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Lobster in a Changing Gulf of Maine: Investigating the Temporal Impact on Molting and the Fishing Fleet

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LOBSTER IN A CHANGING GULF OF MAINE: INVESTIGATING THE TEMPORAL IMPACT ON MOLTING AND THE FISHING FLEET

By

Kevin W. Staples

B.S. University of Maine, 2010

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degrees of

Master of Science

(in Marine Biology)

and

Master of Science

(in Marine Policy)

The Graduate School

The University of Maine

August, 2017

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LOBSTER IN A CHANGING GULF OF MAINE: INVESTIGATING THE TEMPORAL IMPACT ON MOLTING AND THE FISHING FLEET

By Kevin W. Staples

Thesis Co-Advisor: Dr. Yong Chen
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An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degrees of Master of Science in Marine Biology
and Master of Science in Marine Policy
August 2017

We investigated the phenological and fisheries dynamics surrounding the spring molt of American lobster (*Homarus americanus*, Milne Edwards 1847) in the Gulf of Maine. We created a time series from Maine Department of Marine Resources Lobster Sea Sampling data using logistic models to estimate the timing and duration of the spring molt for eastern, central, and western regions of the Maine coast. These estimates revealed substantial inter-annual variability in the timing of the spring molt for all regions and that 2012 was indeed anomalously early relative to other years. Each region experienced significantly different molt timing for any given year, indicating that there are spatially-distinct molting phenologies along the Maine coastline. Generalized Linear Models were constructed using the molting time series and hindcasted bottom temperatures from the Northeast Coastal Ocean Forecasting System using the Finite Volume Composite Ocean Model to analyze how nearshore and offshore bottom ocean temperatures might shape molting trends and differences. This analysis revealed that the

influence of nearshore temperatures was significant in the eastern region only and the relationship between nearshore temperatures and the timing of the spring molt weakened from east to west.

Logistic models were also applied to Maine Department of Marine Resources Landings Program data to estimate and evaluate multiple landings-based proxies for the timing of the spring molt via the fishing fleet’s ability to synchronize with the lobster molting phenology. Newshell landings, as a percent of the annual weekly maximum, were identified as the best proxy, given relative difference from the annual *in-situ* estimates of spring molt timing and lower standard error values. The fleet’s ability to synchronize with variable spring molting phenology was assessed using a correlation analysis. This analysis revealed that both eastern and western fleets followed the same temporal patterns as the lobster molt timing in their region and the western fleet showed a poorer, more variable ability to absolutely synchronize their timing when compared to the eastern fleet.

Maine lobstermen were interviewed to investigate how they achieve an optimal synchrony, revealing the utilization of several environmental and non-environmental variables. General temperature, lunar and tidal phases, and Penobscot River discharge were fishermen-nominated variables tested using correlation analysis. These analyses showed that fishermen methodology and its association with spring molt timing were spatially variable. General temperatures displayed the same weakening association with spring molt from east to west; tidal phase was significant in the east only; and river discharge was significantly associated in the eastern and central regions. River discharge association with molting was also temporally variable, showing strongest significant positive relationships during April.

We discuss these investigations into the temporal and spatial dynamics of the spring lobster molt along the Maine coast and the fishery’s response to inter-annual variation, creating a baseline of information about the spring molt for Maine. We also discuss the degree to which the fleet is able to approximate and adapt to inter-annual variation in this phenology and some of the methods they have been using to accomplish this synchrony.

ACKNOWLEDGEMENTS

I would first like to thank the NSF Coastal SEES program, the University of Maine's School of Marine Sciences, and Maine Sea Grant for providing the financial support necessary for this research and graduate education.

Aside from the important funding sources, my pursuit of a Master's student and the preparation of this document are not accomplished without the support of many people. It takes a village, as they say – but in this case, it took many villages. The names that could be included here are innumerable, but I will do my best to include those that specifically stand out at the time of this writing – if you are reading this and feel that I have forgotten you, I assure you it is an omission of the moment and invite you to consider yourself acknowledged in gracious fashion here. I will work from my office outward, before working back inward again.

To my officemates, Sugandha, Ruleo, Megan, Stephanie and Andrew (Maura, I will include you here as well), thank you for the years of questions asked, questions answered; the years of laughs and distractions that are needed to provide balance on a daily basis to counter the countless hours of research; for letting me listen to music without headphones, further making the office environment that much warmer; and for not judging me when a 12-hour workday passed without any tangible progress.

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More thank yous to the Xue/Chai, Boss and Brady Labs, specifically, Leann and Sean, Chen-Tien, Alice, Ali, Nils, Jordan, and Kelly, who were key soundboards and important lunchtime dining companions and didn’t protest my daily disruptions *too* often. I am grateful for the daily change of pace. Haley, Elisabeth, Josh and Kristina, Jeff, Andy, Garrett, Ashley, Noah, Melissa, Karen, Skylar, and Julek, I would like to thank you mostly for your off-campus contributions to my graduate career. It is important to have people remind you of the value of socialization.

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Thank you to Susie Lizzotte, Linda Costello, and Jeff Wren, as well as the numerous Wallace Pool lifeguards for keeping the pool open for me. Wallace Pool has been a constant in my life for so long and provided me a near-daily escape before lunch. The exercise didn’t only relieve stress and keep me healthy, but also allowed my mind to breathe, likely leading to more coherent research and writing.

Thank you to all of the Maine lobstermen who made time to talk with me. Our conversations were always educational and often provided me with ideas for how to improve my work. Large portions of my research were shaped by these conversations, sometimes overtly, sometimes abstractly.

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To my advisors, Dave and Yong, your contrasting styles as academics produced a broad spectrum of advising. Dave, your constant dedication to the students of this university (and this state) is something I appreciate and admire. This dedication is manifest in your involvement within the university and departmental political sphere, neither of which detracts from your teaching or advising focus. Beyond that, your unquenchable interest in the Gulf of Maine and general excitement about the sciences has given me energy during my time here and hope for a career close to home, much like you have achieved. Yong, I am still dumbfounded at how you are able to provide financial and academic support for so many students and scholars. Your work ethic, international recognition, and sheer size of professionals whom you have advised are bars set very high, which many others now find themselves measured against. The opportunity to travel to China that you provided me has opened doors to international connections that I could not have dreamed about otherwise. I will be forever indebted to you for my time there.

To my entire committee, Drs. Yong Chen, David Townsend, Damian Brady, Keith Evans and Paul Anderson, I thank you for your support academically, professionally and financially. Your diversity, passion and candidness have been a sincerely invaluable part of my graduate experience. I feel enlightened and confident in my work and career path having been under your collective mentorship.

To my friends both on Mount Desert Island and the Great Lakes, thank you for the perspectives you have provided me and the continued informal fisheries-related discussions. Especially Alex Maffucci and Amy Cameron, Maxwell Morgan, and Josh Radford, whose personal experiences with and without fisheries allowed me to ground a lot of theories before flying them.

To my family and special loved one, who have supported my pursuit of higher education from the beginning, but would support me in any endeavor, provided that it is productive in some way, I love you all.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FOREWORD

Before I begin discussing my research methods and findings, I want to provide you, the reader, with some important background information that sheds light on why I chose this research topic. I am a native son of Maine, born on Mount Desert Island, famously the home of Acadia National Park. This island is a magnet for tourists coming from all corners of the country and the world from May-October, mostly. Though seasonal work is dominant within the local economy, there is still a population of people that enjoy living here throughout the year. I grew up as one. This population is made up of small business owners that tap into that tourism industry, tradesmen, and larger company employees such as the Jackson Laboratory and Hinckley Marine. One of the most consistent professions of year-round island residents is fishing. The historically dominant fishery for the area has been lobstering. It is difficult to grow up on Mount Desert Island without being influenced by the presence of the Park, or by the presence of the fishing communities of which many of my childhood friends continue to be involved in to this day. It is an ocean-centric, working-class culture with a mixed-in a conservation ethic that makes it so unique. I have tried to stay as connected to this community as long as possible. I’ve been fortunate to receive both my undergraduate and graduate education in the marine sciences at the University of Maine, only 1.25 hours from my childhood home.

Alas, with Maine’s culture and beauty, there are also the broader troubles of employment. When I received my Bachelor’s in 2010, the unemployment rate was 8.1% in Maine, reflecting national trends after the 2008 financial crisis. So, with limited options at home, I was fortunate to land a job in the Midwestern U.S. working and living on a boat, visiting many Great Lakes ports and cities. Nowhere did I find this culture that I missed so much. I read my hometown newspapers daily, catching up on news and events online, when the 2012 lobster glut and resultant price depression occurred. I read stories describing the hardships and struggles of people with my shared culture. I wanted to investigate why this happened, thinking that understanding the circumstances that created conditions believed to be ‘abnormal’.

Luckily, people at the University of Maine believed this investigation to be worthwhile. Within, you will learn about the approaches I used for this investigation; the trials of optimizing these approaches; the findings they produced; which questions remain unsolved and which questions have arisen from this research.

Thanks for reading,

Kevin W. Staples

CHAPTER 1

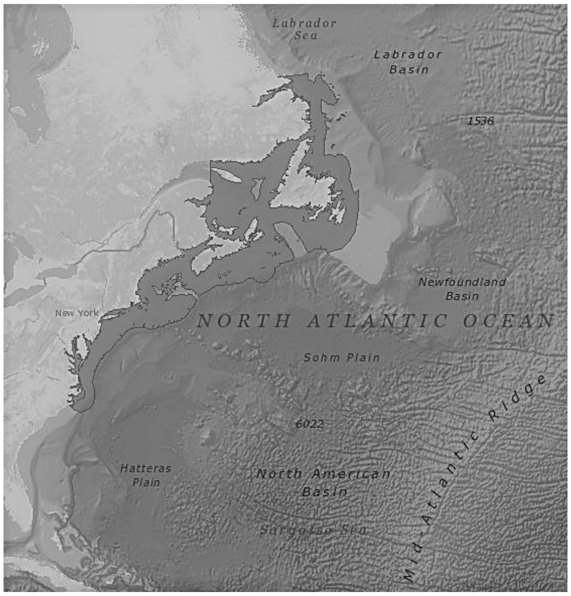
GENERAL INTRODUCTION

This thesis includes research in an array of disciplines, from biology to oceanography to anthropology, and these disciplines are united around American lobster (*Homarus americanus* Milne-Edwards, 1837) in the Gulf of Maine. This connectivity among the phases of my work creates an opportunity to provide background information that provides needed context for these overlapping projects. In this chapter, macro-scale information is provided on the organism (American lobster), the environment (the Gulf of Maine), and the people (Maine lobster fishery).

1.1 The American lobster

The American lobster is a decapod crustacean whose range stretches from Cape Hatteras in the United States of America to Newfoundland of Canada in the northwest Atlantic Ocean (Fig. 1).

Figure 1. Lobster distribution in the northwest Atlantic Ocean. Taken from http://maps.iucnredlist.org/



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This habitat includes a range of depths, from the intertidal to 700m, in areas that are pristine and areas that have been highly contaminated by human actions (Aiken and Waddy 1986) Lobsters, especially juveniles, prefer a rocky cobble substrate that provides shelter during vulnerable early years (Pottle and Elner 1982; Wahle and Steneck 1991) that is abundant within the Gulf of Maine. This substrate is a key factor in the settlement of lobster postlarvae, which recruit to these preferred benthic habitats after their planktonic larval stages are completed (Wahle and Steneck 1991). Their geographical distribution is driven by temperature, with temperature having the most pervasive influence on survival, growth and reproduction of juvenile and adult lobsters (Aiken and Waddy 1986).

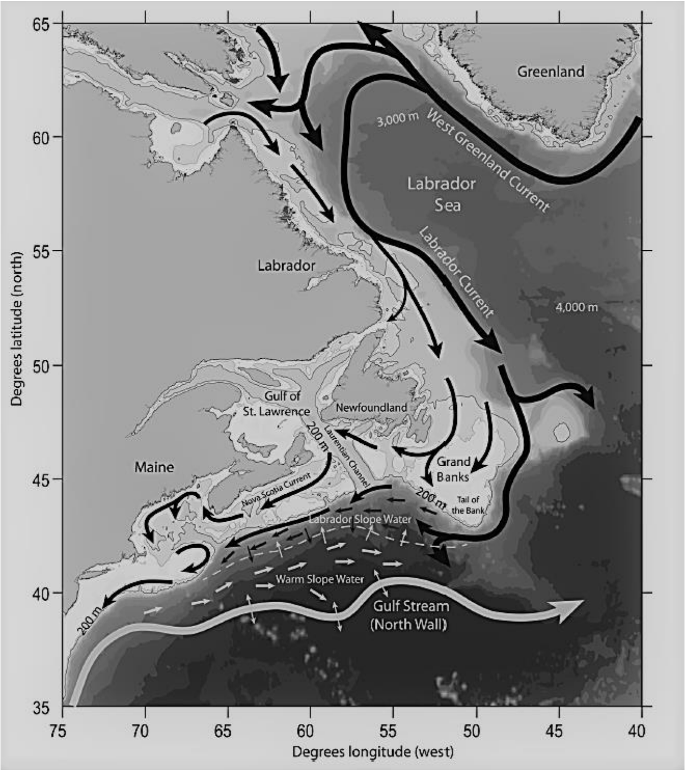
In recorded history, lobsters within the Gulf of Maine have enjoyed an ideal temperature range, something that cannot be said of late for neighboring stocks to the south that are managed by Massachusetts, Rhode Island and Connecticut, for example (Castro et al. 2006; Glenn and Pugh 2006). Much of the concern for future lobster stock resilience within the Gulf of Maine is centered on the problems that may arise due to a warming ocean (Mills et al. 2013; Saba et al. 2016), whether it is directly (Aiken and Waddy 1986) or indirectly related to survival (Castro et al. 2006). In either case, current oceanographic conditions have promoted stock growth within the Gulf of Maine.

1.2 Relevant Gulf of Maine oceanography

The Gulf of Maine (GoM) is a unique region, because of its semi-enclosed nature and pronounced inter-annual variability. Reasons for this variability can be attributed to the Gulf's proximity to a steep latitudinal temperature gradient where different water masses meet and produce the Gulf's water properties (Fig. 2; Townsend et al. 2010, 2015).

Figure 2. Map of currents and oceanic circulation in the northwest Atlantic Ocean.

Figure taken from Townsend et al. 2015.

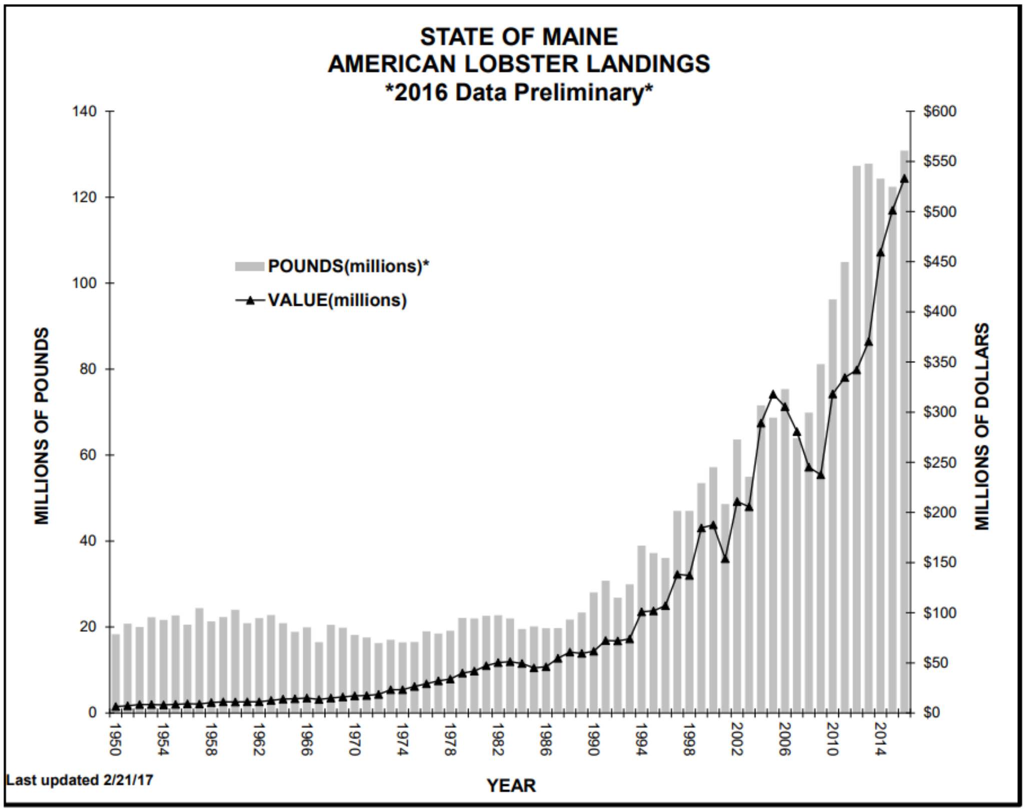


Labrador Slope Water (LSW), from the northwest Atlantic Ocean and Labrador Sea, flows south along the Canadian Maritime Provinces and diverges before reaching Newfoundland, Canada, into shelf and slope currents and contributes to Scotian Shelf Water (SSW), which flows separately along the continental shelf of Nova Scotia. LSW, beyond the shelf edge, is a relatively cold and fresh water mass, that meets and mixes with Warm Slope Water (WSW), of Gulf Stream origin, which resides offshore of LSW and inshore of the Gulf Stream (Townsend et al. 2015). This boundary between WSW and LSW creates a steep thermal gradient and is subject to latitudinal variability on an inter-annual time scale (Csanady and Hamilton 1988; Chapman and Beardsley 1989; Townsend et al. 2010). The location of this cold and warm water boundary influences the proportional influence of these three water masses into the GoM (LSW, SSW, WSW), thereby influencing water temperatures from year to year (Townsend et al. 2010, 2015). Water temperatures in the GoM are also responsive to atmospheric heat flux (Mountain et al. 1996), but advection of different water masses mixing into the GoM are thought to have the greatest influence (Bigelow, 1933; Chen et al., 2014; Lentz, 2010).

1.3 The Maine lobster fishery

The Maine lobster fishery started in the early 1800's, and became more developed with the advent of 'smacks', a type of sailboat (sloop) with recirculating tanks for storing lobster (Acheson 1997). While the early fishery was dominated by canneries, by the late 1800's, it was mostly a live market fishery (Acheson 1997). This fishery is held in high regard, due to its early adoption of conservation measures, continued comanagement practices (Johnson and van Densen 2007; Wilson et al. 2007), and high landings in an era of fisheries depletion (Hilborn 1992; Acheson and Steneck 1997). The landings are so high, in fact, that the Maine fishery has set record high landings (in terms of volume) and value in 2016 (preliminary estimates of ~58967 metric tons worth ~$547.1 million), accounting for roughly 74% of the total value for commercially landed fishery resources in Maine that year (Fig. 3; Maine DMR, 2017).

Figure 3. Graph of Maine lobster landings and ex-vessel value. Graph taken from the Maine Department of Marine Resources website.



Furthermore, Maine is currently landing 81% of the catch in the most valuable fishery in the United States (NFMS, 2017). Though, the lobster fishery does not have a large impact on the national economy, it, like other fisheries in developed countries, has a large impact on local communities (Roessig et al. 2004).

CHAPTER 2

QUANTIFYING THE SPRING MOLT OF AMERICAN LOBSTER IN THE GULF OF MAINE

2.1 Introduction

American lobsters (*Homarus americanus,* Milne-Edwards, 1837) in the Gulf of Maine (GoM) experienced an extreme shift in the timing of spring landings to much earlier in the year in 2012 (Trotter and Staff 2012a; Mills et al. 2013). This shift, believed to be a result of an early spring molt of recruits into the fishery (Holland 2011; Mills et al. 2013), had adverse impacts on the lobster industry supply chain and directly impacted communities where lobster fishing is the primary industry. It is not clear how this event compared to the historical timing of recruitment events because there is no time series describing changes in the spring American lobster molt in the GoM. Those familiar with general trends, fishermen and scientists alike, offer anecdotal perspectives on any deviance from the perceived ‘normal’ spring molting events. The lack of an effective quantitative measure of how the spring molting of lobsters prevents a more concrete understanding of these changes, uninfluenced by qualitative biases. Furthermore, a quantitative time series would open the door to analyses of what changes have occurred, when they have occurred, and what might be the driving forces behind any changes. The importance of the lobster fishery to Maine coastal communities underscores the need for monitoring the direction and magnitude of phenological shifts.

Quantifying these recruitment events is of particular use because those lobsters that molt and recruit to the GoM fishery each year account for an estimated 60% of the total population abundance (Atlantic States Marine Fisheries Commission, 2009). This dynamic of heavily fishing the new recruits is also described by a median size of catch below 90mm (where the legal sizes are 83 to 127 mm) underscoring how critical the spring molt, the first and largest recruitment event in a given year, is to the fishery (Atlantic States Marine Fisheries Commission, 2009).

Molting, also known as ecdysis, describes the event that punctuates the growth cycle in the American lobster and other crustaceans. The molting cycle is continuous, passing through five stages (A, B, C_1-C_3, D_0-D_3, and E) (Aiken 1973), where the soft shell condition immediately after the molt is stage A, stage B occurs when the shell starts to harden, and stage C occurs when the shell hardens further, developing three layers of cuticle (C_2), and a membranous layer (C_3). Stage D describes the formation of a new carapace below the now-hard old carapace and stage E is the active process of splitting and shedding of the old carapace (Aiken 1973; Comeau and Savoie 2001). Physiologically, molting in American lobsters is regulated by the ecdysterone hormone, the sensitivity of lobsters to this hormone had been shown to be particularly affected by temperature (Gilgan and Burns 1977; Aiken and Waddy 1986). The frequency of molting is also dependent on available space, presence of conspecifics and nutrition (Aiken 1980). Lobsters may molt once, multiple times, or not at all in a given year, depending on factors such as length, sex and maturity (Templeman 1936; McLeese 1956; Aiken 1980; Aiken and Waddy 1986).

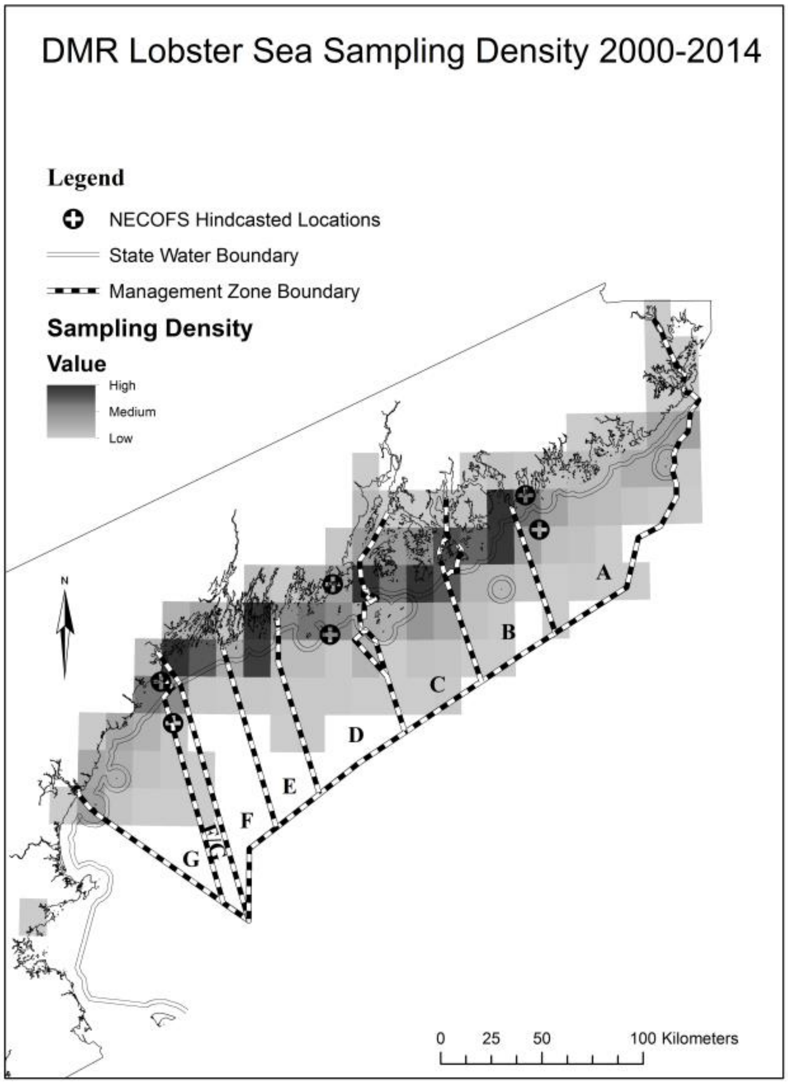
In this thesis, the timing and suddenness of the spring molt of American lobster in the GoM is quantified, producing the first time series for this important phenological event. We expect that this time series will reflect and support the previous findings that sex and size will result in slightly different spring phenologies, that there will be differences between the eastern and western GoM, and that there will be less sudden spring molts when the event occurs earlier in the year.

2.2 Methods

2.2.1 Data source

This research utilized the Maine Department of Marine Resources Lobster Sea Sampling (LSS) program, populated by state-employed observers who collect data on all lobsters that are caught by commercial fishing vessels that volunteer their services. Data recorded include geographic position, sex, length, and an *in situ* qualification of whether a lobster has molted within that calendar year using cues such as shell color and firmness (Reardon, 2015). Spatial coverage of the entire coast of Maine is achieved through an effort to record at least three sampling trips per lobster management zone (Fig. 4) per month (Reardon, 2015). The temporal coverage is concentrated in the months where the fishery is most active. These data initially contained over 2.272 million individual lobster records and were analyzed for the years 2000-2014 (data collection is ongoing) before we removed all data for lobsters collected in waters deeper than 73m, our demarcation depth between inshore and offshore. This reduced confounding effects from offshore sampling trips throughout the year, especially in the months surrounding the annual spring molt, which would complicate the spatial heterogeneity of the LSS. This paring of offshore data removed 26% of all records (leaving ~1.675 million observations), before the data were further divided using the Maine lobster management zone structure into eastern (zones A, B and C; 734,686 records), central (zones D and E; 493,988 records) and western (zones G and F; 446,812 records) regions for analysis. The LSS was selected because real-time, *in-situ* measurements of lobster molt status were recorded, but this qualitative assessment may be confounded by factors such as length, sex and maturity (Templeman 1936; McLeese 1956; Aiken 1980; Aiken and Waddy 1986).

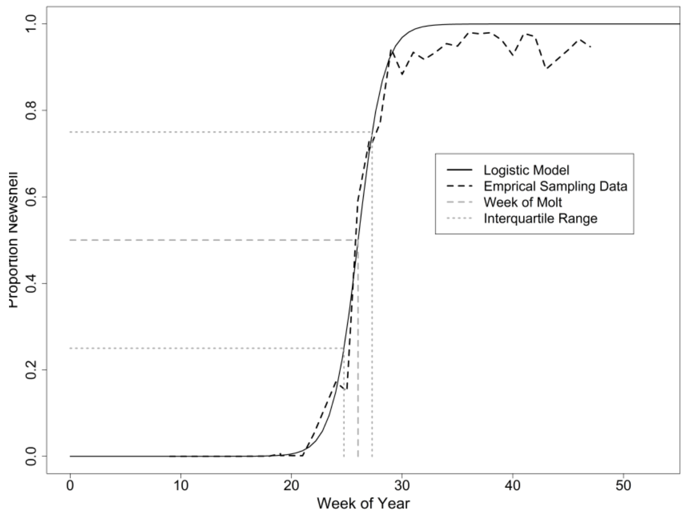
Figure 4. Map of Maine Department of Marine Resources Lobster Sea Sampling effort from 2000-2014. Also included are locations when the NECOFS bottom temperatures were queried.



2.2.2 Logistic model applications

With the LSS data heterogenous with respect to lobster size and sex and time and space, we utilized a logistic model to smooth the data during the year, estimating the average proportion of newshell lobster at depths shallower than 73 m during each week of the year. This application of the logistic model to the data assumed that (1) there are no lobsters with a new shell on January 1st of each year, (2) by the end of the year the proportion of lobsters sampled with a new shell will approach 1 (100%), and (3) all sampled lobsters will have laid a new shell at least once during that calendar year. These assumptions reflect those made by the LSS program. The logistic curves were fit to the LSS data for each individual year of the program using a weighted nonlinear least squares function, so that yearly values for timing and suddenness (heretofore denoted as *Week50* and *R*, respectively) were estimated (Fig. 5), producing a time series for these two variables.

Figure 5. Example of fitting a logistic model to LSS data and *Week50* and *R* parameter estimation. Data shown are from the depths shallower than 73 m in 2012 in the eastern region.



