

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.

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 as 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 LMEs with similar environmental exposure, then similar suites of species would be found within ecoregions.

The National Center Ecological Analysis and Synthesis and the Exxon Valdez oil spill funded a research project designed to examine the evidence for 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)) disturbances.

Boreal marine systems such as the Gulf of Alaska 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. 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. In our study we 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]

The Gulf of Alaska shelf 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). In this paper we extend these 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 km². For reference, the states of Rhode Island and Delaware are 3,140 km² and 6,452 km² 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 km² 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

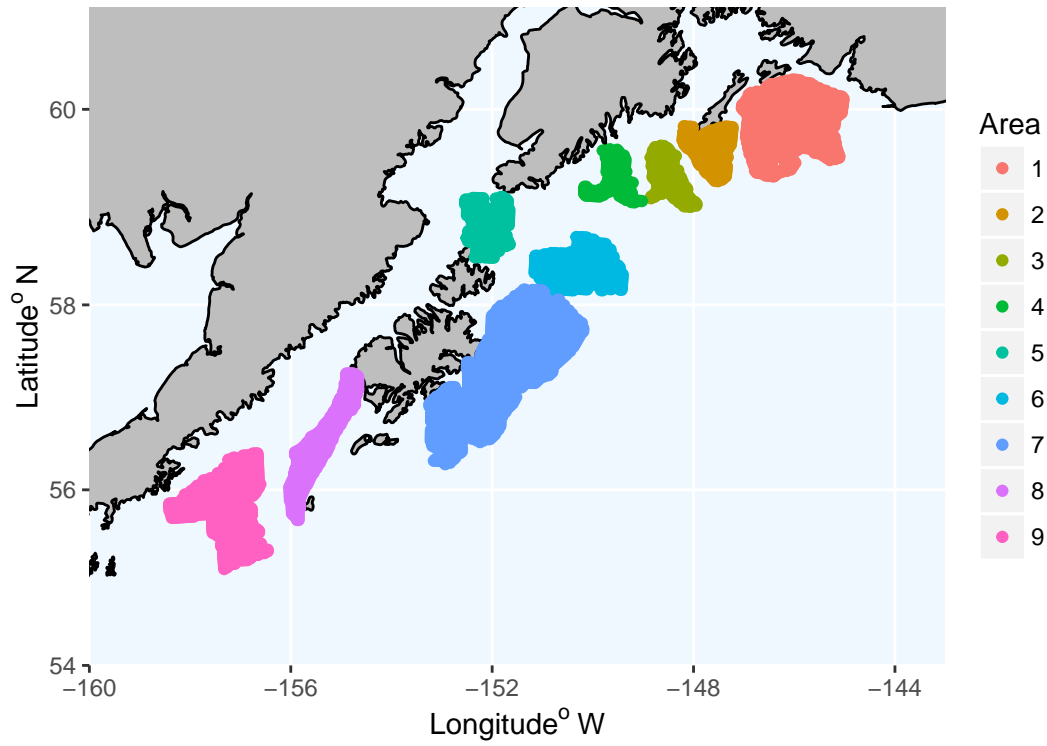


Figure 1: Locations of shallow areas (50-150 m) in Gulf of Alaska.

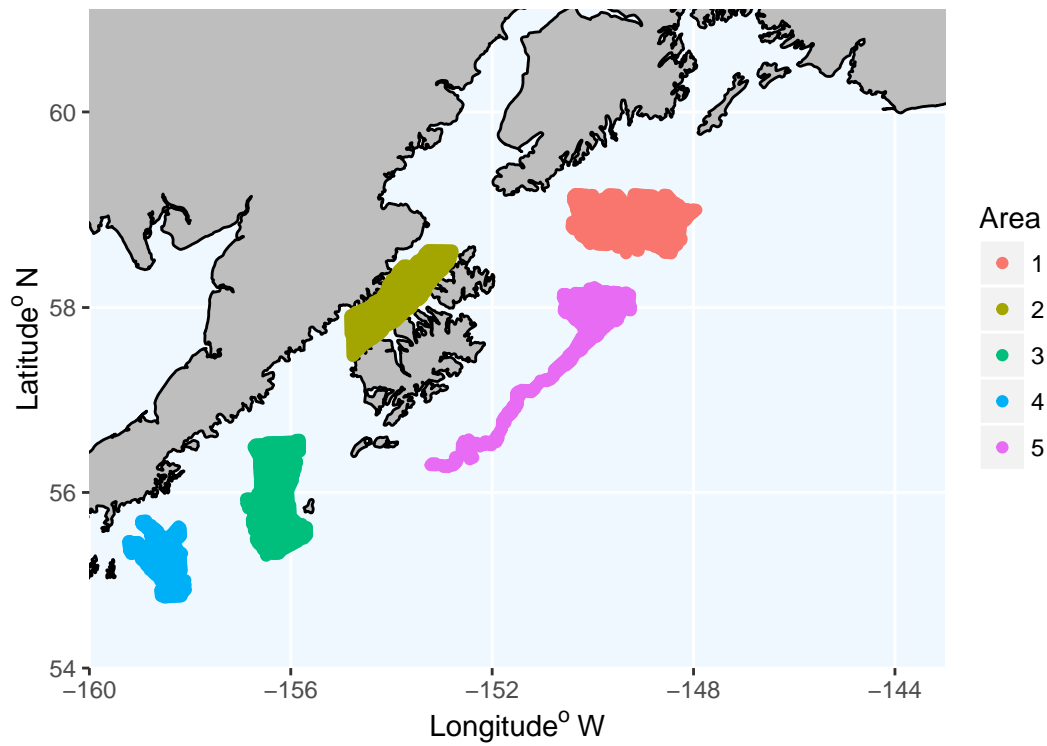


Figure 2: Locations of deep areas (>150-300 m) in Gulf of Alaska.

