

# Diversity Paper Preliminary Results

*May 3, 2016*

## Introduction

The processes underlying species co-existence remain one of the more fascinating questions of ecological study. While numerous theories have been advanced to explain species co-existence, no single unifying construct seems adequate to explain observed patterns of co-existence (Wilson 2011). Most studies of co-existence occur in terrestrial systems where factors governing co-existence could be carefully controlled and monitored with numerous opportunities for Before-After-Control-Impact studies. In aquatic systems identifying opportunities for comparative studies is more difficult (Smith et al. 1993). Therefore there is a paucity of literature on co-existence in ocean settings.

The portfolio effect, which is essentially statistical averaging, is one explanation for stability in multi-species communities. This effect occurs when species have asynchronous responses to environmental perturbations, but when summed across the community the responses average out statistically leading to increased stability with increased diversity (Cottingham et al 2001, Doak et al 1998). This effect can be conveyed through the mechanisms of species' intrinsic responses, the speed of those responses, and a reduction in interspecific competition (Yachi & Loreau 1999, Loreau & de Mazancourt 2013).

Recent literature has suggested that redundancy within marine ecosystems can lead to improved stability within ecosystems through alternative pathways for stability (Schindler et al. 2015; Schindler et al. 2010). The constructs of the portfolio concept intersect with species co-existence through the attributes of redundancy, structure, and the interaction terms. If these concepts do have a stabilizing effect, we hypothesize that portfolios would be preserved across space (ecoregions) within large marine ecosystems that have similar large scale environmental forcing. We further hypothesize that if portfolios are preserved across space within large marine ecosystems (LMEs) with similar environmental exposure, then similar suites of species would be found within ecoregions.

Boreal marine systems such as the Gulf of Alaska (GOA) experience high levels of seasonal, interannual, decadal and multi-decadal variability which in turn impact marine species (Anderson and Piatt 1999; Hare and Mantua 2000; Hollowed et al. 2001; Stachura et al. 2014). These climate driven perturbations create states of non-equilibrium at multiple spatial scales. The Gulf of Alaska provides an excellent region to examine processes governing co-existence and the portfolio effect. The region exhibits complex topography being punctuated by submarine troughs and canyons which act to steer currents (Lagerloef 1983). Previous studies have utilized this complex topography to for natural experiments based on the comparison of responses of selected fish species to natural or anthropogenic disturbance (Hollowed et al. 2007; Logerwell et al. 2007; Walline et al. 2012).

Previous studies have demonstrated that food-webs in the GOA are dominated by short interaction chains with a select group of nodal species (Gaichas and Francis 2008) suggesting that shifts in environmental conditions could be detected relatively quickly. These features of frequent environmental perturbation and short interaction chains that depend on a discrete suite of nodal species makes this region particularly interesting for an investigation the emergent properties of ecosystem change in response to disturbance.

We focused our study on examining the portfolio effect on ecosystem responses to natural (e.g., regime shifts (Anderson and Piatt 1999)) and anthropogenic (e.g., the Exxon Valdez Oil Spill (Incardona et al. 2015)) environmental perturbations. We tested species responses through time, and functional complementarity, two mechanisms of the portfolio effect (Loreau & de Mazancourt 2013).

We also reviewed three of the most promising of the 12 hypotheses governing species co-existence which were reviewed by Wilson (2011):

1. Alpha-niche differentiation – stabilizing

2. Environmental fluctuation – stabilizing [ via relative non-linearity and/or the storage effect see (Chesson 2004)]
3. Allogenic disturbance – stabilizing [intermediate disturbance; although climate variability occurs on large spatial scales, fishing occurs at intermediate scales, therefore this hypothesis is retained here]

We then extended single species studies to explore the evidence for community stability and commonality in regional species portfolios as measured by common members of species complexes, trophic stability (common proportional density of foraging guilds) and stability in species diversity. It is unclear which of the potential ecosystem disturbances: environmental variability, fishing, and predation (Gaichas et al. 2011). We expect that explorations of these relationships on a regional basis will elucidate key processes underlying GOA ecosystems.

## Methods

The shelf region of the Gulf of Alaska was divided into 9 sub-regions (Figure 1). Each region represented an area ranging in size from xxx – yyy km<sup>2</sup>. For reference, the states of Rhode Island and Delaware are 3,140 km<sup>2</sup> and 6,452 km<sup>2</sup> respectively. The mean depth and bottom temperature of each region is shown in Table 1.

NMFS bottom trawl data were used in this analysis. Since 1984, the Alaska Fisheries Science Center (AFSC) has conducted comprehensive bottom trawl surveys in the GOA to monitor trends in the distribution and abundance of groundfish populations. The full survey area includes the continental shelf and upper continental slope (to 1,000 m depth) in the GOA and extends from the Islands of Four Mountains (170° W) 2,300 km east to Dixon Entrance (54° N). The AFSC contracts 3 commercial trawlers during May–August and samples the standard 320,000 km<sup>2</sup> survey area with approximately 820 survey stations. The catch data result in observations of catch-per-unit-area which are averaged and expanded by survey area to estimate the relative abundance of important groundfish species. This multi-species survey is based upon a stratified-random design and the area-swept method of estimating abundance (von Szalay et al. 2010 ). The net is a four-seam, high-opening Poly Nor’Eastern trawl featuring a 27.2 m headrope and a 36.7m footrope equipped with rubber bobbin roller gear.

The net is deployed from the vessel while the vessel steams ahead at 3 knots. Once on the seafloor, the net is towed for 30 minutes prior to 1992 and 15 minutes thereafter. In most years the net was equipped with a bottom contact sensor on the footrope, a Seabird SBE-39 bathythermograph on the headrope. The catch was processed by the scientific crew who identified all living organisms, weighed and counted the catch of each species, and took biological samples (lengths, otoliths, and specially requested tissues) from key groundfish species or other species of interest.

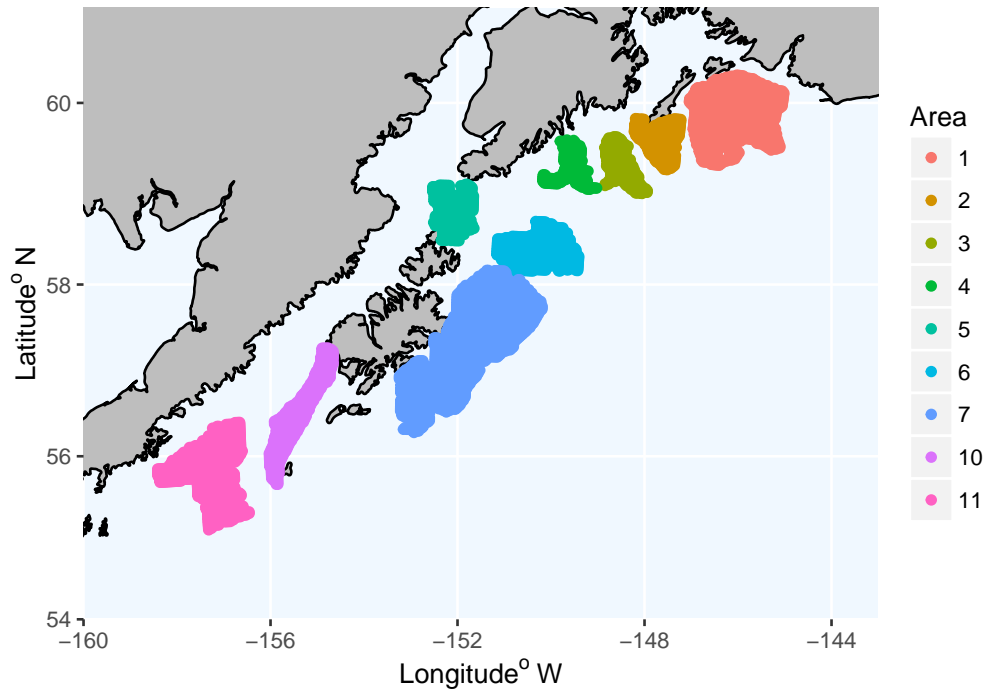
Survey data were smoothed using a geostatistical model developed by (Ono et al. 2015; Shelton et al. 2014). The model treated year and depth as fixed effects on CPUE. Most groundfish exhibit spatial partitions related to depth (). In addition many groundfish also exhibit notable ontogenetic shifts in depth (Figure xx). Including depth as a fixed effect corrects for species specific affinities for a given depth range. To correct for ontogenetic shifts in depth, the depth and temperature distributions were examined by length category for species that had continuous time series of length measurements. In cases where marked spatial shifts due to size were observed, the data were further partitioned into young (small) and adult (larger) size groups.

