Contributions of species and harvest asynchrony to the stability of regional fishing harvest portfolios in Chesapeake Bay, USA

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## Abstract

Ecological diversity can confer temporal stability to ecosystem processes through asynchrony in species’ abundances, and this ecological asynchrony may also contribute to the asynchrony and stability of dependent human systems like commercial fisheries. However, the linkages between asynchrony in ecological and human systems are not straightforward, as resource extraction intensity need not scale with resource availability. We explored human-ecological relationships in asynchrony using harvest data and fisheries-independent trawl surveys in two regions (Maryland and Virginia) of the Chesapeake Bay, USA from 2002–2018 to identify how seasonal (within-year) asynchrony among targeted fish species contributed to: 1) seasonal asynchrony in the harvests of these species, and 2) the within-year stability and economic value of harvests. In Maryland, seasonal closure of striped bass (*Morone saxatilis*) fishing resulted in asynchrony by forcing the harvest of alternative stocks. In Virginia, the natural emigration of target species from the system was positively associated with harvest asynchrony; however, harvest asynchrony in Virginia declined interannually over the study period, possibly due to coincident declines in the abundances of target species and fishing effort following changes in the marketability of target species. Our findings show that both social (management) and ecological factors influence asynchrony in the harvests of fished populations, which goes onto affect the stability of regional harvest portfolios.

## Introduction

The management of social-ecological systems like commercial fisheries is challenged by their immense complexity that limits the comprehension of the drivers of system dynamics (Levin et al., 2013; Link, 2018) and ultimately their predictability (Boettiger & Hastings, 2013). However, in commercial fishing harvest portfolios, defined as dynamic collections of harvests drawn from multiple species and/or populations within a region (i.e, “stocks”), as well as in the ecosystems those portfolios depend upon, it is interestingly the fostering and conservation of complexity that has long been advocated for as a strategy to reduce variability in aggregate system properties like total harvest yield and revenue (Cline et al., 2017; Hilborn et al., 2001; Schindler et al., 2010) or community biomass production (Tilman, 1996; Tilman et al., 1998). When commercial fishing portfolios or biological communities are composed of diverse species assemblages, the asynchronous dynamics of these “assets” leads to reduced variability (enhanced stability) over time in the aggregate system relative to the average asset, otherwise known as a “portfolio effect” (Anderson et al., 2017; Link, 2018; Schindler et al., 2015). Despite the dependence of commercial fisheries on the population dynamics of the species they target, the relationships between asynchrony among species populations in the environment (species asynchrony) and the asynchrony of harvests drawn from those species (harvest asynchrony) are not well integrated. Clarifying these relationships will shed light on the stabilizing role of biodiversity in social-ecological systems like commercial fisheries.

Understanding how asynchrony in harvest portfolios and the biological communities they depend upon relate to each other benefits from first considering how asynchrony emerges from within these systems. While there are many ways to quantify asynchrony (Doak et al., 1998; Moore et al., 2021; Siple et al., 2020; Thorson et al., 2018), we adopt an approach developed in community ecology where, in the context of a community of species, asynchrony () is quantified as the ratio comparing community stability () to an average across-species stability (), such that (Thibaut & Connolly, 2013; Wang & Loreau, 2016; Zhao et al., 2022). While this approach has only previously been applied in an ecosystem context, we extend its application to fishery harvest portfolios that share similar hierarchical structures to communities, i.e., stocks, analogous to populations, comprise a harvest portfolio, analogous to an ecological community or metapopulation (Link, 2018). In all cases, stability is the inverse temporal variability (i.e., the inverse coefficient of variation = 1/CV) of system properties. In this formulation, cannot be < 1, meaning that stability of the community will almost always be higher than average across-species stability due to asynchrony (Doak et al., 1998; Link, 2018). This measure of asynchrony integrates two related processes whose effects can be partitioned mathematically: statistical averaging and compensation (Fig. 1, Zhao et al., 2022).