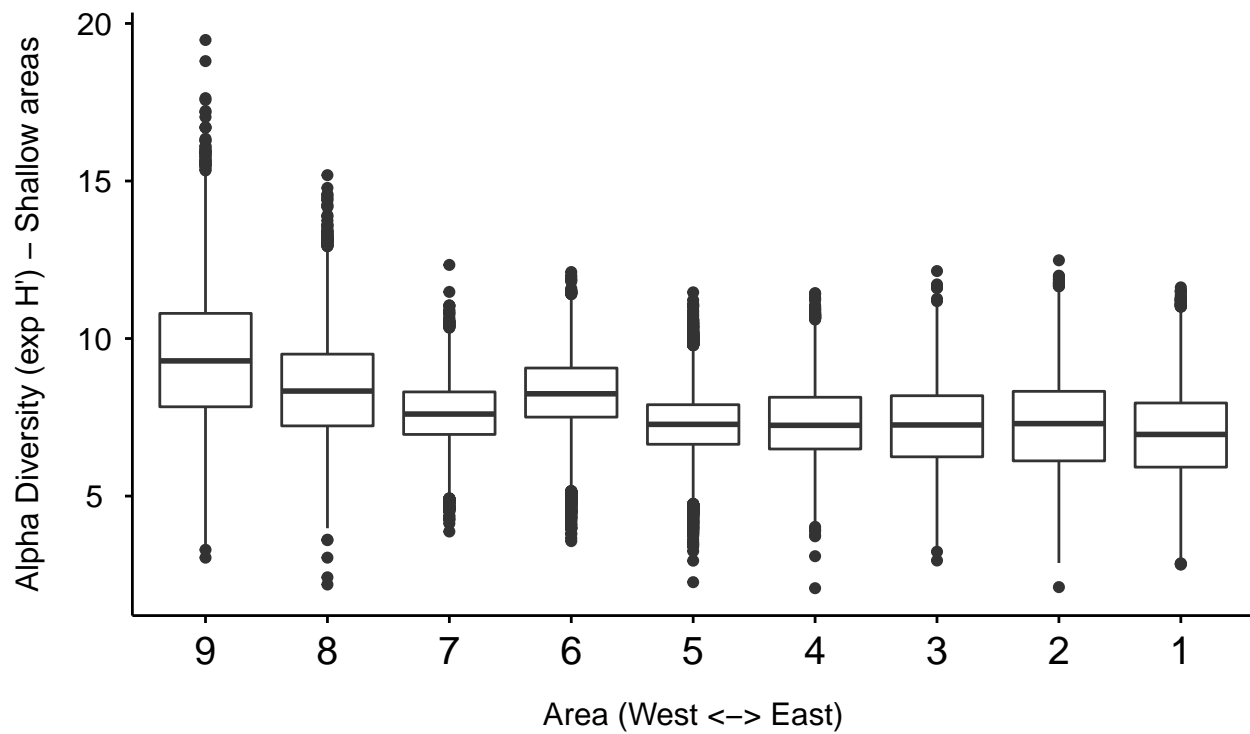


Figure 3: Alpha diversity (exp H') estimated for shallow areas (50-150m). Based on bootstrap sampling (n=1000).

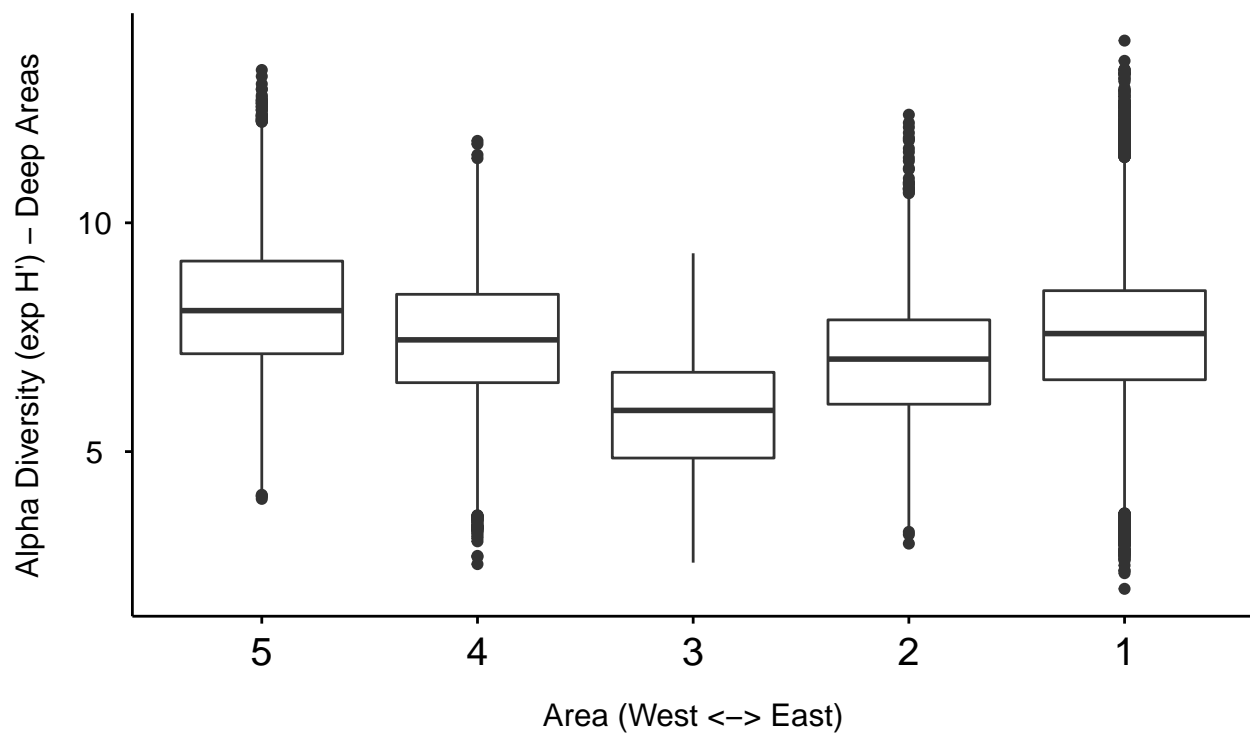


Figure 4: Alpha Diversity (exp H') estimated for deep areas (>150-300m). Based on bootstrap sampling (n=1000).

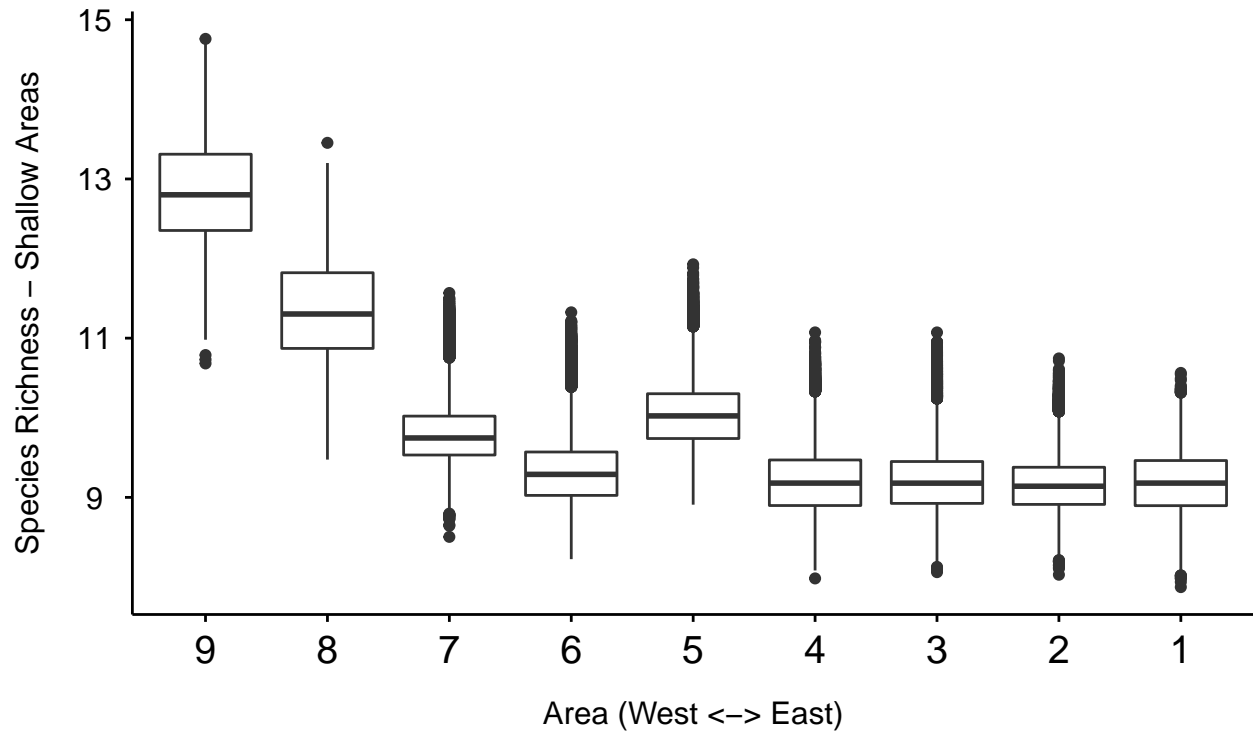


Figure 5: Species richness estimated for shallow areas (50-150m). Based on bootstrap sampling (n=1000).

