Spatiotemporal dynamics of effective fishing effort in the American lobster (*Homarus americanus*) fishery along the coast of Maine, USA

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Abstract

Utilization and interpretation of fishery-dependent data such as fishing effort, although important in quantifying the dynamics of a fishery, tend to be challenging due to non-random sampling and the complexity of quantifying a species' interaction with complex effects of environmental factors. We developed a framework for estimating effective fishing effort from fishery-dependent sampling data for the coastal Maine American lobster (*Homarus americanus*) fishery, where a lack of high resolution effort data does not permit sufficient understanding of fishery dynamics. This framework incorporates environmental covariates in a bootstrapped two-stage generalized additive model to standardize lobster catch per unit effort (CPUE) from 2006 to 2013. Estimated confidence intervals (CIs) of sub-regional standardized CPUE were combined with congruent resolution landings data to estimate CIs of effective effort. Both effort and landings varied seasonally, with the peak of effective effort consistently preceding the peak of landings. Coast-wide from 2006-2013, effective effort increased modestly (4.6%) while landings increased dramatically (69.6%), suggesting assessment of spatiotemporal fishery dynamics may provide important insights for future management. Characteristic northeast-southwest differences in catch and effort suggest spatial non-stationarity of biological, temporal, and geographic processes in the Maine coastal American lobster fishery. The approach developed in this study has utility in situations in which a fishery may be data-limited, or with a surplus of fisheries-dependent data.

Keywords: CPUE standardization, Generalized additive model, effective fishing effort, *Homarus americanus*, Gulf of Maine

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1. Introduction

A comprehensive understanding of the spatio-temporal dynamics of fishing effort can be critical for effective fisheries management (Stefansson and Rosenberg, 2005). However, producing reliable estimates of fishing effort over time and space remains challenging due to the complex interactions between fishing effort and catch rates with many environmental variables, and the nonrandom nature of the fishing process. Nominal effort, such as vessel size, vessel power, vessel density (Stewart et al., 2010), crew size, number of licenses, and/or VMS data (Mills et al., 2007), is commonly measured in a fishery (Hilborn and Walters, 1992). However, nominal effort may not necessarily be proportional to the fishing mortality it generates. In fact, the relationship between the nominal effort and fishing mortality is often complex and nonlinear, making its interpretation difficult (Maunder and Punt, 2004). Use of nominal effort in the calculation of nominal CPUE in monitoring fish population dynamics has been argued to have led to many of the largest fishery stock collapses, including Northern cod (*Gadus morhua*) (Rose and Rowe, 2015) and Peruvian anchoveta (*Engraulis ringens*) (Patterson et al., 1992). Similarly, use of landings data alone as a proxy for stock biomass has been widely criticized (Hölker et al., 2007; Jaenike, 2007; Branch, 2013) after the method led to an extrapolation that world fishery stocks would collapse by 2048 (Worm et al., 2006). Consequently, common practice in fisheries science is to apply a procedure to standardize catch rates to estimate a more reliable index of relative biomass for a stock (Maunder and Punt, 2004; McCluskey and Lewison, 2008).

Traditionally, fishery measurements such as catch per tow or area swept for commercial trawl vessels have been standardized by catchability factors such as depth, temperature, or substrate to estimate relative abundance (Hilborn and Walters, 1992; Murawski et al., 2005). Though these factors may or may not directly influence catchability, they are assumed as proxies for unobtainable or not yet fully-understood mechanisms that govern the interactions between species of interest and their environment. For example, depth, which is simple and relatively inexpensive to measure, may be a highly significant covariate in a model. Realistically, depth probably is not the mechanism that governs species distribution, but may represent less easily quantifiable parameters such as food supply/predator limitations, pressure limits, preferred light levels, and thermal tolerance. Thus, considerable care and caution must be taken when interpreting these relationships and designating causal inference (Palmer, 2016; Pershing, 2016; Pershing et al., 2015; Swain, 2016).

Utilization of fishery-dependent data for estimation of fishery effort presents considerable statistical hurdles. In cases when fishery-dependent data from only a subset of a fishery are available, the data are not necessarily representative of the fishery and are ipso facto not straightforward to interpret. In addition, these data often contain a large proportion of zeros (Maunder and Punt 2004) for which many traditional error distributions (e.g., Gaussian, Poisson) are not sufficient.

The American lobster (*Homarus americanus*) fishery is currently the most valuable wild fishery in the United States, and in Maine alone, is valued at over 533 million dollars annually , or 83% of the state landings by weight (Maine Department of Marine Resources, 2017a). The fishery extends north from Cape Hatteras, North Carolina, to the Maine-Canada border (Atlantic States Marine Fisheries Commission, 2015). Despite the social, biological, and economic value of this species, there exists a gap in the literature concerning comprehensive knowledge of its catch and effort dynamics. It is recognized that the lobster fishery and population center has moved northeast (up the coast) in recent decades, likely due to a relaxation of predation (e.g., the concurrent decline of Atlantic cod, *Gadus morhua* stocks (Swain, 2016) and an ocean warming trend (Pinsky et al., 2013). The majority of the annual catch occurs in the summer and fall months, coinciding with the annual migration of lobster into nearshore waters (< 3 nm) in the summer and fall to molt and reproduce (Campbell and Stasko, 1986; Chen and Wilson, 2000; Steneck et al., 2013). Most lobster catches in Maine result from sublegal lobster newly molted into legal size and thus, is a recruitment-driven fishery. For example, 85% of the legal size catch in 2007 was within one molt of minimum legal size (Atlantic States Marine Fisheries Commission, 2015).

As the lobster population is currently at a time series high (Maine Department of Marine Resources, 2017a), management has become wary of socioeconomic resilience (Henry and Johnson, 2015) and consequences associated with potential future decreases in biomass (Steneck et al., 2011). Attempts have been made to diversify fishermen's harvesting portfolios in the region to aid in abating an over-reliance on the lobster fishery. Given recent efforts to reduce the number of traps fishing in Maine, the Maine Department of Marine Resources (DMR) has begun reducing the amount of trap tags sold. Individual zones have adopted 'exit ratios', where for every trap tag that comes out of circulation, less than one re-enters. Concerns about lack of enumeration for latent effort (trap tags bought, but not fished), leads to uncertainty as to how many traps hauls occur in the Maine fishery. Additionally, recent attention has focused on the potential bycatch of commercially important, but depleted species by the lobster fishery such as Atlantic cod and cusk (*Brosme brosme*). As bycatch is commonly estimated by catch rates or catch ratios, estimation of fishery effort (defined here as effective trap hauls) will serve to lay the groundwork for robust estimation.

Lobster traps in Maine are limited by a maximum volume, entrance size, escape vents, and tend to have similar rectangular designs, but individual fishers are allowed some flexibility in trap design (e.g., color, number of sequential "parlors", and type of bait housing). Vessels range considerably both in size and power, where the offshore (>3 nm) winter fishery tends to be dominated by larger boats. Due to the substantial summer and fall lobster fishing effort in the nearshore (< 3 nm) waters, NOAA's (National Oceanographic and Atmospheric Administration) fishery-independent sampling trawls cannot effectively operative in the area lobster are being fished the hardest due to interaction with fixed gear. A vent-less trap survey meant to quantify lobster abundance is conducted annually (Atlantic States Marine Fisheries Commission, 2015), but these data are not directly compatible with the commercial fishery due to reasons such as unknown density-dependent lobster interactions around and inside the modified survey traps and non-variable soak times.

We employed a delta distribution model and a probability of capture submodel (Maunder and Punt, 2004) based on coastal Maine fisheries-dependent data to account for zero-catch data to estimate spatiotemporally-explicit American lobster effective effort and standardized catch rates. We used a bootstrap approach to provide estimates for confidence intervals of standardized and model-based CPUE's. In conjunction with reported landings data, we estimated fishery effective effort and standardized indices of abundance for the years 2006-2013. Potential management implications of the identified spatiotemporal dynamics of the American lobster fishery are then evaluated.

2. Methods

2.1 Data

The Maine DMR sea sampling survey was established in 1985 as a voluntary observer program designed to measure biological characteristics of individual lobster (e.g., carapace length, sex, v-notch, egg stage) and record abiotic factors including location, date, zone, and depth. The sampling effort is three trips per month for each of the seven lobster management zones (A-G) from May-November, and efforts are made to sample at least once per month during the winter and spring months of December- April (Fig. 1). During this time, lobsters are typically further offshore (Campbell and Stasko, 1986) and cold temperatures and stormy seas are technical limitations for many fishers due to boat size and lower catch rates. Consequently, the most lobster effort and catch occurs in the summer and fall months. Sea sampling survey information from 233,866 individual lobster traps during 2006 -2013 was used in analysis. Due to limited resources, there were no data for 21% of the time series (mostly in the less-sampled winter months). To calculate total effective effort, data were linearly interpolated from bordering months, and if not available, the same month was assumed to be the average between neighboring years.