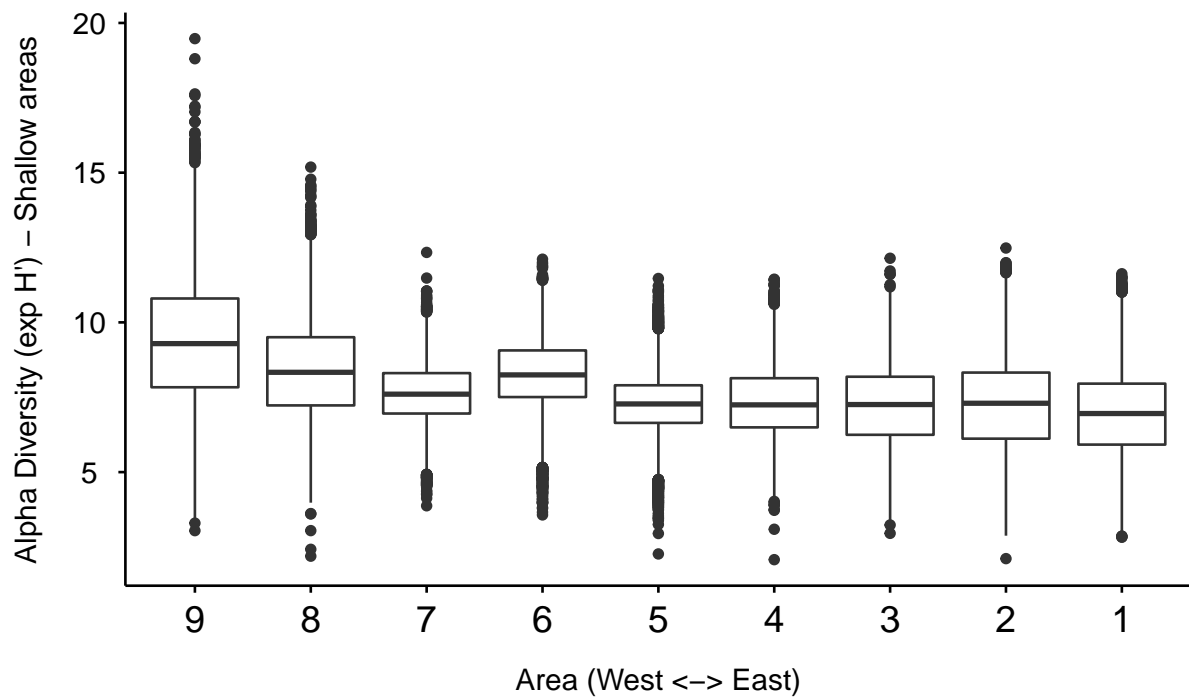
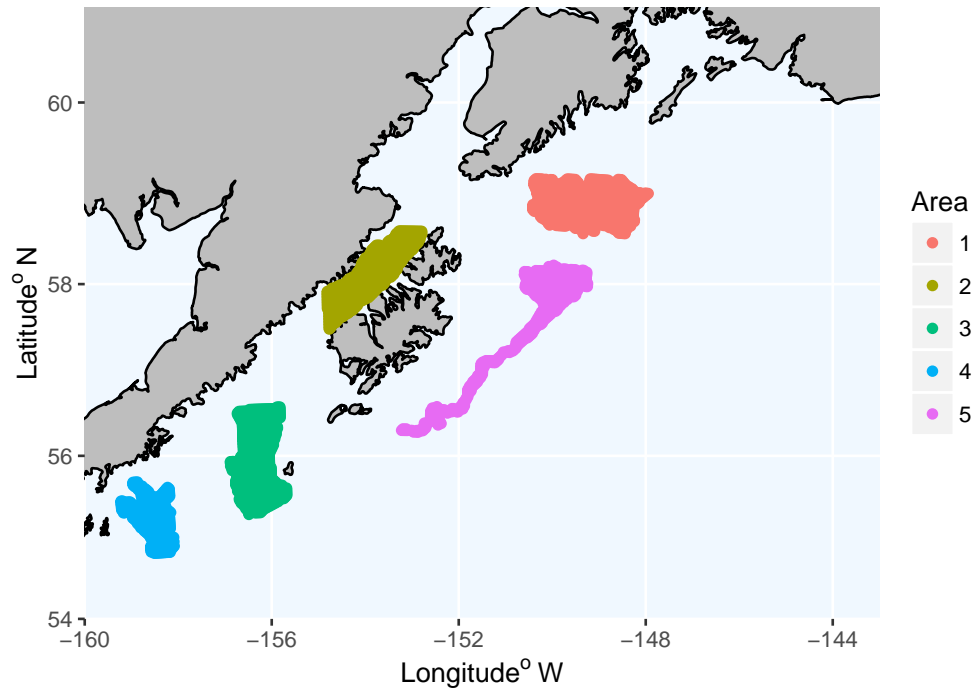
The estimated range at which the spatial correlation in the spatial field falls to 0.05 after accounting for depth ranged from 10km – 500km with most species exhibiting a range of 65km. Species with higher frequencies of occurrence tended to have lower spatial ranges with the dominant species (cod, halibut, sablefish, and pollock) being less than 60km. Area expansions derived from the model were used to estimate abundance for each of the 9 sub-regions. Some information is shared between regions due to the the spatial range of correlations, however in most species/region cases the distances between the 9 regions exceeded the species range. For each of the nine regions the mean and variance of biomass by species was calculated. It should be noted that the species exhibit different vulnerability to the survey trawl. Thus, all results reflect the demersal shelf fish community.