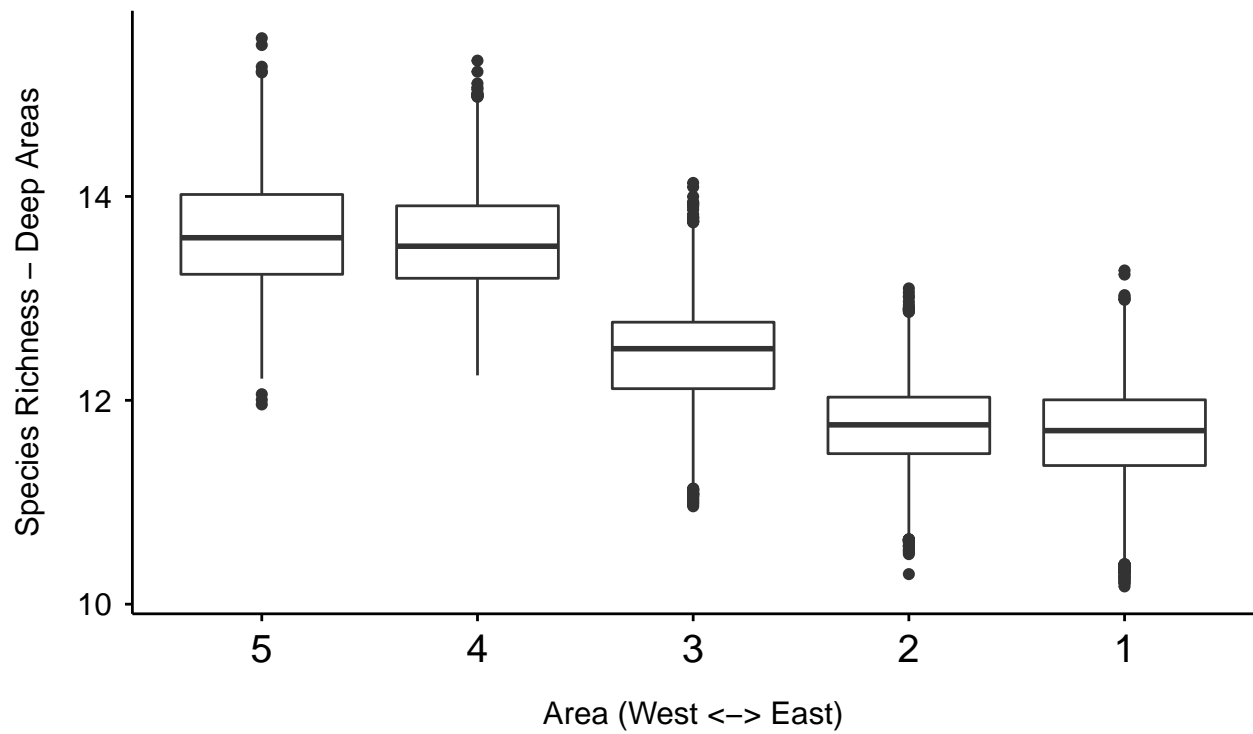


Figure 6: Species richness estimated for deep areas (>150-300m). Based on bootstrap sampling (n=1000).

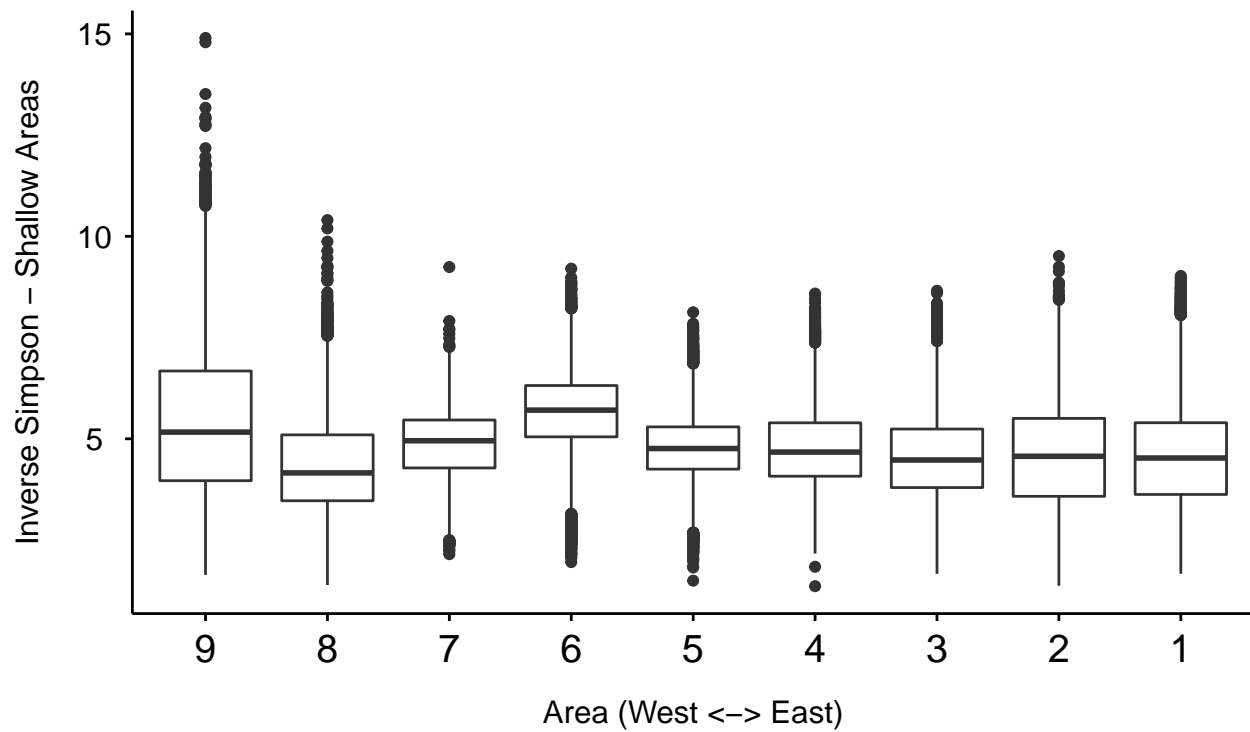


Figure 7: Inverse Simpson's diversity estimated for shallow areas (50-150m). Based on bootstrap sampling (n=1000).