2.2 Landings Data

Monthly-zonal lobster landing reports were available from the DMR from all months and zones (A-G; Fig. 1) during study period. A small portion (<1%) of the data came from ports with fewer than the minimum number of commercial deliveries; information other than the landings magnitude could not be used due to confidentiality issues.

2.3 General Approach

A quasi-stationary (Petitgas, 2001) approach was adopted to account for non-stationarity of biological and fishery processes across the state of Maine, i.e. separate models were applied to each of zones A-G. This approach is useful in situations where a species occupies a large environmental gradient and may exhibit different relationships to environmental covariates (spatial heterogeneity) across the full spatial extent. In modelling, a common way to deal with spatial heterogeneity is to adjust grid size. A preliminary study of the sea sampling data focused on Atlantic cod (*Gadus morhua*) and cusk bycatch suggested that coarse grids typically resulted in a lower percentage of zero observations, and distribution of catch was found to be sensitive to grid size (Zhang and Chen, 2015). Given the high proportion of zero-values in our dataset (>30% trap hauls with no legal lobster), data were aggregated on the zonal management scale to eliminate zero-value grids and provide management predictions on a spatiotemporal scale that spanned coastal oceanographic gradients and was appropriate for regulation. Ranges of effective lobster effort were estimated by dividing zonal-monthly landings data by the 95% confidence interval of respective 'standardized' CPUE distributions.

2.4 Standardized lobster CPUE

We used the mass of legal lobster per trap (kg/trap) as the response variable because landings are measured in mass. Thus, sea sampling data were subset to include only individual lobster within the legal size slot limit (83-128 mm carapace length), lacking visible eggs (lobster with visible eggs must be discarded regardless of size), and lacking a v-notch (a method in the Gulf of Maine (GoM) that protects sexually mature females for multiple molt cycles). Of the subset, we make the implicit assumption that fishers keep all legal lobsters. In the Maine fishery, there is no daily limit or quota, so practices such as high grading (releasing small individuals in favor of larger, more profitable ones) or other illegal practices were considered negligible. We back calculated each legal lobster to estimate mass (M, kg) using carapace length (CL, mm) and GoM combined sex allometric parameters from the 2015 lobster benchmark assessment (Atlantic States Marine Fisheries Commission, 2015): $M = 6.85816 * 10^{-7} * CL^{3.020978}$. Lobster mass was aggregated by individual trap ID number to calculate mass of legal lobster per trap.

Two types of covariates were considered in the models:

- *Environmental* - Initial models for lobster standardized CPUE included depth (*D*; 0 - 179 m), seven categories of sediment (*S*), number of trap soak days (*T*; 1-45). Out of the three, only *D* and *T* were directly measured in the sea sampling survey. *S* data were categorized by grain size into seven bins (gravel, gravel-sand, sand, sand-silt/clay, sand-clay/silt, clay-silt/sand and sand/silt/clay derived from Poppe et al., 2014) and assigned based on location. Covariates were tested for multicollinearity using variance inflation factors (removed if > 4), and Pearson correlation (Supp. Tables 1 & 2). Concurvity was assessed with the 'concurvity' function in the mgcv R package (Wood, 2011) (Supp. Figs 1 & 2).
- *Spatiotemporal-* In our initial models, we included month (*Mo;* 1-12), year (*Yr*; 2006-2013), latitude (*La*; 42.98°- 45.07°), longitude (*Lo*; 66.94° – 70.01°), and distance to shore (*DS*; 0-10 km) to represent spatiotemporal aspects of the fishery dynamics. *DS* was calculated from the NOAA Medium Resolution Shoreline shapefile (NOAA, 2016) using ArcGIS 10.1 (Environmental Systems Resource Institute, 2012). We applied our modeling approach for each individual lobster zone, which were based on known oceanographic differences (Pettigrew et al., 2005), and existing zone-based management.

A delta 2-stage generalized additive model (GAM) (Hastie and Tibshirani, 1990) approach (Pennington, 1983) was used to standardize catch rates (weight of legal lobster per trap). This approach is useful when datasets have a large proportion of zeros (i.e., trap hauls with no legal lobster). GAMs are an extension family of Generalized Linear Models (GLMs) that can accept various error distributions and relate non-linear smoothing functions of predictors linearly to a response variable (Murase et al., 2009; Wood, 2006) .

Though GLMs can accommodate nonlinear predictors (e.g., using a quadratic term), GAM smoothing functions allow more flexibility in modeling both linear and non-linear gradients of environmental covariates. This flexibility allows some assumptions relating to the actual response – predictor relationship to be relaxed, but comes at a cost of being somewhat less interpretable than fully parametric models. Building off methodology from Barry and Welsh (2002) and Li et al., (2015) the first stage GAM predicts probability of legal lobster capture with a logit-link function and a binomial error distribution:

$$\text{GAM 1: logit}(p) = s(Mo) + te(La, Lo) + s(D) + s(T) + Sf + \text{s}(DS) + Yr, \tag{1}$$

where (*s*) represents a spline smoothing function, *te*, a thin plate tensor to account for *la* and *lo* interaction effects, and *p*, probability of some catch of legal lobster. The second stage "positive catch distribution model" predicts legal lobster total mass in kilograms, E(log(*M*)), using an identity-link function, and log-transformed catch data (Ohshimo et al., 2016):

$$\text{GAM 2: E}(\log(M)) = s(Mo) + te(La,Lo) + s(D) + s(T) + S + \text{s}(DS) + Yr. \tag{2}$$

The absolute legal lobster mass per trap haul (M_h, kg), was estimated by multiplying the predictions from (1) and (2):

$$E(M_h) = p * exp(E(log(M))) * exp(0.5 * sig\char`^2), \tag{3}$$

where "sig" is the standard deviation of the random error from the linear regression on a log-scale.

The robustness of hypothesis testing can depend on the smoother degrees of freedom. Based on expectation from similar studies and recommendations in the literature, all univariate smoothed terms were given a maximum of 5 degrees of freedom (knots) (Keele, 2008; Sagarese et al., 2014; Tanaka et al., 2017; Zuur et al., 2009) and bivariate terms (Lat, Long) 15. All GAM computations were performed using R Version 3.1.3 for Windows (R Core team, 2015) and the mgcv package (Wood, 2011). Covariates were selected using a modified guided step-wise selection approach. After each fitting, the least significant covariate was removed (highest p-value) until all were significant ($p < 0.05$). All models had to include the covariates month and year regardless of significance as they are needed for temporal standardization. Final model diagnostic plots were evaluated for residual patterns and to check statistical assumptions.

Zonal models were bootstrapped to generate distributions of average monthly/annual 'model-based' and 'standardized' CPUEs to account for the uncertainty associated with the GAM's and the non-random nature of the sea sampling data. Zonal individual trap haul records were sampled randomly with replacement (maintaining zonal sample size). The number of zonal trap hauls (n) ranged from 30,609 (zone E) to 40,309 (zone A). The final model covariates determined by the original selection process were used for each bootstrap iteration. After each fit, zonal model predictions were made for each month of the study period, and the arithmetic mean of each subset was calculated. This process was repeated 1000 times, generating distributions of zonal-monthly averaged 'model-based' CPUE's (Fig. 2). Individual monthly variance and CV of the bootstrap distributions were checked to evaluate stability. We produced medians and 95% confidence intervals for each estimate (i.e. the 2.5th, 50th, and 97.5th percentiles of the bootstrap distribution). 'Standardized' CPUEs were calculated with a modified version of the above approach where after each bootstrap fit, month (z) and year (t) indices were created by using the individual bootstrap sample covariate means across the study period and the most common sediment category as the basis for prediction.

2.5 Effective lobster effort

To estimate effective lobster effort (in individual trap hauls) per zone and month, $Landings_{z,t}$ were divided by the corresponding upper, mid, and lower bounds of the 95% lobster standardized $CPUE_{z,t}$ confidence interval. This enabled generation of individual zonal-monthly lobster effective effort confidence intervals over all study years.

$$\frac{Landings_{z,t}}{Low\_CPUE_{z,t}} \leq Effective\ Effort_{z,t} \leq \frac{Landings_{z,t}}{High\_CPUE_{z,t}} \qquad (4)$$

2.6 Nominal CPUE

The Maine DMR has conducted a fishery-dependent harvester survey since 2008 (Maine Department of Marine Resources, 2017b). Fishers are selected at random and 10% random sampling is stratified by zone and license type. Selected individuals report categorical fishing location (zone, approximate distance from port), landings, and number of traps hauled for a given trip. Validation of accuracy is not feasible. Consequently, uncertainty cannot be directly estimated due to confidentiality (samples were grouped prior to analysis). With these data, nominal CPUE (landings (kg) per trap haul) was calculated, and effort was estimated by division of zonal-monthly landings by the average harvester CPUE.