The logistic model was set up as follows:

$$Pm_{wk_t} = 1/(1 + e^{-2*\frac{\log(3)}{R_t}} * wk_t - Week50_t) \qquad [1],$$

where *Pm* is the probability of sampling a lobster with a shell laid in a week *wk* of year *t*, estimating the variables *R* (interquartile range) and *Week50* (inflection point) of the logistic curve. The *Week50* variable can be defined as the week when 50% of the sample lobsters would be expected to be classified as ‘newshell’ (Fig. 5). For this analysis, *Week50* represents the week of the year that the spring lobster molt occurs. The value of *R* estimates the number of weeks elapsed between the interquartile values of 0.25 and 0.75 and therefore is a measure of the suddenness of the molting season onset for a given year. An example of variable estimates for timing (*Week50*) and suddenness (*R*) of spring molt seasons in waters 3-73m east and west of the Penobscot for 2012 are displayed in Fig. 5. To quantify the fit of the model to the data for each year, the areas underneath receiver operating characteristic (ROC) curves (AUC) were calculated using the ‘pROC package’ in R (Robin et al. 2011). This value can range from 0.5 (no apparent accuracy) to 1 (perfect accuracy) (Hanley and McNeil 1982). Values under 0.7 are typically poor fits, 0.7-0.8 are considered fair, 0.8-0.9 good and 0.9-1.0 excellent (Hanley and McNeil 1982).

These data were further subset into males and females within the eastern, central, and western regions to assess differences between sexes, and by length into short (<83mm carapace length [CL]) and legal (83-127mm CL) and oversized (>127mm CL) classes to assess the effect of size (relative to the double gauge protections of the fishery) on spring molting seasons. Logistic curves were fit to the sex data in the same manner as described above, complete with

AUC tables and parameter estimations. This process was initially attempted for each size class, but multiple spring peaks confounded the logistic model application, preventing convergence at one value.

2.3 Results

2.3.1 Logistic model applications

The area under curve (AUC) results showed that most logistic fits were ‘fair’ or better, with average AUC values in the west, central and east as 0.799, 0.889 and 0.917, respectively (Table 1). The western region had the poorest average model fit, owing to the years 2007-2013, specifically, with the years 2008 and 2009 having fits classified as ‘poor’. Paring the LSS data to those recorded in depths shallower than 73m had very little effect on the logistic model fits for the observations in the west region (average difference of -0.017), central region (average difference of 0.003), and eastern region (average difference of 0.032). We emphasize that this data paring limits the scope of this research to the molting of those lobsters found at depths 3m and 73m.

Table 1. Regional LSS logistic model fits (all data). AUC (area under receiver operating curve) values, describing logistic model fits, for each region from the years 2000-2014 using all lobster sea sampling (LSS) data (total) and those records shallower than 73 m (adj.).

Year	AUC West Total	AUC West Adj	AUC Cent Total	AUC Cent Adj	AUC East Total	AUC East Adj
2000	0.875	0.849	0.783	0.792	0.556	0.821
2001	0.843	0.843	0.919	0.920	0.854	0.939
2002	0.858	0.858	0.926	0.928	0.814	0.799
2003	0.931	0.924	0.873	0.865	0.941	0.955
2004	0.868	0.876	0.786	0.836	0.846	0.908
2005	0.867	0.869	0.960	0.957	0.948	0.974
2006	0.872	0.880	0.900	0.905	0.925	0.946
2007	0.758	0.739	0.917	0.916	0.939	0.951
2008	0.710	0.691	0.896	0.892	0.880	0.868
2009	0.722	0.685	0.876	0.873	0.910	0.942
2010	0.741	0.728	0.933	0.928	0.901	0.899
2011	0.759	0.745	0.855	0.872	0.930	0.940
2012	0.774	0.710	0.850	0.833	0.924	0.924
2013	0.775	0.734	0.889	0.878	0.946	0.947
2014	0.898	0.861	0.927	0.935	0.954	0.935

The AUC results for inshore males and females (Table 2) demonstrated very good average fits for both sexes in the eastern (0.941 and 0.911 for males and females, respectively) and central regions (0.920 and 0.886) and good average fits in the west (0.813 and 0.814). While 2002 seems to be a rare poor fit for the eastern sexed data, the period 2007-2013 saw fair or worse fits (AUC of 0.637-0.766) in the western region.

Table 2. Regional LSS logistic model fits (inshore data). AUC values, describing logistic model fits, for each sex in each region from the years 2000-2014 using LSS records shallower than 73 m.

Year	AUC West Male	AUC West Female	AUC Cent Male	AUC Cent Female	AUC East Male	AUC East Female
2000	0.950	0.867	0.877	0.786	0.908	0.805
2001	0.940	0.833	0.972	0.907	0.979	0.923
2002	0.921	0.858	0.956	0.921	0.815	0.794
2003	0.969	0.921	0.869	0.870	0.970	0.951
2004	0.914	0.874	0.871	0.829	0.903	0.914
2005	0.902	0.863	0.966	0.958	0.987	0.969
2006	0.914	0.874	0.943	0.899	0.969	0.937
2007	0.766	0.739	0.946	0.910	0.971	0.945
2008	0.643	0.730	0.902	0.895	0.878	0.868
2009	0.672	0.704	0.895	0.878	0.947	0.945
2010	0.735	0.739	0.953	0.926	0.934	0.895
2011	0.697	0.784	0.908	0.867	0.967	0.931
2012	0.637	0.768	0.857	0.843	0.960	0.912
2013	0.681	0.772	0.923	0.877	0.974	0.943
2014	0.853	0.877	0.964	0.929	0.948	0.940

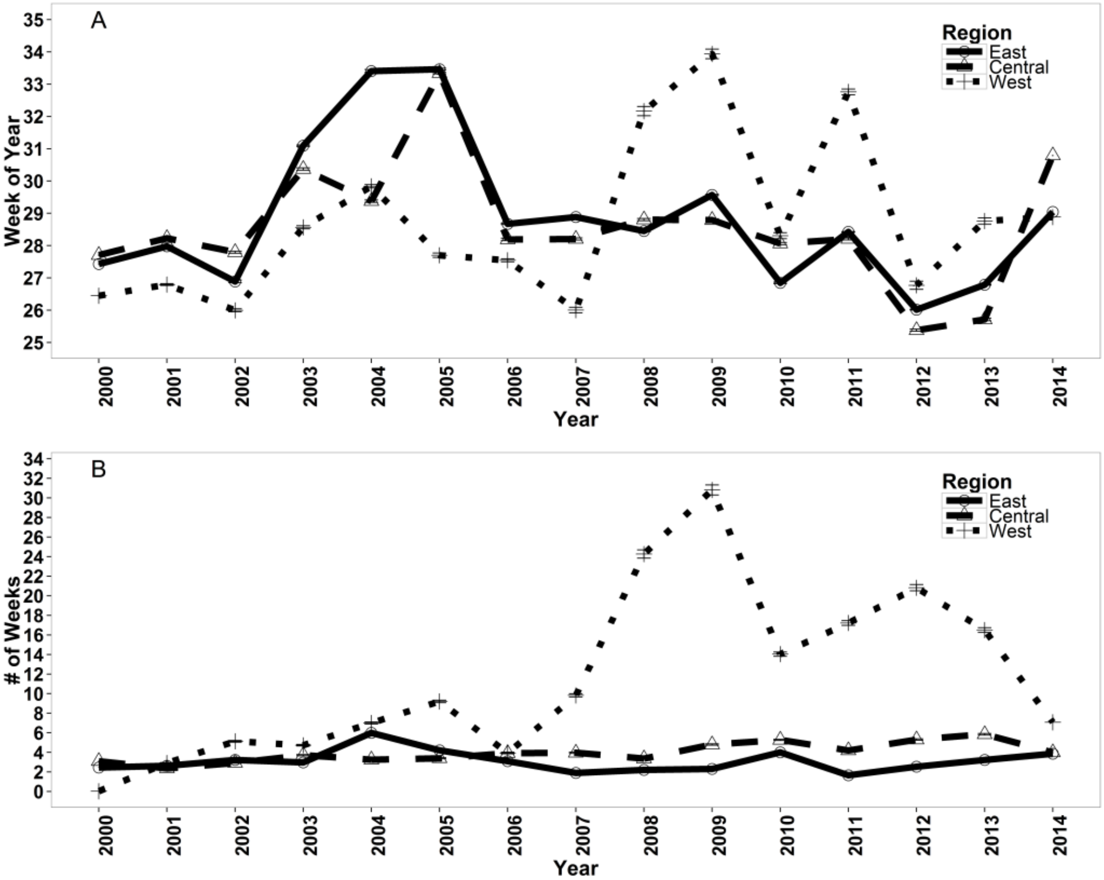
2.3.2 Variable estimation

The time series for *Week50* for all regions (Fig. 6A) consistently displayed small standard errors (maximum 0.149 weeks) around the parameter estimates and a large degree of inter-annual variability. The trends for each region over the time series were similar, aside from those years where western model fits are poor to fair (2007-2013). There is no overall regional order for the

Week50 estimates (*i.e.*, western first, central second, eastern last) that might suggest a “rolling” of the molt from west to east along the Maine coast.

The time series for *R* for all regions (Fig. 6B) consistently displayed small standard errors (maximum 0.514 weeks) around the parameter estimates and inter-annual variability. The western region is shown to be most variable, with the central and eastern regions showing similar magnitudes of variability. The spring molt in the eastern region was consistently less sudden than that of the central region from 2006-2014.

Figure 6. Time series plots for regional spring molt timing (*Week50)* (A) and suddenness (*R)* (B) estimates.



Further exploration revealed that the fit of the logistic model to the LSS data might be influencing the *R* parameter estimation. The Pearson correlation coefficient between the AUC values of the logistic models and the *R* parameter estimates of the western region was -0.879 and statistically significant, indicating that these estimates were unreliable because of their dependence on model fits. This was not the case, however, for the central and eastern regions, where Pearson correlation coefficients of -0.104 and 0.023, respectively, and neither statistically significant.

Pared and non-pared (depths shallower than 73m) estimates demonstrated that standard error (SE) was not inflated due to a reduction in data and that there were no consistent changes in parameter estimation. Time series plots of the timing and suddenness of the spring lobster molt for both east, central and west inshore LSS data (Fig. 6) and sexed LSS data (Figs. 7, 8) consistently displayed small standard errors around the parameter estimates and a large degree of inter-annual variability, though the errors in the west were greater than those in the central and east. Timing estimates for each region were nearly identical on average, with about 0.25 weeks separating the average timing of the central region from the average timing of the western region on either end of the spectrum. The average suddenness of the molt was shortest in the eastern region and increased as a function of distance to the west (3.085 weeks, 4.965 weeks, and 11.565 weeks, respectively).

Figure 7. Time series for males (A) and females (B) *Week50* estimates for each region.

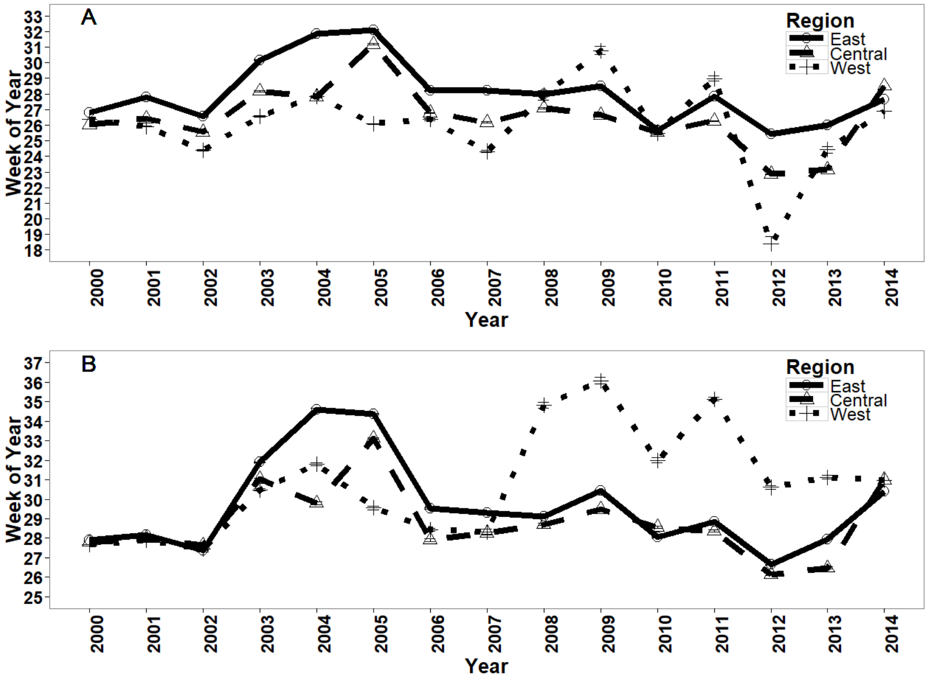
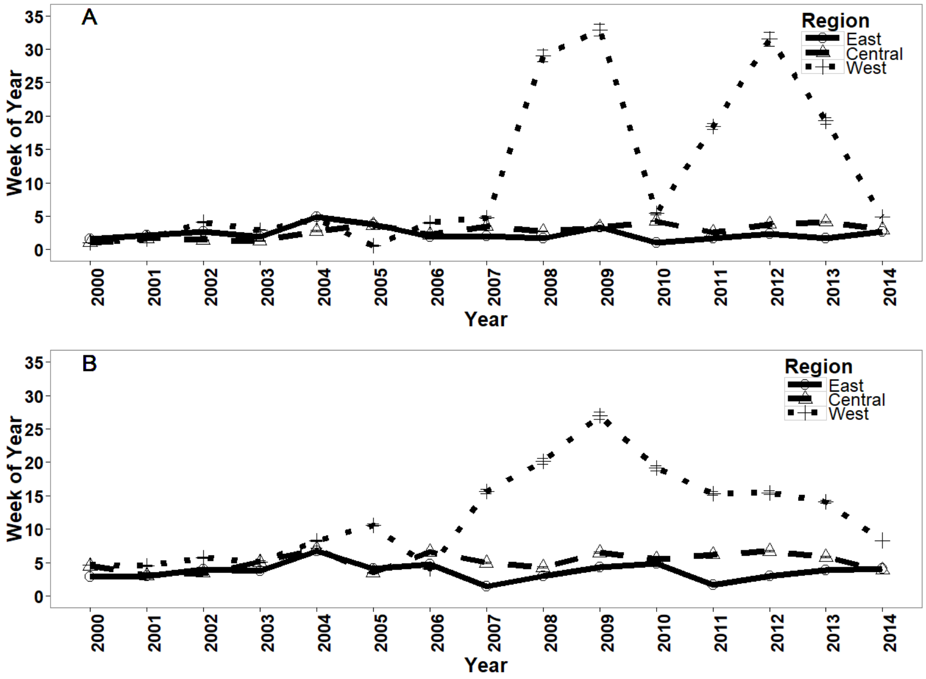


Figure 8. Time series for males (A) and females (B) *R* estimates for each region.



The timing trends are complicated when the data is further divided by sex, with males molting earlier than females on average (1.591, 2.271, 4.772 weeks earlier in the east, central, and western regions, respectively). The spatial dimension of the spring molt timing between the sexes reveals more of a progression from west to east than the combined estimates, save for 2011. Males molted more suddenly than females on average, and this was found to be consistence across regions. The difference between sexes grew between the eastern and central regions (1.30 to 2.33 weeks), but was most similar in the west (0.84).

2.4 Discussion

2.4.1 Spatial variation

Each region and sex exhibited a temporally distinct spring molting season in our data analysis (Fig. 6A). The differences in logistic model fits to the LSS data for each region provided an early hint of this regional variability. The logistic models did not perform as well in the western region compared with the eastern and central regions, probably because of influences including, but not limited to, oceanographic differences, spatiotemporal variance in sampling, and phenological differentiation within the lobster population. The empirical differences in the spring molt season estimates for each region should serve as sufficient evidence to warrant a more geography- and sex- specific discussion of lobster molt timing in the Gulf of Maine.

Most studies that concern molt timing have either focused on an area outside the Gulf of Maine (Northeastern Nova Scotia, Canada; Tremblay & Eagles, 1997), were conducted in autumn (Thakur et al. 2017), or they have utilized data that do not directly determine the molt stage of individual lobsters (Mills et al. 2013); this study). Therefore, there is no truly descriptive time series for spring molting within the GoM, as previous attempts rely on proxies such as shell condition and color, or landings, with no evaluation available on the relationship between such proxies. The LSS is intensive, requires substantial data collection over small time windows, and was not meant to specifically address molting dynamics, so methods such as pleopod-staging (Tremblay and Eagles 1997; Thakur et al. 2017) are not practical to include within the collecting protocol. However, the adoption of a qualitative categorization method, such as that employed by the State of Maine for shell-disease, may provide an adequate solution. If using "light finger pressure" to the lateral posterior of those brightly colored, shiny shells (Tremblay and Eagles 1997) is adopted, more information on the temporal nature of the lobster population's molting cycle will be available for interpretation. It is reasonable to point out the uncertainty and bias that will result from a technique such as shell depression, but perhaps it is no more susceptible to drawbacks than the current technique of a more optical and binary shell evaluation, which the logistic model effectively smoothed during analysis.

2.4.2 Importance

Limited surveys that use a paired approach to directly compare multiple efficient and effective techniques for evaluating lobster molting may be necessary develop a more universally accepted method that would allow for more understanding on finer spatial and temporal scales. Ideally, this method would be employable within existing surveys without burdening samplers and produce a more continuous representation of molting. This would allow for a more detailed investigation into the intra-annual phenology, such as population-scale secondary autumn molts, that cannot currently be conducted with the available LSS data.

CHAPTER 3

QUANTIFYING THE IMPACT OF BOTTOM OCEAN TEMPERATURES ON THE SPRING MOLT OF AMERICAN LOBSTER IN THE GULF OF MAINE

3.1 Introduction

During the period from autumn 2011 through summer 2012, there was a disruption in the lobster supply chain that led to oversupply and ex-vessel price depression (Trotter and Staff 2012a, 2012b; Woodard 2012). This disruption coincided with a warming trend that began in 2004 (Mills et al. 2013; Pershing et al. 2015). This warming event, abrupt in its occurrence and unpredictable in its impact on coastal communities, was investigated to determine its cause (Chen et al., 2014; Saba et al., 2016) and whether such a quantifiable departure from the normal range might be a driver of changes in phenologies of GoM species (Runge et al., 2014; Pershing et al., 2015). Due to the dependence of Maine coastal communities on the lobster fishery, it is imperative to determine whether shifts in the spring lobster molt are possibly a direct result of environmental forcing. Robust quantification of the relationship between spring lobster molting and environmental forcing is necessary and the communicating of such a relationship to industry and managers is important to the resilience of the fishery in the face of climatically-driven changes.

Research on the relationship between temperature and molting in lobsters has been limited to controlled laboratory environments Templeman 1936; McLeese 1956; Aiken and Waddy 1975; Gilgan and Burns 1977; Aiken 1980), with fewer studies focusing on how this relationship is observed in a natural setting (Tremblay and Eagles 1997; Comeau and Savoie 2001; Thakur et al.

2017). Aiken and Waddy (1986) contrasted the molting and reproductive phenology of two populations of American lobsters at high and low latitudes and found that colder winter temperature regimes produced a more pronounced spawning season (with a sharp peak in timing), while warmer regimes produced more muted and protracted spawning seasons. Their study also found that oocyte development and molting are inversely related for American lobsters and that warmer winters may favor more frequent molting events. Given these conclusions about spawning season dynamics, in which colder winter temperatures lead to greater synchronization and a shorter season, it is of interest whether similar phenology is exhibited for the spring molting season in lobsters.

These studies identify temperature as the most important factor for lobster molting, but exactly how this dependence on temperature manifests itself in the environment over time in the GoM region is not well understood. Furthermore, quantifying how temperature affects the inter-annual variability of the timing of the molting season is an issue in need of more attention. Linking bottom water temperature variability in the GoM to variability in lobster molting phenology may provide valuable information to the lobster industry, which is currently the most valuable fishery in the United States (NMFS, 2017) and at a historical maximum for both landings and value (Maine DMR, 2017). The GoM has exhibited a de-coupling between bottom water temperatures and the North Atlantic Oscillation (NAO), a decadal-scale oscillation of atmospheric pressure over Iceland and the Azores that had been correlated with the relative proportion of LSW versus WSW in the GoM since 1990 (Mountain 2012). This de-coupling further complicates the hard-to-predict nature of bottom water temperatures in the GoM. Furthermore, the GoM coastal current (GMCC) exerts a strong influence on dynamics within the

GoM (Pettigrew et al. 1998, 2005). Two distinct branches of the GMCC, the eastern and western Maine coastal currents (EMCC and WMCC), are often separated by cyclonic offshore flow from Penobscot Bay around Jordan Basin (Brooks and Townsend 1989; Bisagni et al. 1996; Pettigrew et al. 1998), while at other times, intermittent connectivity exists between the two branches (Lynch et al. 1997; Pettigrew et al. 1998). This coastal current system contributes to distinct oceanographic regions along the Maine coast, east and west of Penobscot Bay that varies seasonally (Pettigrew et al. 2005). The connectivity between east and west, or the continuation of the EMCC into the WMCC, may be related to wind forcing (Luerssen et al. 2005)

The overall warming trend over the last 35 years or so, highlighted by periods of rapid temperature fluctuations in the last 15 years (Pershing et al. 2015), further increases the uncertainty associated with lobster molting phenology in the GoM. This warming trend and variability was exacerbated by a rapid warming period from 2004-2012 that in 2012 produced the warmest sea surface temperatures on the northeastern continental shelf on record for both satellite remote sensing data and ship-board measurements from the past 150 years (Friedland 2012). The rate of future warming in the GoM, whether it happens at a rapid rate (Pershing et al. 2015; Saba et al. 2016) or at a rate consistent with more tempered, preceding trends (Loder et al. 2001; Shearman and Lentz 2010), will influence species' distribution and phenologies (Gawarkiewicz et al. 2013; Nye et al. 2014; Mills et al. 2013; Pershing et al. 2015). Analysis of lobster phenology during extreme conditions, when water temperatures are anomalously high or low, could provide clues to lobster molting behavior in the GoM in the future. Such a mechanistic understanding would be a powerful tool for stakeholders in the lobster fishery in the face of uncertain future trends in GoM water temperatures.

We report here an analysis of the relationship between the timing and suddenness of the spring molt season of American lobster and bottom water temperatures in GoM. We hypothesized that warmer temperatures lead to earlier and more protracted spring molting seasons than is the case in cooler years. Specific objectives were to evaluate this relationship for shallow and deeper water temperatures and how these relationships are manifest in each region of the GoM. The expectation is that temperatures at deeper depths will prove to be more prognostic and that there will be distinct spring molting phenologies for each region of the GoM.

3.2 Methods

3.2.1 Data sources

This research utilized two datasets: The first is the spring lobster molt time series that was detailed in Chapter 2 of this document, which provided estimates of spring molt timing and suddenness time series for the GoM (Fig. 6). The second dataset was hourly temperatures accessed from NOAA's Northeast Coastal Ocean Forecasting System (NECOFS) using the Finite Volume Ocean Community Model (FVCOM) maintained by the Northeast Regional Coastal Ocean Observing Network (Chen et al. 2003). This model output provides oceanographic hindcasts for the study region for most of the LSS sampling period (1976-2016) and includes oceanographic variables over both hourly and monthly intervals. Only bottom temperature data from the hourly hindcasts were used in this study.

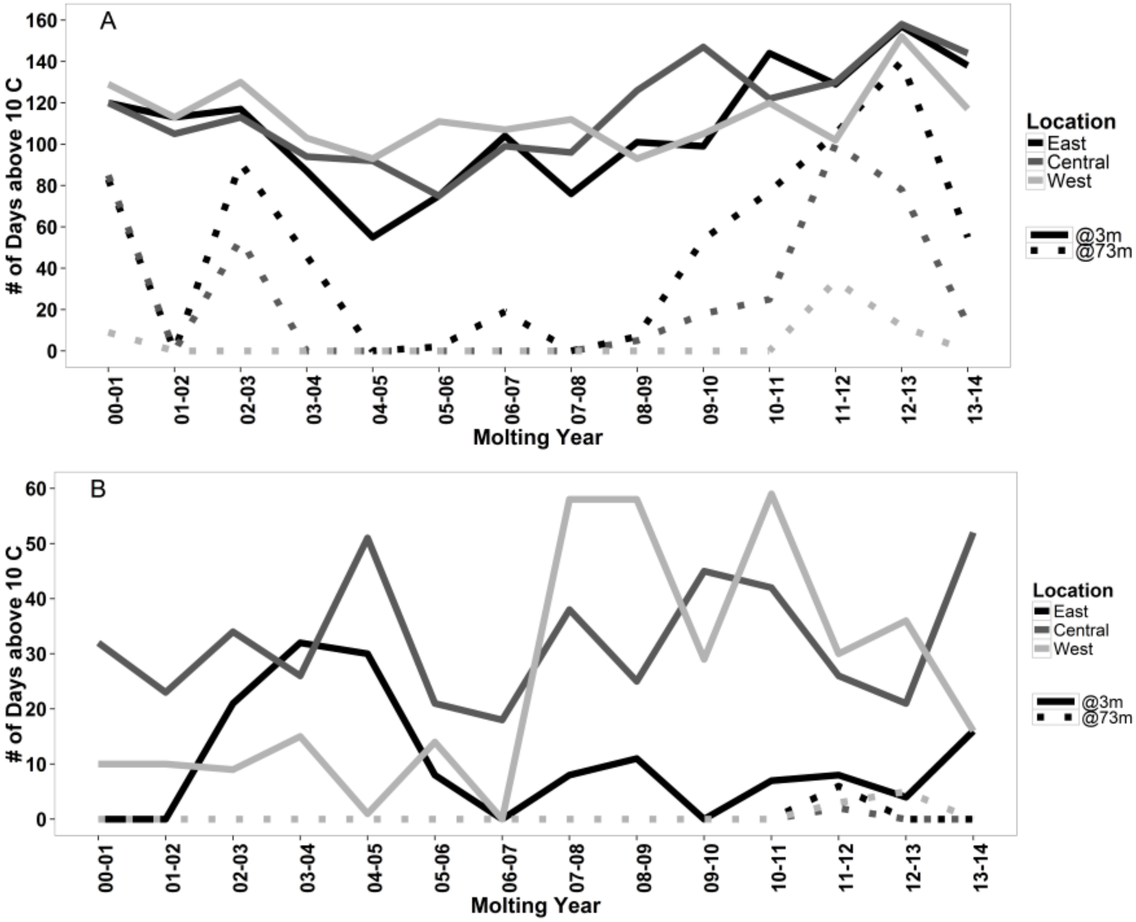
We identified the closest NECOFS node (hindcasted position) to six locations (Fig. 4) within the Gulf of Maine (44.38°N, -67.97°W; 44.23°N, -67.88°W; 43.99°N, -69.16°W; 43.76°N, -69.18°W; 43.55°N, -70.21°W; 43.37°N, -70.13°W). The hourly bottom temperatures were daily-averaged for the period January 1, 2000 through December 31, 2014. These six locations were selected to capture the spatial heterogeneity of water temperatures in the Gulf of Maine, which vary with depth and various oceanographic processes. Locations corresponding to depths of 3 and 73 m in each of the eastern, central and western regions of the Maine coast were chosen for comparison.

These depths were identified by fishermen as likely to provide the most information regarding molting phenology, with 3 m representing a depth where high numbers of molting lobsters were likely to be seen earliest in a standard fishing year. The deeper stations (73 m) were considered to be the extent of nearshore fishing and thus where lobsters may retreat to and beyond for overwintering.

3.2.2 Degree day analysis

Aiken and Waddy (1975) found that temperatures above 10 °C had a significant impact on the ecdysterone hormone, resulting in an acceleration of the molting process. We therefore used 10 °C to define a degree day, or instance when a particular thermal threshold is achieved. The period over which these degree days might impact the molt for a given year was assumed to be the current molt cycle of the lobster population, defined as the period, in days, between $Week50_{t-1}$ and $Week50_t$. We assume that once one hormonal cycle of ecdysis is completed, those temperatures experienced have no bearing on the next cycle. With the molt period defined, we calculated the number of degree days within that period by tallying the days above 10 °C from the NECOFS hindcast data. The result was a time series of degree days, thereby constituting a temperature metric that was used to explain the timing of the molt for lobsters in the Gulf of Maine. Temperature time series were created for 3 and 73 m depths in the eastern, central and western regions of the Gulf of Maine, using paired inshore-offshore locations along the Maine coastline (Fig. 9). These locations were also selected because of their exposure to the Maine coastal current, which strongly influences nearshore oceanographic processes (Pettigrew et al., 2005).

Figure 9. Time series for inshore summer-autumn (A) and winter-spring (B) degree days, derived from the NECOFS hindcast data for the molt periods ending in 2001 through 2014.



3.2.3 GLM analysis

The geographically distinct relationships between the timing and suddenness of the molt and an array of temperature metrics were evaluated using general linear models (GLMs). The utilization of GLMs over simple linear models is appropriate because dependent variables (*i.e.*, *Week50* and *R* for each region) are both restricted to values that lie within the maximum number of weeks in a year (Guisan et al. 2002). The independent variables for each GLM included summer-autumn degree days (those between $Week50_{t-1}$ and $Dec\ 31_{t-1}$) and winter-spring degree days (those between *Jan 1st* and $Week50_{t}$) at 3 and 73 m. Those winter-spring temperature metrics that were included as independent variables within each GLM predicting Week50 values were first vetted by plotting *Week50* values against degree days. Those which displayed significantly positive regressions were excluded from GLMs, as they could not effectively predict *Week50* values because the period over which degree days accumulate while providing no information about the relationship between the two values.