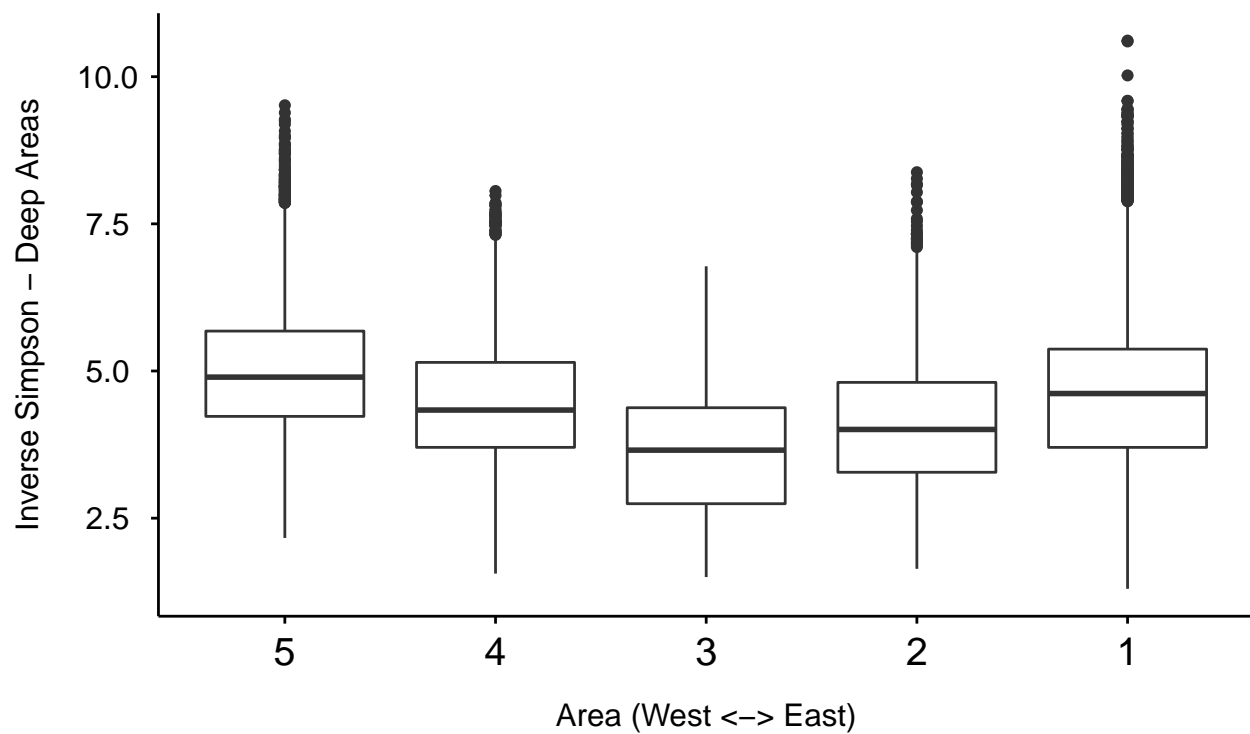


Figure 8: Inverse Simpson's diversity estimated for deep areas (>150-300m). Based on bootstrap sampling (n=1000).

Time series of diversity metrics for 2nd paper?

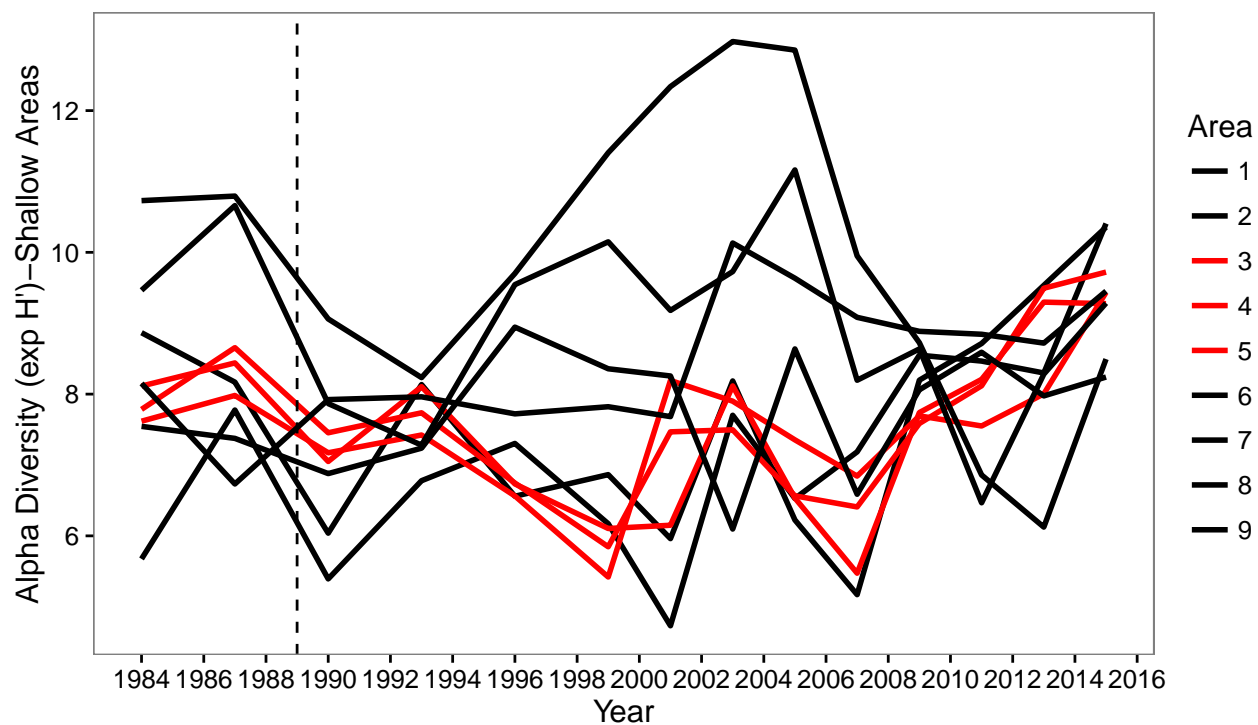
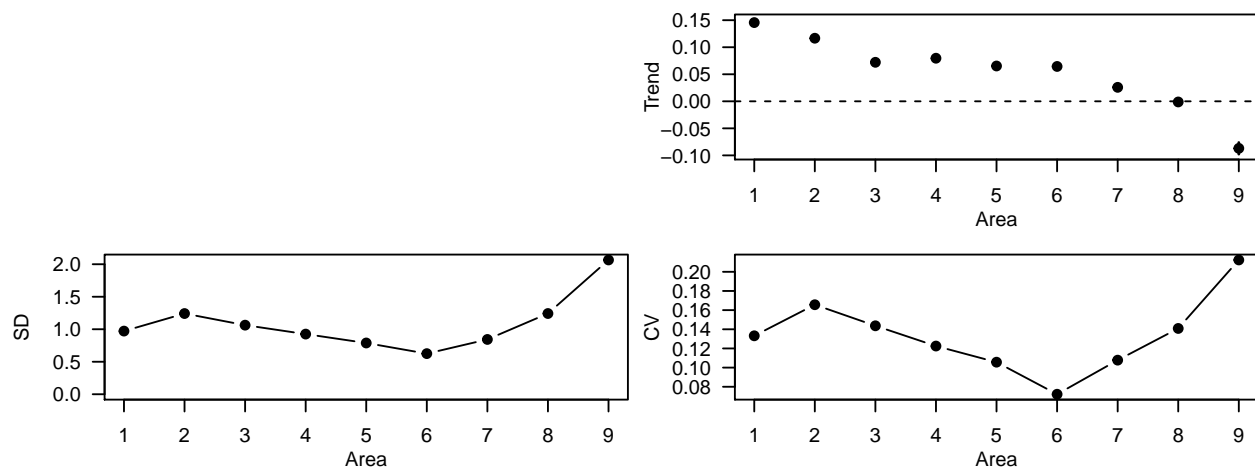


Figure 9: Time series of Alpha diversity for shallow areas (50-150m).