3. Results

3.1 Variable selection

The stepwise selection method produced a single 'best' model for each of the first and second stages for all zones. Visual analysis of Q-Q plots for both first and second stages showed model residuals were approximately normal suggesting that the correct error model was selected

(Supp. Fig. 3). Zones E-G positive catch distribution models exhibited a longer lower tail, likely stemming from a string of similar values (a catch of one lobster near minimum legal size). Concurvity assessments did not indicate any major problems, but suggested that soak days on average had the least identifiability (Supp. Figs 1 & 2). For some zones, the tensor product of latitude and longitude had elevated concurvity with distance from shore. Concurvity plots were similar for both stage GAMs. Covariates selected in the final model were similar over each of the zones. Latitude and longitude were included in all first and second stage final models. Both first and second stage lobster models were statistically significant based on p (<0.05) for all zones.

Zonal first stage models included an average of 5.8 covariates out of 7 with a deviance explained ranging from 4.6 – 16.7%. Second stage models had similar structure, but more explanatory power than the first stage (Table 1, Fig. 3). Deviance explained in the second stage models ranged from 7.6% (zone F) to 28.8% (zone A). While latitude, depth, and set over days were included in nearly all final models, sediment and distance to shore were included only in 35.7% and 64.3% of models, respectively. For both stages, overall more deviance was explained for the northeastern zones (A-D) than the southwestern zones (E-G). Zone F had the lowest deviance explained for both first and second stage (Table 1).

3.2 Spatiotemporal patterns of standardized CPUE

Standardized CPUE's exhibited slightly differing patterns among zones, but these were consistent with the general known seasonal population dynamics of the species (Jury and Watson, 2013, Fig. 3). The average monthly CVs calculated for each bootstrap distribution were narrow across all zones, ranging from 1.1% - 4.5% for standardized CPUE, and 0.7% - 1.0% for model-based CPUE. Annual lobster standardized CPUE resembled a sinusoidal pattern in the northeastern zones (A-D), experiencing lowest standardized CPUE's in April and the highest in September and October (Fig. 4). The general sinusoidal pattern was consistent across all years, but the southwestern zones had subtle difference in fall dynamics (CPUE plots for zones A-G in supplementary material, Fig. 4). Standardized CPUE increased in the southwestern zones typically at least one month before catch rates increased in the eastern zones. In the eastern zones, summer and fall months exhibited more variation between study years than other months. Southwestern zones followed similar patterns in the spring, but exhibited either catch rates leveling off, or a 'double peak', first in July, then again in the late fall (Oct or Nov). All zones however, uniformly had the highest catch rates in the summer and fall (Aug- Nov). Standardized CPUE's increased in all zones (Fig. 5), but disproportionately higher increases occurred in zones A-D than E-G (mean 57.7% and 27.6%, respectively).

Model-based median and nominal CPUEs were highly correlated (r = 0.947) throughout the time series. A linear regression slope of model-based and harvester effort of the non-interpolated months had a slope of 0.86 ($p<0.001$), intercept of -4800 ($p=0.815$), and r^2 of 0.896. Median model-based estimates predominantly occurred inside a ±20% envelope (Fig. 6). Unlike the harvester program, the sea sampling survey allows fine-scale GAM modelling, provides reliable estimates of uncertainty, and allows for standardized CPUE (removal of catchability effects).

Summaries of effective effort are given in Table 2. Over 2006-2013, zones A and B exhibited an increase ranging from 1.02×10^6 (+13.6%) traps hauls to 4.22×10^6 (+42.8%) (Zone A) (Table 2). Over the same period, modest decreases in effective trap hauls occurred in the remaining zones, ranging from -1.33×10^5 (Zone F) to -9.80×10^5. Overall, the relative proportion of total annual trap hauls by zone only increased in the eastern two zones (A and B), 6.04% and 1.10%, respectively (Table 2). We note that landings in the northeastern zones comprised 78% of the Maine total from 2006-2013 while constituting 71% of total effective trap hauls. The modelled net change in effort over the study period was modest (+4.5%, Table 2). Effective effort decreased from 2006 to 2007 drastically (-34.1%), then increased through 2010 (Fig. 7). The level of effort remained relatively high and stable from approximately 2012 through 2013 (Table 2).

Although survey coverage in the winter months is lower, late winter (January-February) and early spring (March-April) consistently had both the lowest catch rates and lowest effective effort (Figs 4 and 7). For all zones combined, effective effort ranged from 3.38×10^5 (February, 2007) to 1.51×10^7 (July, 2012) trap hauls per month, reflecting the major contrast in summer/fall to winter/spring effort levels. Effective effort was highest in the eastern zones (A-D) and F, but similar relative effort patterns existed for all zones (Fig. 8).

The characteristic patterns of fishery timing showed a distinction between northeastern and southwestern zones that was robust throughout the study period. Zone-normalized (highest zonal CPUE corresponding to 1) fishery standardized CPUE increased first in the southwestern zones, but by August were relatively equal across all zones (Fig. 8). Catch rates remained high in the southwest through November in most years and declined moderately through December. Conversely, northeastern zones experienced a much more prominent ‘boom and bust’ type catch pattern. The northeast lagged behind the southwest in the timing of initial catch rate increase, but experienced a much larger peak (generally in August), and a faster decline. Depending on the year, the lag of peak effort ranged from 0 months (2007 and 2013) to 2 months (2006). The remaining years had an approximately 1-month lag. We found that the southwestern three zones tended to have two effort peaks while the northeastern zones did not. The second peaks tended to occur in October-November and were smaller in terms of CPUE, effort, and landings than the main peak (e.g., comparing northeastern to southwestern zones in Fig. 8).

4. Discussion

4.1 Lobster fishery dynamics

With the increase in lobster catches over the past two decades (1994-2013 increase of 229%; Department of Marine Resources, 2017b), we expected an increasing trend in lobster effective effort. Maine’s lobster fishery has become more lucrative as catches have increased and prices have remained relatively stable, providing an incentive for overcapitalization (see Steneck et al., (2011) for characterization of this being a ‘gilded’ trap). Dealer reports suggest all licenses do not get fished on an annual basis (Kathleen Reardon, Maine DMR, West Boothbay Harbor, ME, pers. com), thus the fishery likely is harboring substantial latent effort. Over the period of study, the number of lobster licenses in Maine decreased 16% (Department of Marine Resources, 2017b) from the DMR’s strategy to reduce effort on a zonal basis. Thus, we speculate the increase in effective effort is explained by a combination of fewer unfished licenses and more trap hauls per license.

In all study years, the peak of zonal effective effort preceded the peak of landings. The peak in landings tended to occur in the same month for all zones (though the month differed among years), while the peak in effective effort was more variable. In instances where peak standardized CPUE occurred after peak landings, both density-dependent trap dynamics and lobster ecology probably play important roles. For example, if effort is excessively high in a particular location, dependence on nominal catch rates will be a poor predictor of abundance due to high fishing mortality (Maunder and Punt, 2004). Although the rates of lobster migration are unclear, it is not unreasonable that high localized fishing pressure can act as a pseudo-depletion experiment, thus interpretation of nominal catch rates should be treated with caution. Using aerial surveys, (Kelly, 1993) found trap density in Maine could be quite high, up to 749 traps/km^2 around inshore (<2 km of mainland) regions. Since the early 1990’s lobster landings have more than doubled, which may suggest that inshore trap densities are still as high if not higher.

Large scale repeated patterns of peak effort preceding peak landings are also understandable from an economic perspective. Fishers likely have an economic advantage to have gear in the water before the peak both to claim a competitive edge through “establishing” fishing territory, and by reducing the chance they may begin fishing after a significant portion of the seasonal molt has passed. This behavior is well-founded as Maine lobstermen have a reputation for intense territoriality (Acheson, 1975) and certain years (e.g., 2008 and 2012 from our study period) experienced earlier than expected catches.