These GLM constructs were put through a forwards and backwards stepwise regression function within R statistical freeware (McLeod and Xu 2014; R Core Team 2015) and returned the GLM that explained the most deviance using the fewest variables, paring the initial list of inputs down to the most critical independent variables. Those significant variables ($p < 0.05$) within an optimized model were deemed to be the most influential temperature metrics for explaining variance in the response variables, *Week50* and *R*. Two separate groups of GLMs were created to test the sensitivity of the timing GLMs to temperature metric start and end points. The control group treated $Week50_{t-1}$ and $Dec\ 31_{t-1}$, while the test group treated $Week75_{t-1}$ and $Dec\ 31_{t-1}$ as the endpoints in determining the number of degree days that influenced the resulting

$Week50_t$ value. If the influential variables were consistent for the two methods, the model was considered robust. This method was then replicated for molt season suddenness, but without comparing the sensitivity of optimal control models to a test model, as $Week75_{t-1}$ is a function of R.

Standard errors (SE) were calculated for each independent model, after the optimization and robustness processes were completed, to ensure that the model possessed reasonable predictive power. Temperature metrics were deemed to be influential on spring molt timing if they were present and significant within both control and test optimized models, with both models possessing a SE near 0. The same criteria were used to determine the influence of temperatures on suddenness, without the consistency within control and test model, as there were no test models for molt suddenness. GLMs were also created to test whether the relationship between molt season timing and suddenness was significant. Once again for suddenness, p-values were used to test significance of within the model and SE was used to ensure the usefulness of the model. These GLMs were employed to distinguish clear connections between temperatures at distinct locations during specific seasons, the timing of the spring molt season and the suddenness of the spring molt season.

3.3 Results

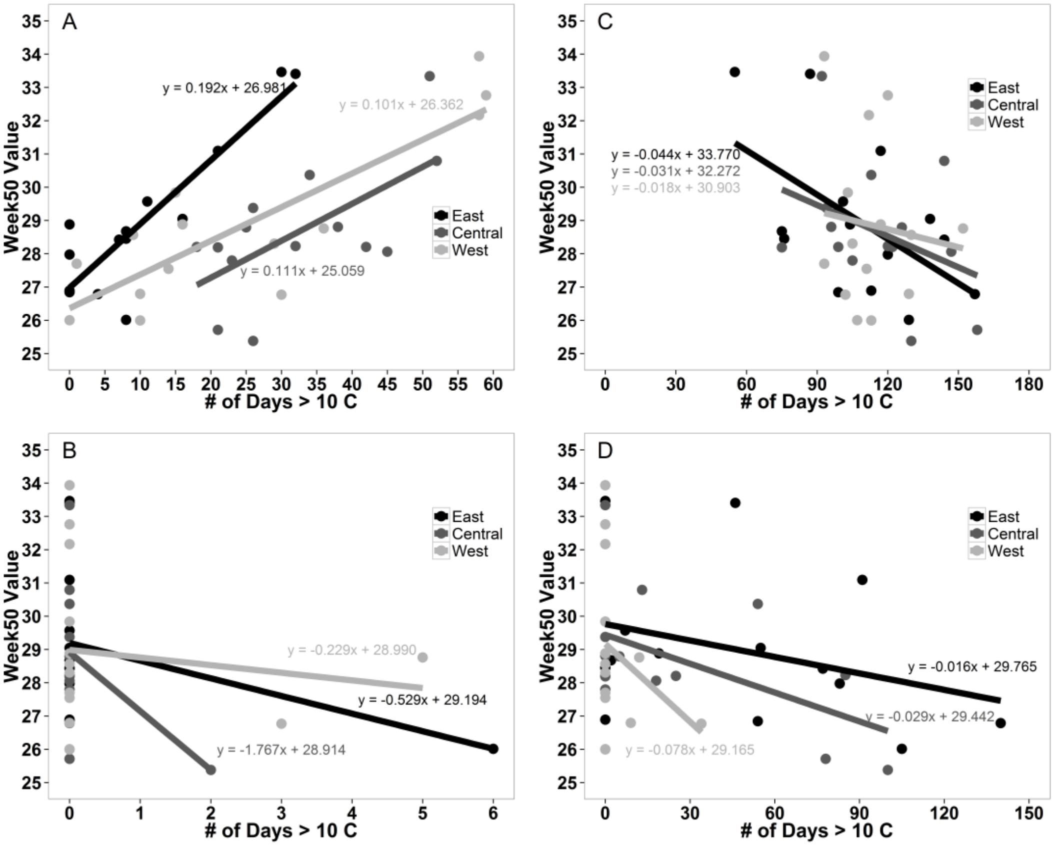
3.3.1 Degree day calculations

Trends in degree day inter-annual variability were similar across all region, depth, and season combinations (Fig. 9). The trends for total degree days for a given molt period are largely driven by summer-autumn temperatures. In addition, results reflect that offshore temperatures are cooler than inshore temperatures. Furthermore, the difference between inshore and offshore temperature decreases substantially during this period, especially in the central and western regions, where the inshore and offshore lines are nearly identical. There is also a distinct lack of winter-spring offshore degree days (save for molt periods ending in 2012 and 2013.

3.3.2 GLM results

The inshore winter-spring and *Week50* regression plots for all regions (Fig. 10A) show positive slopes, indicating that later *Week*50 estimates allow for the accumulation of additional winter-spring degree days.

Figure 10. Regression plots of winter-spring inshore (A), winter-spring offshore (B), summer-autumn inshore (C), and summer-autumn offshore (D) *Week50* values against degree days for each region.



This relationship, which does not provide any information on the relationship between the spring molt season of GoM lobster and winter-spring temperatures, coupled with the dearth of winter-spring offshore degree days (Fig. 10B), led to the removal of winter-spring days from the GLM analyses, leaving only summer-autumn degree day metrics. This contrasts with the regression of $Week50$ estimates and both inshore and offshore summer-autumn degree days for all regions (Figs. 10C, 10D), which had ample number of offshore degree day and were not affected by a soft end-date boundary like the winter-spring degree days.

The resulting GLM formulas were developed as:

Timing and Suddenness Control Group

Timing: $Week50_{t,r} = \alpha_1 ITF_{t,r} + \alpha_2 ITF_{t,r}\colon OTF_{t,r} + \alpha_3 OTF_{t,r}$ + C [2]

Suddenness: $R_{t,r} = \beta_1 ITF_{t,r} + \beta_2 ITF_{t,r}\colon OTF_{t,r} + \beta_3 OTF_{t,r}$ + C [3]

Interaction East: $R_{t,r} = \mathit{\Gamma}_1 Week50_{t,r}$ + C [4]

Timing Test Group

Timing East Test: $Week50_{t,r} = \alpha_1 iTF_{t,r} + \alpha_2 iTF_{t,r}\colon oTF_{t,r} + \alpha_3 oTF_{t,r}$ + C [5]

where $Week50_{t,r}$ and $R_{t,r}$ are timing and suddenness estimates for each of the eastern, central, and western regions *(r)* in a given year *(t)*; *IT* and *OT* denote 3m and 73m degree days, respectively; *iT* and *oT* denote 3 and 73 m degree days between the week where the estimated probability of new shell was 0.75 in the preceding year and the end of that calendar year, respectively; *F* indicates the summer-autumn time period; α, β, and $\mathit{\Gamma}$ represent estimated independent coefficients; and C represents a constant.

Table 3. GLM analysis outputs. Optimized GLMs and their significant independent variables, with corresponding beta-coefficients, standard error, and p-values. Asterisks and shading indicate a statistically significant effect within the final model.

Final Model	Dependent Variable	Included Variables	Beta-coefficient	Standard Error	p-value
Timing East	Week50	ITF	-0.044	0.019	0.039*
Timing Central	Week50	ITF	-0.049	0.024	0.063
Timing West	Week50	NULL	-	-	-
Timing East Test	Week50	ITF	-0.087	0.016	0.000*
		OTF	0.021	0.014	0.165
Timing Central Test	Week50	ITF	-0.076	0.022	0.005*
Timing West Test	Week50	ITF	-0.056	0.011	0.000*
		OTF	0.055	0.041	0.208
Suddenness East	R	NULL	-	-	-
Suddenness Central	R	NULL	-	-	-
Suddenness West	R	NULL	-	-	-
Interaction East	R	Week50	0.269	0.113	0.033*
Interaction Central	R	Week50	-0.228	0.126	0.093
Interaction West	R	Week50	2.534	0.683	0.003*

The ability to predict molt suddenness using spring molt timing was significant in the eastern and western regions, but not in the central region (Table 3). If the timing of the spring molt season was delayed one week, the effect in the eastern and central regions was a protraction of 0.269 and 2.534 weeks of the spring molt suddenness, respectively. Summer-autumn temperatures at 3 m had a statistically significant predictive effect on spring molt timing in the eastern GoM region for both the control (0.044 weeks earlier per degree day) and test (0.076 weeks earlier per degree day) models. No such consistent, significant temperature predictor was found in the west (Table 3). No significant direct predictive effects of temperatures on spring molt suddenness were found in this analysis (Table 3).

3.4 Discussion

3.4.1 Temperature influence on spring molt season

The number of summer-autumn degree days at 3 m had a significant effect on the spring molt timing in the eastern region. Furthermore, the coefficient for this metric, which indicates the temporal effect per degree day, was negative, which supports the hypothesis that warmer inshore temperatures in the east were likely to result in earlier spring molting. This inshore effect was not as apparent in the central and western regions, where the control models did not exhibit the significance present in the test models. This indicates that there may be regional differences in how water temperature affects the timing of the spring molt.

The hypothesis that spring molting seasons will be longer and less sudden during periods of warmer temperatures was not supported by the GLM results, as no significant temperature metrics were included in the final models for suddenness. This finding is complicated by another: that molt suddenness in the western region exhibited much more variation than its central and eastern counterparts, possibly an artifact of poor logistic model fits (Fig. 6B), though there is a smaller range of degree day temperatures in the west (Fig. 9). This study cannot determine whether this is further evidence that molt suddenness is unrelated to temperatures or if it is additional evidence that eastern- and central-located individuals respond to temperatures differently than western ones.

3.4.2 Spatial variation

The differences in final GLM variable selections reinforce the idea that lobsters along the Maine coast are influenced by different factors that vary by location. Indeed, the relationship between spring molt timing and suddenness was shown to be connected in the eastern and western regions, but not in the central region (Table 3). Though this research indicates that east and west regions exhibit some level of synchrony in the direction of timing anomaly (*i.e.*, later or earlier than the average), the magnitudes of those anomalies are commonly uncorrelated (Fig. 6). This study underscores the importance of understanding spatial variability in the relationship between temperatures and spring molt timing. If a forecast is to be created for the spring molting event, changes in this relationship along the coast must be considered.

3.4.3 Importance

The need to understand the mechanisms driving the phenology of lobsters is only growing in importance. Lobstermen along the Maine coast have offered that this once ‘predicatable’ phenology has become much less predictable in recent years, which are the focus include this study. Though anecdotal, these musings correspond with a significant increase in ocean temperature variability in the Gulf of Maine during this same period that has garnered attention for the rate of warming during the last prolonged warming period (2004-2014; Pershing et al. 2015; Chen et al. 2014). Periods of abrupt temperature changes may provide a glimpse into future ecosystem dynamics, where extreme spring molting events similar to 2012 may begin to become the new normal with increased variability in ocean temperatures in the Gulf of Maine. The results we present here do not establish an absolute link between bottom water temperature and spring molt phenology, nor do they unequivocally indicate the absence of such a relationship. Instead, our results underscore the complexity that a variable temperature regime has upon phenology. As the GLM results indicate, warmer temperatures inshore during the latter part of the year are more likely to coincide with an earlier molt in the following year. Again, the post-spring molt phenology of the GoM lobster population may provide clarity as to how individuals that molt later in the year might influence the results seen in this study.

The skill with which the logistic model approximates the timing of the spring molt, especially in the eastern and central regions (Chapter 2), offers promise that an accurate forecast of the spring molt can be developed for lobster populations. However, the inconsistent effect of model inputs at a broad spatial scale described here suggests that this model requires more development before it can be operational. It is necessary to be critical of potential forecasting abilities, or lack of ability, because of the economic repercussions of such projections. Markets are sensitive to such information and incorrect forecasts (or correct forecasts, for that matter) result in lobster pricing shifts that may not reflect future fishery harvests. Previous attempts at forecasting the spring molt of lobsters in the GoM have employed a statistical model to generate forward-looking predictions (http://www.gmri.org/sites/default/files/resource/lobster_forecast_methods.pdf, unpublished). Such models give only a probabilistic estimation based on the historical association of outcomes and independent variables and do not provide a framework that allows for input values to create specific outcomes (Spanos 2006), which the authors readily acknowledge. It is the intent of our research to identify appropriate inputs for utilization within mechanistic models to create such specific projections for spring molt timing and the uncertainty of those estimates.

Even in the absence of an ideal molt index for the Gulf of Maine, research should continue to build upon the work that has previously been completed, including what we present here. The connections among the molting phenology of American lobsters, fishery dynamics, and economic dynamics are important, yet variability in this phenology could portend an evolution towards a fundamentally different fishery. Understanding the mechanisms behind such variability buffers managers and industry stakeholders alike against ineffective policies and practices.

CHAPTER 4

QUANTIFYING THE SYNCHRONIZATION OF THE MAINE LOBSTER FLEET WITH THE SPRING MOLT OF AMERICAN LOBSTER IN THE GULF OF MAINE

4.1 Introduction

If the timing of the American lobster spring molt in the Gulf of Maine varies from between years (as outlined in Chapter 2 of this thesis), and if that variation is driven by temperature (as outlined in Chapter 3 of this thesis), then it is important to understand how the Maine American lobster fishery responds to these yearly differences. The significance of this response is underscored by the role that the spring molt plays as a recruitment event, where a large number of sub-legal individuals molt and achieve a body size that makes them legal to harvest (Wilson et al. 2007). This large, population-scale recruitment event replenishes the number of individuals within the legal size window (83-127mm; *Lobster Measurement* 2017) that were depleted the from the prior year’s fishing effort.

This “double-gauge” legal size management practice, which restricts the effects of recruitment overfishing (Pauly 1988) to a specific size range, coupled with the population-wide spring molt phenology of American lobster, manufactures a pseudo-“derby fishery”. The typical derby fishery is driven by fishery-wide quotas (shares of common-pool stock), and seasonal openings and closings, where the best conditions for fishing occur at the beginning of each season, creating a race, or “derby”, for harvesting the stock when the cost of catching the exploited stock is low (Hackett et al. 2005). In the Maine lobster fishery, shares of the stock are distributed (*Lobster and Crab Fishing Licenses* 2017), but there is no cap on how much each license may harvest, just the aforementioned legal lengths of individuals. There are no seasonal closures in the Maine lobster fishery, either, but the biological response of lobsters to temperature in terms of catchability (McLeese and Wilder 1958) and molting phenology (Ennis, 1984; Crossin et al., 1998) creates some semblance of a season where the exploitable stock is larger and catches are higher. This phenology is the driving force behind the pseudo-derby characteristics of the lobster fishery, where fishermen allocate their effort inshore to catch the newly recruited individuals, which also happen to be at their maximum catchability (Miller 1990; Wilson et al. 2007).

It is common, when discussing how changing climate has altered, and will continue to alter, commercially exploited and non-exploited species to speak to inter-annual distribution shifts (Perry, 2005; Nye et al., 2009; Pinsky & Fogarty, 2012; Kleisner et al., 2016), but less common to address how changing climates will alter intra-annual species phenologies (Sims et al., 2001; Stenseth et al., 2002). Similarly, this is the case when discussion climate impact on fisheries (Brander, 2010; Dufour et al., 2010; Pörtner & Peck, 2010). The lobster fishery in Maine has experienced the inter-annual distributional effects (Pinsky and Fogarty 2012) that have helped the industry achieve all-time highs in landings (Maine Department of Marine Resources, 2017), but it the intra-annual phenological effect of climate change (Chapters 3 and 4), that tests the ability of fishermen to optimize their fishing behavior for maximum gain.

The seasonal spatial allocation of effort is important to a lobsterman’s business operation, and must balance the seasonal catchability, input costs as fuel and bait, and competition for space with other lobster fishermen (Miller, 1990; Acheson & Gardner, 2005; Wilson et al., 2007). This balance on the margin is exacerbated in the spring, when inshore catches are at their nadir prior to a near maximum (Miller 1990). If a fisherman allocates effort inshore, either by moving gear from offshore or by re-entering the inshore region after a winter spent ashore, without tending gear, too early, then they are not recuperating their input costs effectively. If they are too late, they have likely missed a period of profitable fishing. Here, we quantify the ability of the fleet to track the variable spring molt timing among Gulf of Maine lobster and evaluate the potential of landings data as a proxy for the spring molt by doing so. We hypothesize that the fleet, in the interest of maximizing profitability, accurately tracks this changing intra-annual phenology.

4.2 Methods

4.2.1 Data sources

Two Maine Department of Marine Resources (DMR) data sets were used to estimate the timing and suddenness of the spring molt for American lobsters along the Maine coast: the lobster sea sampling program (LSS) and the lobster landings program (LP). The LSS data is described in Chapter 2. For this analysis, only those data on legal sized (83-127mm) collected during 2008-2014 were used, totaling over 618,000 individual records. The LSS was selected to describe the baseline *in-situ* timing of the molt, without proxy.

The LP data are provided by seafood dealers who are involved in the first purchase (initial transaction from harvester to dealer) from the harvesting fishermen and harvesters that also possess dealer licenses. These dealers report the weight of purchased lobster that was legally landed (i.e., with a carapace length between 83-127mm). Like the LSS protocol, dealers also assign a qualitative grade to their product that approximates whether it is old shell, new shell, or unknown designation, though it is unclear what metrics are used for such a qualitative distinction. Unlike the LSS, the LP data provided by the DMR came pre-aggregated by week and by region (east and west of the Penobscot River, as management zones ABC and DEFG, respectively) because of confidentiality restrictions. The region west of the Penobscot River is a combination of the previous sections' central and western regions, so we will call it the central-western region for this analysis. These concerns were minimized using a two-region demarcation and weekly aggregation, but some weekly values were not present within the dataset because of such restrictions. There was still plenty of information to investigate spatial and temporal differences in the GoM. The LSS data was aggregated in the same spatial manner to maintain congruence between the two datasets. The LP data were divided by grade, a crude measure of molt status, separated into newshell and total landings, before aggregation into weekly cumulative total landings for each year (substituting the average of the preceding and following weeks in cases where values were absent) so that both datasets shared common temporal intervals.

The LP data was further manipulated beyond the weekly cumulative landings to ensure that the most descriptive representation of the temporal nature of the LP data was available. These different representations included weekly averaged landings and value as a percent of the maximum weekly landings for a given year, which allowed for a time series that more effectively showed the weekly differences in landings. These varying representations of the LP data allow for a more thorough testing of how well the industry synchronizes its season of higher effort with the LSS data representing spring molt timing.

4.2.2 Analyses

Logistic models, using the same formula as described in Chapter 2, were applied to each of these time series to once again estimate the week where 50% of the response variable is achieved (molt timing approximation; *Week50*) and the number of weeks between 25% and 75%

of the response variable (molt suddenness approximation; *R*). The landings data which were standardized against the maximum weekly newshell landings for each year, did not make the assumptions that the LSS data does, where there is assumed to be 0% newshell lobster on Jan 1st and 100% newshell lobster on Dec 31st of each year, with all individuals molting at least once in each year. Rather, instantaneous appraisals of whether a lobster has an oldshell or newshell are made for each lobster throughout the year.

It is because the lobster fishery newshell landings follow similar patterns of low catches, rising to a peak before declining near the end of for each fishing year, that the window to which logistic models were fit to the percent of maximum weekly landings data was cropped to a consistent window (between 10 and 35 weeks of each year). This is the time of year that newshell landings first increase at high rates toward the yearly maximum. This process enabled logistic models to make more accurate estimates of *Week50* and *R*. Standard errors (SE) were calculated to quantify the ability of variable estimates to fit the given data.

Quantification of the similarities between the analyzed time series was conducted using a Pearson correlation coefficient matrix. This matrix not only quantified the degrees of similarity, but indicated when correlations between time series were statistically significant ($p\text{-value}<0.05$). From this matrix, the best proxy for the *in-situ* timing of the spring molt was empirically evaluated for its ability to approximate the timing of the spring molt by first plotting the differences between the proxy approximations and yearly *in-situ* approximation and second plotting the anomalies relative to the mean for both proxy and *in-situ* approximations against each other. The first evaluation will show the absolute difference in ability to quantify the spring molt between the two metrics, while the second evaluation will show the relative difference.

4.3 Results

4.3.1 Landings data logistic model estimations

The various logistic model estimations of spring molt timing revealed that the LSS estimations had larger standard errors than the LP estimates, and that cumulative landing estimates were smaller than the percent of weekly maximum estimates, especially in the case of total landings. The largest errors were associated with the central-western LSS estimations, topping out at 1.382 weeks (Table 4), while the largest errors for LP estimates were associated with the central-western percent of total weekly maximum total landings, which reached 0.763 weeks (Table 4).

Table 4. LSS and LP logistic model fits. Logistic model-derived estimates and associated standard errors (SE) for eastern (A, B) and western (C, D) regional cumulative annual landings (A, C) and landings as a percent of the annual maximum weekly landings (B, D).

A

Year	LSS Timing	SE	LP Newshell Timing (Cum.)	SE	LP Combined Timing (Cum.)	SE
2008	27.851	0.521	36.501	0.080	36.102	0.109
2009	28.941	0.322	37.029	0.086	37.069	0.092
2010	26.168	0.487	35.830	0.123	35.323	0.093
2011	27.683	0.250	35.997	0.101	35.518	0.074
2012	25.589	0.134	34.528	0.096	34.368	0.078
2013	26.490	0.307	34.995	0.109	34.559	0.084
2014	28.739	0.374	36.990	0.076	36.410	0.082

Table 4. Continued.

B

Year	LSS Timing	SE	LP Newshell Timing (% of max.)	SE	LP Combined Timing (% of max.)	SE
2008	27.851	0.521	29.200	0.074	29.332	0.423
2009	28.941	0.322	30.192	0.142	30.145	0.318
2010	26.168	0.487	27.887	0.128	27.343	0.299
2011	27.683	0.250	29.400	0.092	29.041	0.352
2012	25.589	0.134	26.866	0.293	26.682	0.440
2013	26.490	0.307	28.497	0.189	28.307	0.371
2014	28.739	0.374	30.259	0.089	29.868	0.246

C

Year	LSS Timing	SE	LP Newshell Timing (Cum.)	SE	LP Combined Timing (Cum.)	SE
2008	27.929	0.900	36.773	0.066	36.028	0.111
2009	29.481	1.382	37.440	0.073	36.887	0.091
2010	26.724	0.832	36.687	0.095	36.153	0.101
2011	28.620	0.981	36.686	0.097	36.239	0.091
2012	25.647	1.242	34.565	0.108	34.378	0.113
2013	26.463	0.994	35.287	0.103	34.800	0.098
2014	28.716	0.401	37.227	0.087	36.840	0.120

D

Year	LSS Timing	SE	LP Newshell Timing (% of max.)	SE	LP Combined Timing (% of max.)	SE
2008	27.929	0.900	29.145	0.136	28.822	0.349
2009	29.481	1.382	29.599	0.090	29.216	0.291
2010	26.724	0.832	27.408	0.112	27.018	0.285
2011	28.620	0.981	29.126	0.079	28.681	0.271
2012	25.647	1.242	26.915	0.777	26.910	0.763
2013	26.463	0.994	27.466	0.149	27.077	0.485
2014	28.716	0.401	30.230	0.094	29.787	0.327

4.3.2 Proxy evaluation

The Pearson correlation coefficient matrices revealed that both newshell and total landings data estimates of the spring molt timing were strongly and significantly correlated with the LSS estimates (Figure 11). They also revealed that, in both eastern and central-western regions, landings as a percent of the weekly maximum had a higher correlation coefficient. This evidence, in addition to the relatively lower standard errors around the spring molt timing estimations, identified newshell landings as a percent of annual weekly maximum as the best proxy for fleet behavior. For the subsequent investigations, this was the chosen proxy.

Figure 11. Pearson correlation coefficient matrices for the (A) eastern region and the (B) central-western region.

A)

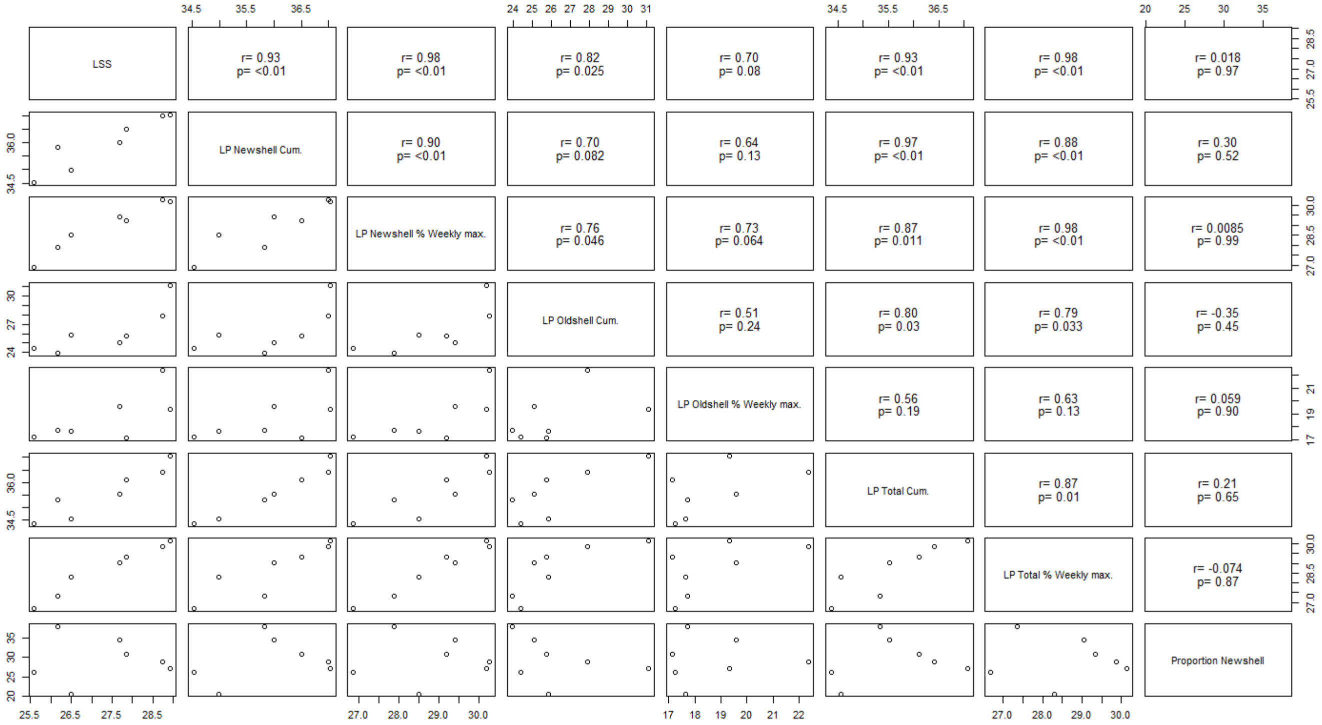
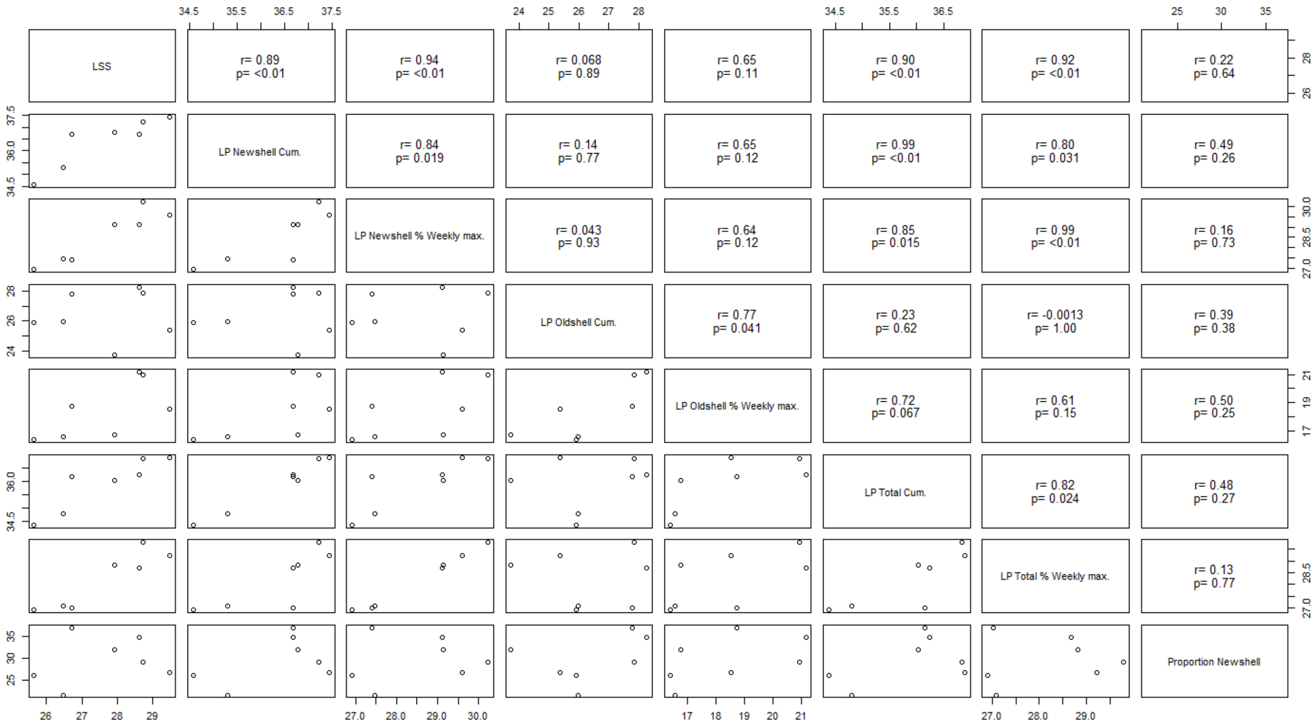


Figure 11. Continued.