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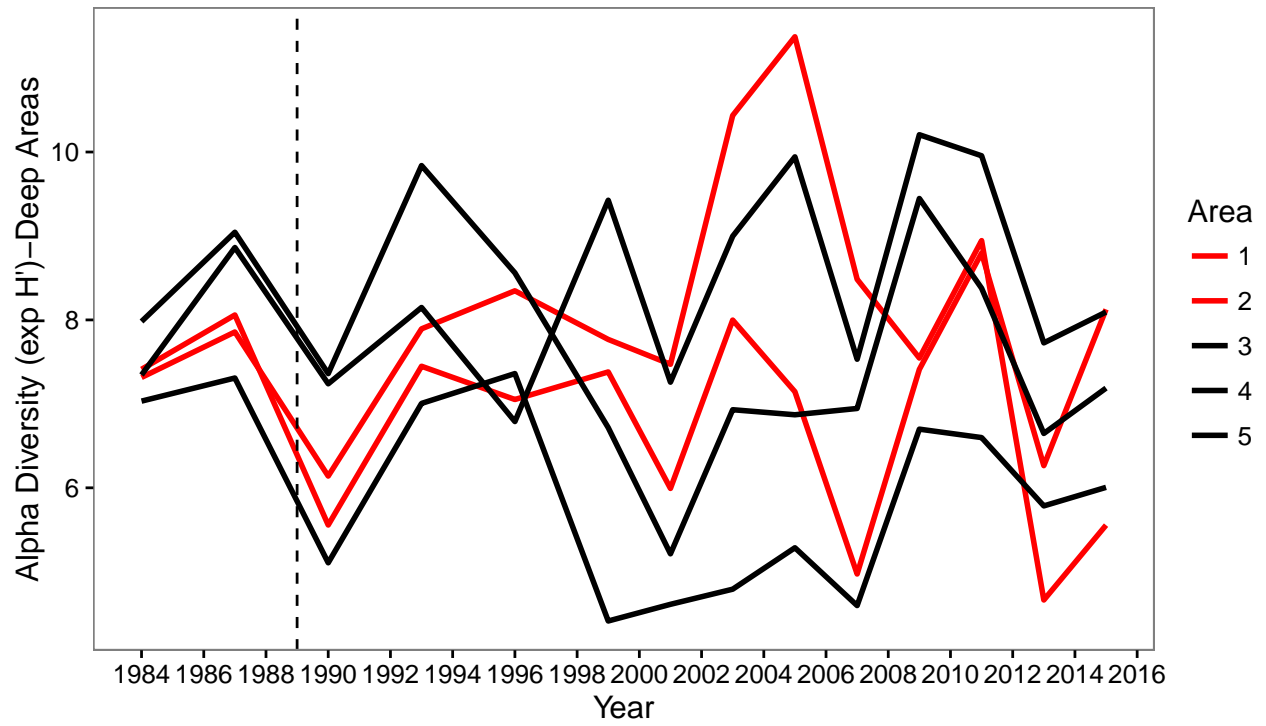
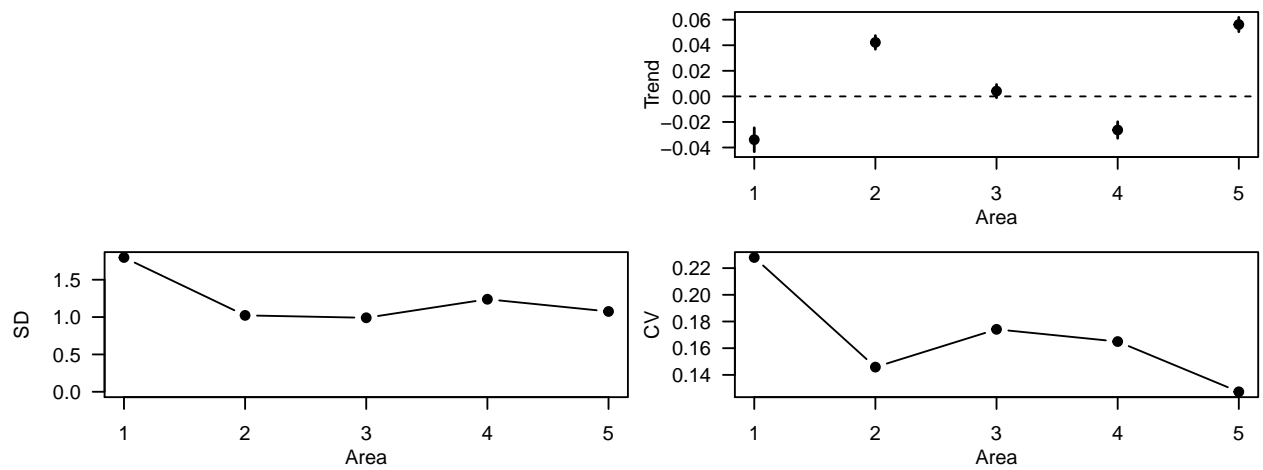


Figure 10: Time series of Alpha diversity for deep areas (>150-300m).



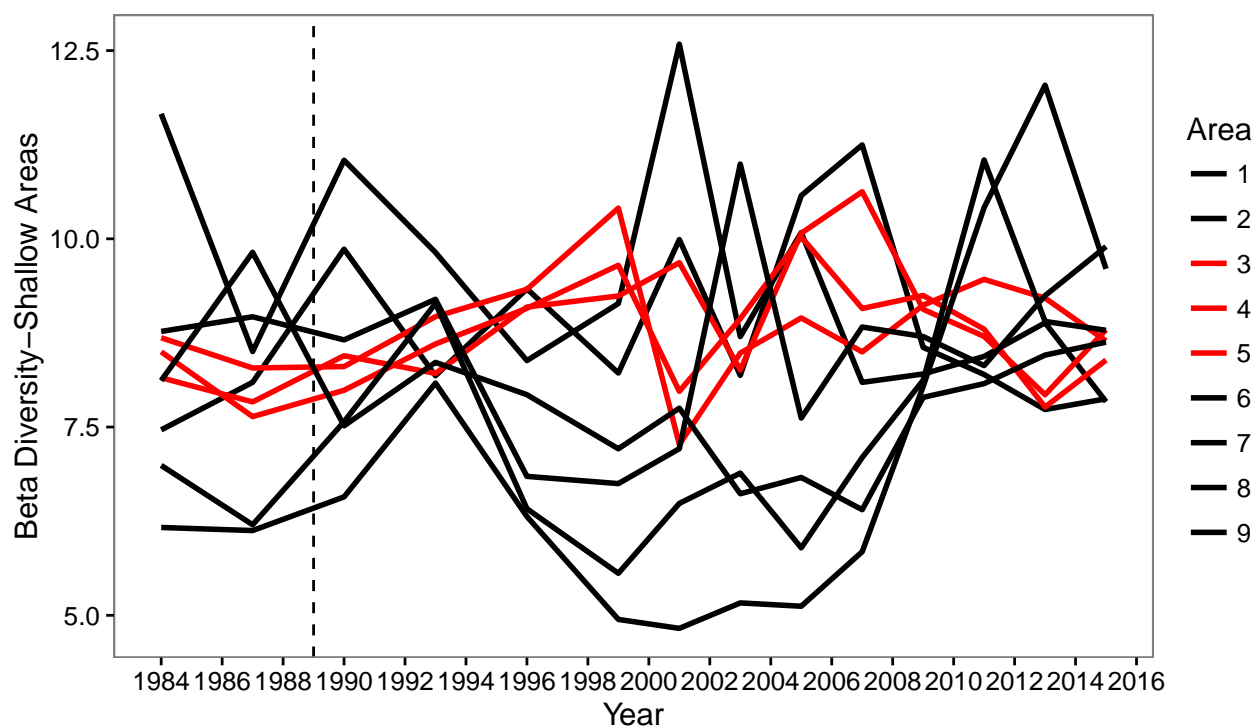


Figure 11: Time series of Beta diversity for shallow areas (50-150m).