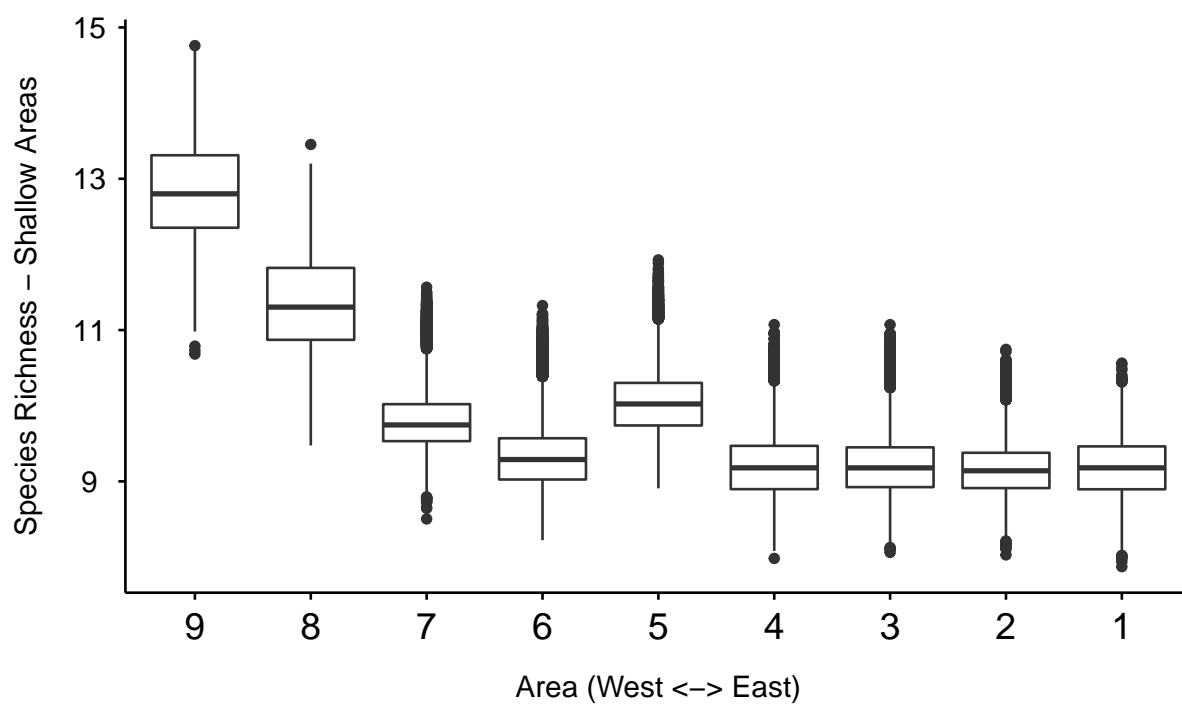
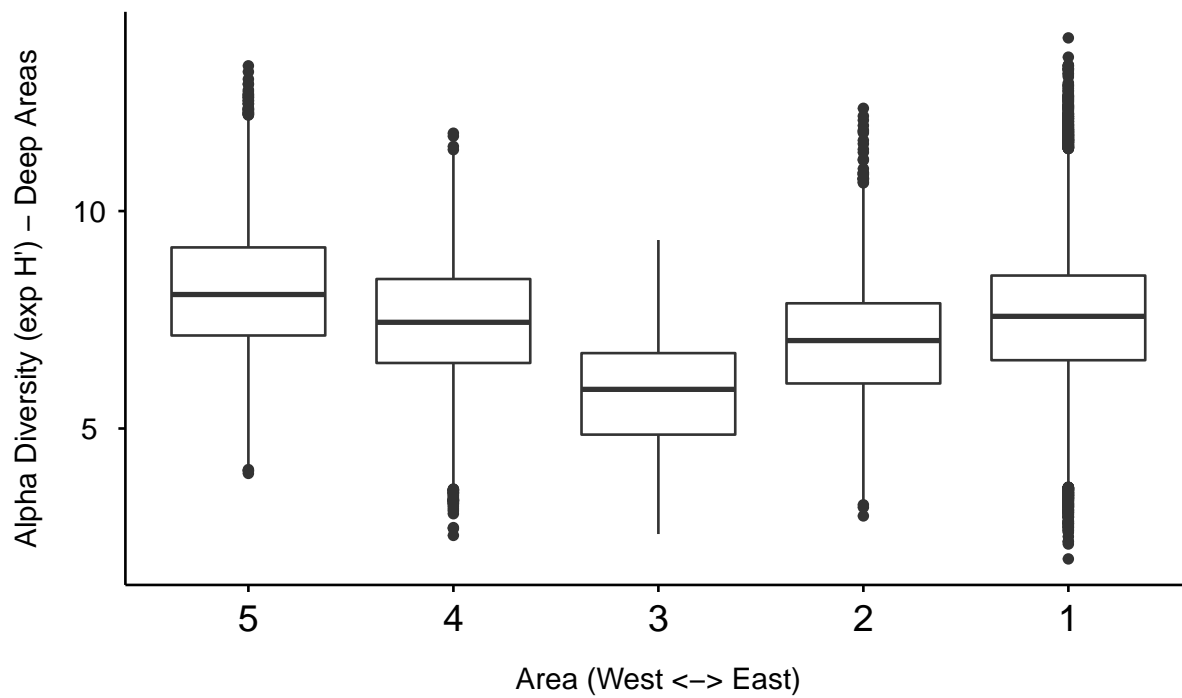
Alpha (within sub-region) and beta (across sub-regions) components of species diversity were estimated based on (Jost 2007). Components of species diversity were derived from estimated mean biomass for each species within a region. To correct for uncertainty in regional abundance we resampled the expected distribution of species within each region 1000 times using bootstrap methods.