B)

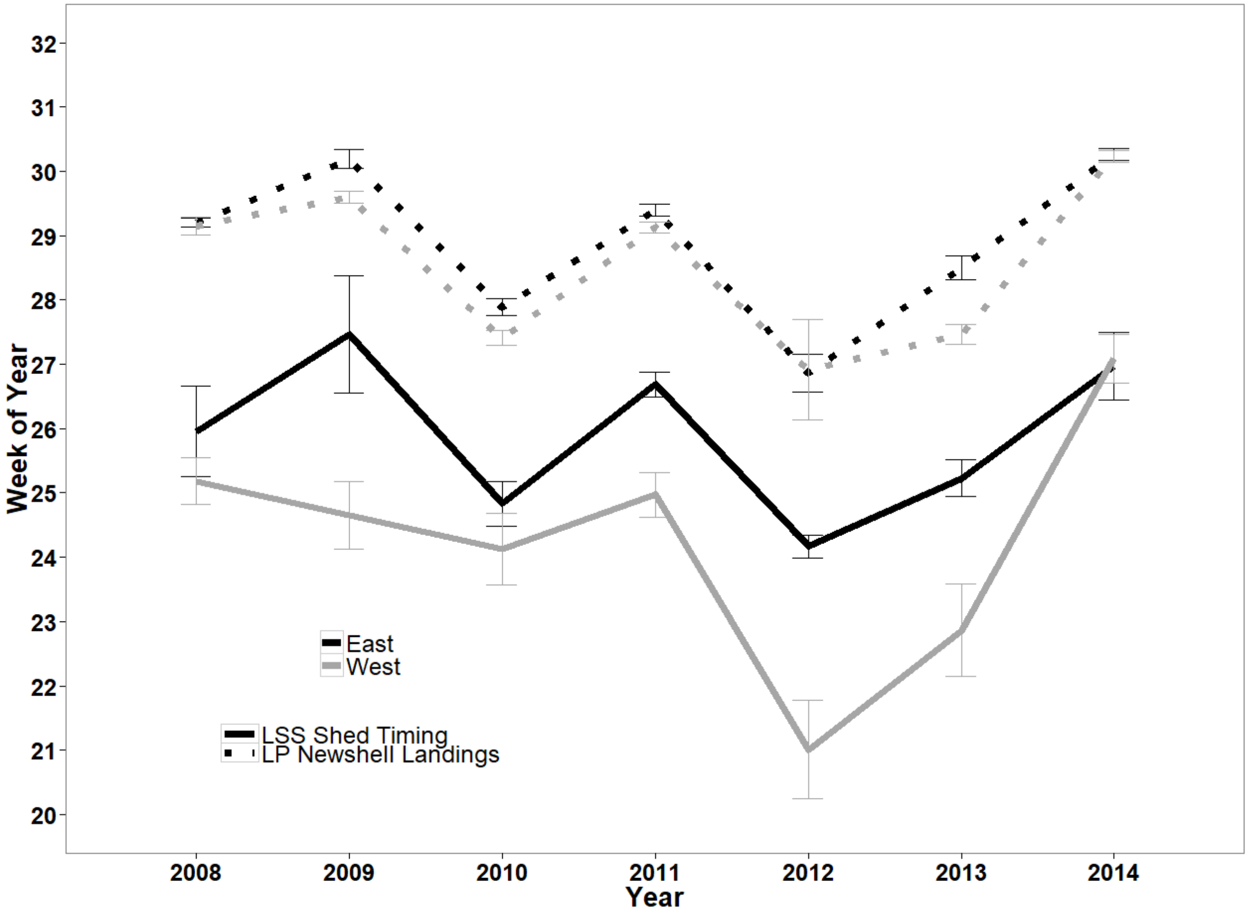


4.3.3 Fleet evaluation

A qualitative comparison of these LP proxy and the LSS estimations show a tighter coupling between the eastern and central-western regions for the LP proxy, but a general tracking of the LSS estimate time series pattern. The biggest differences between the LSS estimates and the LP proxy occurred during relatively earlier LSS estimates of the spring molt in the central-west during 2009 and 2012 (Figure 12). The absolute effectiveness of the proxy to mirror the LSS estimate of spring molt timing was evaluated by taking the differences of the LSS estimates from the LP proxy estimates (Figure 13).

This time series shows the consistency between LSS and LP proxy estimates of the spring molt timing in the eastern region, and that there is more variability between the estimates in the central-western region. It also shows that the lag between the fleet and the lobster phenology is greatest in the central-west, where the molt generally is estimated to occur first.

Figure 12. Time series of LSS and LP % maximum newshell spring molt timing estimates.



The evaluation of the fleet’s responsiveness to changing spring molt phenology was conducted via a comparison of LSS and LP proxy estimates. The time series revealed that, even with inter-annual variability of lobster spring molt timing, there was a tight coupling of the patterns through time where changing lobster molting phenology was mirrored closely by fleet phenology (Figure 14).

Figure 13. Time series of the difference between LP proxy estimates and LSS estimates for spring molt timing.

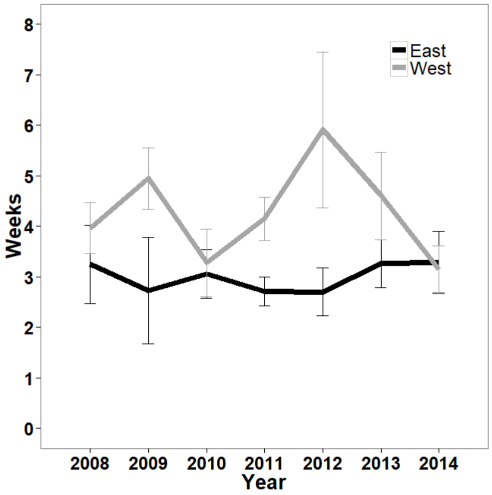
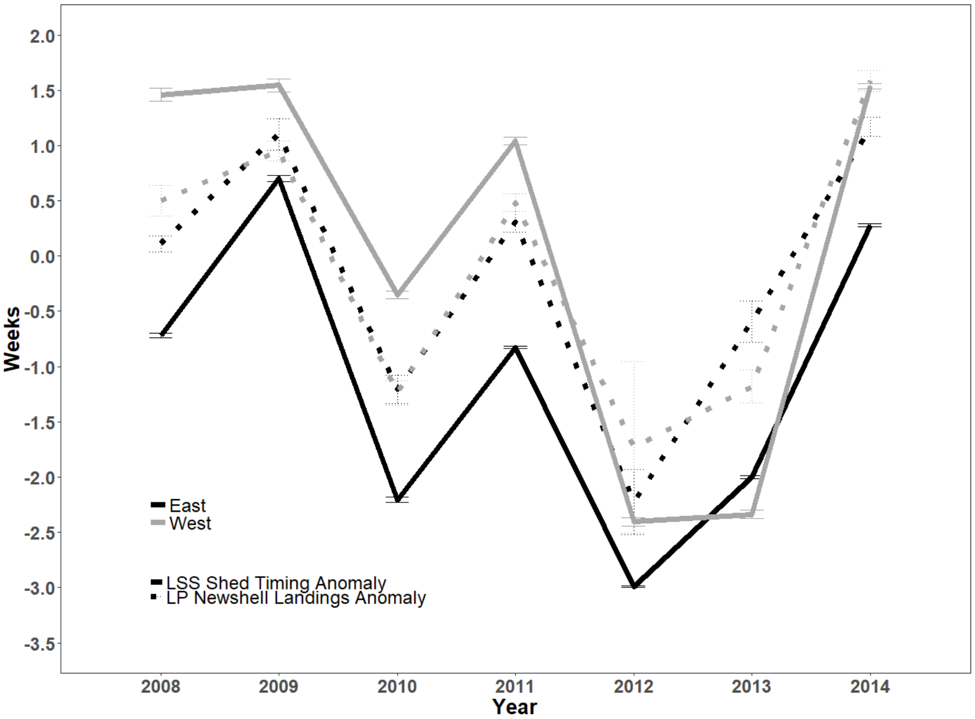


Figure 14. Time series of LSS and LP proxy estimates for spring molt timing in the eastern and western regions, as anomalies relative to the mean value for the years 2008-2014.



4.4 Discussion

The use of a proxy, derived from the newshell LP data, was effective for describing the general patterns and trends of the spring lobster molt timing in Maine, especially considering the correlation between the two time series (Figure 11). There was a lag between the LSS estimation and the LP proxy, however, and this lag proved to be variable through time in the central-western region (Figure 13). These differences might indicate that strict use of the LP data leads to perceived changes or characterizations of molt phenology that do not exist. A more accurate takeaway might be that the different LSS and LP estimates of spring molt timing demonstrate how difficult it is to characterize the timing of the spring molt accurately using qualitative metrics in fishery-dependent datasets, where the spatiotemporal nature of the sampling (fishing) at locations where lobster are expected to be caught in high volume may lead to biased results.

As previously discussed (Chapter 2), there is no ideal monitoring program for the molting of lobsters. The LSS data inclusion of any molting metric is likely tied to evaluation of the impact that shell disease is having on the population, which is amplified for those individuals which have had their shell for a longer period of time (Castro et al., 2006; Glenn & Pugh, 2006). The LP data, which are evaluated by primary buyers in the lobster supply chain, has economic complications attached. Newshell lobster is considered an inferior product, fetching a lower price that hardshell lobsters due to lower meat content and higher shipping and handling mortality (Holland 2011) and dealers are often accused by fishermen of artificially depressing the ex-vessel price to benefit their profit margins. We do not make any accusations here, but rather underscore the hazards that come with unstandardized qualification of whether a lobster has molted or not.

With the assumption that buyers and sea samplers use the same qualitative criteria to assess the molt status of lobster, the LP data demonstrate an effective tracking of the inter-annual variability of spring molt timing. This is shown clearly in Figure 14, where LSS and LP estimate anomalies exhibit the near-exact pattern. There are absolute differences between the east and central-western regions' ability to mirror this lobster phenology, likely attributable to the anecdotally typical 'rolling up the coast' of the spring molt, enabling the eastern regions to better predict to occurrence of the molt in their area. This additional information and its utilization is reflected by the consistent difference between the eastern fleet and the eastern molt, whereas the central-western fleet's synchronization is not as consistent (Fig. 13).

Something to consider, is the hypothetical optimal fleet response to the spring molt timing. These results confirm that lobstermen are very good at catching lobster after some 150 years of tradition (Acheson 1997). Confirmation of the obvious aside, the results which show the mirroring the molt's variability with some accuracy (Fig. 14) are impressive, but the lag between the LSS estimated and LP estimated molt timing (Fig. 13) is something that one might initially consider sub-optimal. Context is needed to re-frame expectations, however. The lobster population does not simply flip from hardshell to newshell at once, as growth is mediated by size, sex, thermal history, nutrition, and a myriad of other factors (Wilder, 1953; Aiken, 1980; Waddy et al., 1995; Glenn & Pugh, 2006). These differentiated growth processes result in a staggered molting progression on the population scale, and so it is possible that fishing practices have evolved to ensure that effort allocation to inshore areas is conducted once an overwhelming proportion of the population has not only molted, but hardened their shells to the point where movement outside of molting shelters for feeding in traps can occur, which can take 2-6 weeks

(Templeman 1933). This is the true target of the fishery and a possible reason for the lagging of the LP estimates behind the LSS estimates.

Maine Department of Marine Resources Commissioner Patrick Keliher stated that a "more predictably timed shed improved industry's ability to manage the supply" (*Mount Desert Islander* 2015), echoing to the public the significant connection between the timing of the molting season and the socio-economic impact on coastal Maine populations. This comment on the timing of the spring molt was made because of the economic impact (via ex-vessel price depression) that an unforeseen extreme early molt had on the industry in 2012. Ramifications were so strong and so negative, that the United States' Secretary of State at the time, Hilary Clinton, was pressured by industry stakeholders and U.S. senators alike to contact her Canadian counterpart in an effort to break a Canadian blockade on American lobsters, which were flooding the market (Trotter and Staff 2012b). The commissioner's comment, however, omits the ability of the fishermen to supply the product in the first place. One might speculate that a significant portion of the industry's inability to manage the supply was because the fleet is so effective at catching lobster, even during years of pronounced variation, whereas other components in the supply chain were less adaptable. Certainly, it would appear that lobstermen have, over time, developed fishing practices that are able to respond fluidly to the uncertainty of when the spring molt occurs from year to year.

CHAPTER 5

AN INVESTIGATION INTO THE DRIVERS OF FLEET FISHING BEHAVIOR SURROUNDING THE SPRING MOLT OF AMERICAN LOBSTER IN THE GULF OF MAINE

5.1 Introduction

We have discussed how a fisherman's timing of the spring molt is important for maximizing catches, and in turn, profits (Chapter 4) and that there is annual uncertainty in when the spring molt will happen (Chapter 2). We have also discussed that this uncertainty of timing coupled with extreme events (2012 early molt) and negative outcomes (glut of supply and price depression) have created an apparent need for increased certainty for the industry at large. This call was answered (Bell 2014), opposed, and discontinued (Press 2017). This progression is a prime example of the oversimplified Two Cultures Theory of Fisheries Knowledge (TCFK), where Research Based Knowledge from academic institutions (RBK) and Local Ecological Knowledge of fishermen (LEK) are often incompatible with each other because of how each group interacts with the resource (Wilson, 2003). In this case, a research institution's attempt to provide certainty is rebuffed by an industry that viewed the attempt as too oversimplified and narrow, and too far removed from the processes that create the variability in the first place.

A challenge for today's fisheries managers is bridging the gap between RBK and LEK, as LEK has the potential to enhance RBK management, and to do so in a scientific way that is compatible with traditional RBK (Pauly et al., 1993; Ruddle, 2000; Wilson, 2003). Traditional managers often dismiss LEK as anecdotal (Palsson 1998) because of its local, qualitative, and hard-to-translate-into-RBK nature (Palsson 1998; Neis et al. 1999), though some researchers emphasis the benefits for integrating LEK into management research and regulation (Johnson and van Densen 2007).

The timing of the spring lobster molt provides a topic whose drivers, environmental and otherwise, have not been definitively identified and robustly tested by RBK (Chapter 2; Tremblay & Eagles, 1997; Thakur et al., 2017), and therefore a vehicle in which LEK can be explored for novel approaches to better explain the timing of the spring lobster molt along the coast of Maine. While there is considerable uncertainty around any given year's molt, there is less uncertainty surrounding the responsiveness of the fleet to any changes (Chapter 4). This synchronization between the fleet and the lobster spring molt phenology is shaped through LEK acquisition by individual fishermen through the years and generations. This LEK acquisition is done in ways that larger management institutions cannot, using multiple sources of imperfect information in chorus at fine spatial and temporal scales. The frequent interactions with the environment and species allow fishermen to use this information to match their business operation with their surroundings. Fishermen's interactions on and off the water with other fishermen with frequent interactions (Acheson & Gardner, 2005; Wilson et al., 2013) allow for individual information to aggregate on a fishery-wide institutional level. This is an example of institutional learning and accumulation of institutional knowledge (Ostrom 1990; Hilborn 1992), which may provide either new information or a new perspective on old information to help better understand the spring molting phenology.

We interviewed fishermen along the Maine coast and asked them what sources of information they used to synchronize their fishing effort so effectively (Chapter 4), both spatially and temporally, with the spring lobster molt. Selected responses were then quantitatively compared to the LSS estimates (Chapter 2) to see if these variables could be useful from a RBK perspective.

5.2 Methods

5.2.1 Recruitment of participants

Interview participants were required to be a current Maine commercial lobster license-holder and at least 18 years of age. They were selected through a variation of snowball sampling (Goodman 1961), where interviewees nominate other fishermen to participate in the interview series. The initial interviewees were fishermen from zones B, D and F who had previously offered their thoughts surrounding the spring molt to the author. Where Goodman (1961) describes a random drawing of interviewees to begin the series, we have started with a handpicked set of three individuals, in an attempt to foster coast-wide sampling of a fleet known for its regional nature (Acheson & Gardner, 2005; Wilson et al., 2013). A total of 21 interviews were conducted, with at least one occurring in each of Maine's seven lobster management zones. With this, geographic coverage of the fleet was achieved, as was a quantity with which to identify key themes through common responses (Huntington 2000).

5.2.2 Interview methodology

All interviews were conducted in person by the author in a manner that attempted to put fishermen at most ease during conversations. Locations were chosen at the discretion of the interviewees, which included restaurants, diners, coffee shops, dining rooms, garages, and workshops. Conversations were recorded with written notes, not voice- or video-recorded, leaving the door open for future deniability, in attempt to coax fishermen to tell the most truthful version of their experiences and decisions. The creation of an informal setting of free-flowing conversation was important and being recorded adds a degree of formality to any interaction. Interviews followed a semi-structured format, following a consistent set of questions for each interview (Appendix B). The order of the questions was not adhered to, instead following the course of the conversation until a natural dead end, before using questions from the list to restart the dialogue. This method allowed for the fishermen to share as much of their decision-making processes as possible, rather than responding to a narrow list of prepared questions. It also allowed the author to pursue interesting digressions and engage the interviewee in disarming, natural conversation.

5.2.3 Fisherman-suggested variable analysis

From these interviews, variables were selected for individual analysis against the LSS-derived, spatially explicit time series of spring molt timing (Chapter 2). These variables were quantifiable and either commonly described by fishermen or of interest to the author. These variables that fishermen used to inform their inshore effort allocation included the commonly described general winter and spring temperatures and lunar cycle, and the less commonly described, but of interest to the author, spring precipitation and snow melt runoff.

To quantify the general temperatures in the winter (December-March) and spring (April-June), we used the same NECOFS-derived data for each region of the Maine coast as Chapter 3. To mimic a more general concept of these temperatures, we simply calculated the annual mean temperatures for these two seasons. Annual anomalies relative to the means of each season were then calculated for the time series 2000-2014, in congruence with the LSS spring molt timing estimates, which were also recalculated as anomalies relative to the mean.

The lunar data was downloaded from the U.S. Naval Observatory website as a daily percentage of the moon disk illuminated from the perspective of some imaginary observer at the center of the Earth, where 0.00 represents a new moon, 1.00 a full moon, and 0.50 a quarter moon ("Fraction of the Moon Illuminated" 2017). In addition to moonlight, the lunar phase is tied to the tidal cycle (Keeling and Whorf 2000). To calculate the daily tidal cycle (T_d), the absolute value a difference of 0.5 was taken from the daily disc illumination values (I_d), where values closest to 0.5 represented the spring tides of the new and full moon phases, and 0.0 represented neap tides during quarter moon phases.

$$T_d = |I_d - 0.5| \qquad [6],$$

The river discharge data in the Penobscot River at Eddington, Maine United States Geological Survey station no. 01037050 was used as a statewide proxy for spring precipitation and snow melt runoff for the years 2008-2014. Daily data were aggregated into annualized monthly means. Those months that preceded the spring molt and were available for all years (April, May, and June) were transformed into monthly anomalies relative to the monthly means for the entire time series.

Four separate Pearson-correlation matrices were produced from these data. Those variables which were significantly and highly correlated with the spatially explicit estimation of spring molt timing were identified as potentially robust decision-making inputs.

5.3 Results

5.3.1 Interview results

The pool of interviewees was experienced (Table 5; mean = 30 years) and generally ran larger fishing operations, with one or more crew and near the maximum number of traps allowed by law, and were generally involved in other fisheries. When asked about which environmental factors influenced the timing of the spring molt, fishermen often (>70%) cited the general temperatures of the preceding winter and spring seasons. Over 30% of respondents cited the moon phase or tide, and some remarked about how snow melt runoff from the previous winter's snowfall and precipitation events affected the molting of lobsters. These environmental metrics were quantifiable and used in further analysis.

Other responses were not as quantifiable (Table 5). There was no non-environmental metric as common as general temperature was for environmental factors, but there were multiple suggestions that substrate (22%), sentinel trap information (22%), trapping rate (33%), and communication with fellow fishermen (28%) helped them to synchronize their fishing behavior with the molt phenology of lobster. When framed another way, and asked what strategies lobstermen used to detect the molting of lobster, fishermen mentions of using sentinel traps rose to 61% and specific placement of traps (either on certain substrate or bathymetry) was 33%, while the mention of temperature dropped to 16%. When asked what information might indicate the approach of a molt, fishermen commonly pointed to the happenings occurring within the traps they hauled, citing shell color (33%), where the darkening of the shells (especially on the ventral side) indicated a lobster that was very close to molting. The also pointed to the volume of catches within their traps (55%), where a lull in catches, an increase in trapping sub-legal

Table 5. Table of interview responses. Participants by zone: A (4), B (4), C (0), D (5), E (2), F (1), G (5).

Demographics	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	V
Zone	E	E	E	E	E	E	E	E	C	C	C	C	W	W	W	W	W	W	W	W	W
License Class	1	3	2	3	2	2	3	3	3	1	3	2	3	3	3	3	3	2	3	3	3
Crew	1.5	1.5	1.5	2	1	1	2	2	1.5	1	2	1	1.5	2	1	1.5	1.5	0.5	2	2	2
Tags	800	800	800	800	800	800	800	800	800	600	600	400	800	800	800	800	800	800	800	800	800
Experience (Years)	35	30	38	26	35	10	40	13	30	43	30	33	40	12	20	10	50	35	22	13	35
Family Tradition	X	X	X	X		X	X	X	X	X	X		X	X		X	X	X	X	X	
Other Fishery Partic.	X	X		X	X				X	X	X		X	X			X	X	X		
Environmental Drivers																					
Specific Temp.					X																
General Temp.	X	X	X	X			X	X		X	X	X	X	X	X	X			X	X	
Precip./Runoff			X			X			X			X				X			X		
Tide/Moonphase	X	X		X										X		X		X			
Non-Env. Drivers																					
Bottom Type								X	X							X	X			X	
Depth								X	X					X							
Sentinel Traps		X						X						X			X		X		X
Trapping Rate						X	X	X	X	X	X										
Cooperation	X	X		X				X				X							X		
Other			X	X	X	X					X		X	X	X	X		X	X	X	X

lobsters, or an increase in trapping males only, could be precursors to a coming molting event. Fishermen also had varying interpretations of how molting progressed through the year. 16% believed that there was one peak, 50% believed that there were two, and 27% believed that there were three peaks in a given year. In terms of how previously extreme (early or late) spring molts impacted individual fishing strategies, 33% said they have not changed their behavior, while 50% said that they fish in deeper waters during warmer than average years, citing that recently warm years saw higher catches at depth compared to ‘normal’ years.

5.3.2 Fisherman-suggested variable analysis

The correlation matrices revealed that temperature anomalies in the winter and spring were significantly and negatively correlated with the eastern spring molt timing anomalies (Fig. 15), while only winter temperatures were significantly correlated in the central region (Fig. 16), and neither were significantly correlated to western spring molt timing anomalies (Fig. 17). In addition, the correlation coefficients for winter and spring temperatures were largest in the eastern region and lowest in the western region.

While no responses from each region were significantly correlated with the lunar phase, the western region by far had the highest correlation coefficient (r=0.48, *p*-value=0.072). Conversely, the tidal phase was only significant in the eastern region (r=0.62, *p*-value=0.013). Both the western and eastern region early spring molting appears to occur during the same tidal cycle, with values around 0.25-0.030.

Figure 15. Pearson-correlation matrix for spring molt timing anomalies in the eastern region, winter and spring average temperature anomalies, lunar phase and tidal phase.

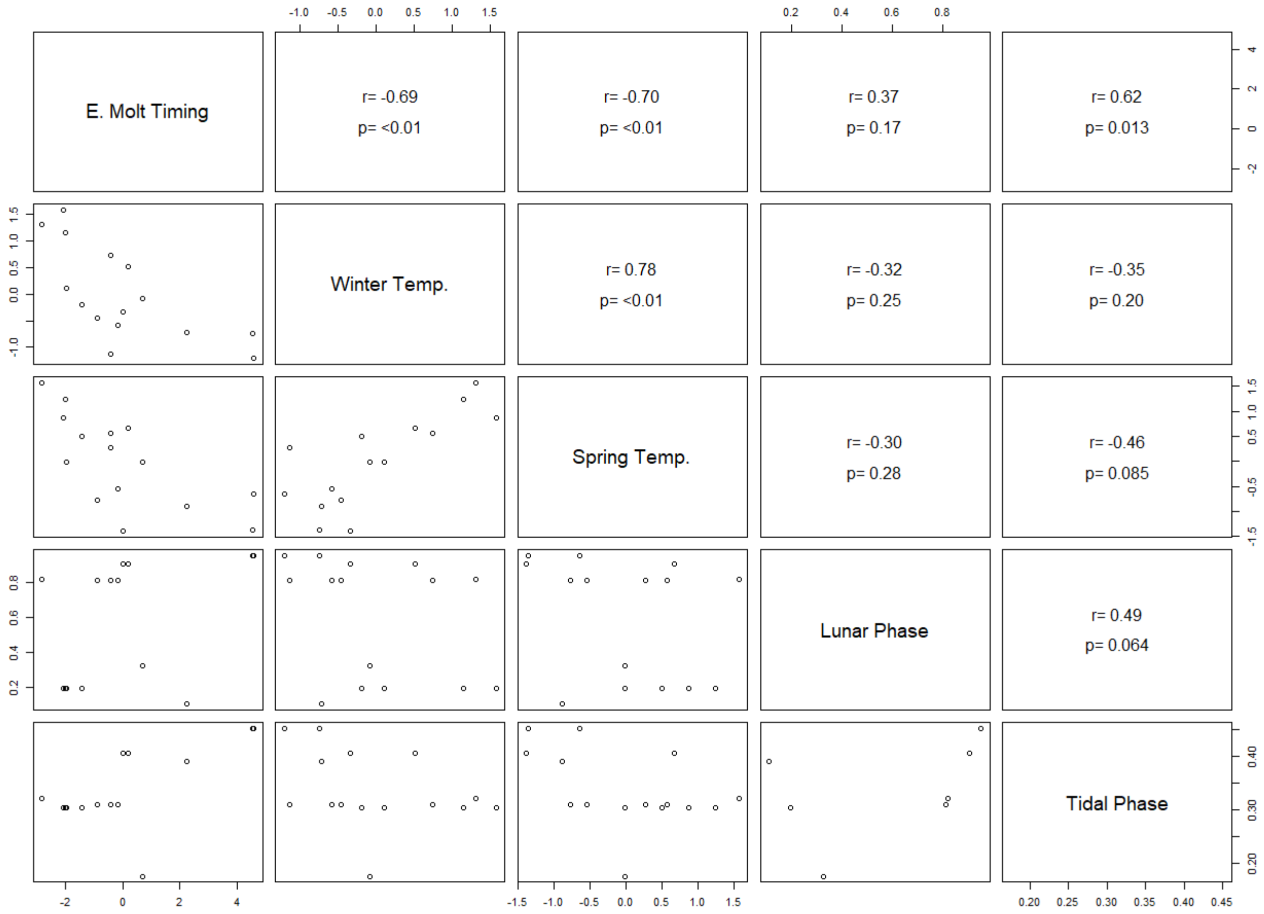


Figure 16. Pearson-correlation matrix for spring molt timing anomalies in the central region, winter and spring average temperature anomalies, lunar phase and tidal phase.