Statistical averaging is the enhancement of system stability that occurs when system components fluctuate independently of one another through time, thereby reducing variability of the system in aggregate (Doak et al., 1998; Link, 2018). In the mathematical partitioning of , Zhao et al. (2022) showed that statistical averaging depends on the quantity and evenness of species variances. For example, the contribution of statistical averaging to will be low in a community characterized by few species whose population dynamics are independent and with highly unequal variances. This unevenness in variances is a common feature of communities, which are almost universally skewed in abundances among species (Avolio et al., 2019; Pedersen et al., 2019) and where population variances tend to increase non-linearly with their means (Anderson et al., 2013; Mikkelson et al., 2011). In contrast, compensation effects also contribute to , but increase when species’ dynamics in a community are negatively correlated. In other words, different species may rise to (and fall from) dominance through time in response to, for example, changing conditions in the environment or availability of resources, such that any given ecosystem property is steadily provided by a rotating cast of characters. Compensation effects can occur in ecosystems due to species interactions (Del Río et al., 2017) or due to the differential responses of species to their environments (Brown et al., 2016).

While asynchrony among species dynamics within a community—or among harvest dynamics within a harvest portfolio—will stabilize the aggregate properties of these systems, how asynchrony within a community relates to asynchrony in the harvests derived from that community depends on both ecological and social factors (Moore et al., 2021; Oken et al., 2021). Asynchrony in stock population dynamics can enhance the stability of the fishery portfolios derived from those stocks, as fishing effort can switch among individual stocks as they become more or less productive from year to year (Hilborn et al., 2003; Moore et al., 2021; Nesbitt & Moore, 2016; Oken et al., 2021; Schindler et al., 2010). Similarly, seasonal (within-year) compensatory dynamics among stocks extend fishing seasons as harvestable biomass remains accessible to fishers for longer (Nesbitt & Moore, 2016; Schindler et al., 2010). However, the stability imparted to the fishery portfolio by stock population asynchrony is mediated by fisher behaviors in response to regulatory and economic factors. For example, if the harvest of a particular stock is limited due to management regulations (e.g., an inability to attain licenses to target a particular stock or seasonal closures), if fishers are specialized in the harvest of a particular stock, or if diversifying across stocks is cost prohibitive or not profitable (Kasperski & Holland, 2013; Sethi et al., 2014), stability may arise not from inherent asynchrony in the population dynamics of targeted stocks, but rather from societal changes in how fishing effort is distributed across stocks. We note that these processes are not mutually exclusive, and in fact may operate in tandem to further impact fisheries stability.

In this study, we tested the hypothesis that within-year asynchrony in commercial fishing harvest portfolios is driven by within-year asynchrony among the species comprising the harvest portfolio. To accomplish this, we partitioned asynchrony into compensatory and statistical averaging effects among species and then among harvests. We predicted that seasonal compensation in population dynamics would be positively associated with the seasonal compensation of harvests. We then extended this analysis to test the hypothesis that within-year harvest asynchrony increased within-year fishery economic stability and the overall value of the harvest portfolio.

We explored these hypotheses within communities of demersal finfish and the associated commercial fisheries in the mainstem of Chesapeake Bay, USA (Fig. 2). The Chesapeake Bay (hereafter, ‘the Bay’) is among the largest and most economically and ecologically valuable estuaries in the world and supports numerous economically and culturally valuable fisheries (Sanchirico et al., 2008). Like many other temperate estuaries, fishes in the Bay are transient and migrate into and out of the estuary seasonally (Buchheister et al., 2013; Schonfeld et al., 2022). The fish community in the Bay is also heavily structured by salinity, with distinct communities dominating more saline waters near the mouth versus those in the comparably fresher headwaters (Lefcheck et al., 2014), and commercial fisheries operating in these regions fall under different management regimes, although several species within the portfolio of stocks are collectively overseen by a regional authority. The relatively low estuarine diversity, naturally asynchronous dynamics among harvested species through time, and well-documented regulatory structuring along a prominent spatial environmental gradient make the Chesapeake Bay an ideal test case for evaluating how asynchrony among populations of exploited species relates to asynchrony in dependent fisheries.