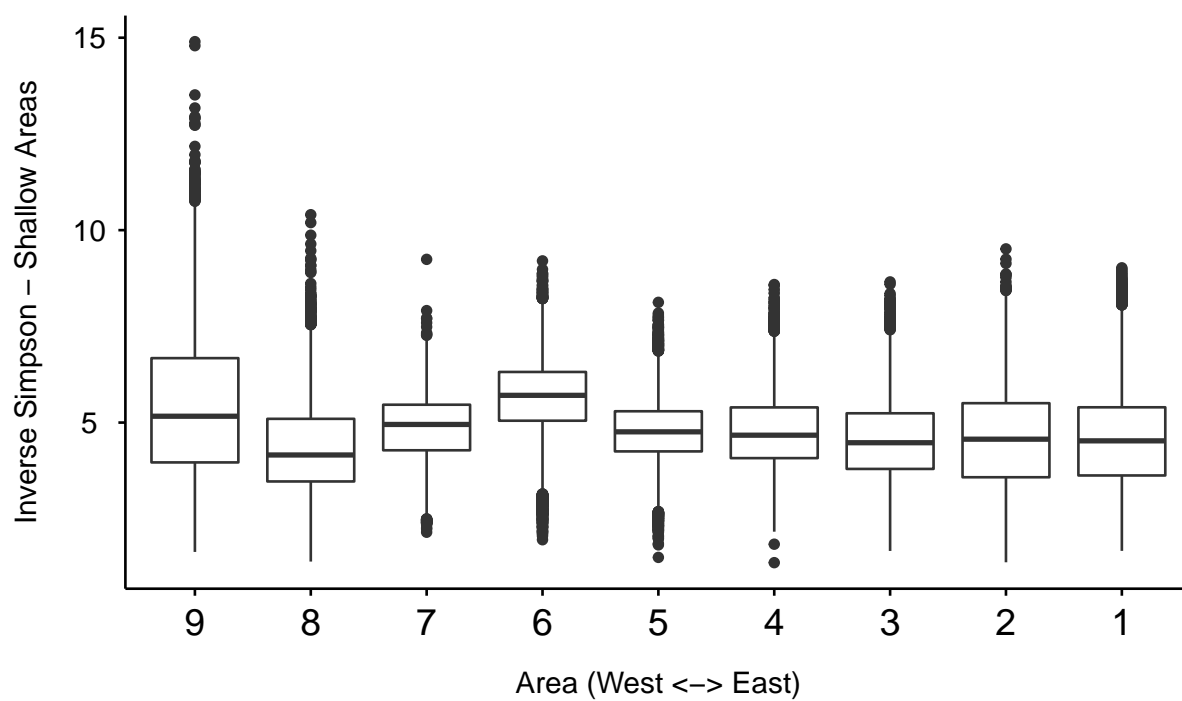
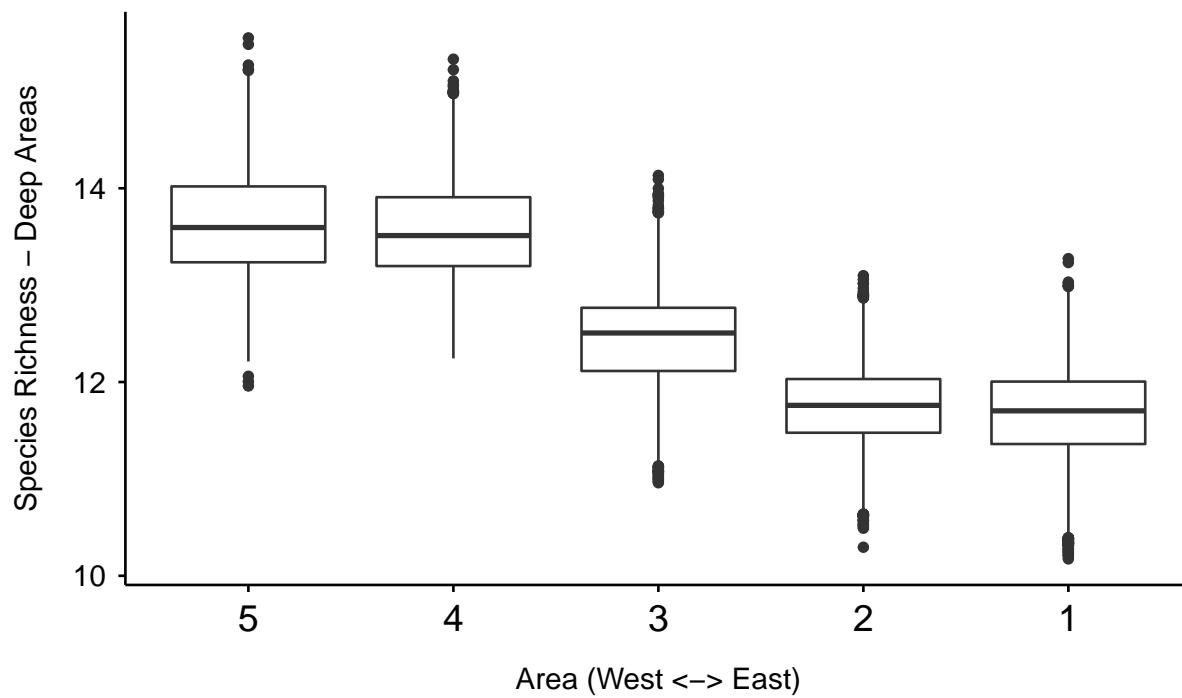
To evaluate regional differences in ecosystem structure we partitioned the predicted mean biomass for a given species into functional groups using based on the NMFS food-habits database (xxxx). For each ecoregion the mean density for each region was plotted and the biomass in each trophic guild was estimated (Table 2, Figure 2) for the entire time series 1984 – present.