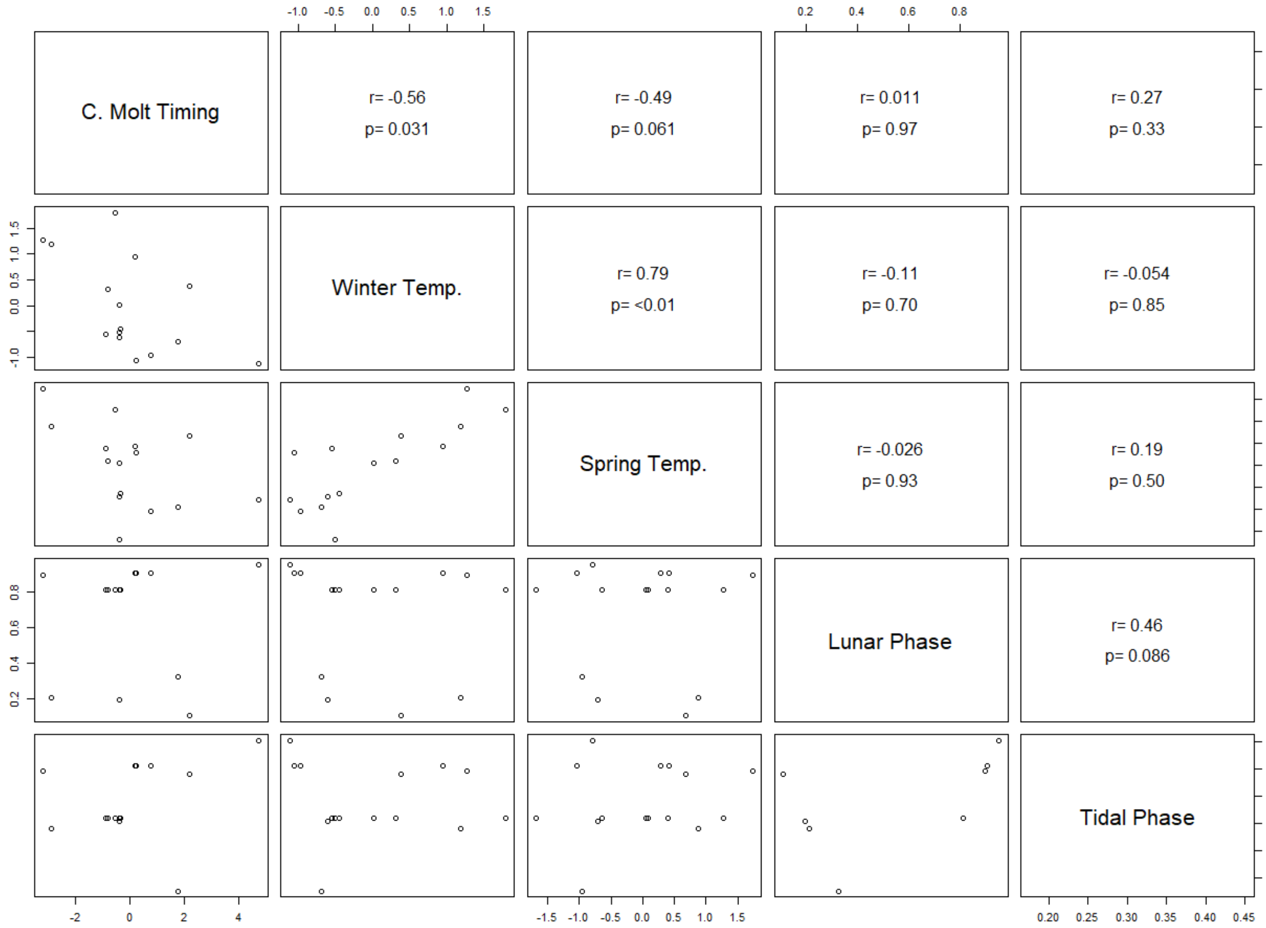


Figure 17. Pearson-correlation matrix for spring molt timing anomalies in the western region, winter and spring average temperature anomalies, lunar phase and tidal phase.

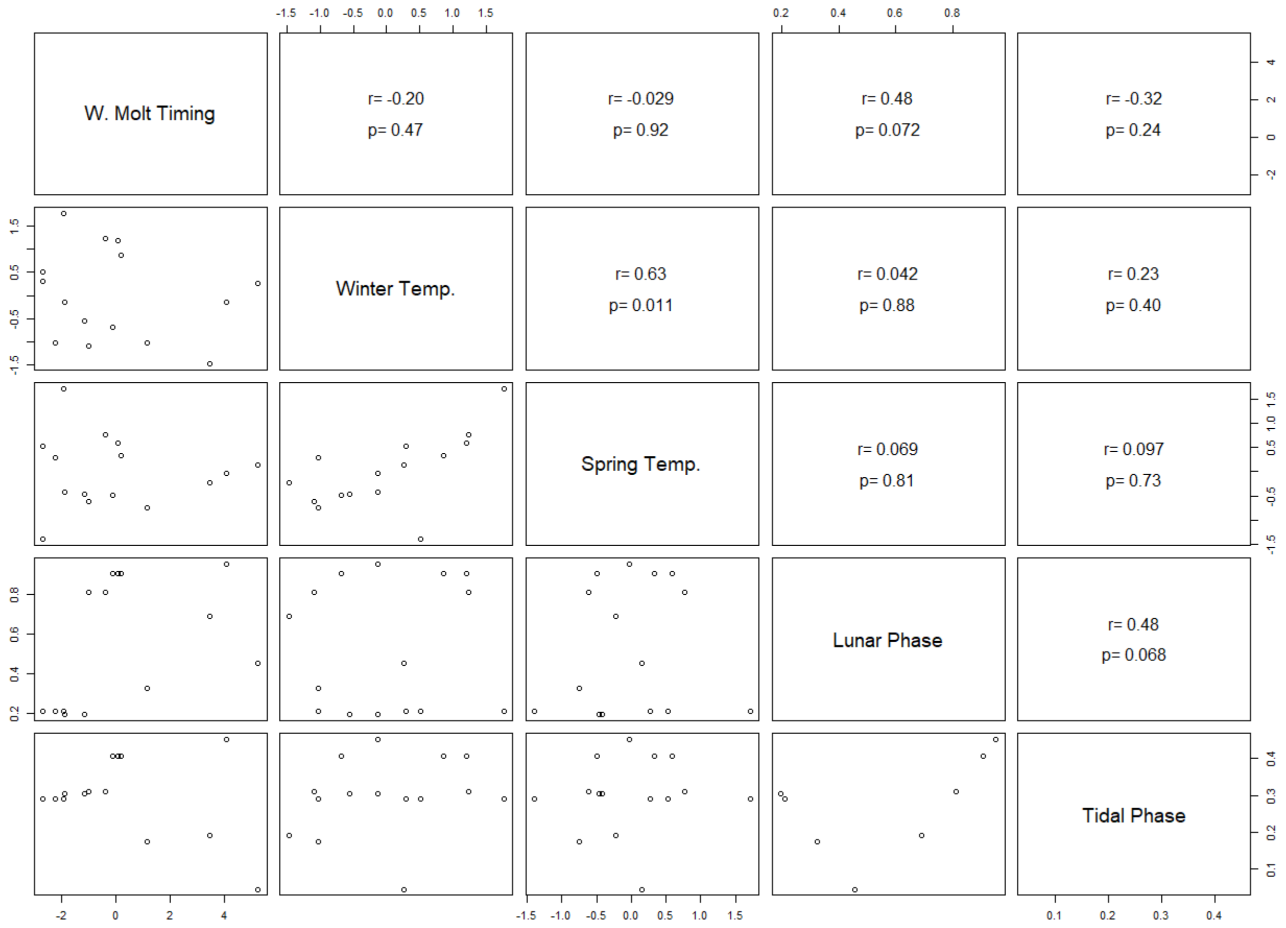
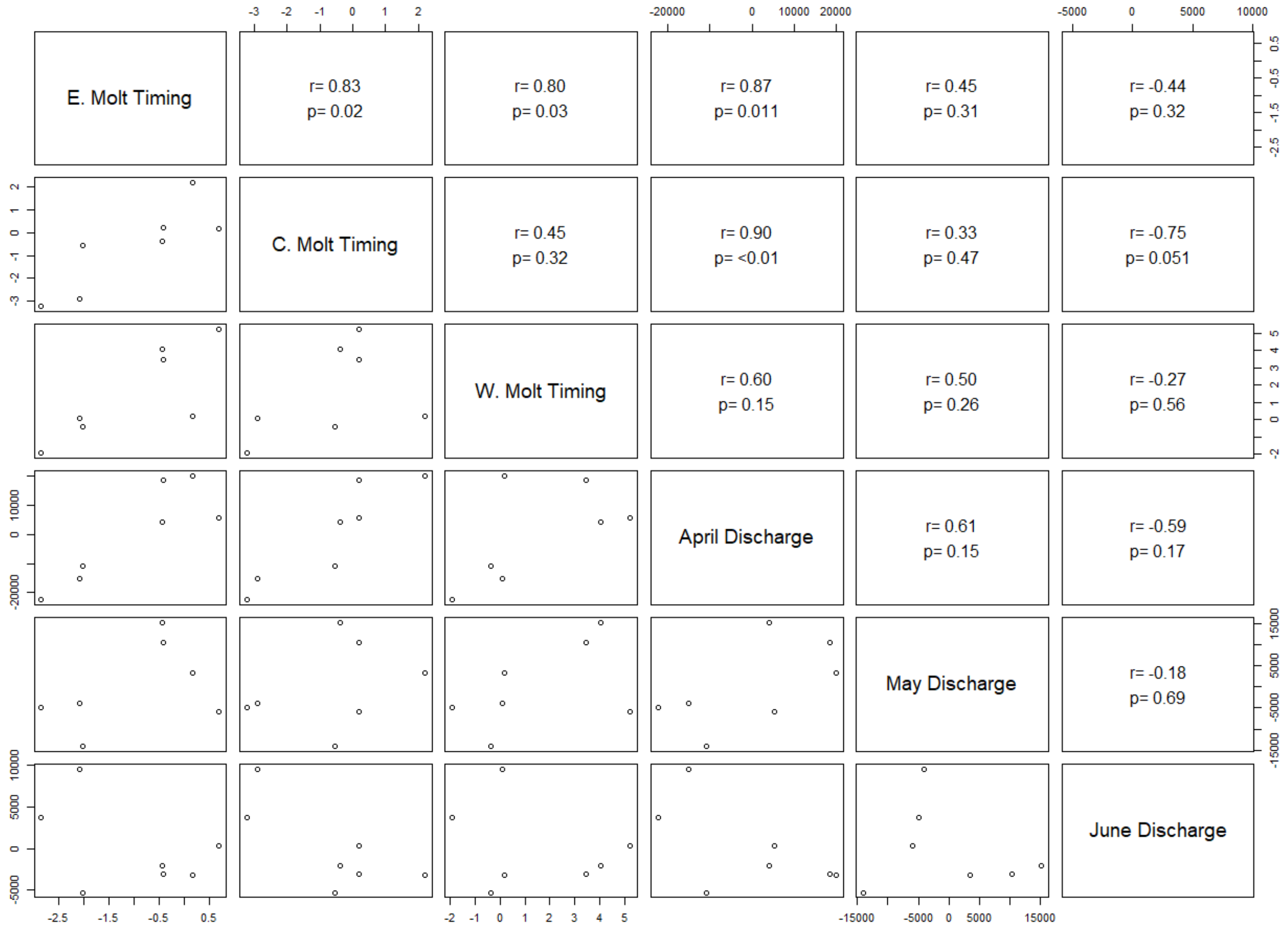


Figure 18. Pearson-correlation matrix for spring molt timing anomalies in the eastern, central, and western regions, and Penobscot River discharge anomalies for April, May and June.



Penobscot River discharge anomalies in April were positively, strongly, and significantly correlated with the spring molt timing anomalies in the eastern and central regions, and highly correlated (but not significantly) in the western region (r=0.60) (Fig. 18). River discharge anomalies in May and June were not significantly correlated with the molt timing of any region, but the correlation coefficients for June discharge anomalies were all negative and largest for the central region (r=-0.75, *p*-value=0.051).

5.4 Discussion

5.4.1 Fishermen responses and knowledge

The discussions with fishermen revealed a general understanding of lobster ecology and biology. The high rate of responses concerning the general temperature effects speak to an understanding of the connection between temperatures and the molt cycle (Templeman, 1936; Wilder, 1953; Aiken, 1980; Waddy et al., 1995). The responses surrounding substrate and the lull before the high landings speak to an understanding of habitat utilization, where lobsters will seek shelter for their molt before emerging to feed after ample shell hardening (Cobb 1971; Cowen and Atema 1990) and even the description of males molting before females shows a recognition of the molt staggering for mating purposes (Cowen and Atema 1990).

What these responses and conversations show is just how close RBK and LEK are for the lobster molt. Fishermen, however, hold the upper hand in understanding any spring molt because of their interactive relationship with the lobster population, which is not something easily substituted through research. Whereas the studies above are mostly done in controlled settings and laboratories, fishermen conduct experiments on a much finer scale, sometimes daily. This is the sentinel trap strategy that was commonly discussed, where fishermen will essentially design their personal fisheries sampling program. Sometimes the dispersal of traps is simply a shifting of the center of gravity within an established, consistent area and sometimes feeler traps are continually identifying areas where reallocation of effort follows in full. Any design allows the fishermen to observe the catch rates and shell status of the unseen lobster population below. Sometimes these experiments are done 100 replicates at one time, comparing variables that include the depth, substrate, and bottom complexity that fishermen identified in the interviews. If traps set on hard bottom start to catch individuals at a higher rate in any given week, a fisherman will likely move those less effective traps set on mud to areas of hard bottom, for example. This small-scale feedback loop allows for short-term tuning of fishing behavior to track lobster, which is undoubtedly why fishermen have gotten so good at catching them. It is the initial application of sampling effort inshore that is the difficult part, but fishermen use low-cost methods such as communicating with those sentinel fishermen within fishing groups, who lower the cost of information for a larger number of fishermen. Individual fishermen will also use a reduced amount of sampling effort (fishing less traps or hauling traps less often) until it is more cost-effective to do so.

Fishermen also described the adaptability in their methods for approximating the timing of the molt. When asked if extreme events had affected their methods, many indicated a conscious change in their response to warmer years that included fishing in deeper water, where trapping rates were high during previous warm years. Those that declared their methods static, described how such decision-making processes had previously led them to a similar endpoint as those making the direct change to deeper water and higher catches. The method was static, but the outcome of that same process was different and adaptable to changes in lobster phenology.

Given their adaptable fishing behavior and frequent interaction with the fishery, it is surprising that there is such variety in characterizing molting throughout the year as one, two, and even three distinct molting events, separated by an average of two months, for those characterized with multiple peaks. Some fishermen explained how each independent peak occurred at different depths or at least had some spatial variation. This may be a clue that leads to a better understanding of lobster molting, at least underscoring the somewhat cryptic nature of the lobster molting phenology, for those who study them from academic settings or those who interact with them on a frequent basis.

5.4.2 Correlation testing fishermen’s knowledge

The fishermen-suggested drivers of the spring molt, general temperature, tides and moonphase, and freshwater input had similar results to those degree day temperatures in Chapter 3. Average temperature anomalies showed that relatively cooler years were more associated with later spring molts and that temperatures were more associated with molting in the eastern and central regions than the western region. While moonphase in terms of moonlight did not have any association with molting, its impact via the tidal cycle did in the eastern GoM, where tides are greatest (Garrett 1972; Brooks and Townsend 1989). The association of increased Penobscot River discharge, through April snow melt runoff, was significant in delaying spring molting in the eastern and central regions, similar to general temperatures, confirming the strategy put forth by some fishermen. Curiously, though, river discharge did not have any effect in May, and the opposite association in June, where increased discharge was associated with earlier spring molts.

5.4.3 Bridging local ecological knowledge and research-based knowledge

In an arena, fisheries, where fishermen often feel that their expertise is overlooked (Palsson 1998), it may be more effective to show how much fishermen and scientists have yet to learn about a cryptic topic, such as the spring lobster molt and what influences its timing each year. In this example, we attempted to formalize how the fishing fleet was able to achieve such synchrony with the spring molting phenology shown in Chapter 4, using interviews to identify common cues that fishermen use to track the spring molt, and then using correlation analysis to test these variables’ association with the LSS derived spring molt timing (Chapter 2). What we learned was that fishermen identified similar variables to those within molting literature and some novel approaches, most of which were qualitative. Given the varied correlations of fishermen-selected variables to the timing of the spring molt, it is easy to understand how using a combination of cues and inputs allows individual fishermen to track the phenology of lobster with some accuracy. They are paying attention to environmental cues, non-environmental cues, and even biological cues to maximize their fishing practices and businesses. It is unclear what information scientists can provide fishermen that they do not already possess, as one fishermen said, “We’re always early,” referring to the fleet’s ability to use small-scale sampling to tune their behavior and also the need to stake one’s claim to preferred fishing areas (Acheson and Gardner 2005). These sentiments put the complex nature of lobster molting phenology in a different frame of increased complexity, where even perfect knowledge of molt timing may not alter the fishing practices along the coast of Maine.

CHAPTER 6

SYNTHESIS OF HOW LOBSTERS, THE OCEANIC ENVIRONMENT, AND THE LOBSTER FLEET INTERACT DURING THE SPRING MOLTING SEASON OF AMERICAN LOBSTER IN THE GULF OF MAINE

6.1 Trickle-down loop interactions

This research has shown that the spring lobster molt has a social-ecological dynamic. The spatial and temporal variability of the timing of the spring molt (Chapter 2) was shown to have some connection (robustly in the eastern region, at least) with inshore bottom ocean temperatures (Chapter 3). Fishermen, also using ocean temperatures (somewhat), along with many other environmental and non-environmental variables to approximate the timing of the pending spring molt (Chapter 5), consistently synchronize their behavior with that of the lobster they aim to catch (Chapter 4). These interwoven interactions highlight the effect that a variable (and changing) environment has upon fisheries dynamics, not just the marine species they target. The fishermen who have been noticing these fundamental changes in lobster phenology are part of the reason (as all humans are) for the changing (warming and increased variability) ocean temperatures that are affecting their own fishing practices.

6.2 Spring: nature’s jack-in-a-box

Springtime in temperate regions, like the Gulf of Maine, is a time of rapid change. The sunlight shines over a longer period of each day, temperatures begin to rise, snow begins to melt and flow toward the ocean, and thermoclines begin to develop. This changing environment produces suddenly favorable conditions for primary production, and herbivores feed upon these huge blooms, followed by their predators, looking for feasts of their own. The onset of spring also produces favorable conditions for lobsters looking to molt and the fishermen looking to catch the soon-to-be-legal sized bounty. As important as the timing of spring is, in the non-astronomical sense, it is also difficult to predict.

This difficulty was apparent in this research, especially relating to how bottom ocean temperatures might influence the timing of the lobster molt. While our results showed some signals that inshore temperatures might drive the timing of the molt, the analysis showed that it was hardly a smoking gun. Much of this difficulty can be attributed to quantifying temperature in a ‘correct’ way. Certainly, there is a lot of analysis to be done on how different representations of the same temperatures might better predict the timing of the spring molt, but the value is greatest in developing some sort of ocean temperature forecast. Such a forecast would provide a base to number of species-specific predictions, lobster included. Achieving forward-looking projections of lobster molting using the relationship between the timing of the molt and temperatures are hardly useful if future temperatures are going to continue to be a mystery.

The conversations with fishermen reinforced this point. As fishing is their main source of income (for most, anyway), identifying ways to synchronize their business model with that of the resource they are exploiting is most important. While they paid attention to temperature in a broad sense, their use of frequent sub-sampling of the environment and lobster population speaks to the difficulty in prediction when spring, in a phenological sense, will arrive. For them, temperature is only one of many inputs; a slow crawl of information that finely tunes their fishing practices. In the end, as many fishermen said, “It’s about what’s in the trap,” when it comes aboard their vessels. It is hard to provide better information than that.

6.3 Admissions, reflections, and hope

Here, we should discuss some of the limitations and assumptions that were made during this research. First, we will reiterate the fisheries-dependent and spatiotemporal variation within the LSS and LP data. While these were the best data available for investigations into a population-scale phenology, this variation was apparent in the differences between logistic model fits. While these differences are results on their own, any errors made during the logistic approximation process propagated throughout each subsequent analysis. Degree days were calculated using these estimates as starting and endpoints of molting periods, over which degree days were summed. Landings proxies were compared to these estimates, which were assumed to be ‘true’ or ‘observed’ scenarios, for the purposes of analysis. Moon and tidal phases were queried from these estimates as well. Each one of these examples highlights the dependency on these initial estimates. This is why, if molting phenology is to be of concern to management in the near or distant future, a fisheries-independent survey must be created (or modified) with satisfactorily standardized molting quantification to provide the observed data that are estimated throughout this research. That said, much of the impetus for this research was the need for the creation of some reasonable baseline for spring lobster molting and potential drivers of lobster molting at the population-level. The ability to point to a quantified history of events and influential factors carries more weight, especially relative to qualitative and anecdotal characterizations, as many fishermen will tell you. The quantification of these characterizations, of both scientists and fishermen, may be the starting point for a more formal evolution of studying lobster molting phenology. Hopefully, this research helps to establish that starting point and quickly gives way to more robust findings which provide greater understanding.

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APPENDICES

Appendix A: Logistic model fits

Figure A1: Logistic model applications for all eastern molt data.

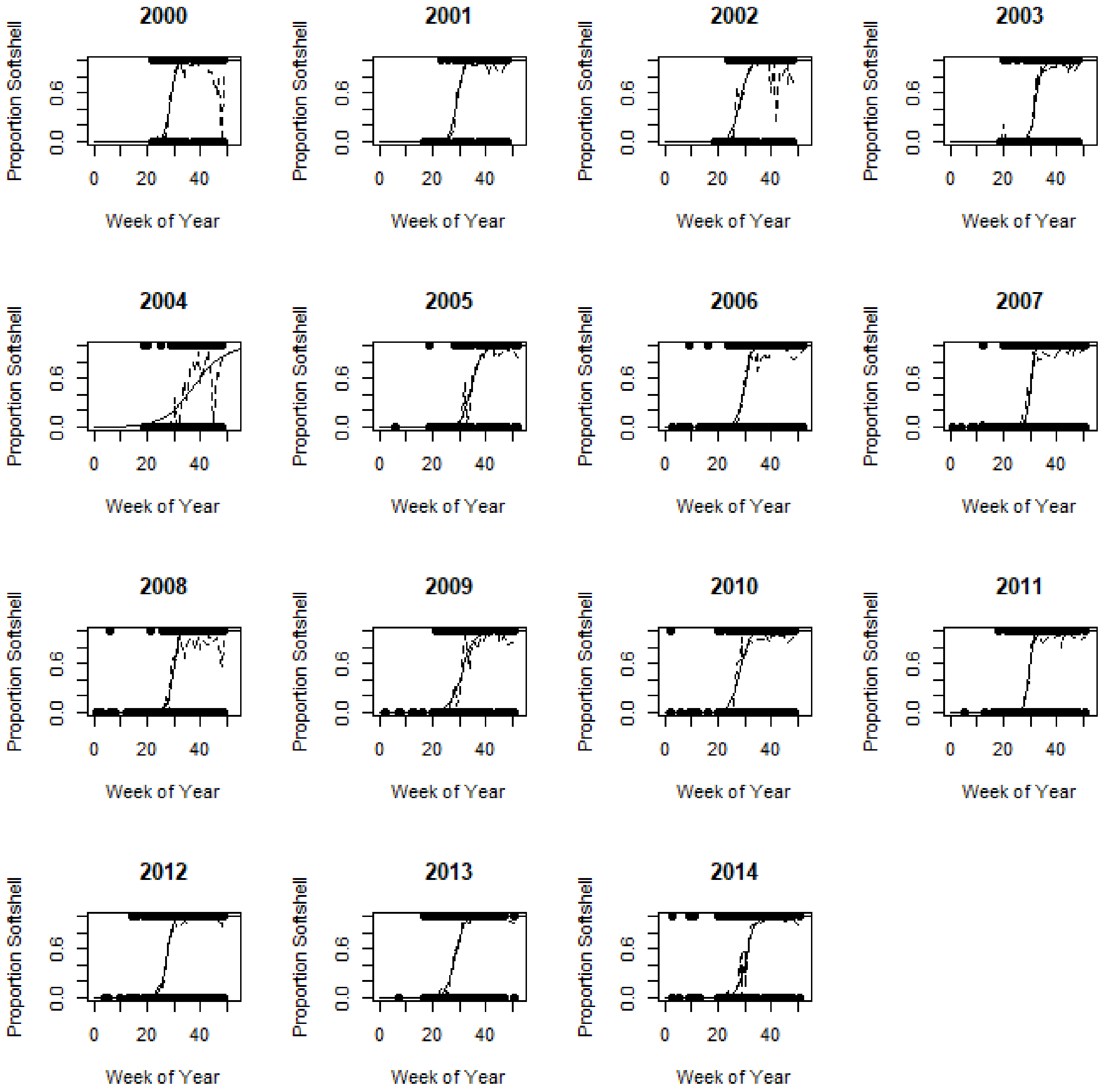


Figure A2: Logistic model applications for all inshore eastern molt data.

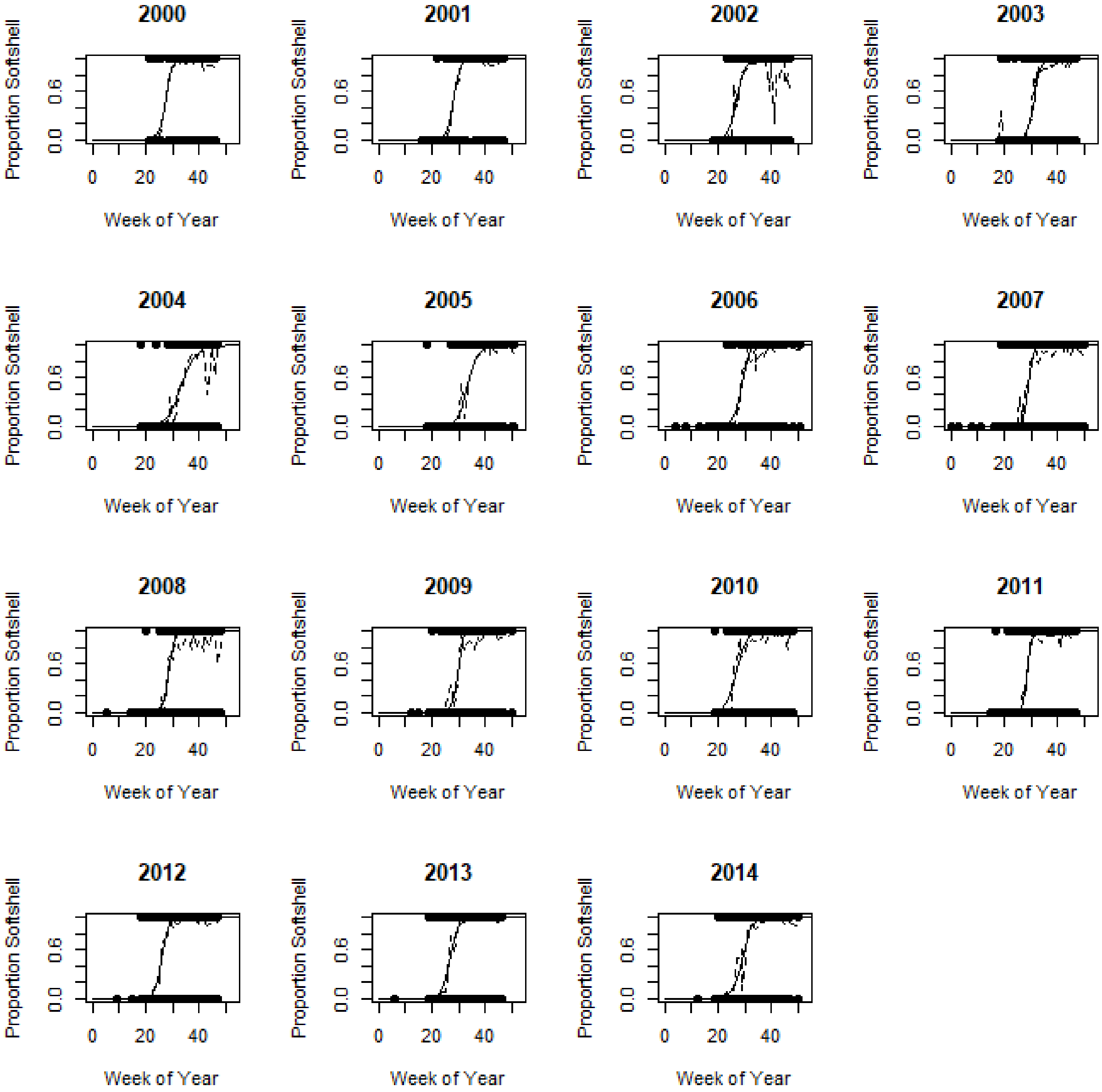


Figure A3: Logistic model applications for all male inshore eastern molt data.