The GoM and Georges Bank American lobster ‘stocks’ are treated as a single population in the stock assessment (Atlantic States Marine Fisheries Commission, 2015), but it is likely that some regionally or sub-regionally-specific differences in stock structure and phenology exist. These may to a large part be explained by temperature regime and bathymetric differences along the coast of Maine (Hadley, 1906). Thus, regional differences between the first and second peaks may be explained by changes in suitable habitat. In the fall, warm water extends further off the coast than in the late spring and as a result, lobster may find habitat suitable for molting further from shore. Additionally, the southwestern portion of the GoM warms earlier closer to shore than further up the coast (Bai Li, School of Marine Sciences, University of Maine, pers. com). In addition, the Eastern Maine Coastal Current (EMCC) runs southwestward and brings relatively colder water along the coast before dissipating near Penobscot Bay, (i.e. between zones D and E, Pettigrew et al., 2005). If the bathymetry and current dynamics dictate differential warming patterns, it is reasonable to expect an earlier increase in southwestern catch rate. One explanation could be that faster growth rates precipitate a stronger second molt due to a longer warm period in the southwest. Considering the magnitude and regional importance of the lobster fishery, further research should be done comparing the size, sex, and age compositions of the first and second molt.

The main advantage from the bootstrap approach comes from the ability to consider spatiotemporal trap dynamics explicitly in the calculation of confidence intervals. Random sampling of zonal-explicit data is a useful way to characterize fishing practices when a larger sample size is unavailable. The sea sampling survey does not take a random sample of fishers, and due to space limitations (sufficient room for measuring lobsters), focuses more effort on mid-size to large boats. Thus, inherent is the assumption that the mean (across time) values from the sea sampling survey are representative of the whole fishery, thus the standardized CPUE scales with the absolute values of fishery and allows rough equalization of standardized and modelled DMR values of effort. Our approach was to examine the trap dynamics as opposed to traditional boat ‘power’ dynamics (Marchal et al., 2001). As all fishers are required to follow the same trap guidelines and most effort occurs in the coastal waters, we determined that the dynamics governing when and where the trap was fished would be more appropriate for characterizing effort than vessel ‘power’.

For the sea sampling data, the measurement of carapace length is relatively precise, but specific details regarding weight-length relationships were assumed to be negligible. As lobster undergo ecdysis, we expect variability of the weight-length relationship to be sexually- and/or regionally-dynamic. Further, because molting is accepted to be a seasonal phenomenon largely governed by temperature (Hadley, 1906), it would not be unreasonable to question whether a seasonal and spatially-explicit allometric key may be more precise. Unfortunately, these data were not available but may be fruitful for a future study.

The goal of CPUE standardization is to remove the effects of nominal CPUE that are unrelated to stock abundance. For trawl surveys, standardization is often done by depth strata and time towed to create unbiased estimates of relative abundance (U.S. Department of Commerse, 2004). Regardless of sampling procedure, assumptions regarding representation of sampling are necessary. Fishery-independent surveys are typically designed based on known spatial variance structures. An example may be random stratified surveys in which variance may be estimated (Pennington, 1986). Fisheries-dependent data are non-random by nature, and may not conform to a rigid sampling design, thus interpretations of these data are generally viewed more cautiously than findings based on fisheries-independent surveys (Paloheimo and Dickie, 1964). Nonetheless, it is not uncommon for an assessment scientist to have access to fishery-dependent data, but a dearth of fishery-independent data. Therefore, it is necessary for further development of fishery-dependent methodologies in regions where independent surveys are non-existent or data-poor.

We confirmed that most temporal effort for the Maine lobster fishery occurs in the summer and fall months and most catches during this time come from the inshore component of the fishery (Chen and Wilson, 2006). It should be noted that effort has been recorded further offshore in recent years. Mostly likely, extirpation of predator species (e.g. Atlantic cod) (Ames, 2004; Fogarty et al., 2008) and recent warming trends have created additional available habitat and facilitated population growth. Density dependence may affect the relative importance of physical environment and space (Leibold and Loeuille, 2015; Steneck, 2006). With more offshore effort in recent years, it is unclear how standardized CPUE estimates based on the sea sampling dataset have changed over time in terms of representativeness. We included all landings (state and federal) in the analyses, but acknowledge the sea sampling survey has more coverage of more productive inshore waters and months in which catches are highest. Notwithstanding, sea sampling data cover an extensive environmental and spatiotemporal extent, thus, the bootstrap procedure we argue sufficiently characterizes the fishery. Large agreement between harvester and model-based CPUE provide support of this claim.

Fisheries are commonly characterized at yearly or seasonal scales but this may not be sufficient to capture relevant biological or fishery dynamics for migratory species such as lobster. We were able to characterize striking spatial differences between months in terms of standardized catch rates and effective effort. Understanding fishery timing simultaneously in terms of catch rates, effort, and landings hold promise to aid in management decisions. Specifically, collecting effective effort at a higher temporal resolution can serve as a useful tool to spatially monitor fishing pressure due to its proportionality with fishing mortality (Ricker, 1975). For coastal Maine lobster, it is uncertain how long high catches will persist, though we expect knowledge of high-resolution fishery dynamics will make management capacity more flexible and precise.

Spatiotemporal patterns on the zonal-monthly scale are a considerable improvement to current knowledge, but limitations remain. Changes in the lobster fishery were detected on the zonal-monthly resolution, but we recognize changes occur on the microscale both through time and space. As the northeastern lobster zones in Maine experienced an average first peak in standardized CPUE lag of approximately one month, certainly we can expect individual zonal, or port to port lag to be a fraction of a month, week, or day. Estimating peak months for effective effort comes with similar caveats. For the Maine lobster fishery specifically, monthly-zonal resolution provides a reasonable balance of the complex oceanographic and fishery dynamics of the Maine coastline.

We applied a quasi-stationary approach in this study to account for mesoscale oceanographic differences across coastal Maine but note the management zone lines used for separating catch statistics are arbitrary, thus do not necessarily reflect changes in habitat. Additionally, lobstermen in Maine can fish up to 49% of their gear in a neighboring zone, but probably deliver most often to their registered home port or co-op (Department of Marine Resources, 2017a). Given the available fishery-dependent and landings data however, these problems are not easily overcome. Habitat dynamics are undoubtedly complex, requiring small and meso-scale empirical studies to tease apart a more detailed understanding on lobster phenology, behavior, and fishery dynamics. Fortunately, the sea sampling data are geographically referenced, so exact zone is known. Therefore, the assumption made was that overall, landings are accurate and come from the registered zone of the individual lobstermen.

The generalized framework we propose for standardizing CPUE and estimating effective effort can have wide-ranging applications in other data-poor, or fishery-dependent data dominated fisheries. We suggest careful consideration of spatiotemporal fishery dynamics for choosing appropriate grid or sector size for implementation of this methodology. More specifically, prior knowledge of biological and oceanographic conditions should be weighed by investigators to select appropriate geographical and temporal extents for CPUE standardization and effective effort estimation. Generally, if known gradients across a fishery exist, accounting for spatial non-stationarity by modeling processes at smaller geographic or temporal interval (quasi-stationary) would be more advantageous than a stationary approach (Petitgas, 2001). Regardless of methodology, estimates of uncertainty associated with each available dataset and modeling approach should be an integral part of crafting robust fishery CPUE standardization strategies. Elucidation of more precise fishery dynamics from fisheries-dependent data holds promise to aid in setting and successfully reaching management goals.