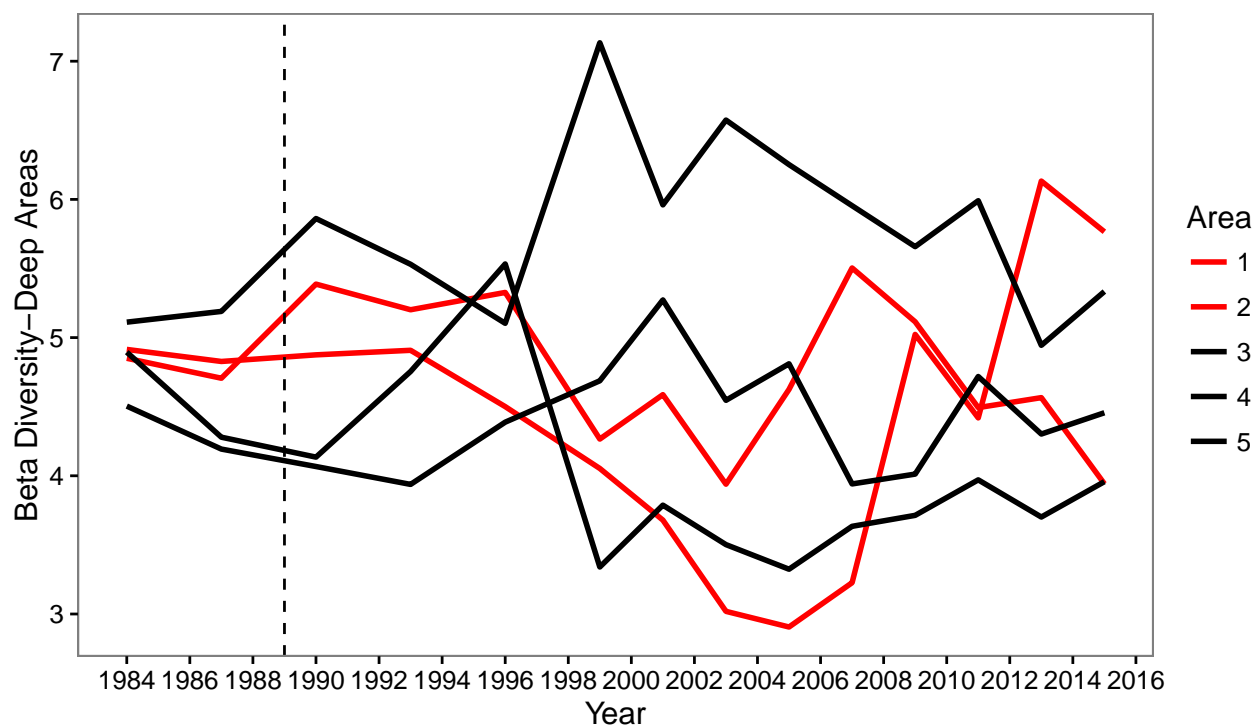


Figure 12: Time series of Beta diversity for deep areas (>150-300m).

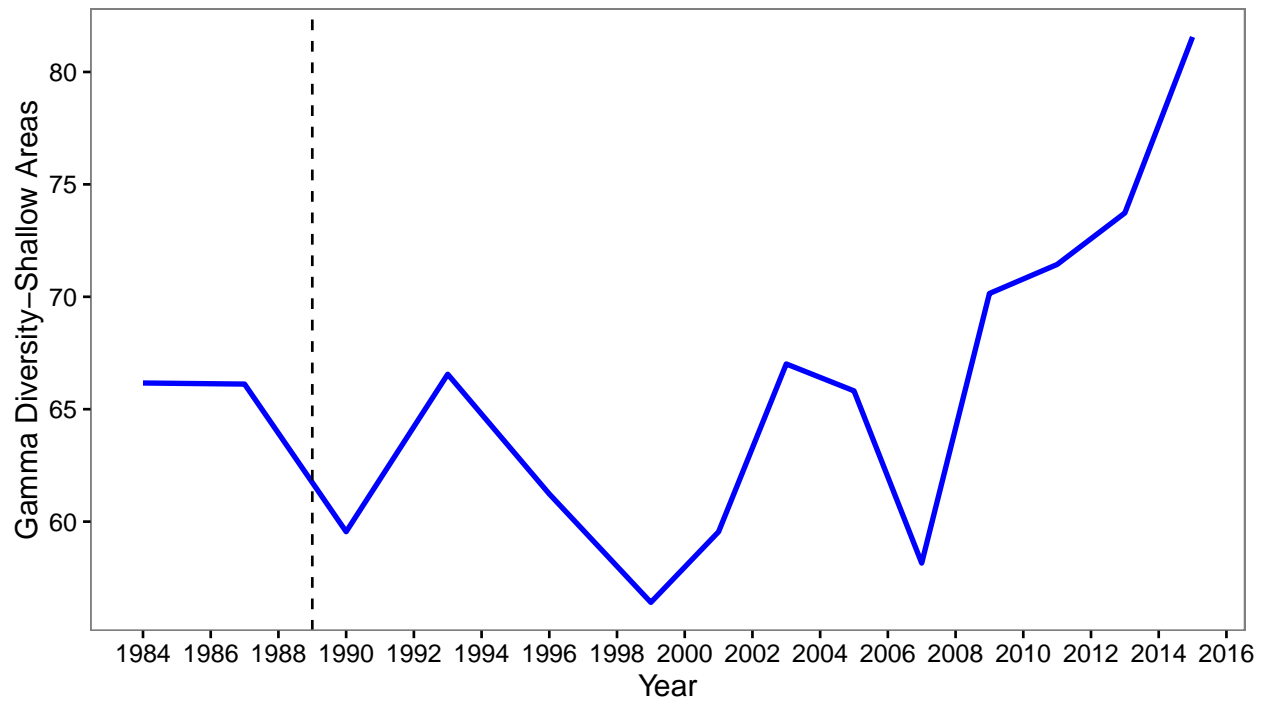


Figure 13: Time series of Gamma diversity for shallow areas (50-150m).