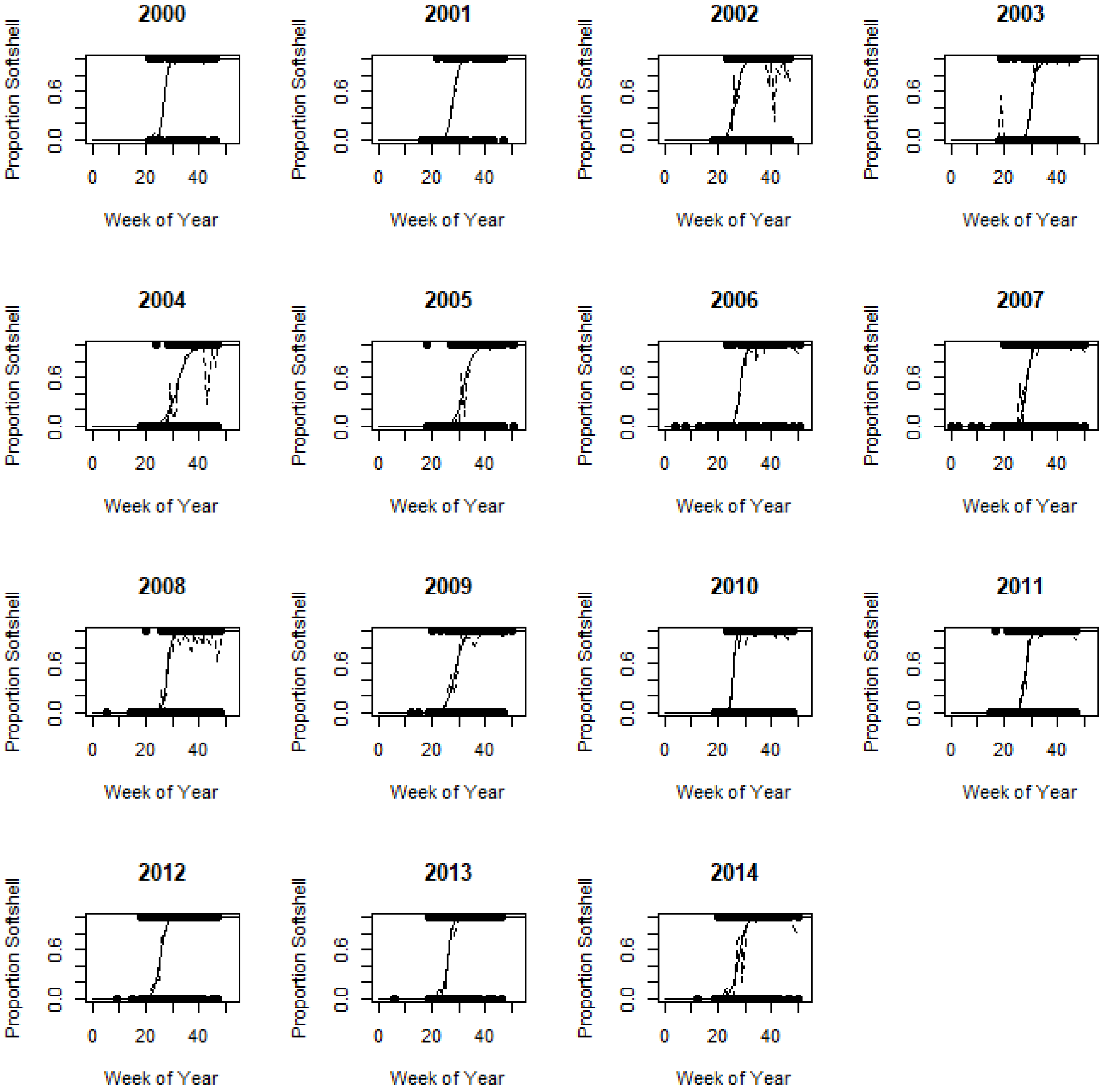


Figure A4: Logistic model applications for all female inshore eastern molt data.

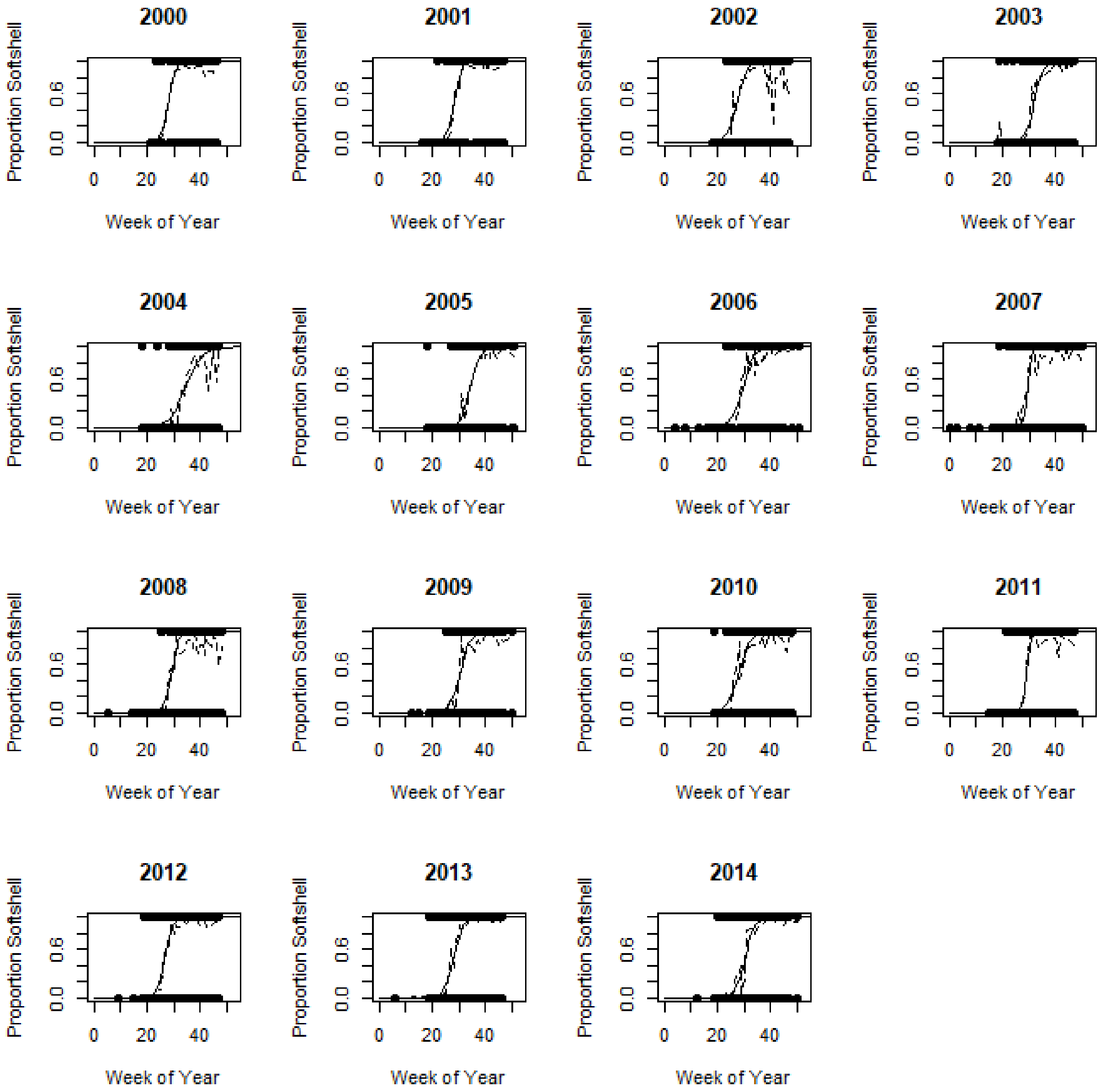


Figure A5: Logistic model applications for all central molt data.

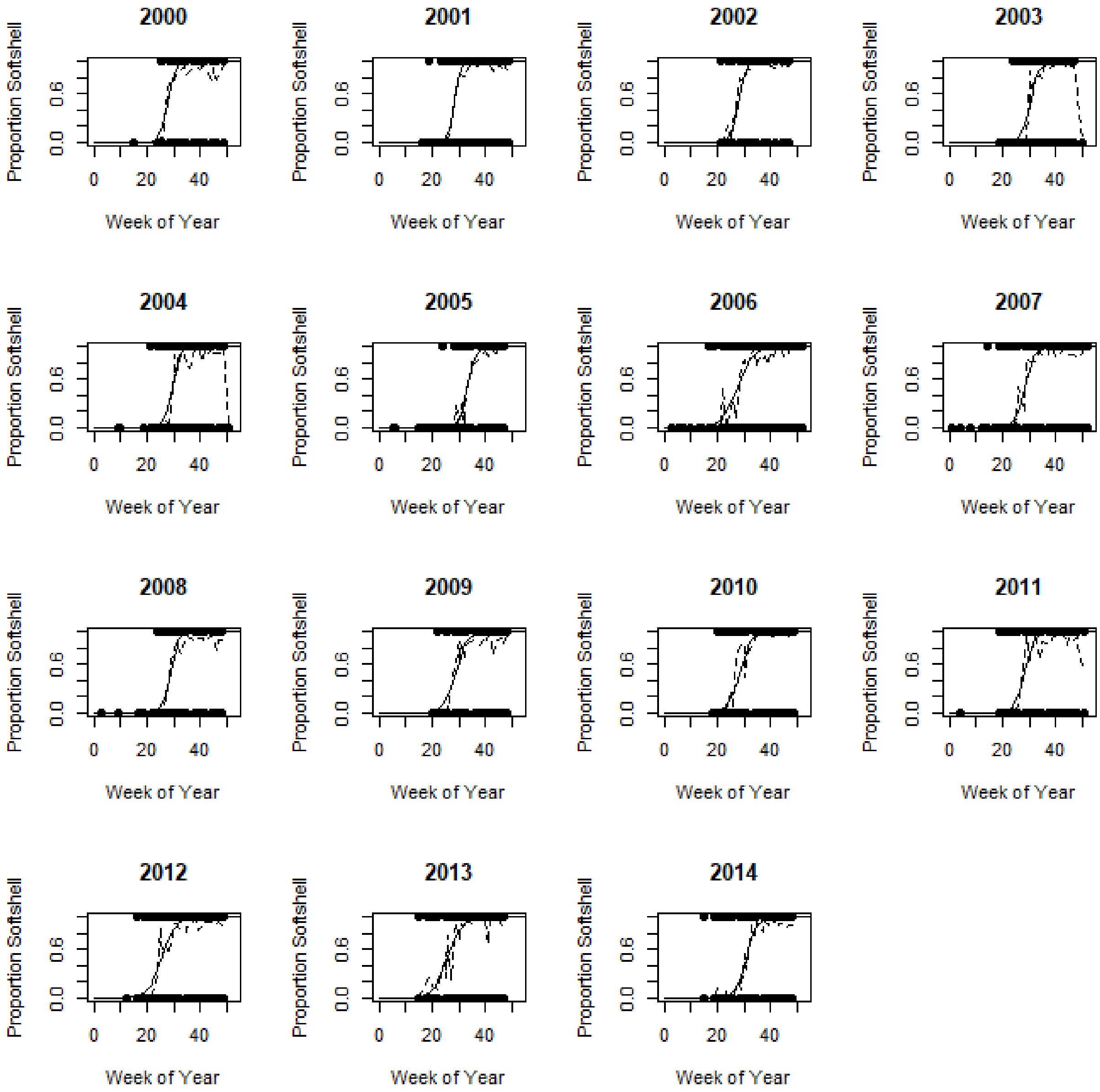


Figure A6: Logistic model applications for all inshore central molt data.

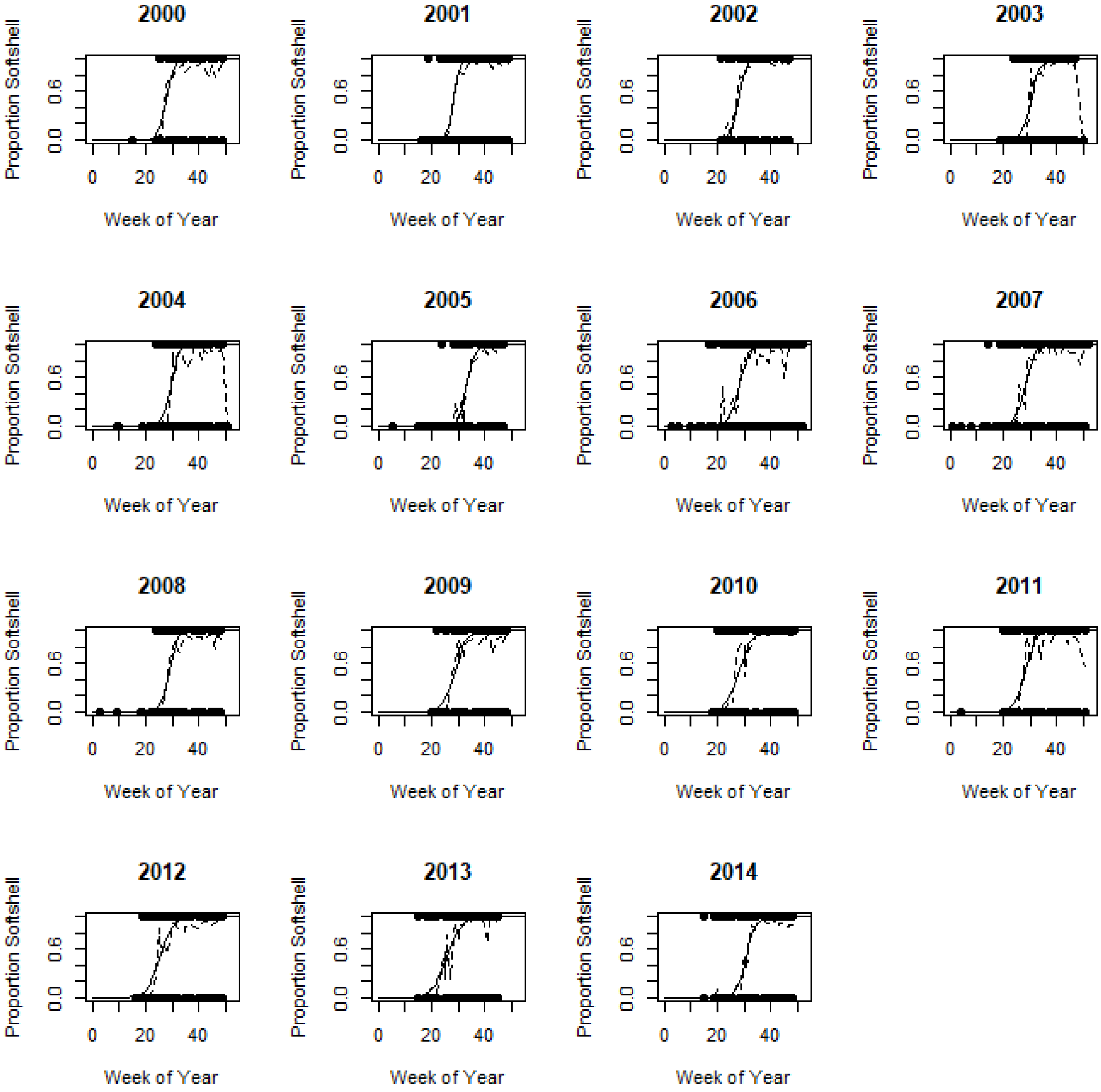


Figure A7: Logistic model applications for all male inshore central molt data.

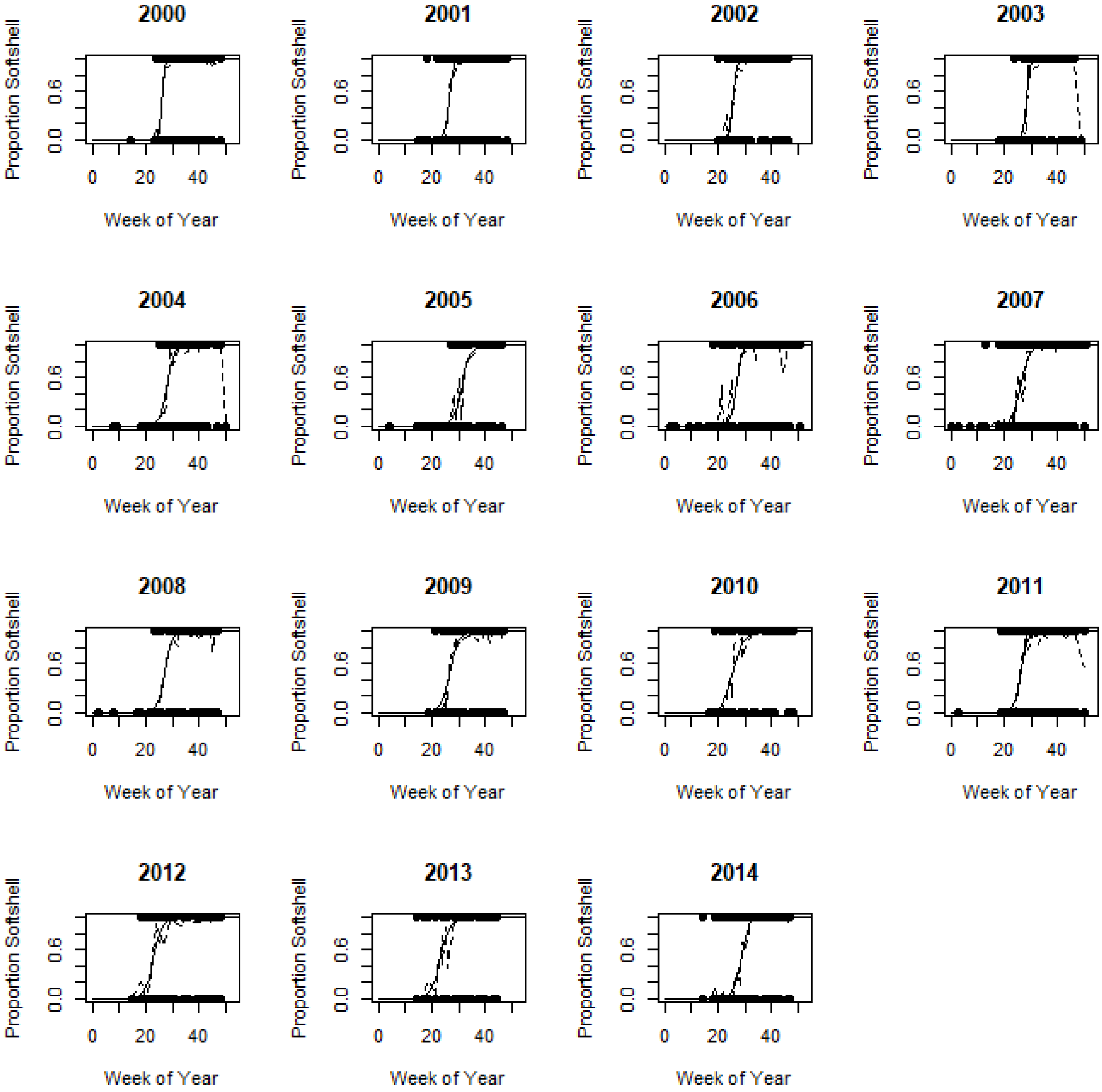


Figure A8: Logistic model applications for all female inshore central molt data.

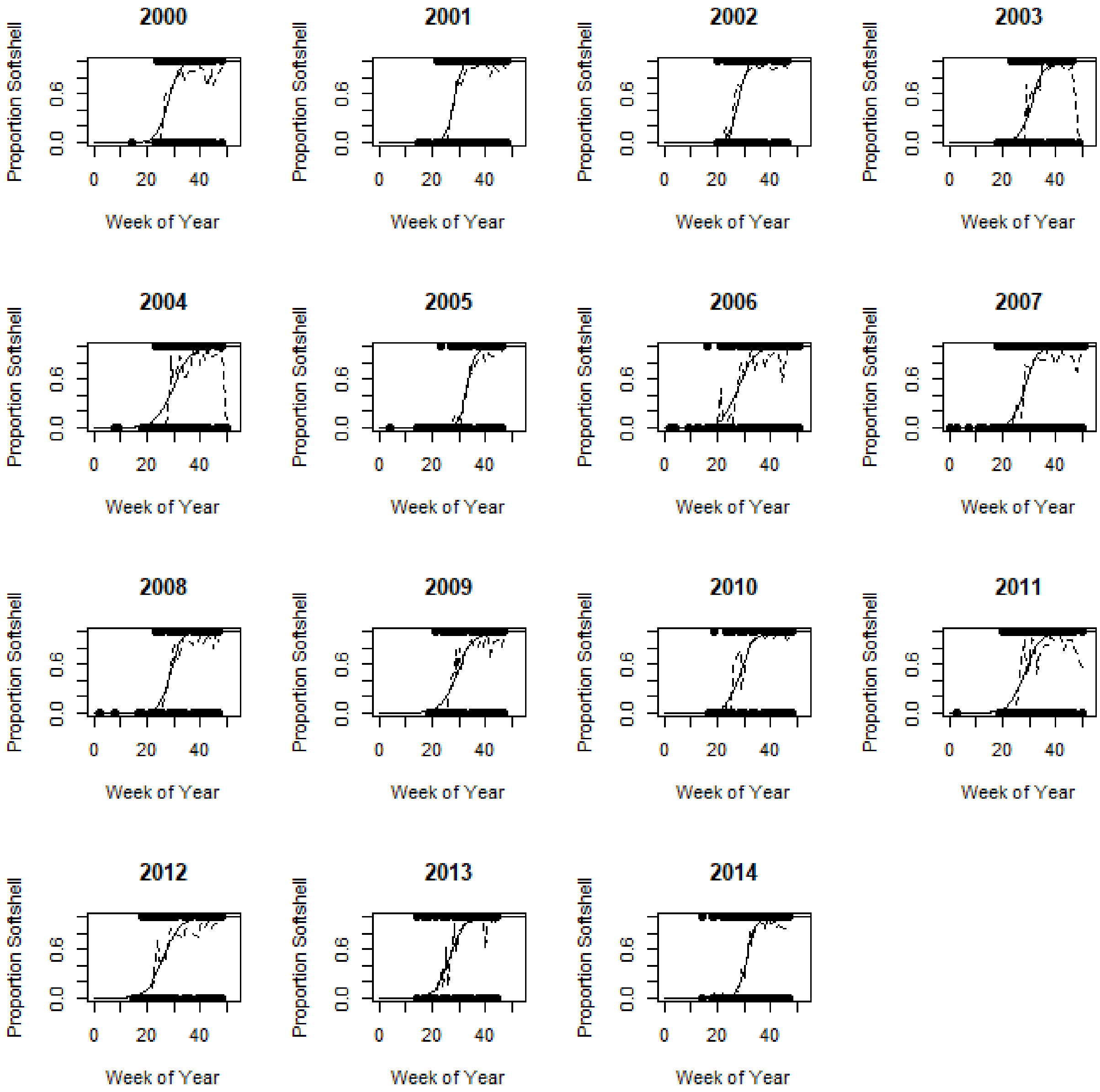


Figure A9: Logistic model applications for all western molt data.

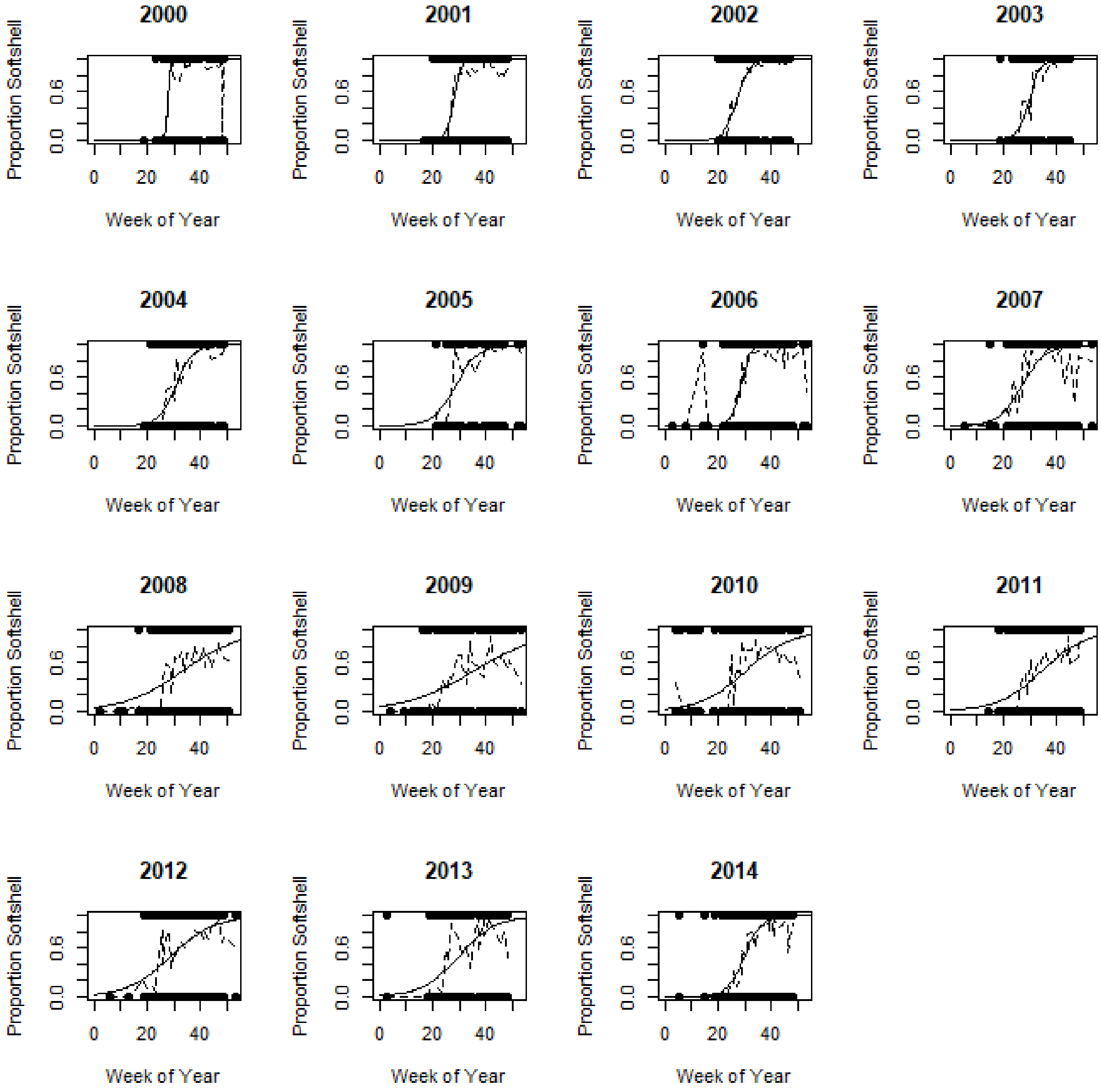


Figure A10: Logistic model applications for all inshore western molt data.

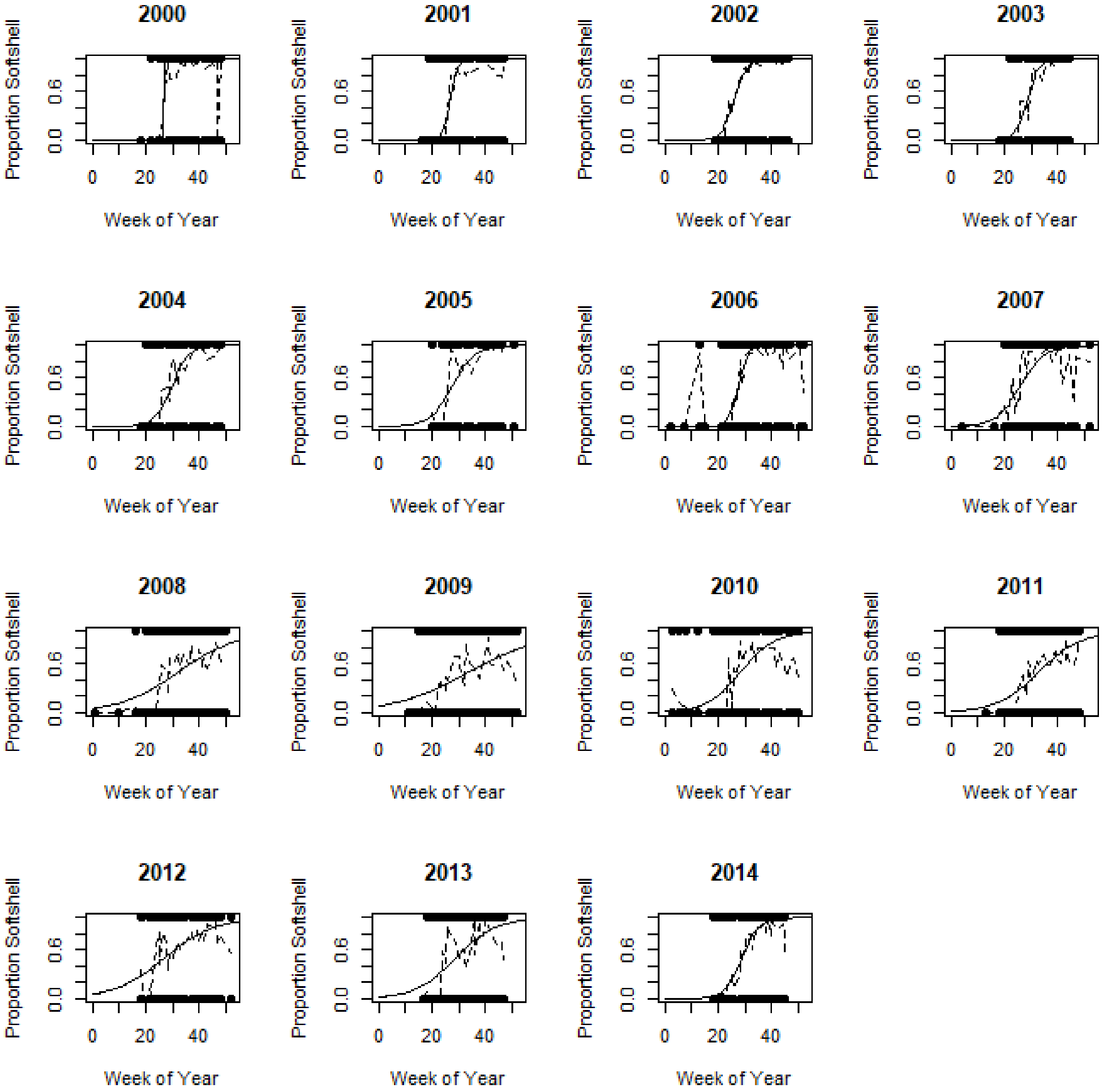


Figure A11: Logistic model applications for all male inshore western molt data.