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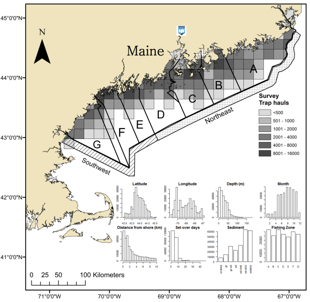
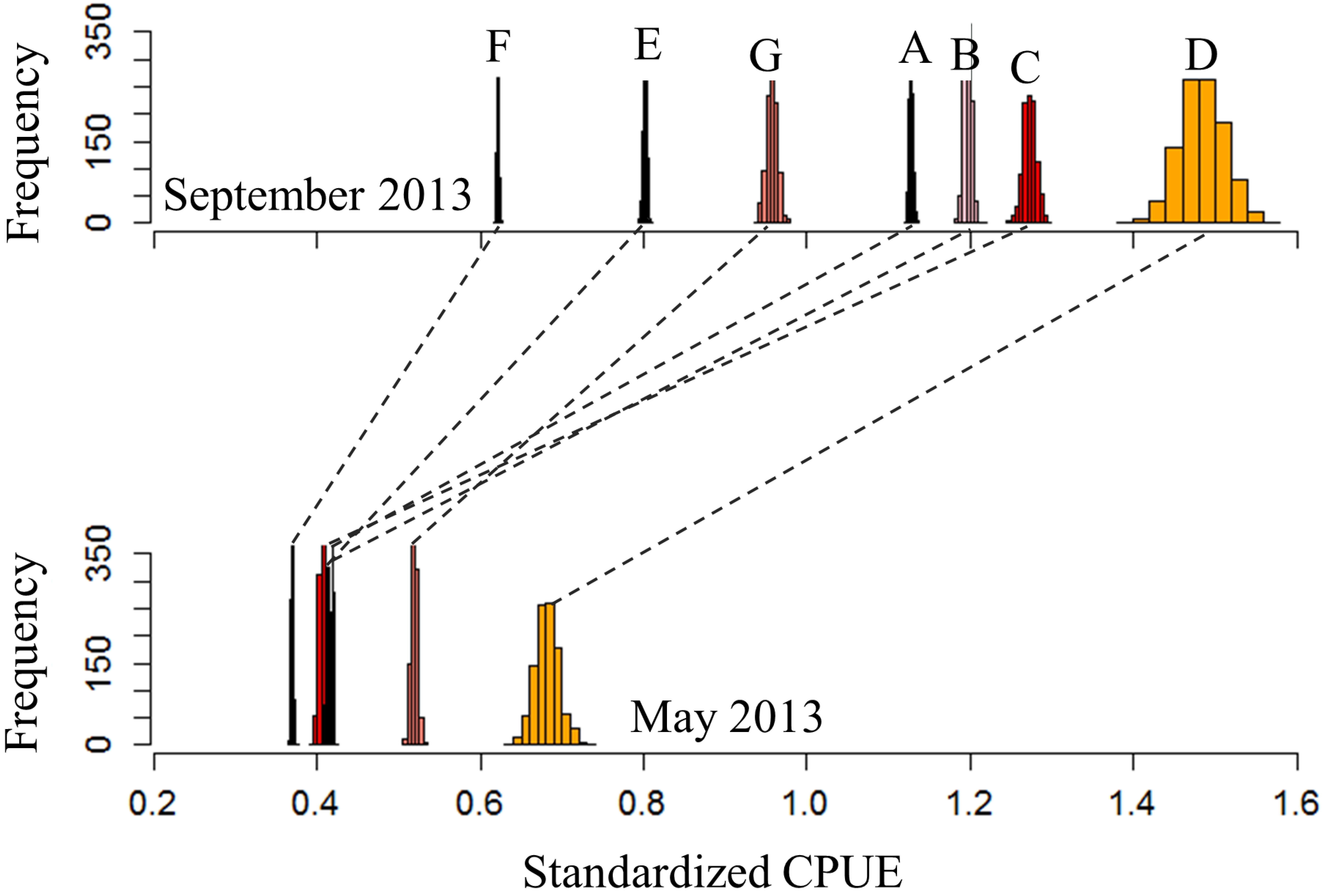