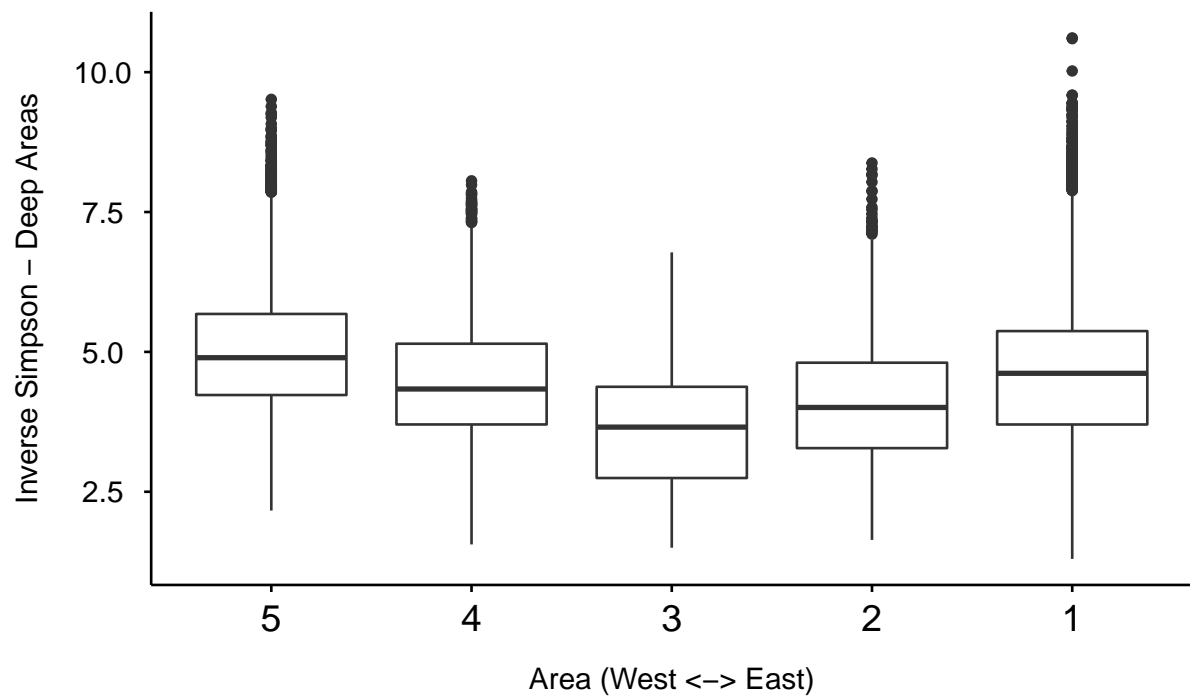
## Results



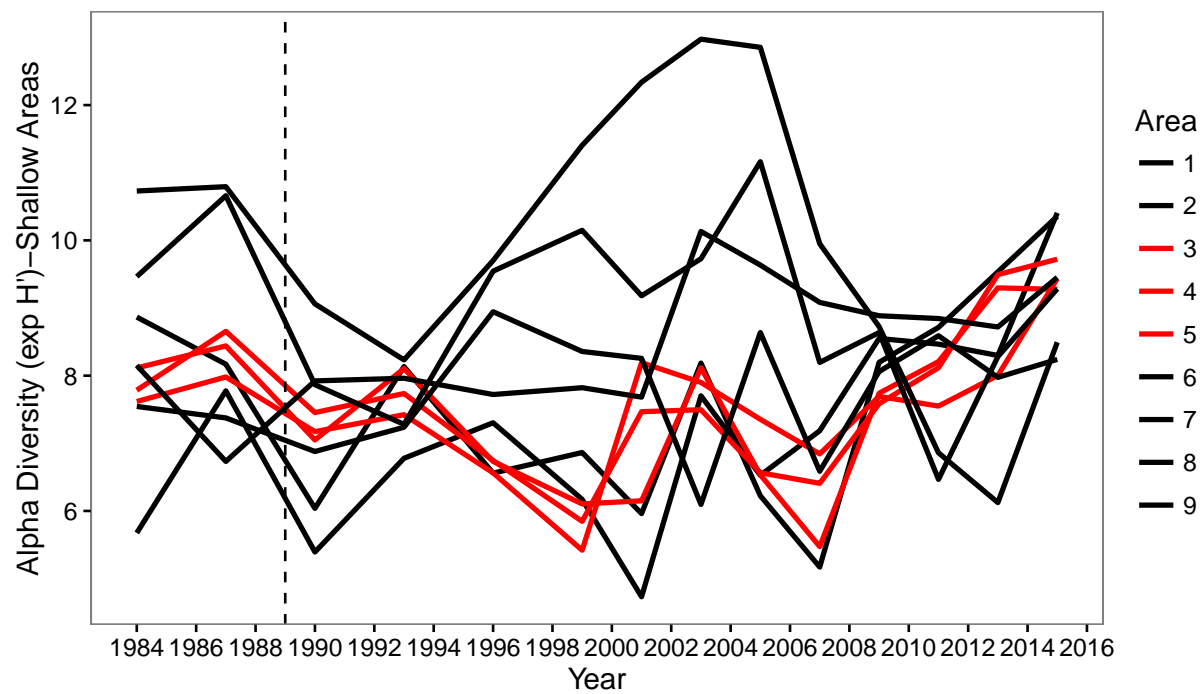




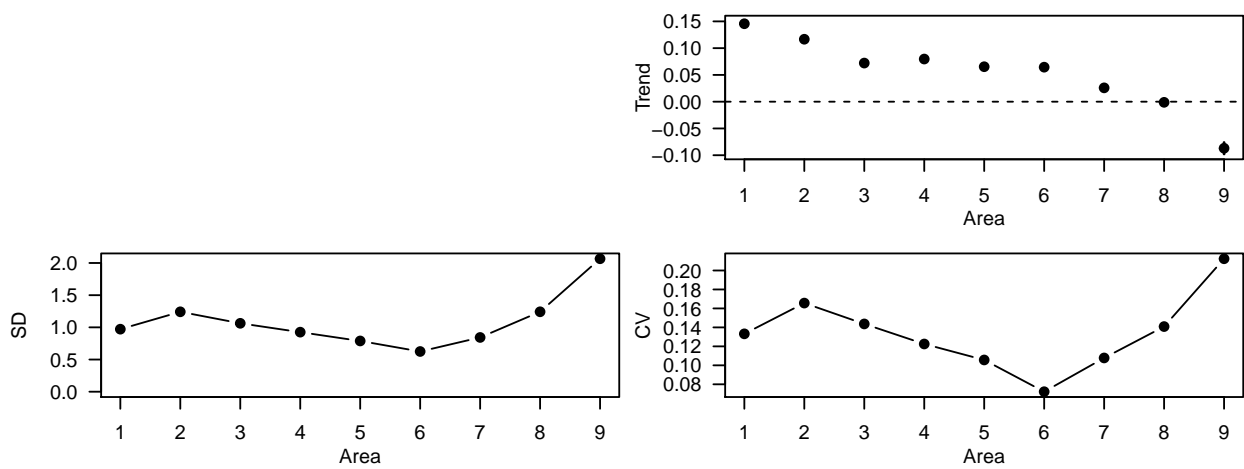




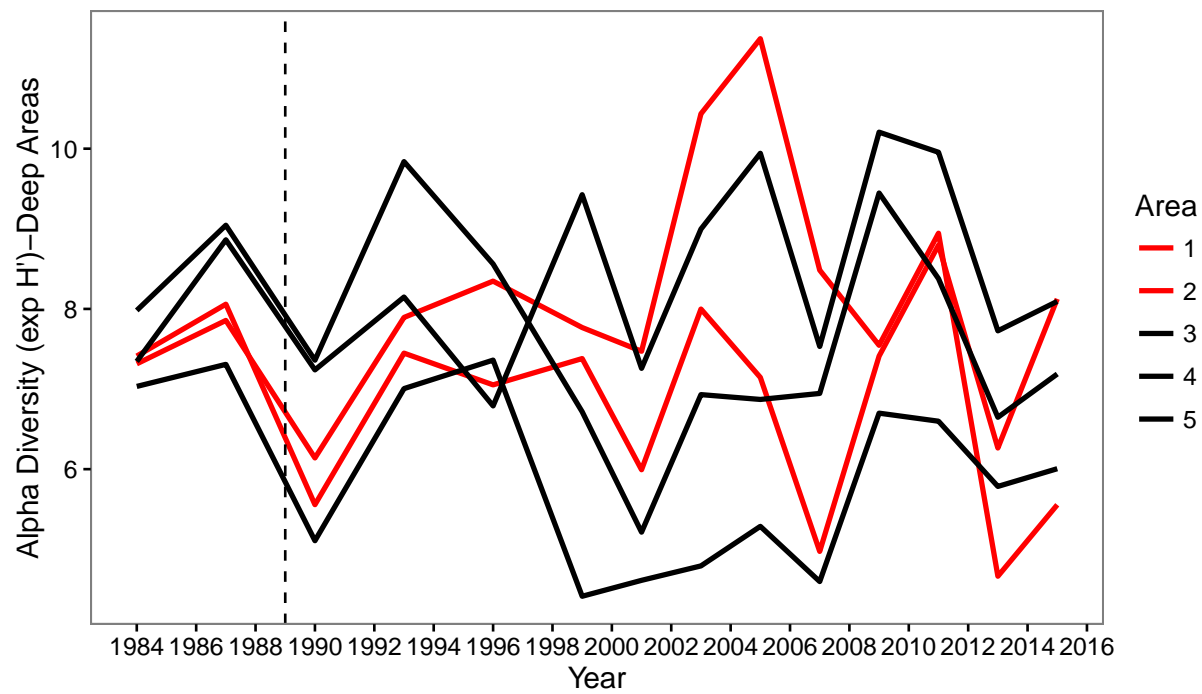
Time series of diversity metrics for 2nd paper?