## Methods

### Methods overview

To test the hypotheses that within-year species asynchrony among targeted fishes in Chesapeake Bay led to within-year harvest asynchrony and harvest portfolio yield, stability, and economic value, we first developed monthly time series of species-specific total biomass estimates (“biomass indices”) for six species of finfish commonly targeted by commercial fishing in the Maryland and Virginia regions of the Bay mainstem (Fig. 2). We used these indices to calculate within-year species asynchrony and its components—species compensation and species statistical averaging effects—within both regions.

We then used the total monthly harvests of these six species from the mainstem of the Bay in Maryland and Virginia to calculate harvest asynchrony and its components—harvest compensation and harvest statistical averaging effects. Next, we related seasonal species compensation and statistical averaging effects to seasonal harvest compensation and statistical averaging effects using structural equation models (SEMs). We predicted that harvest and species compensation would be positively associated given strong seasonal patterns in fish abundances in the Bay and the expectation that seasonal harvests from these species would correlate with their seasonal abundances. In Maryland, the striped bass (*Morone saxatilis*) fishery is closed for part of the year, so we expected that harvest diversification outside of striped bass during this closure would increase harvest asynchrony.

Lastly, we summed harvest yields and harvest values across species within-years to create monthly indices of portfolio harvests and value. We used these indices to calculate annual harvest yield and value stability, as well as total annual harvest yields and value. We extended the SEMs from the previous analysis to evaluate the indirect linkages between species asynchrony (partitioned as species compensation and statistical averaging effects) and harvest portfolio yield, stability, and economic value. We identified that commercial fishing effort declined over the study period, and so we related an index of overall fishing effort to harvest asynchrony in SEMs.

### Fish community dynamics and commercial fishing in the Bay

In the northern mainstem of the Chesapeake Bay (blue region in Fig. 2), fisheries management falls under the jurisdiction of the US state of Maryland (MD; via the Maryland Department of Natural Resources [MD-DNR]), and long-term average salinities within this region vary from fresh to mesohaline with proximity to freshwater inputs to the north and west (Harding et al., 2019). Demersal fish biomass in MD waters is dominated by anadromous white perch (*Morone americana*) and striped bass (*Morone saxatilis*), especially in spring prior to moving into Bay tributaries to spawn and in autumn when these fishes aggregate in deeper waters (Buchheister et al., 2013). In the mainstem alone, commercial striped bass harvests in 2002–2018 were valued at $3.1 million USD per year (annual average), making them the most valuable finfish harvested in this region, and white perch $276,000 USD per year, the third most valuable species (this study; data from MD-DNR). In the MD waters of Chesapeake Bay, commercial striped bass harvests are prohibited during the spring spawning season (March–May).

In the southern mainstem of the Bay (orange region in Fig. 2), fisheries management falls to the Commonwealth of Virginia (VA; via the Virginia Marine Resources Commission [VMRC]). Salinities in this region increase to euhaline at the interface of the Bay and Atlantic Ocean, and demersal fish biomass is frequently dominated by species that seasonally migrate onto the adjacent continental shelf to spawn (Buchheister et al., 2013). These species include the major fishery targets Atlantic croaker (*Micropogonis undulatus*) and spot (*Leiostomus xanthurus*), whose biomasses tend to peak in the spring and summer following the migration and recruitment of adults and young-of-the-year fish into the Bay from the continental shelf, as well as the ontogenic movement of juveniles from shallow Bay nurseries to the Bay mainstem (Buchheister et al., 2013). In the VA mainstem, the three most valuable commercial finfish fisheries include Atlantic croaker (average harvest value in 2002–2018 was $2.2 million USD/year), striped bass ($1.55 million USD/year), and spot ($1.24 million USD/year) (this study; data from VMRC). Regulations in the Bay prevent commercial harvest of Atlantic croaker prior to January 15 of each calendar year, striped bass prior to January 16, and spot prior to April 15 or after December 8. Given the unique regulatory, environmental, and ecological characteristics of the northern (MD) and southern (VA) regions of the Bay, we considered the ecosystems and fisheries in these regions to be distinct and analyzed them separately.