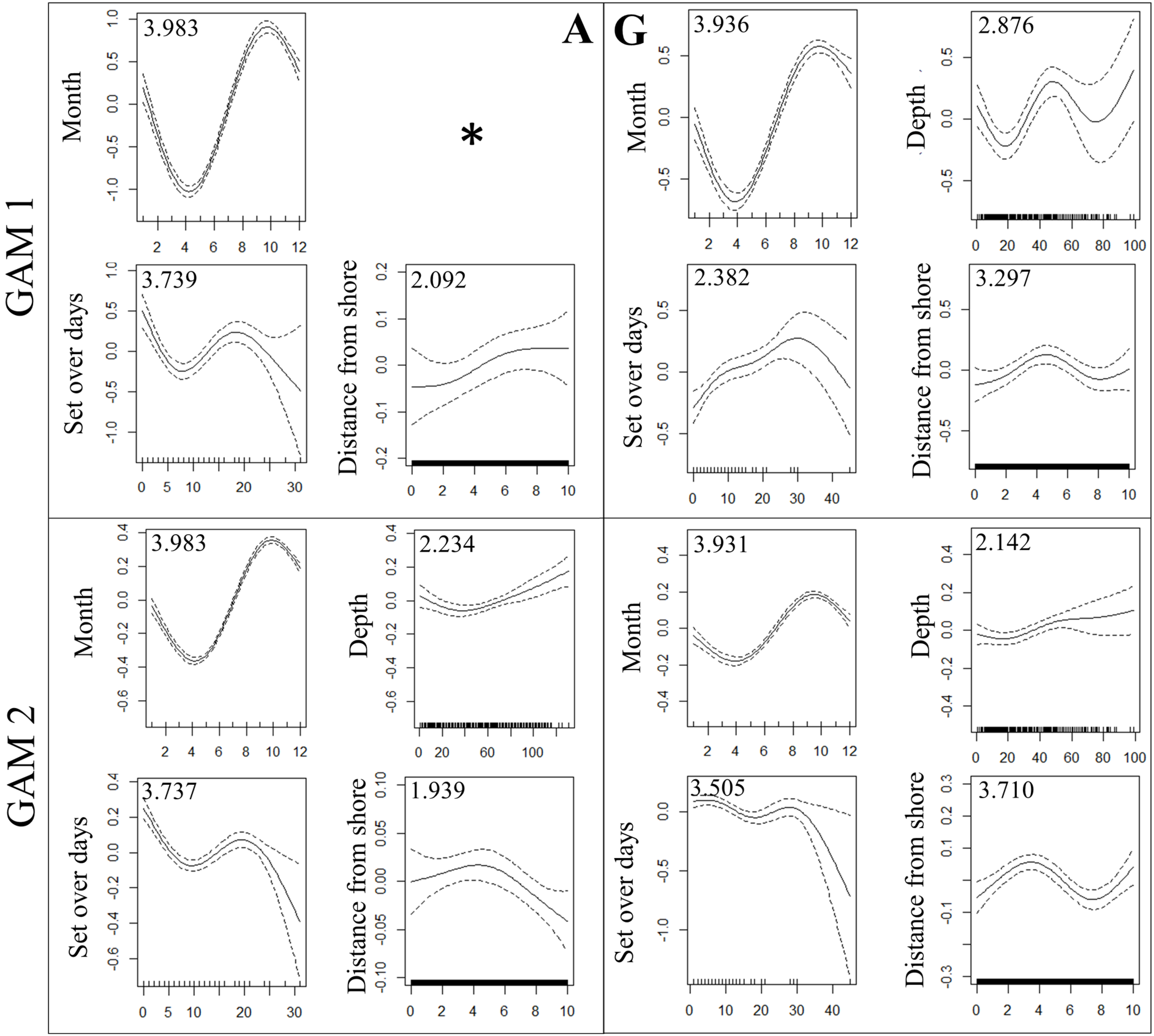
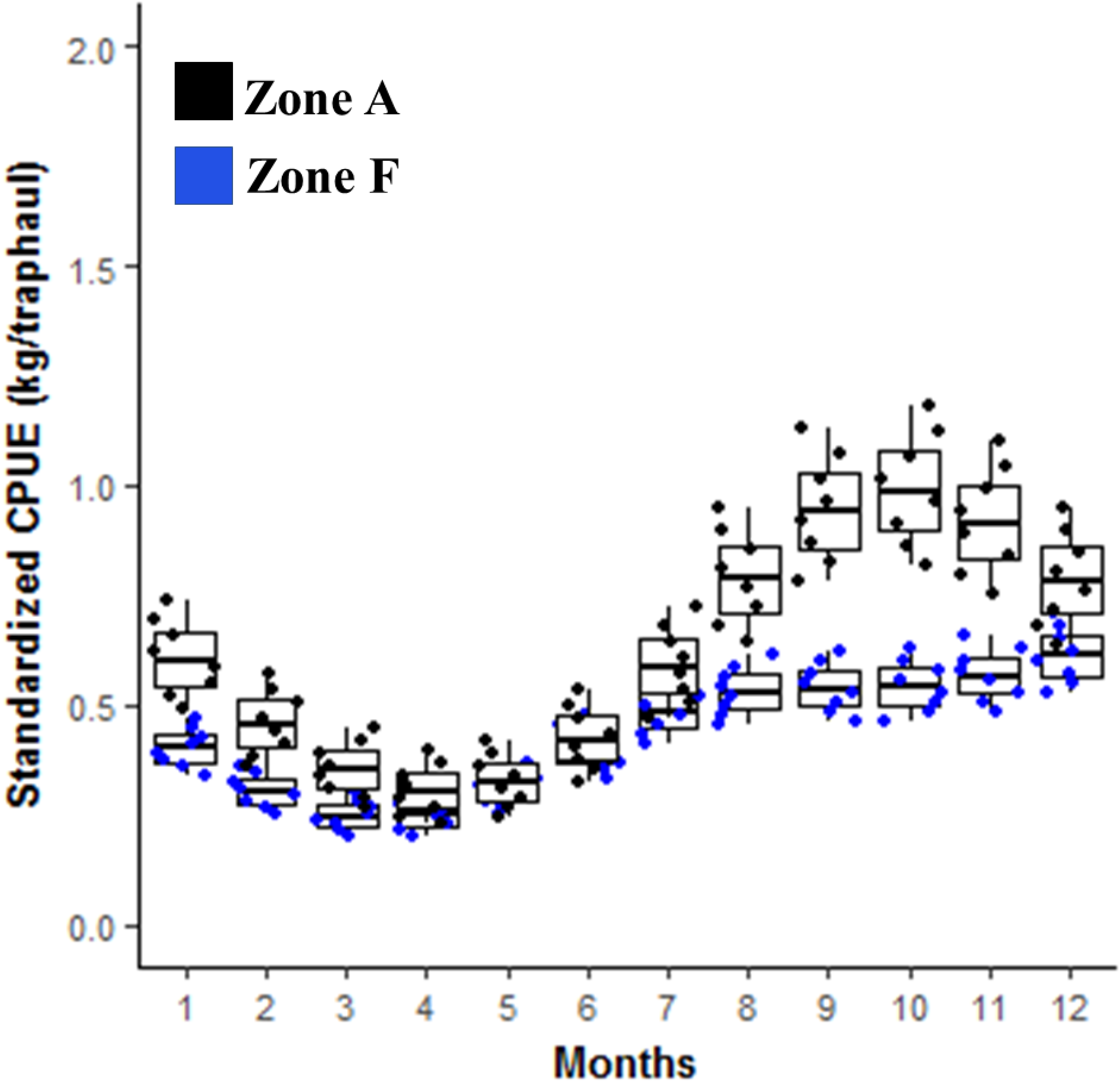
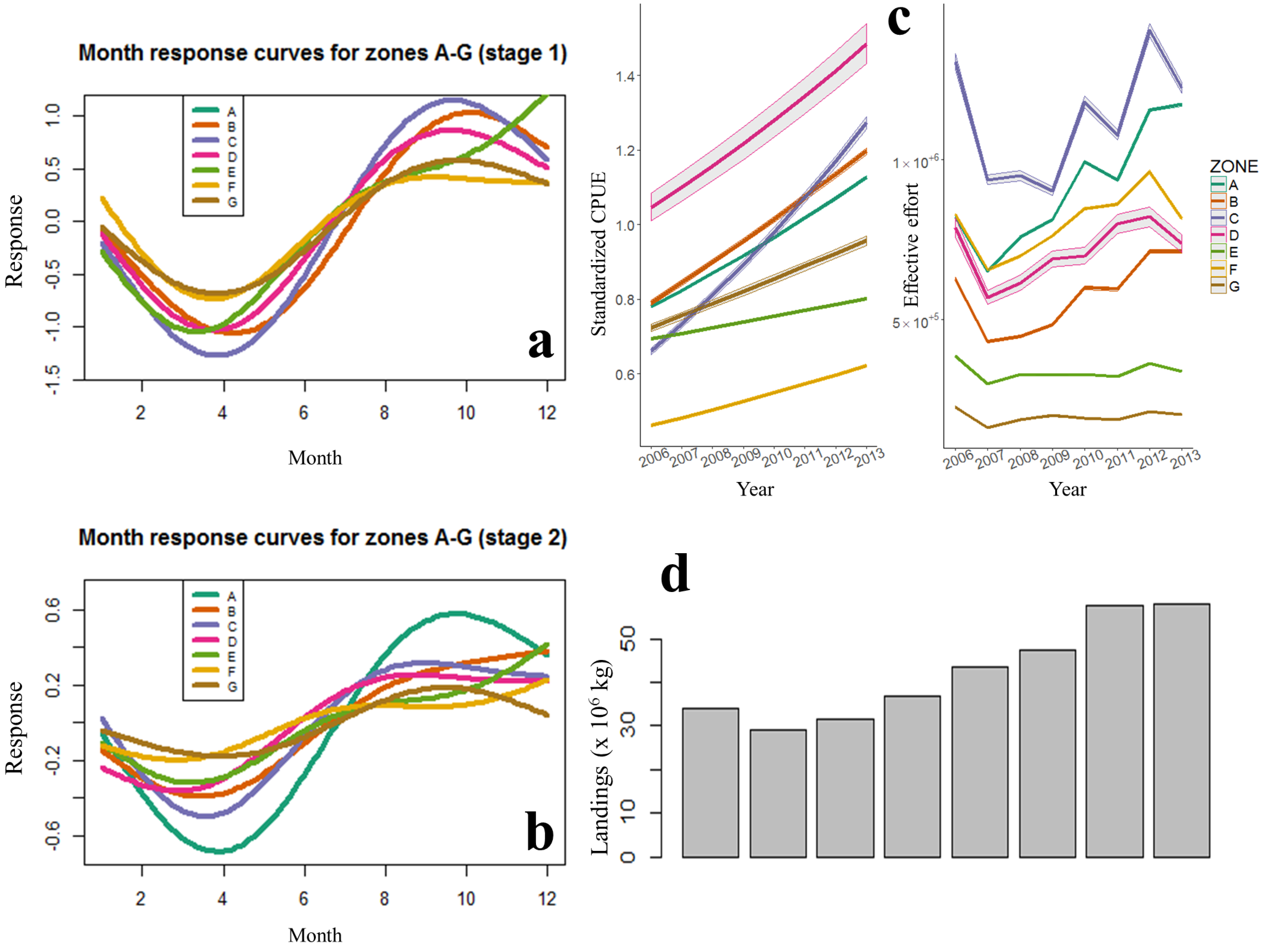