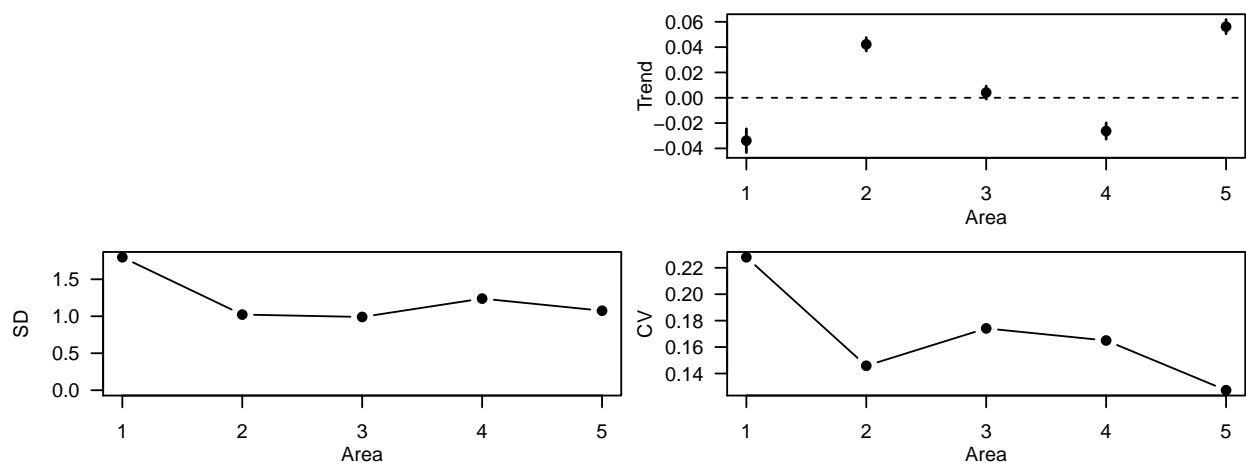
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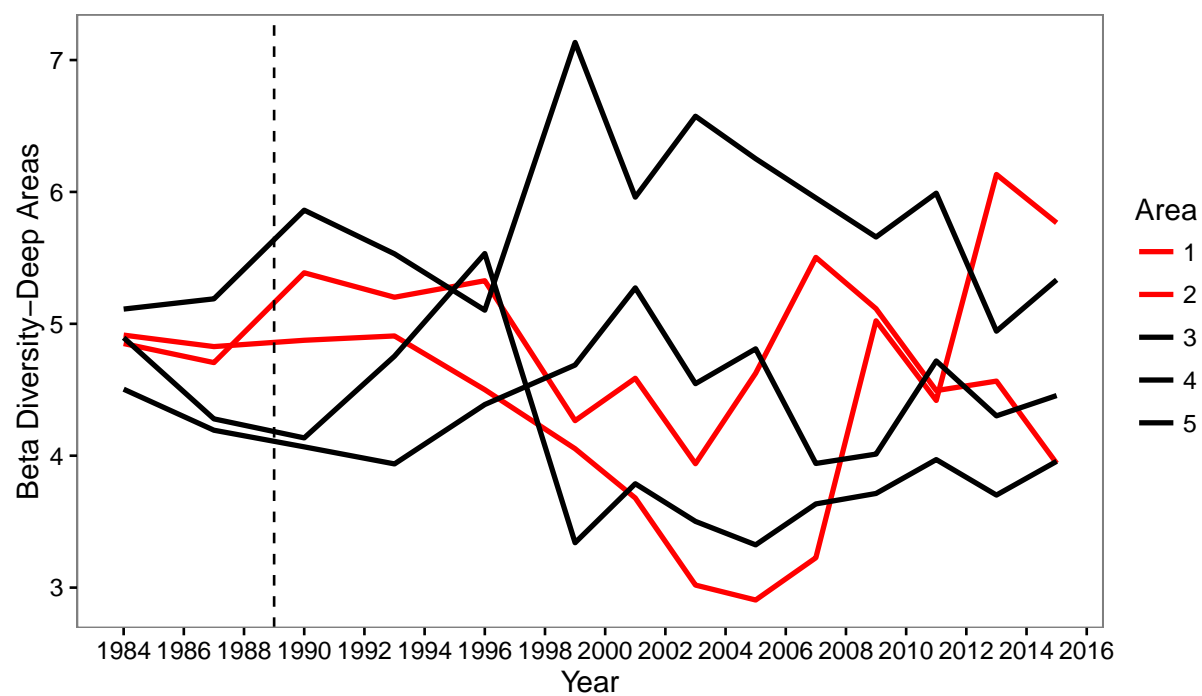
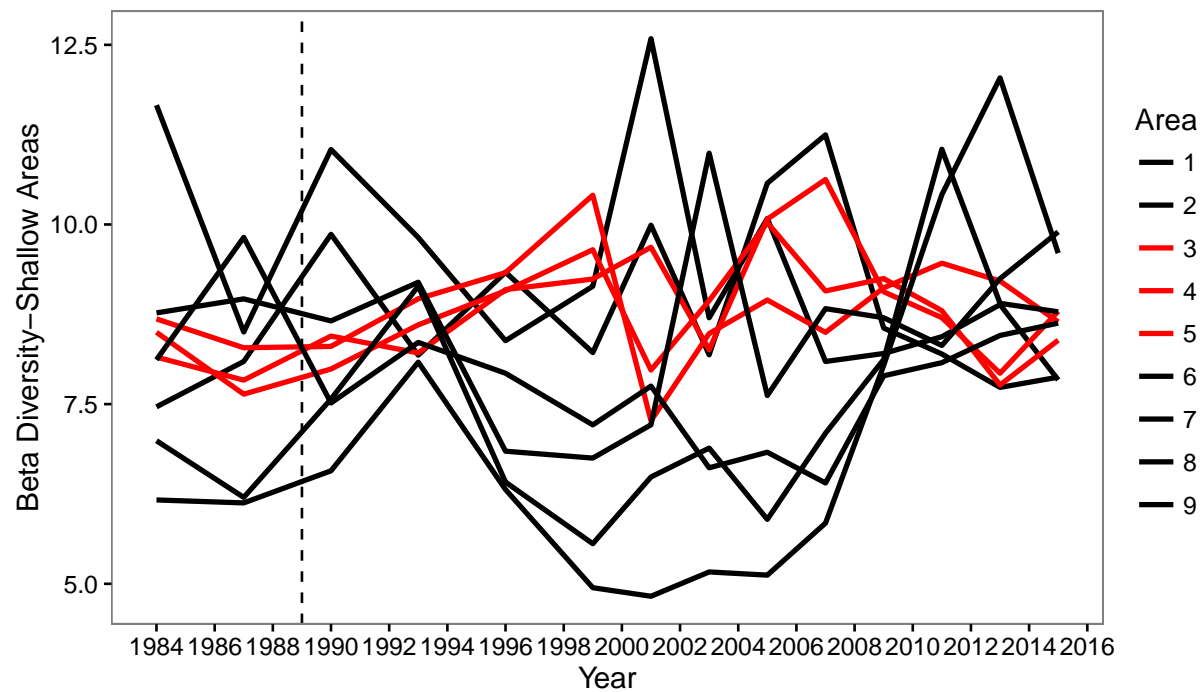