### Bottom-trawl survey and commercial harvest data

In order to characterize demersal finfish population dynamics, we derived within-year biomass indices from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) bottom trawl survey (Latour et al., 2003). During 2002–2018, ChesMMAP cruises usually surveyed the entire Bay mainstem five times annually (targeting March, May, July, September, and November), sampling 300–400 locations per year. However, surveys in some month-year combinations did not occur, and in others sample coverage was relatively sparse (detailed below). The survey followed a stratified random design within three depth ranges (3.0–9.1 m, 9.1–15.2 m, and >15.2 m) (Buchheister et al., 2013).

We estimated biomass indices for demersal finfishes that were both well-sampled by the bottom trawl survey (see Buchheister et al., 2013) and for whose cumulative commercial harvests made up >90% of total harvest yield over the study period. In MD, these species included Atlantic croaker, striped bass, white perch, gizzard shad (*Dorosoma cepedianum*), and channel catfish (*Ictalurus punctatus*). While gizzard shad and channel catfish were only found in ~5% and ~2% of ChesMMAP trawls, respectively, these species are considered well-sampled in the Bay mainstem by the bottom trawl (Buchheister et al. 2013). After excluding blue crabs and Atlantic menhaden (a pelagic species poorly-sampled by the bottom trawl [Bucheister et al., 2013]), the combined harvests of these five species contributed to ~94% of total harvests in the MD mainstem over the study period. In VA, these species included Atlantic croaker, spot, and striped bass. We selected these species because their combined harvests accounted for ~93% of total harvests over the study period after excluding blue crab and Atlantic menhaden.

We evaluated commercial harvest dynamics for these species in the regions of MD and VA that overlapped with ChesMMAP surveys using monthly harvest yield and value data provided by MD-DNR and VMRC (Fig. 3). We also received data on fishing effort in the form of the number of trips per month that fishers encountered each species in both MD and VA. We created a combined index of trips across species within each region defined as the mean number of trips across species annually. To understand how the closure of the striped bass fishery impacted the stability and value of the portfolio, we created an index called the seasonal harvest ratio (SHR). The SHR was the ratio of the average monthly harvests occurring during the striped bass fishery closure to the average monthly harvests occurring outside the striped bass fishery closure. When the SHR was high, harvests of species other than striped bass were compensating for the absence of striped bass harvests during the closure.

### Biomass index modeling

We used generalized additive mixed models (GAMMs) to develop within-year biomass indices for these species in MD and VA waters to compare with harvests in these regions. The GAMMs included penalized smooth terms and spatial and spatiotemporal Gaussian Markov random fields. We modeled biomass indices with Tweedie observation error and a log link (Tweedie, 1984). All models included categorical predictors corresponding to each of five target sampling months for the ChesMMAP survey. We allowed for interannual variability in month-year predictions by including factor-smooth interactions (bs = “fs” in the R package *mgcv* [S. N. Wood, 2006]) for numeric month by year; treating month as numeric because surveys sometimes occurred in months adjacent to the “target” month. For the spot biomass model, we included a thin-plate regression smoother for the numeric year-month combination (Wood, 2006), and for the gizzard shad and channel catfish models, we included categorical predictors for year factors. These changes improved convergence and residual behavior for these models.

There were four instances where cruises did not occur in 2002–2018 (out of 85 possible; 4.7%). In fitting each model, we also excluded trawls collected from regions where a given species was not found throughout all surveys (Commander et al., 2022). This reduced the number of observations available for fitting these models, especially for anadromous fishes whose distributions were limited to the northern mainstem. However, the inclusion of smooth terms allowed us to interpolate reasonable biomass estimates representing typical seasonal densities for each species during these periods and for when there were relatively few observations (e.g., in 3 of 85 month-year combinations, there were fewer than 30 trawls available for fitting the white perch model). To calculate area-weighted biomass indices, we predicted from each model over a grid with 6.25 sq. km cells derived from the boundary of the ChesMMAP survey (Fig. 2) and summed these predictions within months. The model for species besides spot, gizzard shad, and channel catfish can be represented as

(1)

where represents the mean at location *s* and time *t*, an overall mean for each target month, the numeric month-year factor-smooth interaction with common wiggliness, a spatial random field value (varies by space but is constant with time), and a spatiotemporal random field value that is independent each year. The Gaussian random fields were approximated as Gaussian Markov random fields using the Stochastic Partial Differential Equation (SPDE) approach (Lindgren et al., 2011) with covariance matrices and , each constrained by a Matérn covariance function (Cressie & Huang, 1999). We fitted these models in R using the package *sdmTMB* (Anderson et al., 2022) via maximum marginal likelihood (see S1 and associated R scripts for further details).