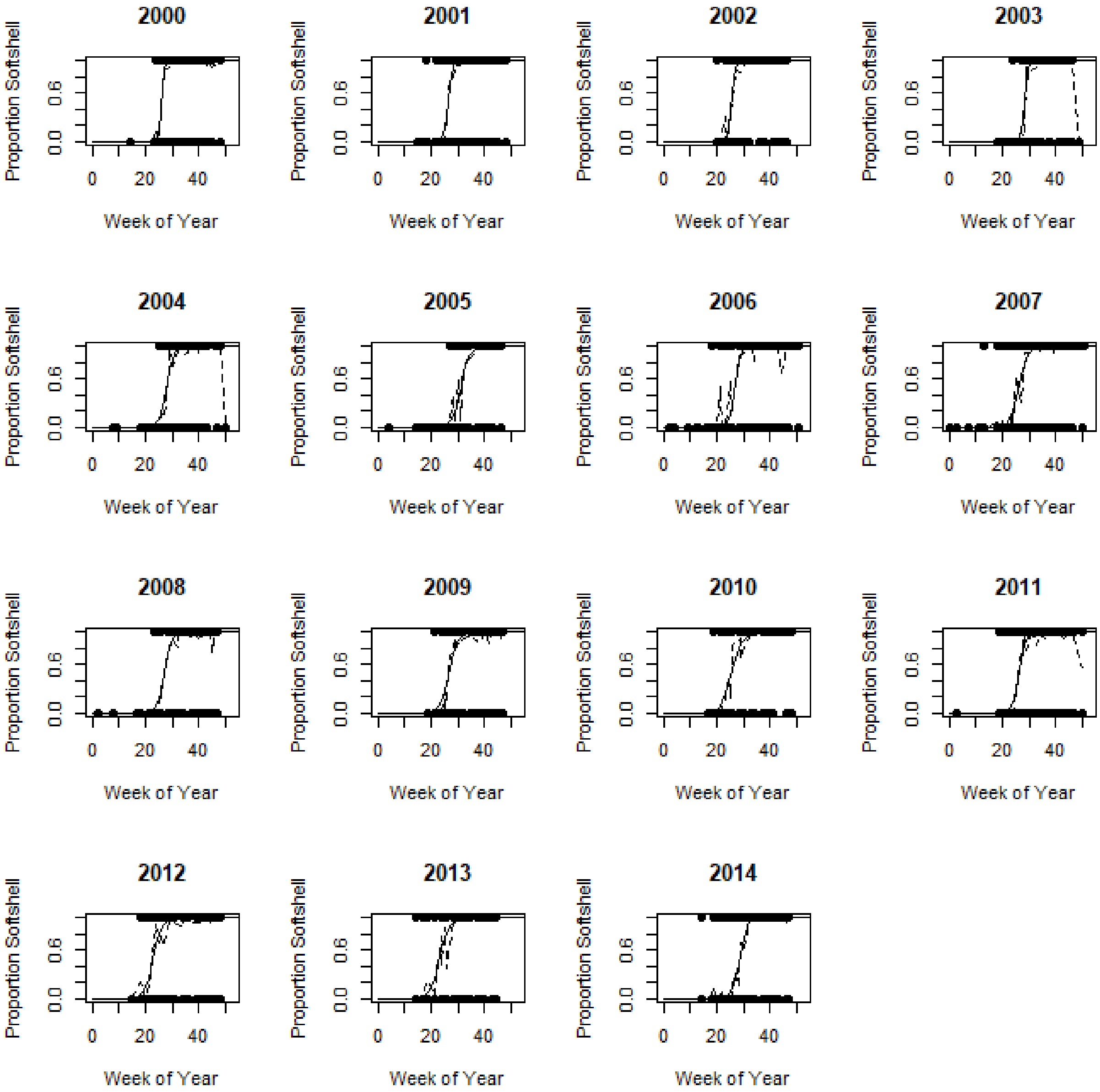


Figure A12: Logistic model applications for all female inshore western molt data.

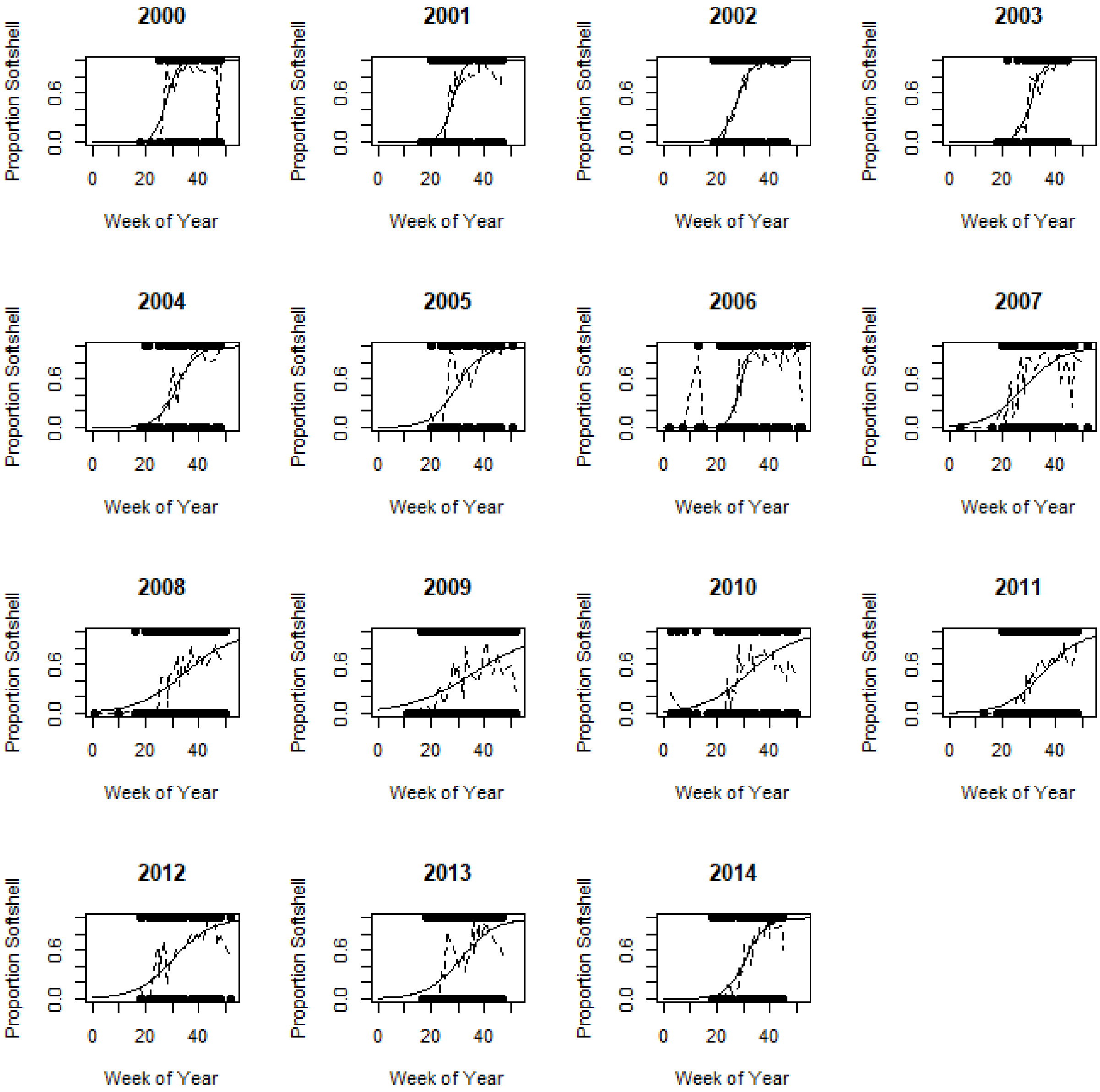


Figure A13: Logistic model applications for all legal-sized eastern molt data.

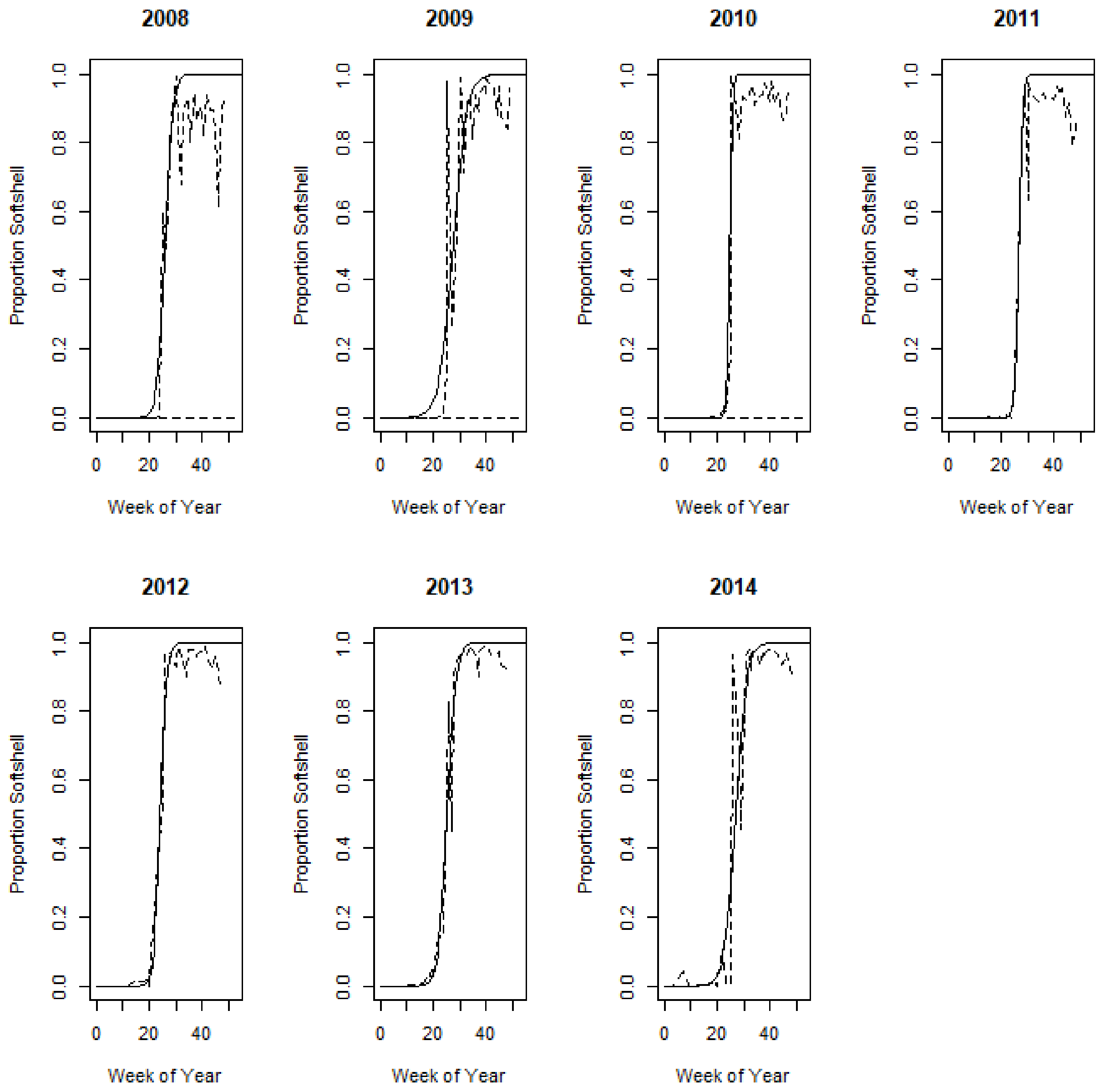
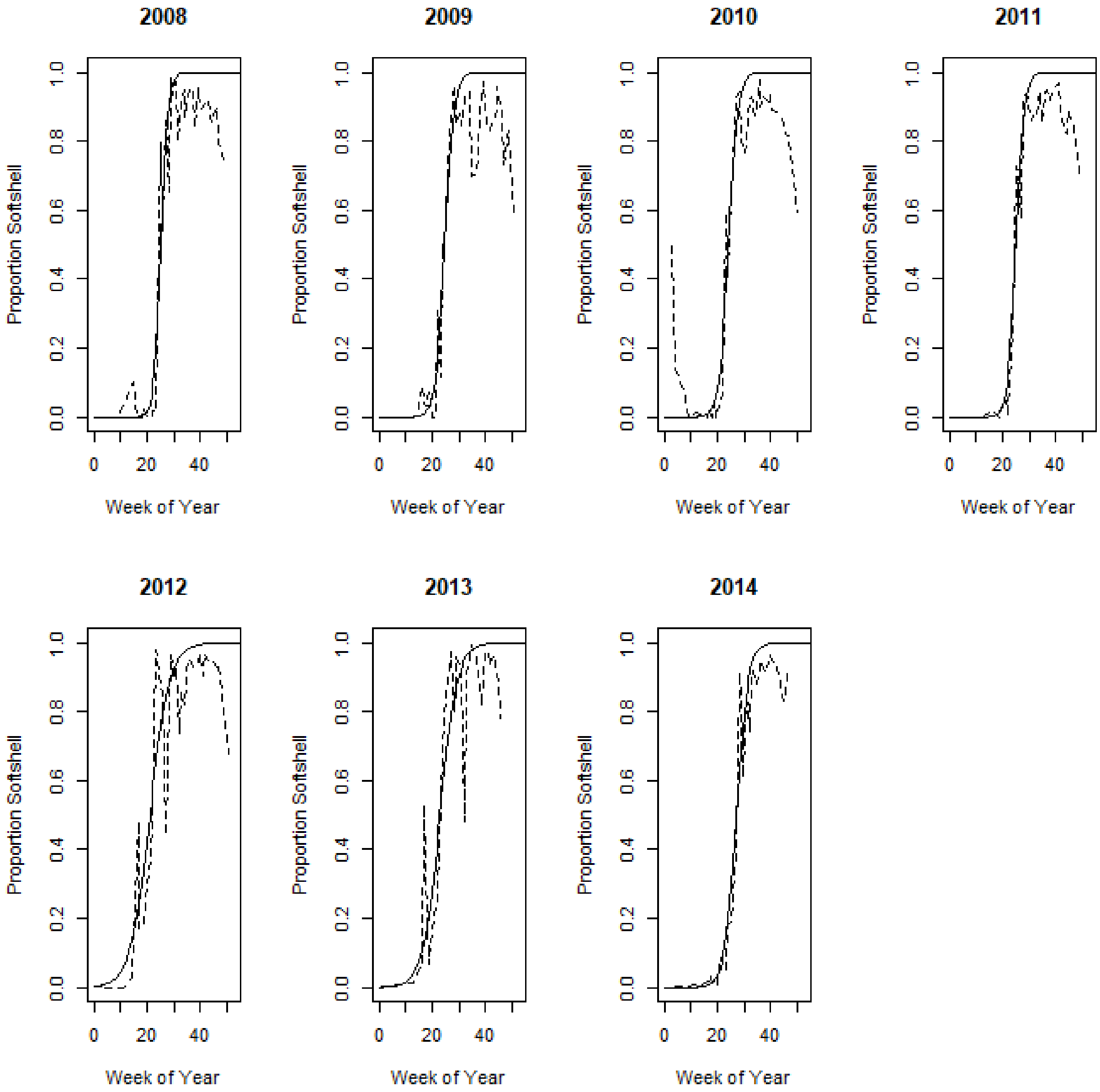


Figure A14: Logistic model applications for all legal-sized central and western molt data.


2008

2009

2010

2011

2012

2013

2014

Figure A15: Logistic model applications for newshell eastern landings data as a proportion of total landings.

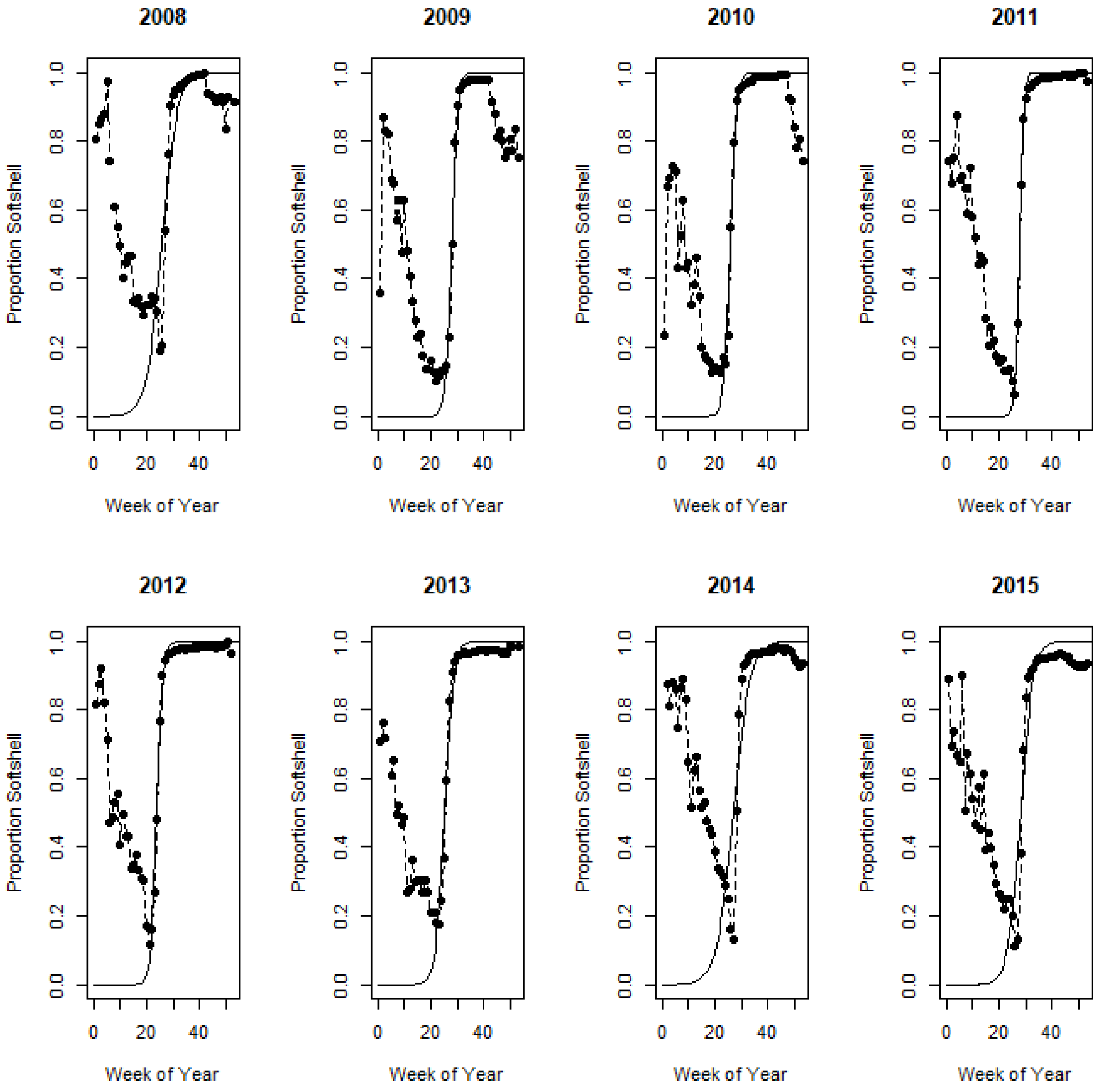


Figure A16: Logistic model applications for newshell eastern landings data as a cumulative percent of annual newshell landings.

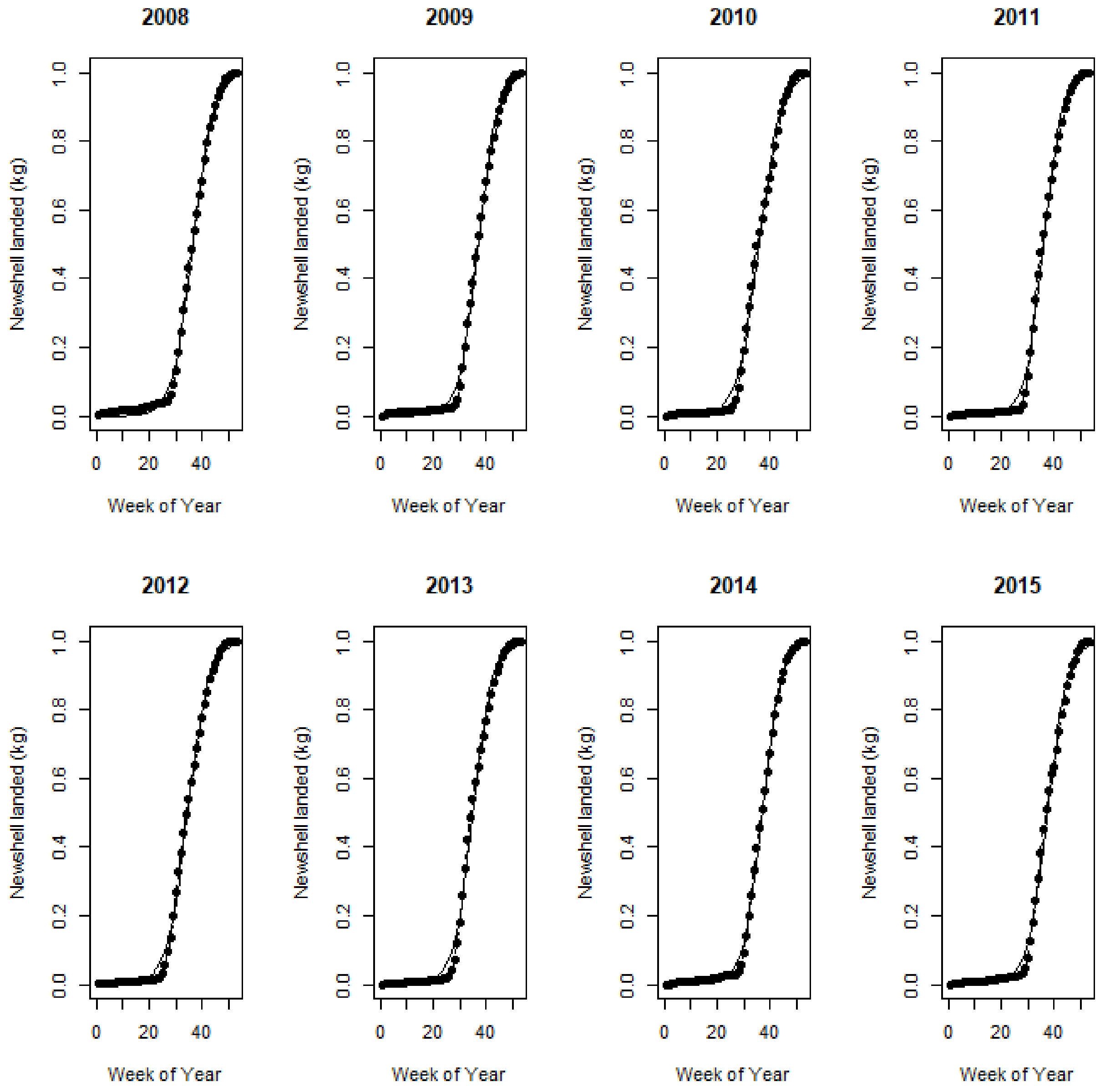


Figure A17: Logistic model applications for newshell eastern landings data as a percent of annual newshell weekly maximum.

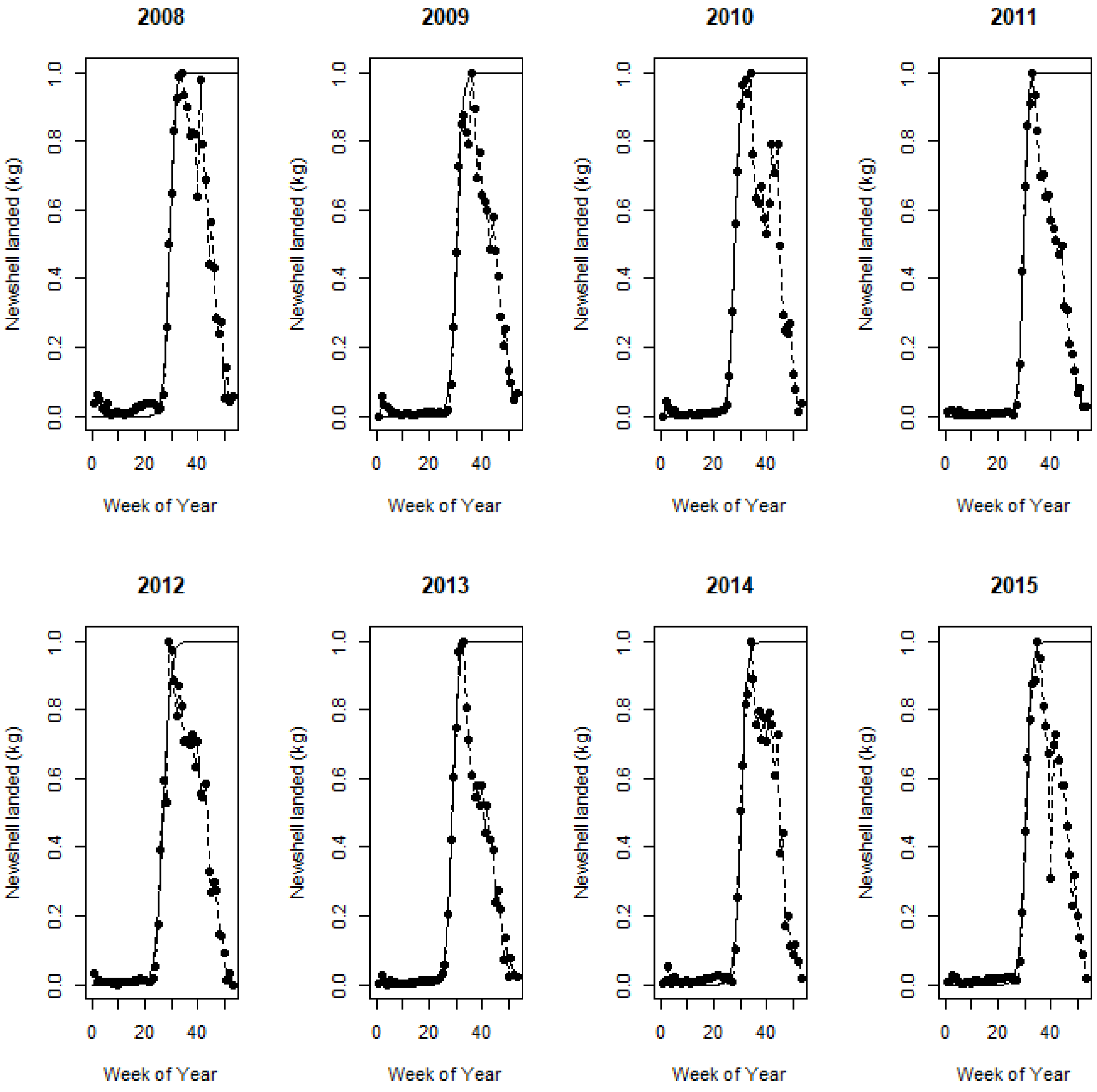
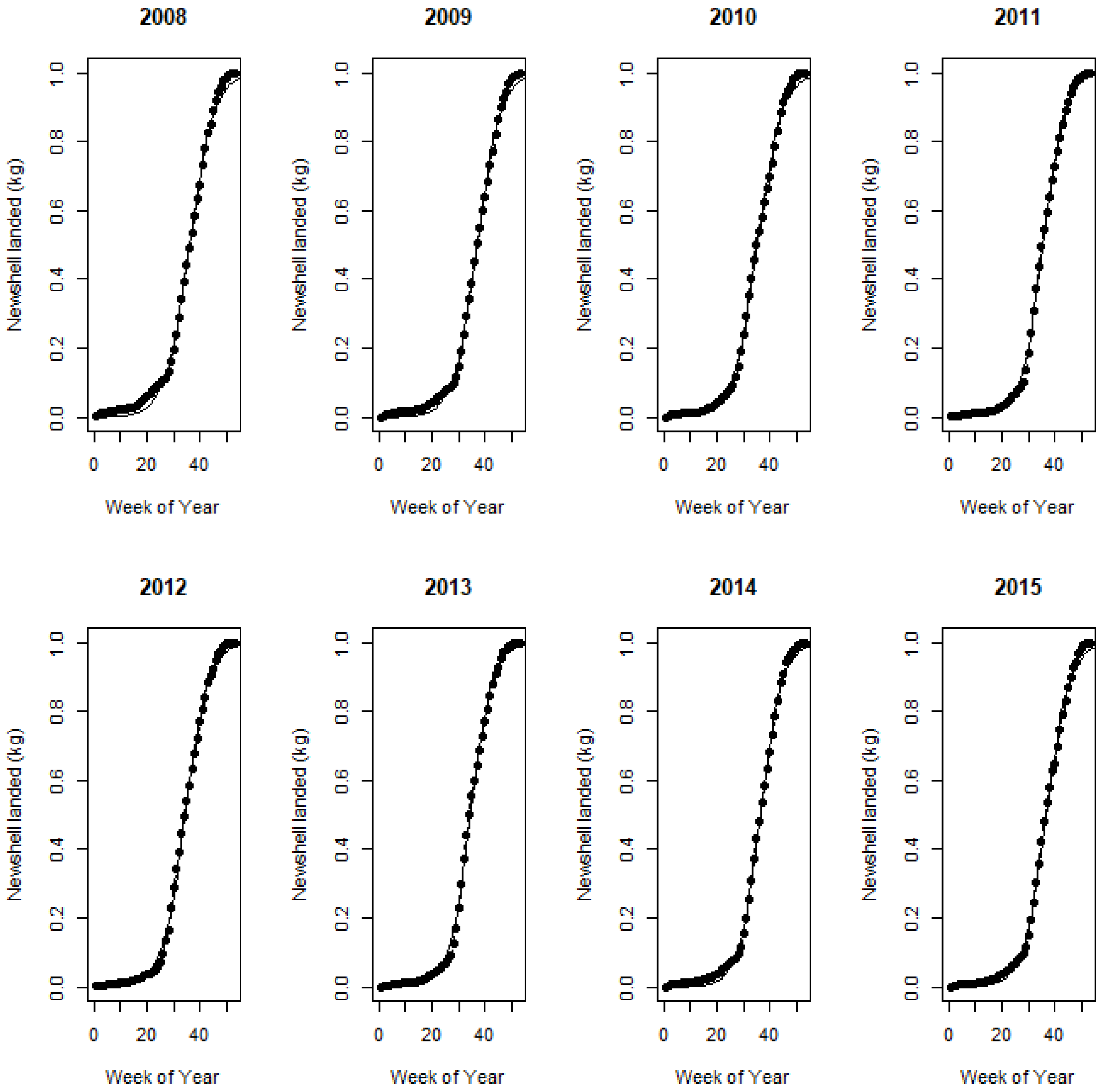


Figure A18: Logistic model applications for total eastern landings data as a cumulative percent of total annual landings.