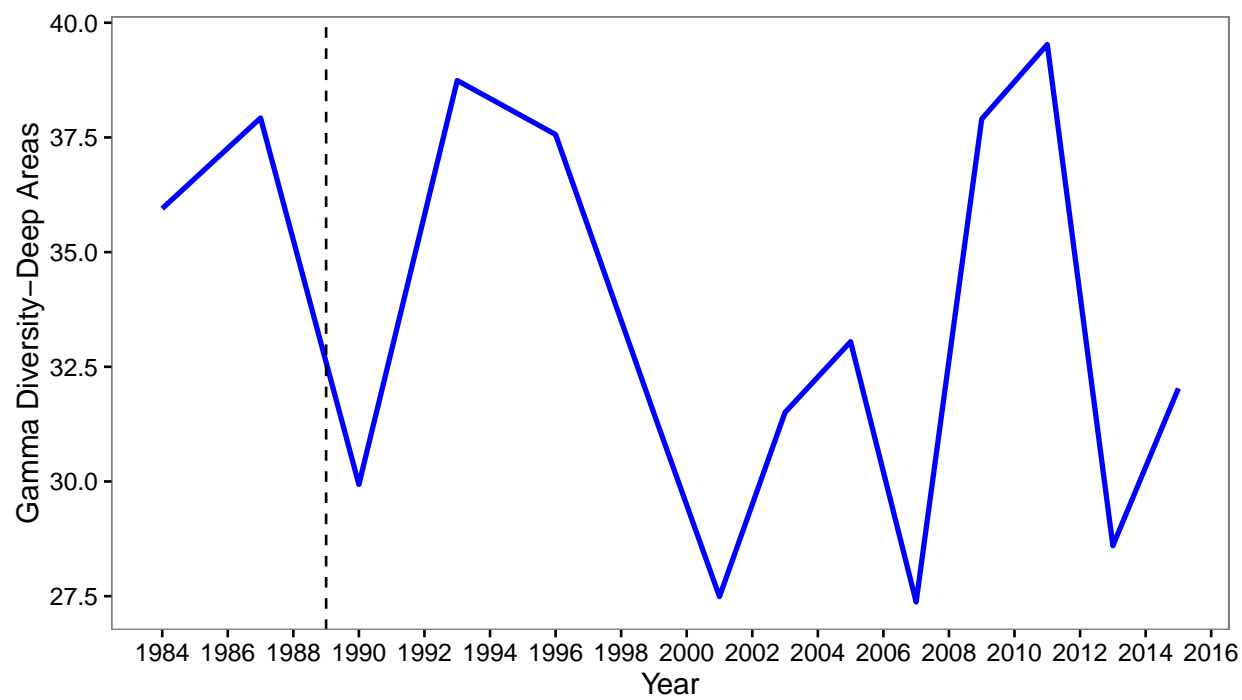
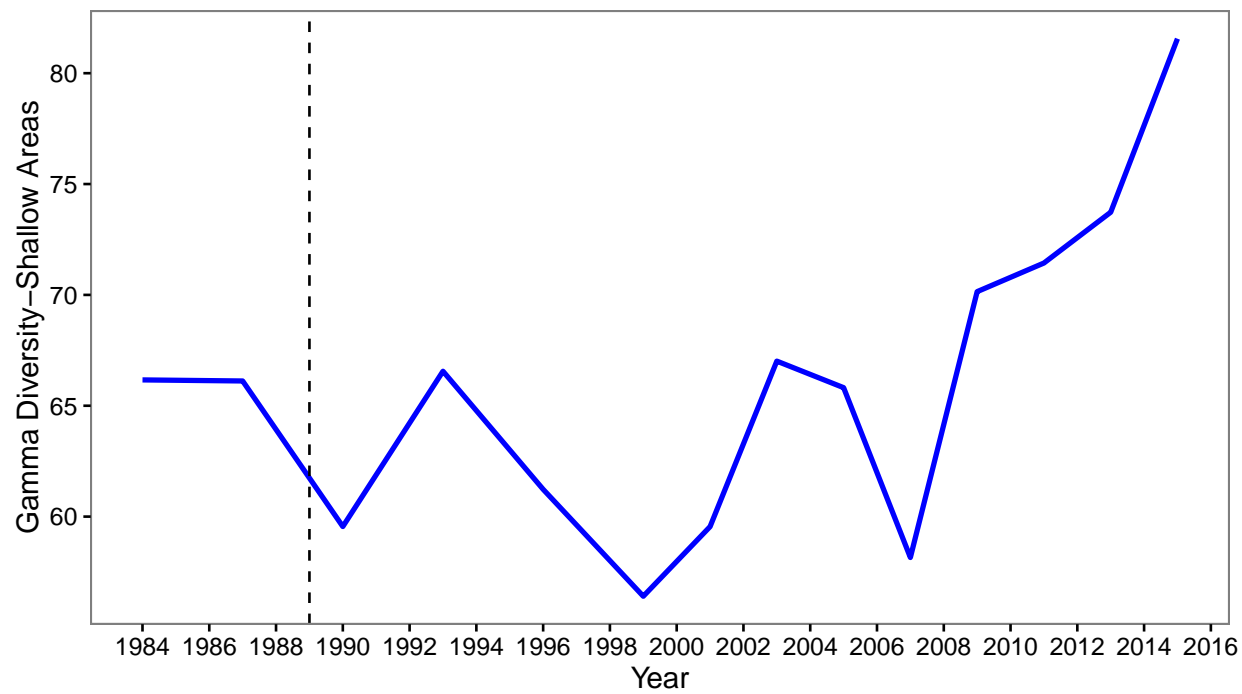