### Partitioning stability and asynchrony and hypothesis testing

We applied the stability and asynchrony partitioning framework developed by Thibault & Connolly (2013; who considered the related quantities of variability and synchrony) that is commonly used in ecological contexts (Lamy et al., 2019; Wang et al., 2019) to both the communities of species being targeted by commercial fisheries in the Bay and to the harvest portfolios in MD and VA. When applied to the fishery harvest portfolio, the stability of intra-annual portfolio harvests is , or the inverse of total harvest variability, given by

. (2)

Here, is the temporal standard deviation of total harvests and the temporal mean of total harvests in a region *R*. is equivalent to the product of harvest asynchrony () and species stability (), the latter term being given by

, (3)

where is the temporal coefficient of variation of harvests of species i, and is weighted by species harvest contributions to . Stated plainly, is the inverse of weighted average harvest variability (Zhao et al., 2022). We calculated twice: once corresponding to the 5 months for which biomass estimates were available (, and again for all 12 months of the year . We similarly calculated the stability of portfolio value by calculating the inverse temporal variability of summed harvest values (all months included).

We next partitioned species asynchrony and harvest asynchrony into compensation () and statistical averaging effects () (Zhao et al., 2022). Continuing in the context of the commercial harvest portfolio, harvest asynchrony is given by = . Zhao et al. (2022) showed that

, (4)

where the is the ratio comparing the portfolio harvest stability if all species harvests were uncorrelated and independent to the portfolio harvest stability if species harvests were perfectly synchronous. is then

(5)

Zhao et al. (2022) noted that the is equivalent to the inverse of the square-rooted variance ratio (Schluter, 1984), a commonly used measure of synchrony/asynchrony in the ecological literature. indicates greater portfolio harvest stability than what would be expected if species harvests fluctuated independently of one another. We partitioned identically to (Table 1).

We used piecewise structural equation models (SEMs) to relate asynchrony and stability indices across ecosystem and fishery systems (Lefcheck, 2016). Within each SEM, we evaluated sub-models for residual independence, normality, and homogeneity of variances. When residual autocorrelation was present, we modeled residual error as an AR(1) process using generalized least squares (Pinheiro et al., 2017). All stability and asynchrony indices were log-transformed prior to fitting models relating these indices across systems given their multiplicative relationships within-systems. To provide context to these results, we used linear models to model interannual trends in population and harvest dynamics and generalized least squares models with varying error structures to account for residual autocorrelation when evident.

## Results

### Relationships between the components of species and harvest asynchrony

Across Chesapeake Bay, we found that harvest compensation was an important driver of harvest asynchrony and the stability of fisheries yields. However, the drivers of harvest asynchrony differed geographically. In MD (Fig. 5, MD SEM 1), harvest compensation was positively associated with the seasonal harvest ratio (SHR) —or the degree to which species other than striped bass dominated the fishery during closed season. This result therefore represents the diversification of harvests (at the regional scale) during the annual striped bass fishery closure that compensates for the engineered loss of harvestable biomass of this fish (Fig. 6). In contrast, there were no relationships between compensation and statistical averaging in the MD community and fishery portfolio, indicating that seasonal asynchrony among populations of target species was not responsible for enhancing the portfolio effect in this state. Ultimately, then, asynchrony in MD fisheries harvests was found to be largely promoted by fisher behaviors occurring in response to management strategies, rather than natural fluctuations among exploited species here.