2008 2009 2010 2011

2012 2013 2014 2015

Figure A19: Logistic model applications for total eastern landings data as a percent of annual total weekly maximum.

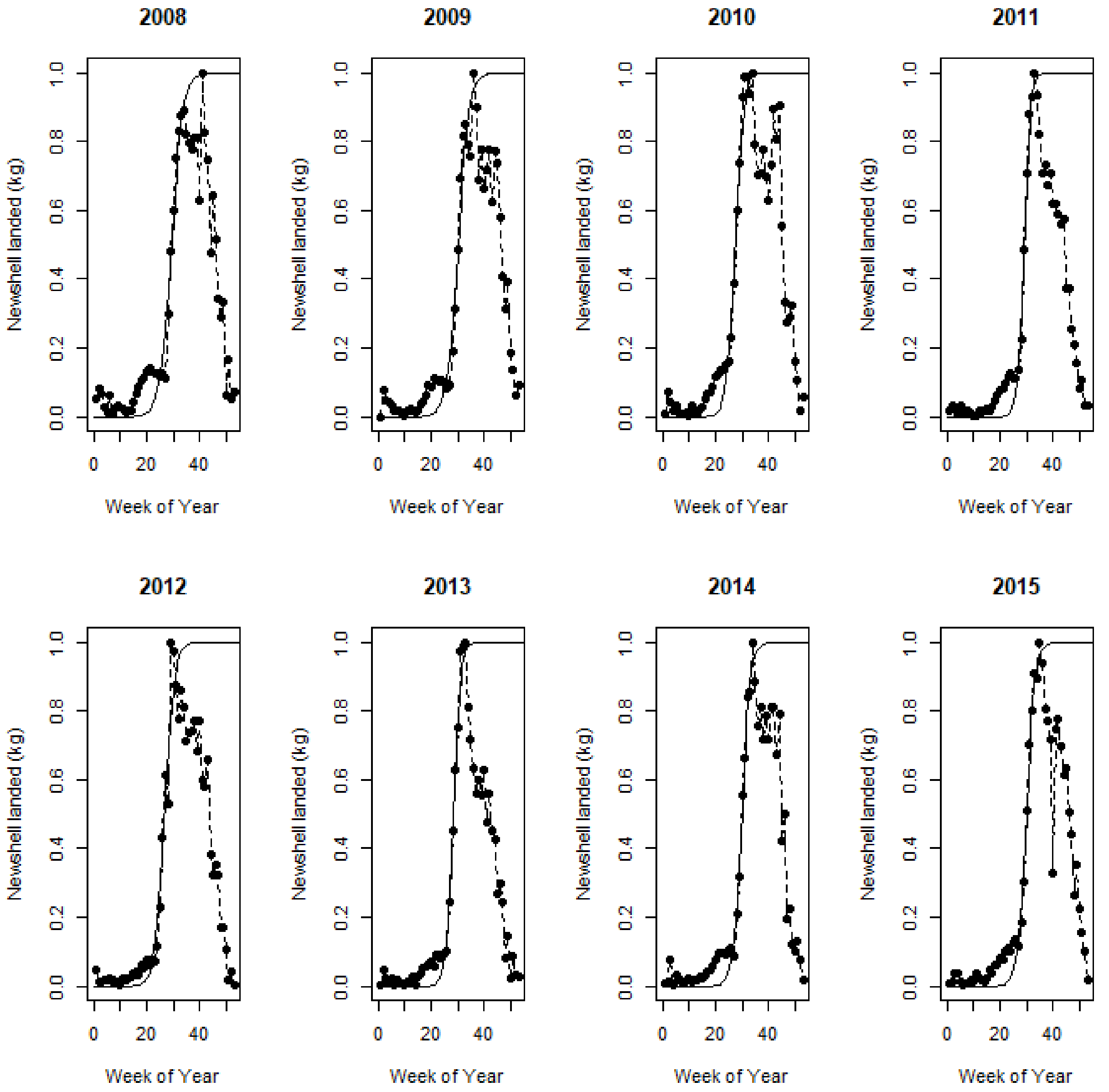


Figure A20: Logistic model applications for newshell central and western landings data as a proportion of total landings.

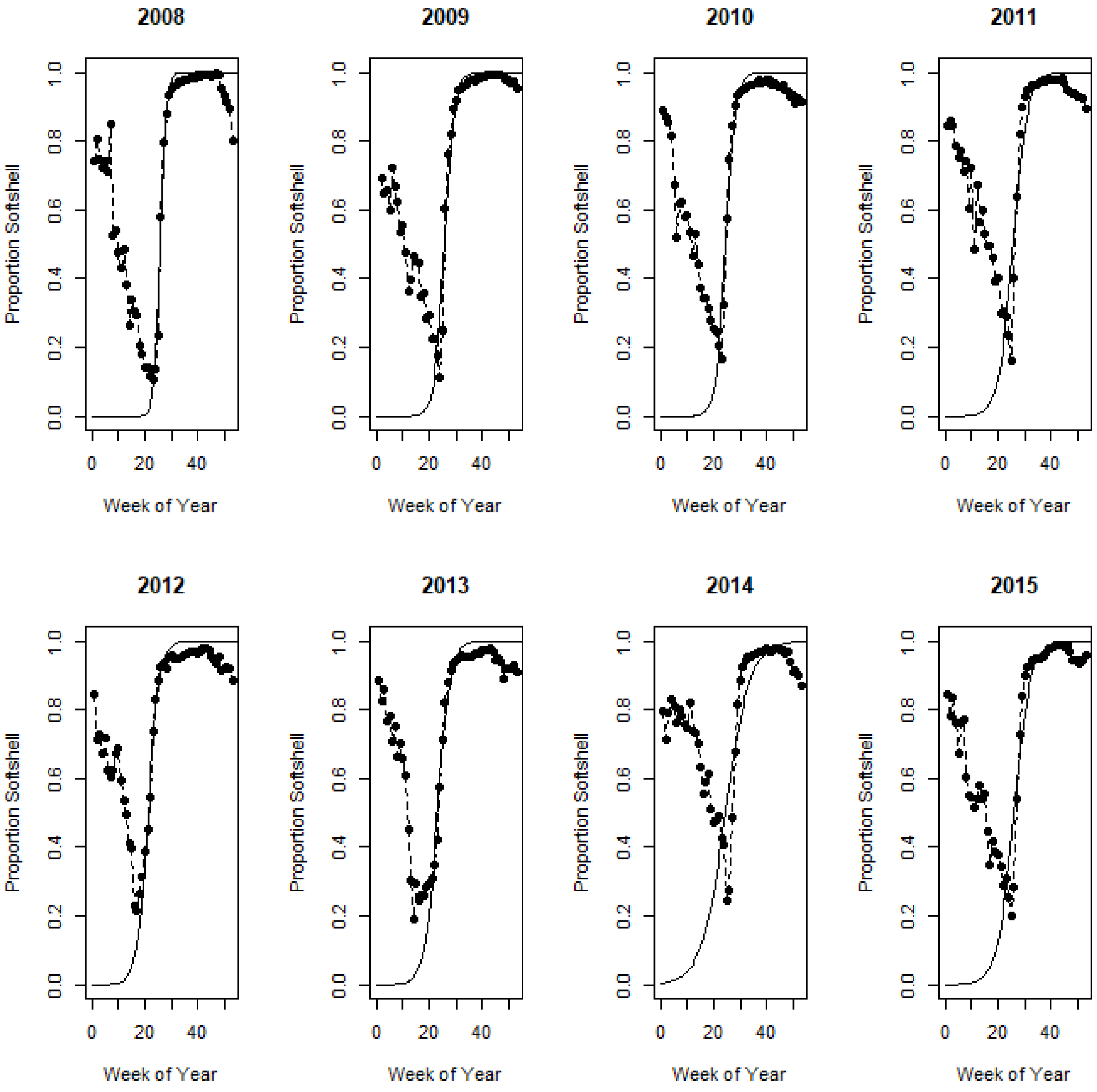


Figure A21: Logistic model applications for newshell central and western landings data as a cumulative percent of annual newshell landings.

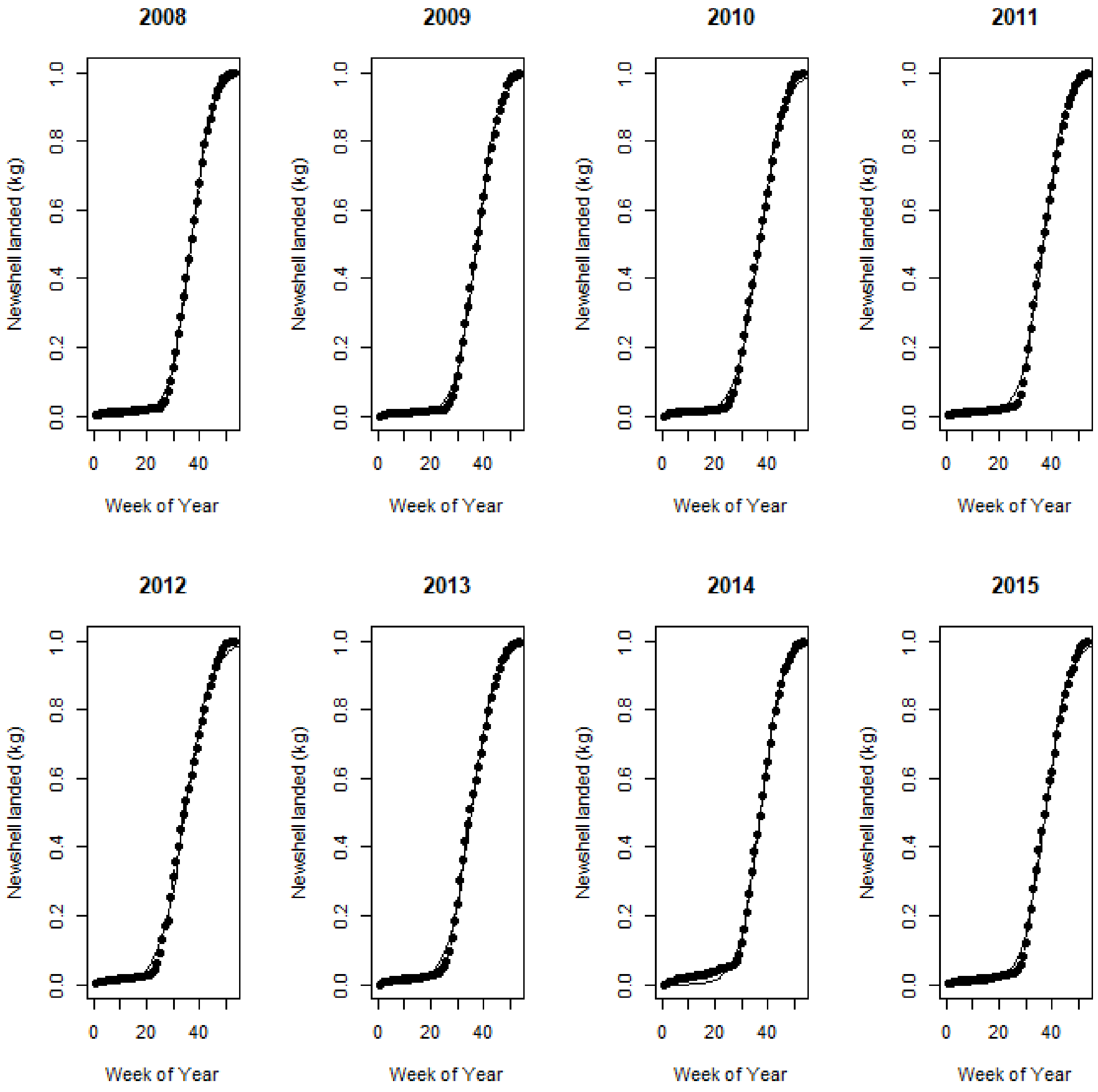


Figure A22: Logistic model applications for newshell central and western landings data as a percent of annual newshell weekly maximum.

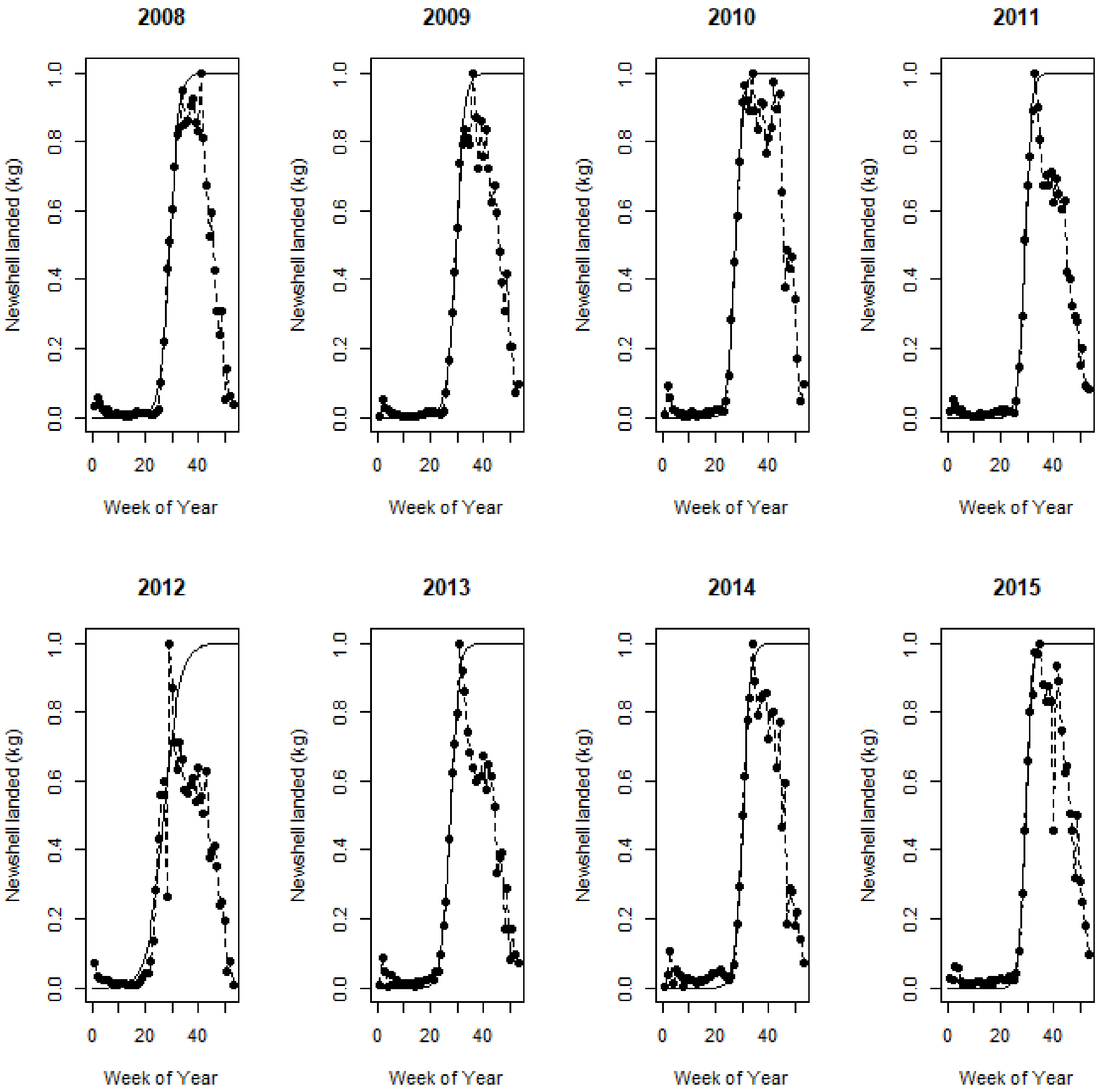


Figure A23: Logistic model applications for total central and western landings data as a cumulative percent of total annual landings.

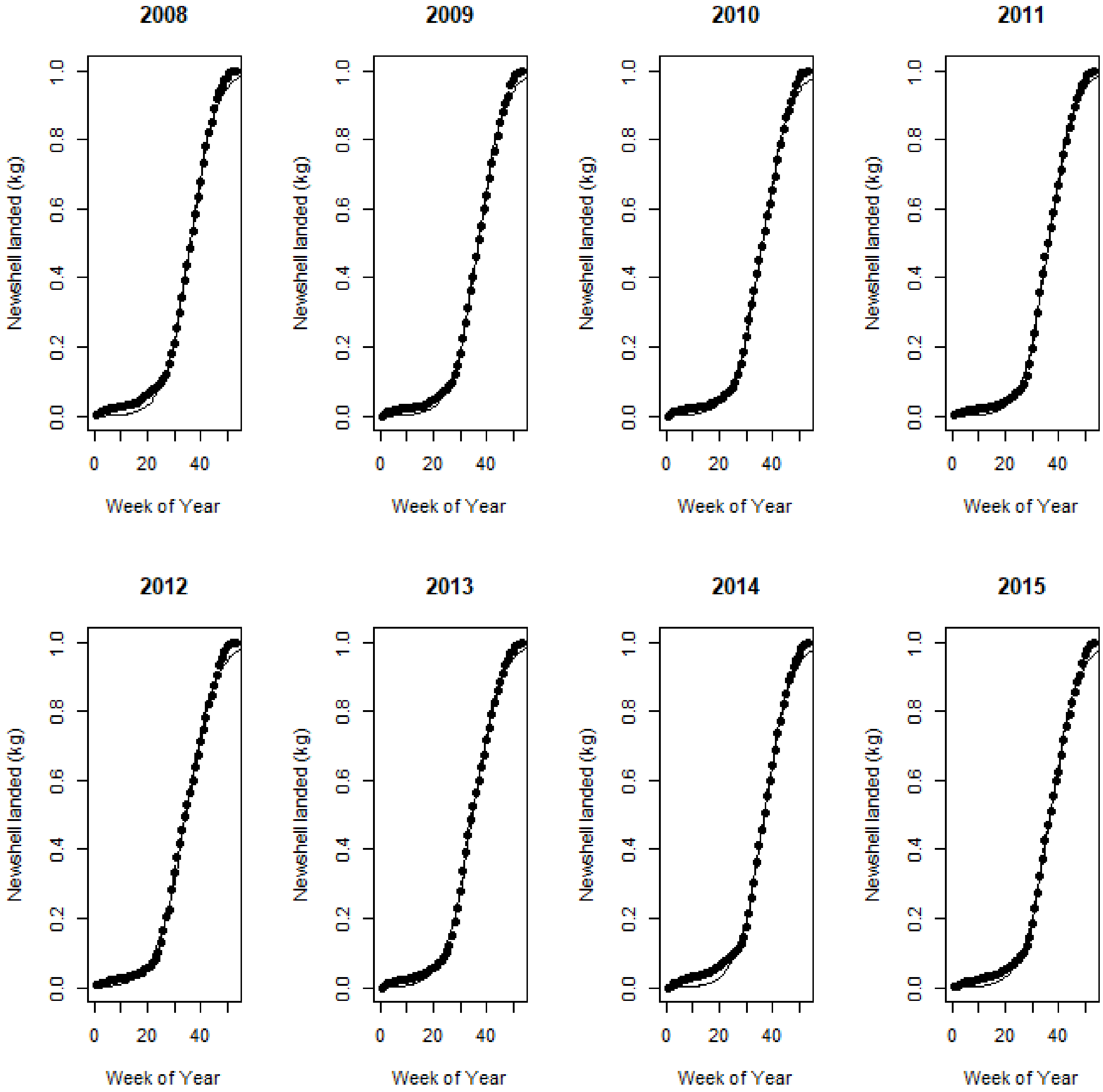
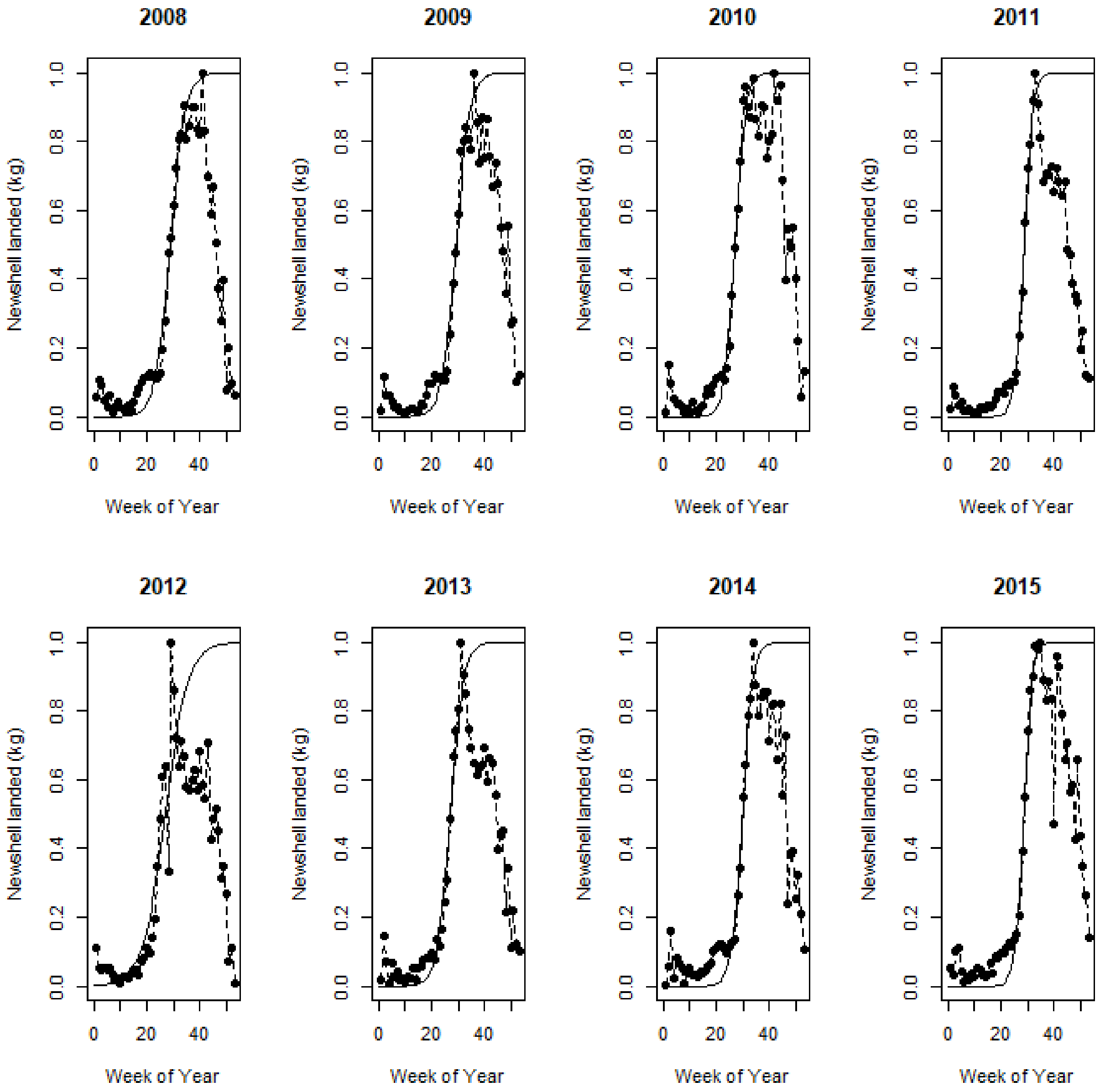


Figure A24: Logistic model applications for total central and western landings data as a percent of annual total weekly maximum.



Appendix B: Interview questions

[Identification] What is your name? What is your vessel's name? What port do you fish out of?

[Size of operation] How many crew do you employ? How many tags do you currently have? What license do you currently possess? Do you participate in any other fisheries?

[History] How long have you been fishing for lobster as an owner-operator? How did you get your start in the fishery?

[Timing questions] Can you describe any environmental factors that contribute to how fishermen decide where to place gear in time (over the course of the year) and space (inshore/offshore)? If there are other factors that influence your decisions, please describe them.

What are the different strategies fishermen use to detect the timing of this activity? Are there early indicators of the molt that fishermen in your area tend watch for? (e.g. Condition of hard shells? Change in trapping rate? Other?)

Do fishermen in your area tend to first detect signs of lobsters becoming active after the molt in a certain geographical area near your home port?

How is the softshell season spread over any given year? Would you describe it as having one peak, two peaks or a combination of the two?

How does any involvement in other fisheries affect your fishing strategy?

[Concerns] Can you provide specific personal examples of how the environment affects your fishing methods?

[Future] Can you tell me about extreme conditions in your past that affected fishing practices and how you might approach the same conditions in the future?

Do you believe there is any appetite for an evaluation of any of the strategies you have outlined? Would you be interested in the results of this research?

Would you consider any distributed results in your future fishing practices?

Are you interested in following up on our discussion today at a later date to be determined?

If you are interested in a follow-up or distributed results, please provide your contact information.

BIOGRAPHY OF THE AUTHOR

Kevin William Staples was born on Mount Desert Island, Maine in 1988 to Joyce MacIntosh and Clifton Oliver Staples where he grew up sailing, hiking, swimming and exploring. He graduated from Mount Desert Island High School (Class of 2006) an accomplished scholar-athlete, whose accomplishments included 3 straight Class B team (2004, 2005, 2006) and individual swimming titles (500yd, 100yd, 200yd freestyle events), resulting in the dedication of a plaque on the MDI athletic department's Wall of Fame. Kevin then attended the University of Maine, where he received his Bachelor of Science degree in Marine Science (Class of 2010), with a concentration in marine biology. Here, he was able to continue his swimming career at the Division I level for 4 years, earning Scholar-Athlete awards each year, including the team's Palmer Academic Award in 2009, given to the most academically impressive individual on the team. Kevin was also able to study abroad at James Cook University in Townsville, Queensland, Australia, where he studied and explored tropical rainforests and the Great Barrier Reef (before chronic bleaching events became common). After graduation, he spent over two years as a marine technician aboard the R/V *Lake Guardian*, an EPA owned-vessel charged with the long-term limnological monitoring of all five Great Lakes, before returning to the University of Maine to pursue a dual-Master of Science in marine biology and marine policy. This pursuit included a two month stay in China, studying and working mostly at Shanghai Ocean University, a tremendous opportunity and experience. He is currently the English language editor for the journal "Aquaculture and Fisheries", based at Shanghai Ocean University and a 2018 Finalist for the NOAA/Sea Grant Knauss Fellowship. He is a candidate for the Master of Sciences degrees in Marine Biology and Marine Policy from the University of Maine in August 2017.