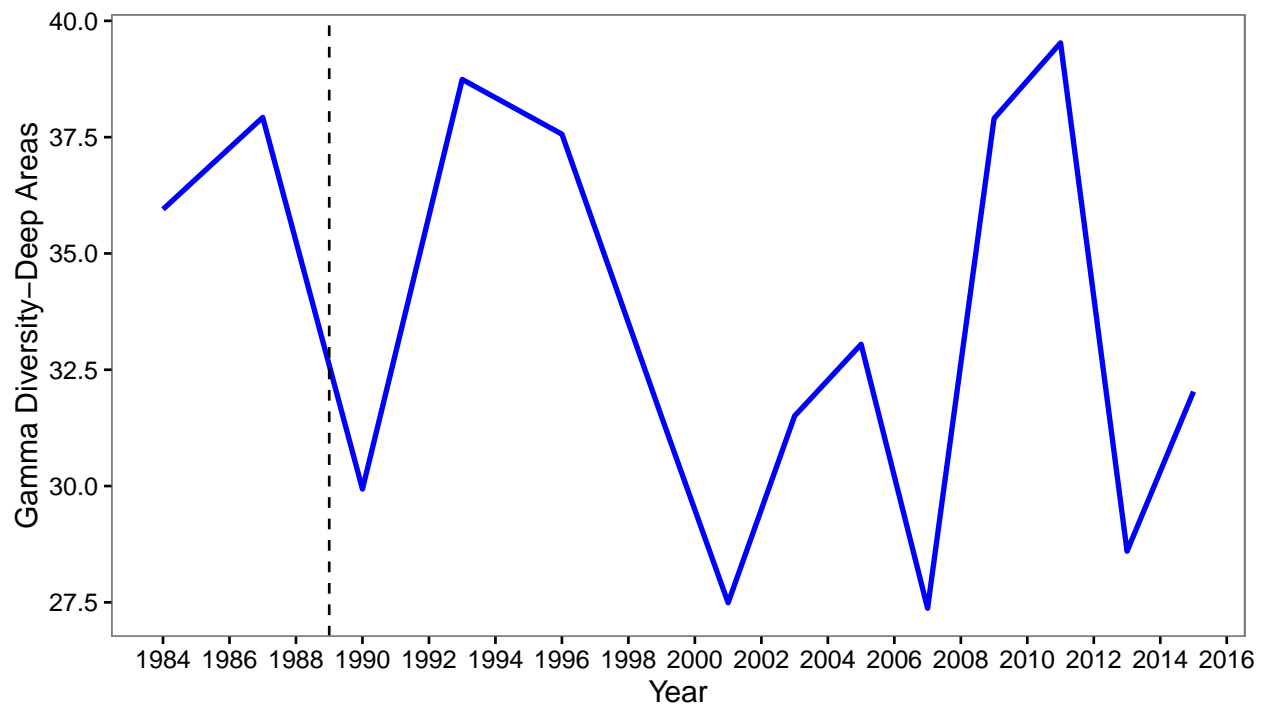
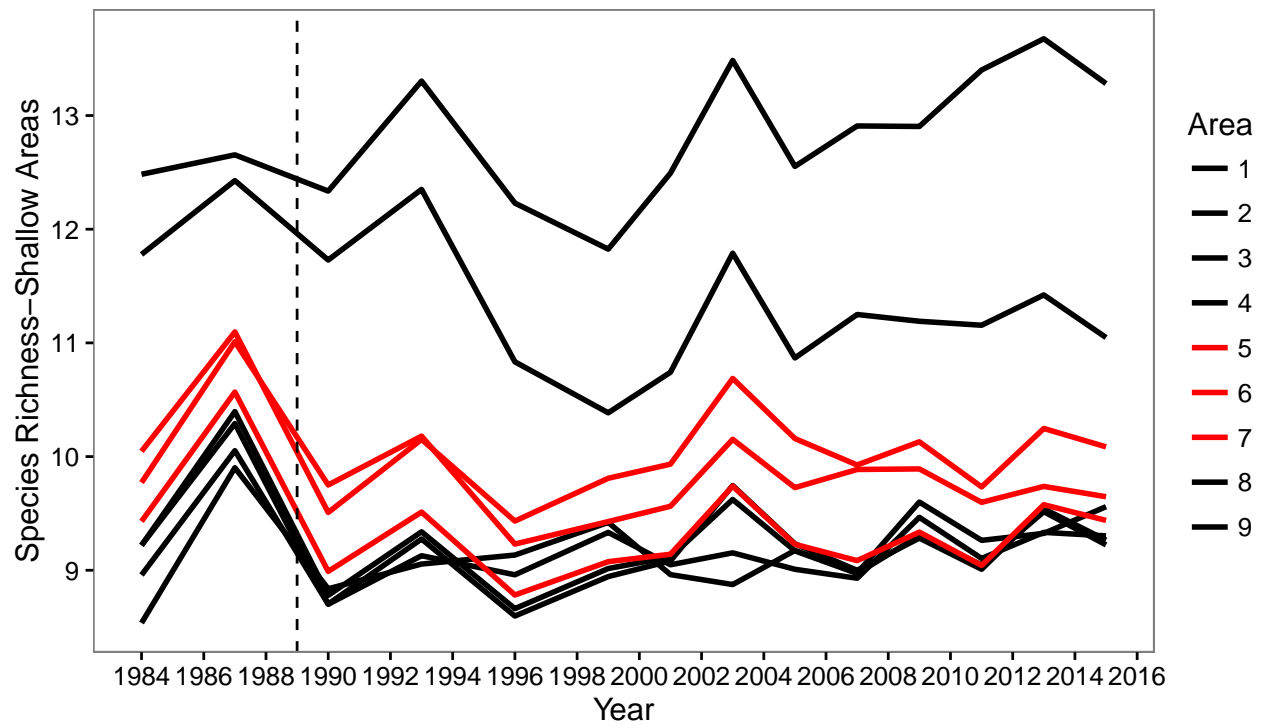
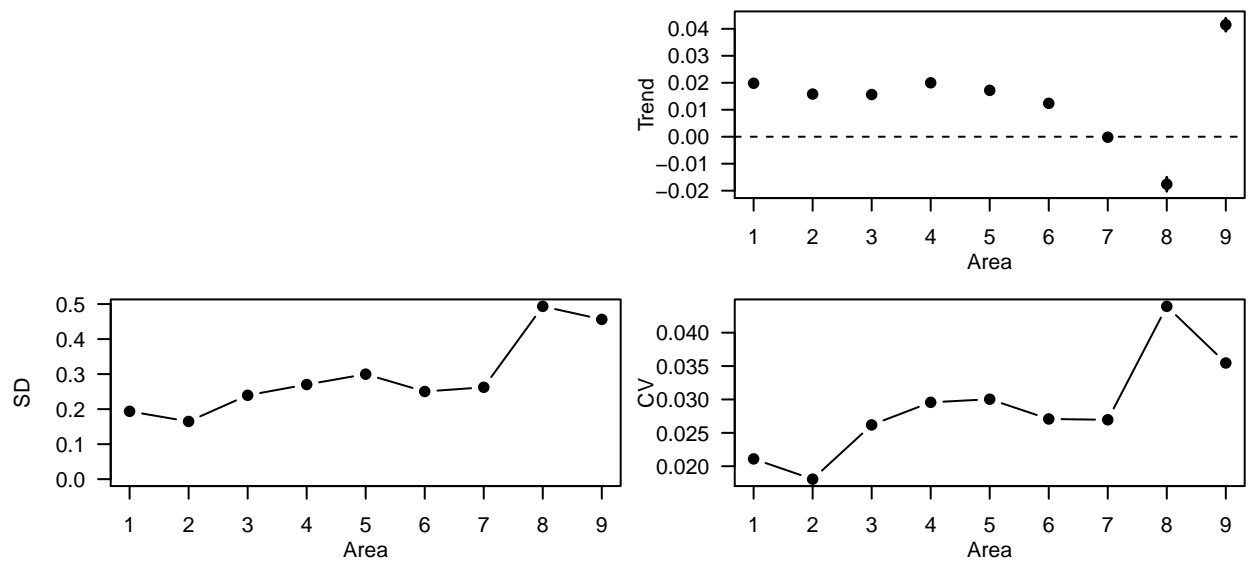
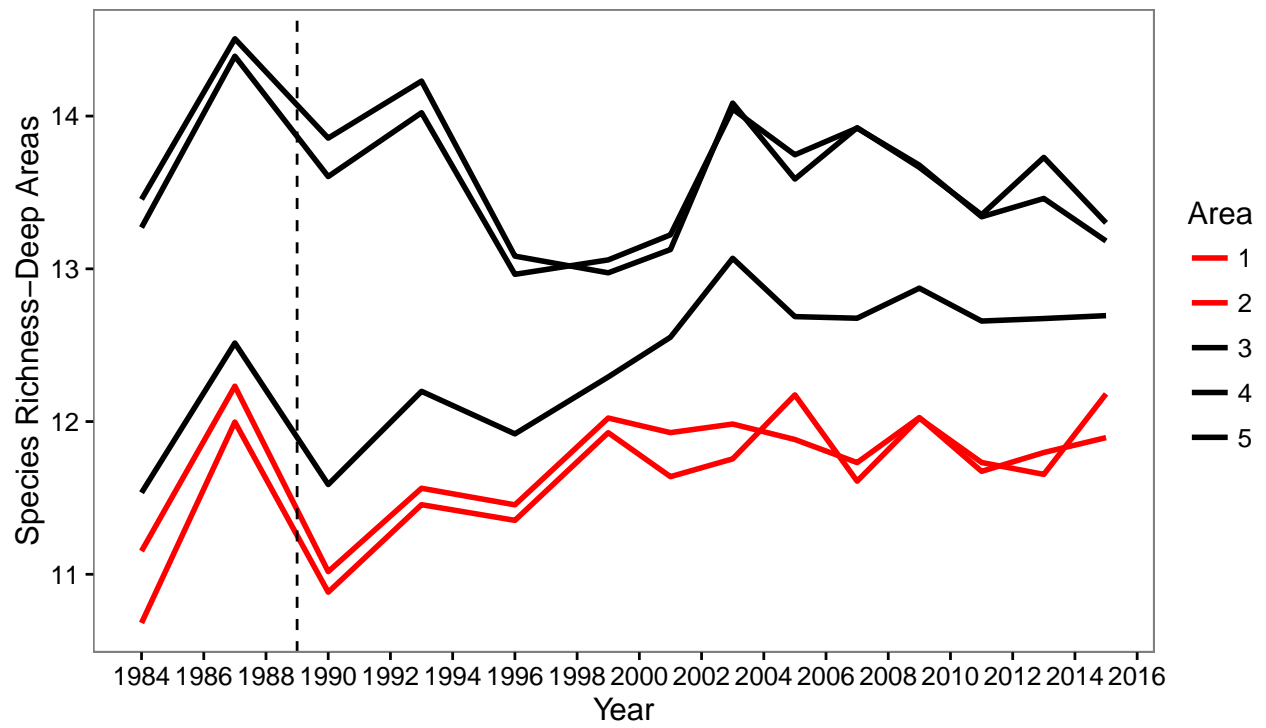