During the study period in VA, the total annual biomass of all three dominant species (Atlantic croaker, spot, and striped bass) declined significantly in the lower mainstem of the Bay (Table S2, Fig. 7). However, these biomass declines were not equivalent in magnitude: Atlantic croaker saw the largest declines overall (linear trend = -1.14x 106 kg year-1, *P* < 0.001), followed by spot (-1.69 x 105 kg year-1, *P* = 0.002) and lastly striped bass (-3.69 x 104 kg year-1, *P* = 0.03). After the substantial loss of Atlantic croaker biomass, the variabilities of species biomasses became more evenly distributed, thereby increasing the species statistical averaging effect over the study period (Fig. 8a). Increases in the species statistical averaging effect due to increased evenness of biomass variabilities among species were then positively associated with species compensation (*P* = 0.001, Fig. 5, VA SEM 1). In other words, following the steep declines in Atlantic croaker biomass, species population dynamics became more seasonally compensatory and therefore asynchronous (Fig. 8b), albeit with substantially lower biomass overall.

While species statistical averaging and compensation increased in the VA fish community over the study period, harvest compensation effects showed a weak negative trend (*P* = 0.079, Fig. 8d, Table S3), and harvest compensation was most strongly associated with species statistical averaging (, *P* = 0.017, Fig. 5, VA SEM 1). This suggests that declines in target species biomass in the Bay (leading to greater evenness of variabilities and increased species statistical averaging) were associated with shifts in the timing of harvests that resulted in a decline of harvest compensation. We identified timing shifts in the harvests of Atlantic croaker and striped bass, whose harvests predominately shifted to later and earlier the year, respectively (both *P* < 0.001, Fig. 9, Table S4). This meant that the timing of Atlantic croaker harvests became more similar to the timing of spot harvests, whereas striped bass harvests became more dominated by harvests in the spring months. In addition to species statistical averaging being associated with declines in harvest compensation, we also found a strong negative relationship between species statistical averaging and the average number of fishing trips across species (*P* < 0.001, VA SEM 1, Fig. 5), which declined throughout the 2002-2018 period across stocks (Fig. 10a).

We found that harvest compensation was positively associated with species compensation (, *P* = 0.04, Fig. 5, VA SEM 1), suggesting that seasonal compensatory dynamics in population biomasses drove seasonal harvest compensation. However, the magnitude of the standardized partial effect of species statistical averaging on harvest compensation was greater than that of species compensation on harvest compensation and opposite in sign ( vs ). This result means that the stabilizing effects of seasonal species dynamics on harvest compensation were overwhelmed by the decline of target species biomasses and the homogenizing of their within-year variabilities (i.e., high species statistical averaging) that was associated with more temporally synchronous harvests (Fig. 8d, 9).

### Portfolio harvest stability and economic performance

We find that portfolio harvest stability was enhanced by harvest asynchrony, which the previously discussed results show was driven by fisher behavioral responses to the striped bass closure (MD) and to the relative biomasses and variabilities of fish populations as they naturally migrate into and out of the Bay mainstem seasonally (VA). Using two additional SEMs, we expanded this analysis to evaluate how portfolio harvest stability associated with portfolio value stability and overall value.

In MD (Fig. 5, MD SEM 2), we found that portfolio harvest stability quantified at the same temporal resolution as the population biomass indices (i.e., SPortfolio, S) was positively associated with portfolio harvest stability quantified using all months of harvest data (SPortfolio, L). We quantified harvest stability at both resolutions because biomass indices were only resolved at the five-month timescale, whereas fishing harvest data were available for all 12 months. This finding shows that harvest asynchrony induced by target diversification in response to the striped bass fishery closures (Fig. 6) was positively linked to the within-year harvest stability of the portfolio. However, portfolio harvest stability was not linked to the economic stability of harvests. In other words, active switching by fishers buffered the stability of the regional portfolio against regulatory measures, in the form of the seasonal closure, but that this stabilizing effect did not translate to enhanced economic stability. Lastly, we identified a strong positive relationship between total yield and total value (P < 0.001), showing that years with greater harvests were associated with greater portfolio value (Fig. 5, MD SEM 2).