45°0'0"N
44°0'0"N
43°0'0"N
42°0'0"N
41°0'0"N
71°0'0"W
70°0'0"W
69°0'0"W
68°0'0"W
67°0'0"W
N
Maine
A
B
C
D
E
F
G
Northeast
Southwest
Survey
Trap hauls
<500
501 - 1000
1001 - 2000
2001 - 4000
4001 - 8000
8001 - 16000
0 25 50 100 Kilometers
Latitude
Longitude
Depth (m)
Month
Distance from shore (km)
Set over days
Sediment
Fishing Zone

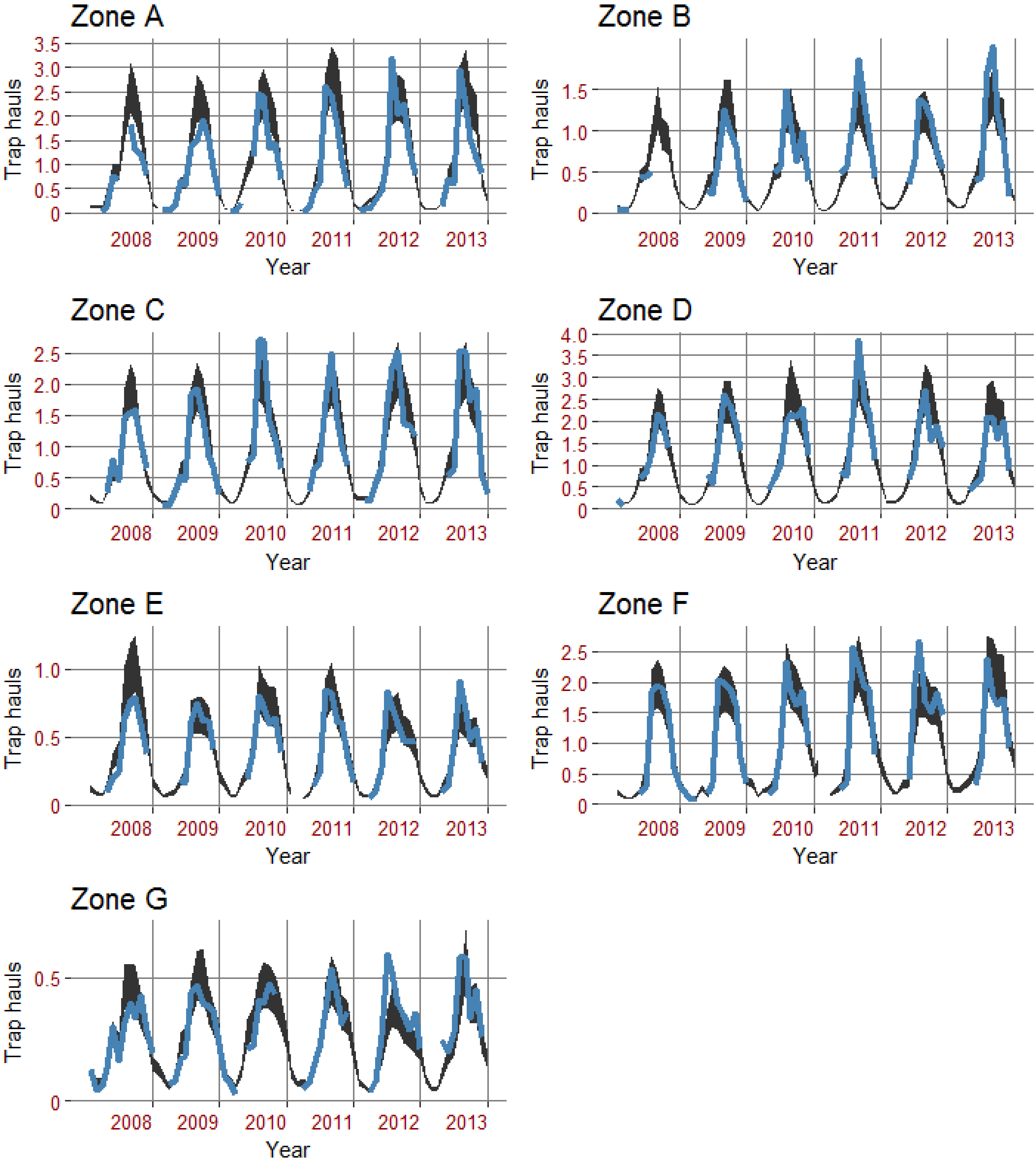


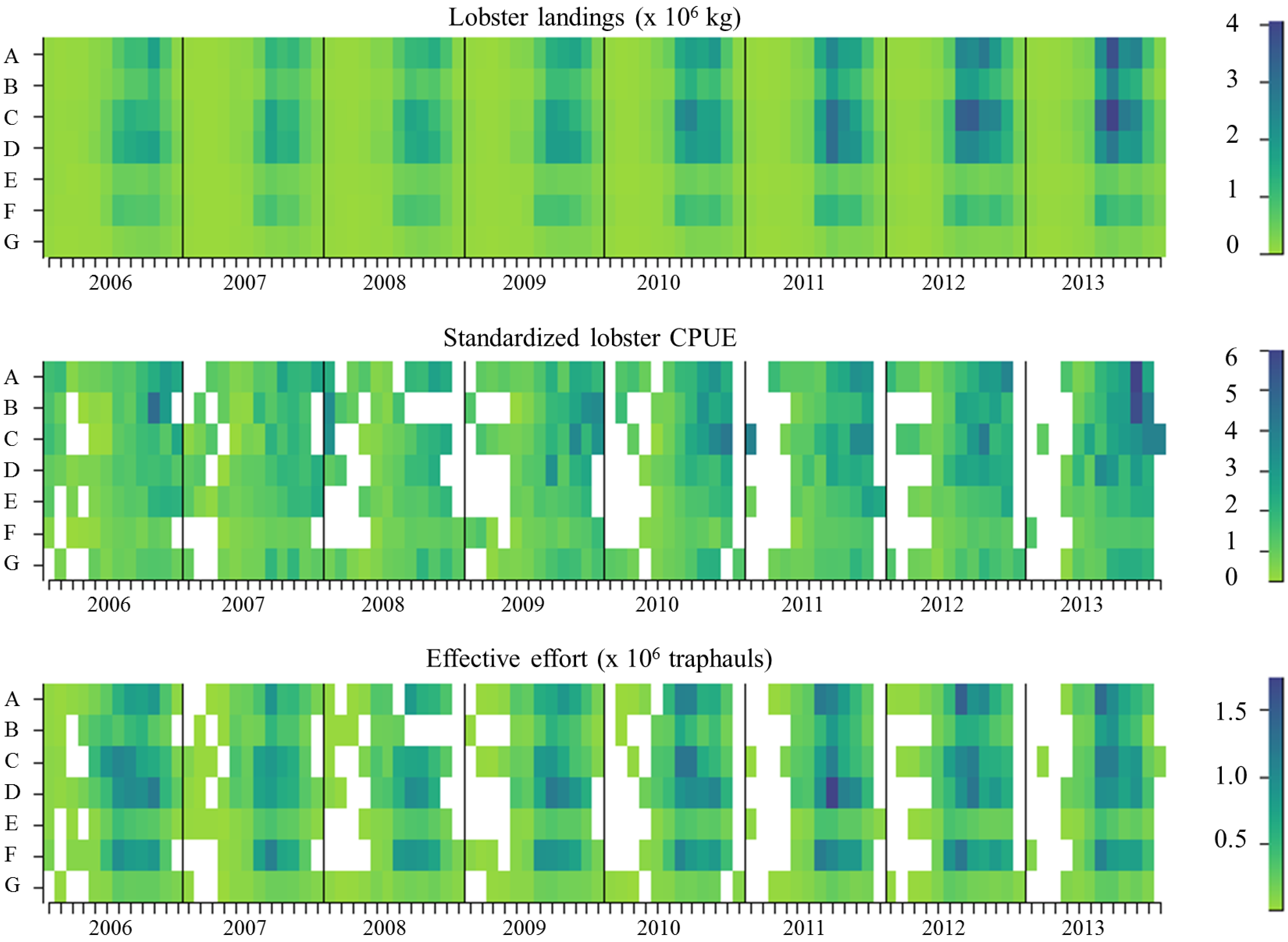
Frequency
0
150
350
F
E
G
A
B
C
D
September 2013
May 2013
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Standardized CPUE

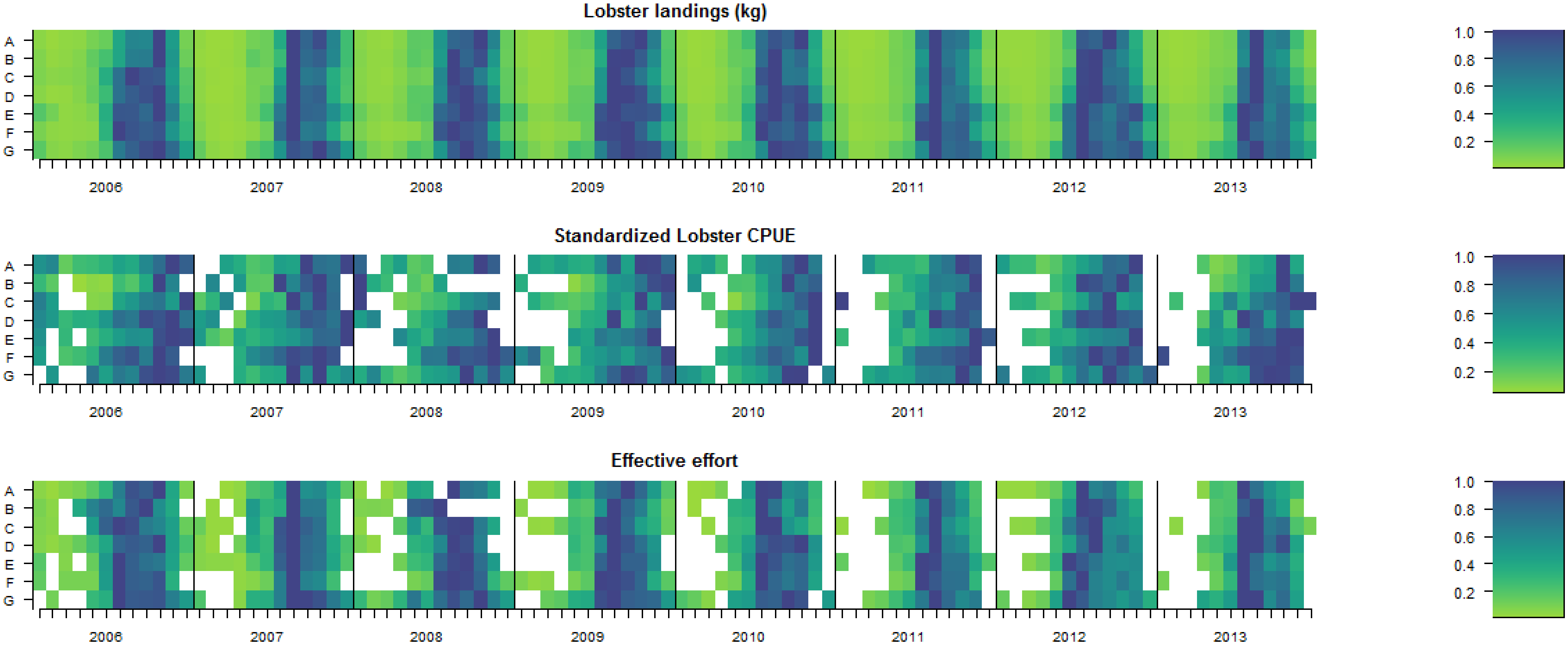

GAM 1
GAM 2
A
G
*
3.983
Month
3.739
Set over days
2.092
Distance from shore
3.983
Month
2.234
Depth
3.737
Set over days
1.939
Distance from shore
3.936
Month
2.876
Depth
2.382
Set over days
3.297
Distance from shore
3.931
Month
2.142
Depth
3.505
Set over days
3.710
Distance from shore
2 4 6 8 10 12
0 5 10 20 30
0 2 4 6 8 10
0 20 60 100
0 20 40 60 80 100
0 10 20 30 40
-1.0 -0.5 0.0 0.5 1.0
-0.2 -0.1 0.0 0.1 0.2
-0.6 -0.4 -0.2 0.0 0.2 0.4
-0.10 -0.05 0.00 0.05 0.10
-0.5 0.0 0.5
-0.4 -0.2 0.0 0.2 0.4
-1.0 -0.5 0.0
-0.3 -0.1 0.1 0.2 0.3