Figure 14: Time series of Gamma diversity for deep areas (>150-300m).

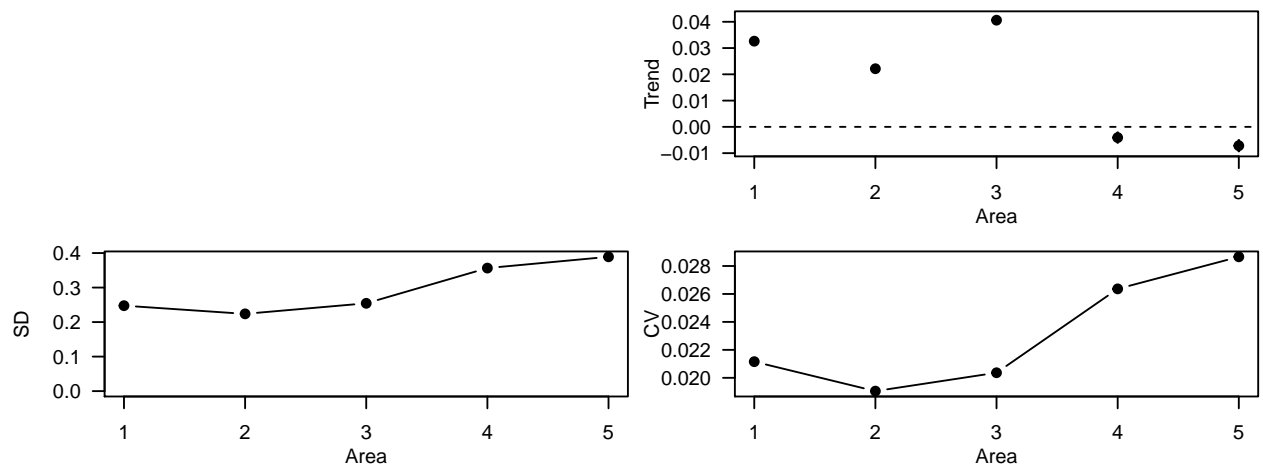


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References

- Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117-123.
- Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236-253.
- Gaichas, S., and R. C. Francis. 2008. Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web. *Canadian Journal of Fisheries and Aquatic Science* 65:1965-1982.
- Gaichas, S. K., K. Y. Aydin, R. C. Francis, and J. Post. 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 68(9):1553-1578.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47(2-4):103-145.
- Hollowed, A. B., S. R. Hare, and Wooster, W. S. . 2001. Pacific basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography* 49:257-282.
- Hollowed, A. B., C. D. Wilson, P. J. Stabeno, and S. A. Salo. 2007. Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). *Fisheries Oceanography* 16(2):142-154.
- Incardona, J. P., and coauthors. 2015. Very low embryonic crude oil exposures cause lasting cardiac defects in salmon and herring. *Scientific Reports* 5:13499.
- Jost, L. 2007. PARTITIONING DIVERSITY INTO INDEPENDENT ALPHA AND BETA COMPONENTS. *Ecology* 88(10):2427-2439.
- Lagerloef, G. 1983. Topographically controlled flow around a deep trough transecting the shelf off Kodiak Island, Alaska. *Journal of Physical Oceanography* 13:139-146.
- Logerwell, E. A., P. J. Stabeno, C. Wilson, and A. B. Hollowed. 2007. The effect of oceanographic variability and interspecific competition on juvenile pollock and capelin distributions of the Gulf of Alaska Shelf. *Deep Sea Research II* 54:2849-2686.
- Ono, K., and coauthors. 2015. Space-time investigation of the effects of fishing on fish populations. *Ecological Applications*.
- Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13(5):257-263.
- Schindler, D. E., and coauthors. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465(7298):609-612.
- Shelton, A. O., J. T. Thorson, E. J. Ward, and B. E. Feist. 2014. Spatial semiparametric models improve estimates of species abundance and distribution. *Canadian Journal of Fisheries and Aquatic Sciences* 71(11):1655-1666.
- Smith, E. P., D. R. Orvos, and J. Cairns Jr. 1993. Impact Assessment Using the Before-After-Control-Impact (BACI) Model: Concerns and Comments. *Canadian Journal of Fisheries and Aquatic Sciences* 50(3):627-637.
- Stachura, M. M., and coauthors. 2014. Linking Northeast Pacific recruitment synchrony to environmental variability. *Fisheries Oceanography* 23(5):389-408.
- von Szalay, P. G., N. W. Raring, F. R. Shaw, M. E. Wilkins, and M. H. Martin. 2010 Data report: 2009 Gulf of Alaska bottom trawl survey. , volume 208. U.S. Dep. Commer. , Seattle, WA.
- Walline, P. D., C. D. Wilson, A. B. Hollowed, and S. C. Stienessen. 2012. Short-term effects of commercial fishing on the distribution and abundance of walleye pollock (*Theragra chalcogramma*). *Canadian Journal of Fisheries and Aquatic Science* 69:354-368.

Wilson, J. B. 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22(1):184-195.