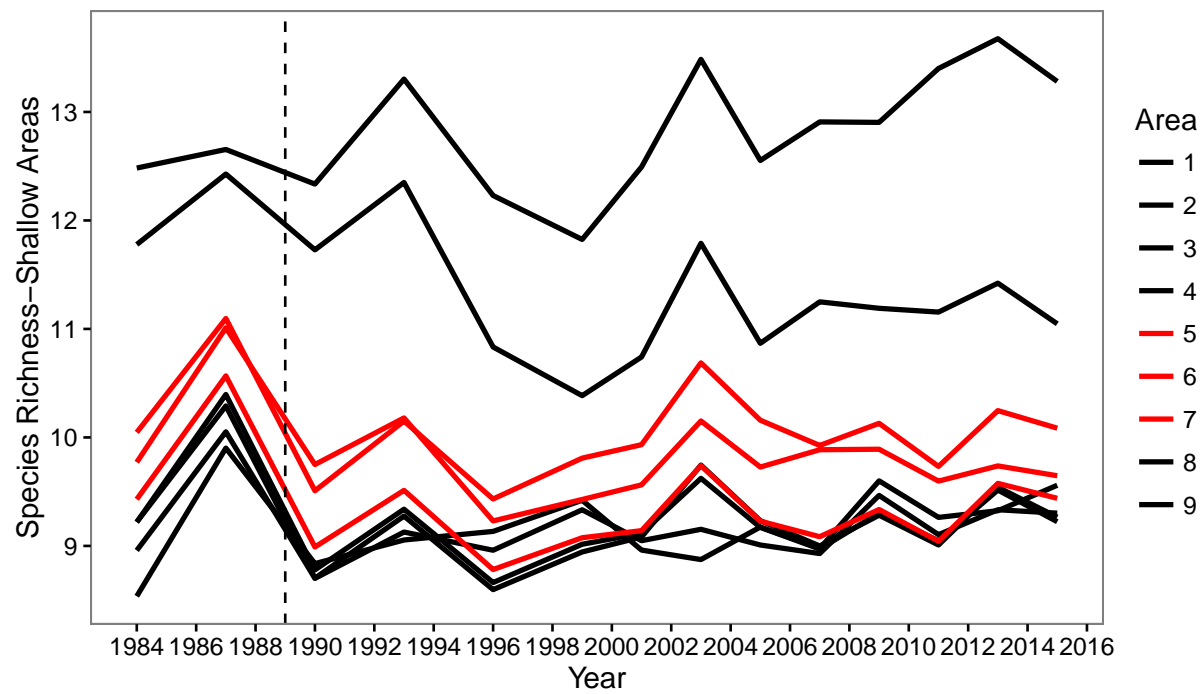


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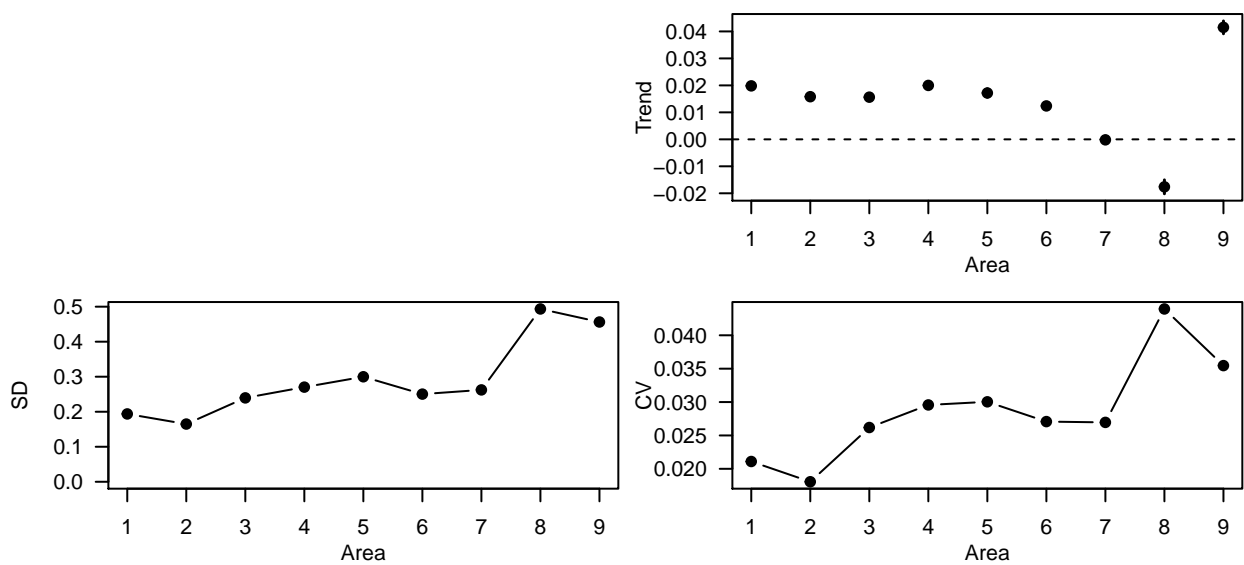


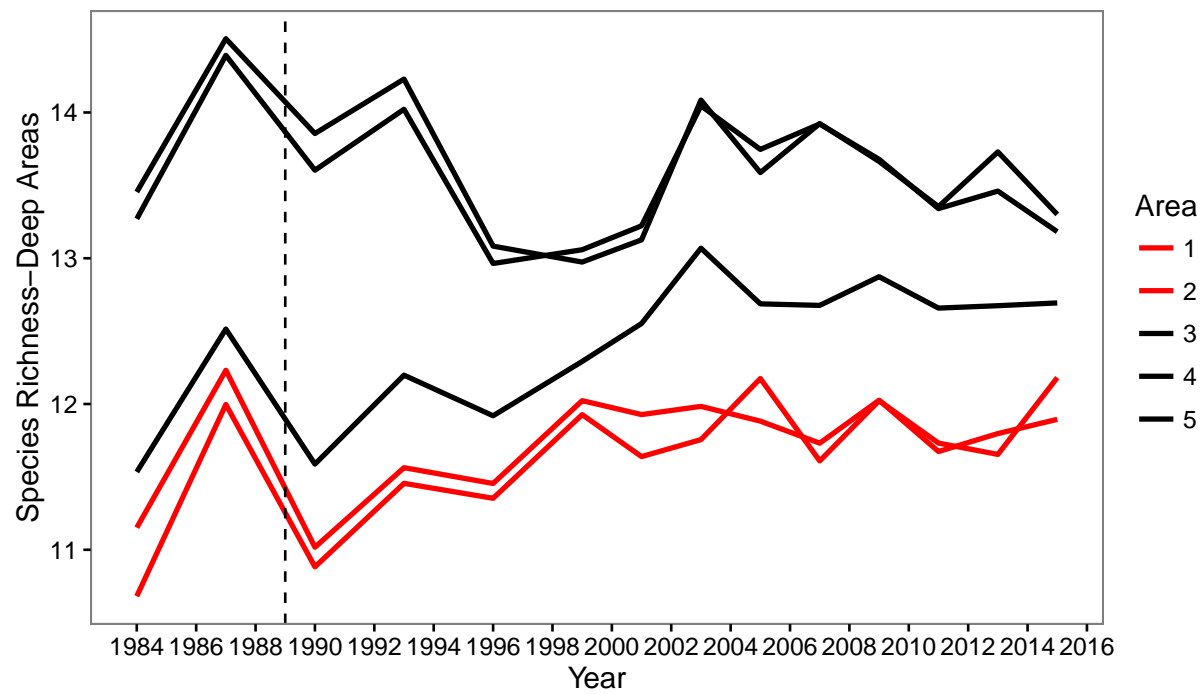




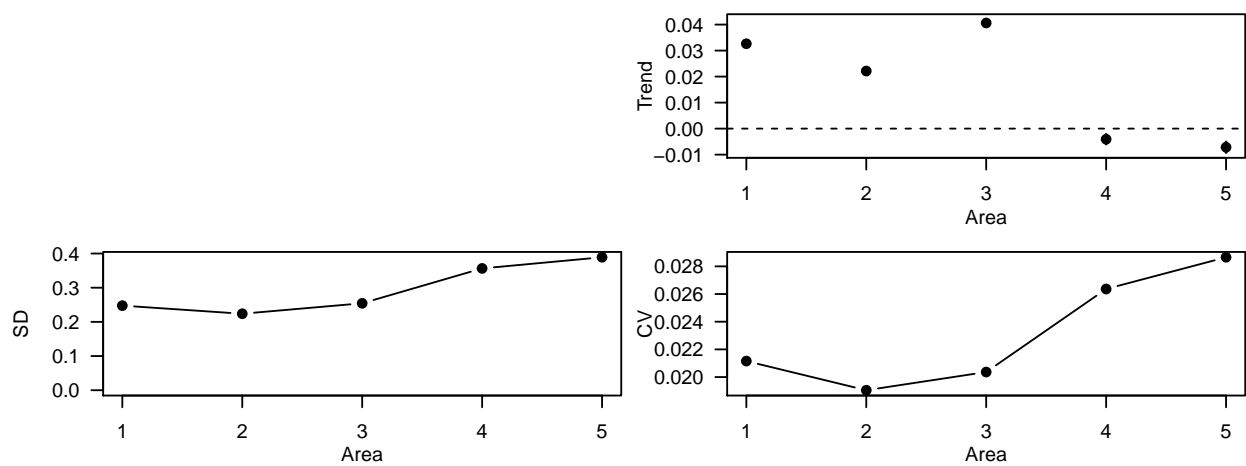


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