Zone A
Zone F
Standardized CPUE (kg/traphaul)
2.0
1.5
1.0
0.5
0.0
1
2
3
4
5
6
7
8
9
10
11
12
Months


Month response curves for zones A-G (stage 1)
Response
1.0
0.5
0.0
-0.5
-1.0
-1.5
2
4
6
8
10
12
Month
A
B
C
D
E
F
G
a
Standardized CPUE
1.4
1.2
1.0
0.8
0.6
2006
2007
2008
2009
2010
2011
2012
2013
Year
c
Effective effort
$1\times10^{+6}$
$5\times10^{+5}$
2006
2007
2008
2009
2010
2011
2012
2013
Year
ZONE
A
B
C
D
E
F
G
Month response curves for zones A-G (stage 2)
Response
0.6
0.2
-0.2
-0.6
2
4
6
8
10
12
Month
A
B
C
D
E
F
G
b
d
Landings (x 10^6 kg)
0
10
30
50


Zone A
Trap hauls
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
2008
2009
2010
2011
2012
2013
Year
Zone B
Trap hauls
0
0.5
1.0
1.5
2008
2009
2010
2011
2012
2013
Year
Zone C
Trap hauls
0
0.5
1.0
1.5
2.0
2.5
2008
2009
2010
2011
2012
2013
Year
Zone D
Trap hauls
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
2008
2009
2010
2011
2012
2013
Year
Zone E
Trap hauls
0
0.5
1.0
2008
2009
2010
2011
2012
2013
Year
Zone F
Trap hauls
0
0.5
1.0
1.5
2.0
2.5
2008
2009
2010
2011
2012
2013
Year
Zone G
Trap hauls
0
0.5
2008
2009
2010
2011
2012
2013
Year


Lobster landings (x 10⁶ kg)
A
B
C
D
E
F
G
2006
2007
2008
2009
2010
2011
2012
2013
4
3
2
1
0
Standardized lobster CPUE
A
B
C
D
E
F
G
2006
2007
2008
2009
2010
2011
2012
2013
6
5
4
3
2
1
0
Effective effort (x 10⁶ traphauls)
A
B
C
D
E
F
G
2006
2007
2008
2009
2010
2011
2012
2013
1.5
1.0
0.5



Lobster landings (kg)

Standardized Lobster CPUE

Effective effort

Spatio-temporal dynamics of effective fishing effort in American lobster (*Homarus americanus*) fishery along the coast of Maine, USA

Figures and figure captions

Figure 1. Distribution of Maine Lobster (*Homarus americanus*) sea sampling trap hauls (10-minute squares) over lobster management zones (A-G) for the years 2006-2013. Overall frequency distribution of eight spatiotemporal covariates include month (12 months), depth (m), latitude & longitude (decimal degrees), distance from shore (km), fishing zone (A-G), sediment (categorized by composition of clay, silt, and gravel), and number of trap set over days. Blank squares indicate space with no sea sampling data.

Figure 2. Example spring (May) and fall (September) two-stage generalized additive model bootstrap distributions of average standardized American lobster (*Homarus americanus*) CPUE (kg of legal lobster per trap haul) as estimated for Maine lobster management zones (A-G) for the year 2013. Dashed line indicates increase corresponding to seasonal inshore migration. Fall standardized CPUE exhibits more pronounced increases in the northeastern zones (A-D) than the southwestern zones (E-G), while spring CPUE is more similar (but much lower) across zones.

Figure 3. GAM 1 (probability of capture) and GAM 2 (positive catch distribution) thin plate regression spline partial dependence plots with 95% confidence intervals for lobster (*Homarus americanus*) zones A and G (columns). Estimated degrees of freedom denoted in top left of subplots. Asterisk denotes covariate excluded from final model.

Figure 4. Example Maine lobster (*Homarus americanus*) management zones (A, G) model-derived CPUE's (kg of legal lobster per trap haul) by month. Black and blue dots represent individual year values; boxes represent variation over years 2006-2013. Remaining zones found in supplementary figure 3.

Figure 5. Annual Maine American lobster (*Homarus americanus*) abundance indices, effective effort, landings, and monthly partial dependence plots for all zones (2006 -2013). a) Probability of legal lobster capture (GAM 1) monthly partial dependence plots (all zones). b) Positive catch distribution model (GAM 2) monthly partial dependence plots (all zones). c) Effective effort (standardized trap hauls) and indices of abundance by year (all zones) with 95% confidence intervals. d) Total Maine American lobster landings (combined zones).

Figure 6: Comparison of Maine harvester survey (± 20%) (dark blue) and bootstrapped Generalized additive model-derived (light blue) effective trap hauls (x 10^6) by month and zone (A-G) from 2006-2013. Grids denoted increments of 5 x 10^5 trap hauls for all zones.

Figure 7. Mapped spatiotemporal trends of lobster (*Homarus americanus*) landings (kg), standardized CPUE (kg of legal lobster per trap haul), and Effective effort (individual trap hauls) for Maine lobster management zones A-G for years 2006-2013. Missing data are represented with white space.

Figure 8. Zone-normalized (0-1) American lobster (*Homarus americanus*) landings, standardized catch per unit effort, and effective effort (traphauls).

Tables and Table captions

Table 1. Frequency of variables being selected in final bootstrapped GAM models and percent of null deviance explained across all fishery zones.

Model	Zone	Year	Month	Latitude, Longitude	Depth	Set over days	Sediment	Distance to shore	Deviance Explained
GAM 1	A	X**	X**	X**	-	X**	-	X*	10.7%
	B	X**	X**	X**	X**	X**	-	X**	15.7%
	C	X**	X**	X**	X**	X**	-	-	16.7%
	D	X**	X**	X**	X**	X**	-	X**	10.4%
	E	X**	X**	X**	X**	X*	-	-	6.13%
	F	X**	X**	X**	X**	X*	-	-	4.6%
	G	X**	X**	X**	X**	X**	X**	X**	5.4%
GAM 2	A	X**	X**	X**	X**	X**	-	X*	28.3%
	B	X**	X**	X**	X**	X**	X*	X**	27.2%
	C	X**	X**	X**	X**	X**	X**	X**	28.8%
	D	X**	X**	X**	X**	X**	X**	X**	19.0%
	E	X**	X**	X**	X**	-	-	-	10.1%
	F	X**	X**	X**	X**	-	-	-	7.6%
	G	X**	X**	X**	X**	X**	X**	X**	14.6%

Table 2. Summary of modelled Maine American lobster (*Homarus americanus*) fishery total zonal effort (trap hauls) for year 2006-2014. Percentages indicate relative proportion of hauls by zone. “West” denotes management zones E-G and “East” corresponds to zones A-D. “*” represents covariate p-value <0.05, and “**” represents p <0.01.

Year	Traphauls (x 10^7)	A	B	C	D	E	F	G	West	East
2006	5.98	16.50%	12.60%	26.20%	15.80%	7.80%	16.60%	4.50%	28.90%	71.10%
2007	4.46	17.60%	11.60%	25.30%	15.40%	8.00%	17.70%	4.36%	30.06%	69.94%
2008	4.78	19.02%	11.20%	23.86%	15.40%	8.20%	17.50%	4.69%	30.39%	69.61%
2009	5.01	19.50%	11.50%	21.60%	16.50%	7.79%	18.30%	5.30%	31.39%	68.61%
2010	5.8	20.54%	12.40%	24.40%	14.50%	6.76%	17.50%	3.90%	28.16%	71.84%
2011	5.73	19.60%	12.44%	22.54%	16.70%	6.70%	18.03%	3.88%	28.61%	71.39%
2012	6.76	20.54%	12.67%	24.90%	14.60%	6.40%	17.10%	3.70%	27.20%	72.80%
2013	6.25	22.54%	13.70%	23.50%	14.16%	6.48%	15.67%	3.89%	26.04%	73.96%