In VA (Fig. 5, VA SEM 2), where we also identified a positive link between portfolio harvest stability at the 5-month and 12-month temporal resolutions, portfolio harvest stability (SPortfolio, L) declined substantially over the study period (Fig. 11, Table S5, P < 0.001) in response to diminished harvest compensation (Figs. 8b) and species harvest stability, the latter of which was associated with fishing effort (Fig. 10). In other words, the loss of harvestable biomass, primarily of Atlantic croaker, was associated with more temporally synchronous harvests, and this coincided with decreasing fishing effort that drove more temporally variable and lower harvests within-years. Both factors contributed to interannual declines in harvest portfolio stability overall. Portfolio harvest stability was positively associated with the stability of portfolio value, as well as total harvest yield (Fig. 5, VA SEM 2).

## Discussion

Asynchronous population dynamics among species targeted by fisheries can promote stability in the harvests of those species over time (e.g., Moore et al. 2021), but the links between population and harvest asynchrony are not straightforward. We approached this problem by analyzing 17 years of data from fisheries-independent surveys (i.e., community data) and fisheries landings across one of the largest and most economically valuable estuaries in the world, the Chesapeake Bay. We found that asynchrony in Chesapeake Bay fish harvests within a given year emerged from two sources: fisher-behavior responses to management strategies (i.e., the closure of the striped bass fishery in Maryland), and from the components of asynchrony among fish species that emerged due to seasonal population dynamics (compensation) and the unevenness of population variabilities (statistical averaging effects). However, while species compensation was a positive contributor to harvest compensation, these effects were counteracted by the negative effect of species statistical averaging on harvest compensation, which reflected a decline in overall biomass availability and increased evenness of variabilities in the ecosystem. In Virginia, we also found that the stability of the harvest portfolio was positively associated with the stability of the value of the harvest portfolio. These findings demonstrate that conserving asynchronously fluctuating exploited natural resources can enhance the within-year stability of their associated harvest portfolios and their value, but that these stabilizing effects can be overwhelmed by the relative availability and variability of targets in the environment, human behavior, and management regulations.

Our application of this framework to a coupled social-ecological system is highly relevant, as it more fully considers the mechanisms through which asynchrony among species in a biological community contributes to stability while the system is simultaneously being both exploited and actively managed. Several authors have explored similar relationships between community dynamics and harvest asynchrony (Moore et al., 2021; Nesbitt & Moore, 2016; Schindler et al., 2010), but have not treated the populations targeted by fisheries and their associated harvests as hierarchically structured portfolios that are linked by asynchrony. By conceptualizing these systems separately, we were able to identify the specific components of asynchrony that contributed to or diminished the stability of associated fishery harvest portfolios.

Cross-system asynchrony relationships were limited in MD, where harvest asynchrony was strongly related to the adaptive response of fishers to management strategies limiting access to the valuable striped bass fishery. During the closure, fishers targeted species like Atlantic croaker, white perch, and gizzard shad. In this sense, the striped bass closure ultimately enhanced the stability of the regional harvest portfolio that became more diversified as a result, although this stabilizing effect did not translate to stability of the value of the harvest portfolio, possibly due to the lower value of species being targeted during the striped bass closure compared to striped bass.

Portfolio harvest stability in VA waters declined over the study period, and this decline was related to ecological and social factors impacting species and harvest asynchrony and species harvest stability. First, through the declines in the biomass of Atlantic croaker and spot in the lower Bay (also documented in Buchheister et al., 2013; Schonfeld et al., 2022), a relationship that was captured in VA SEM 1 (Fig. 5) through the effect of species statistical averaging on harvest compensation. When species biomasses were most uneven (high biomass availability), their harvests tended to be more seasonally compensatory, contributing to the stability of the harvest portfolio overall. However, as population variabilities became more even (low biomass availability), species harvests became more synchronous, and this contributed to declining harvest stability interannually.

The mechanisms through which biomass declines impacted the timing of harvests, and therefore harvest compensation, could be both biological and behavioral in nature. For one, a decline in the abundance of Atlantic croaker during the spring and summer months could have contributed to smaller harvests during those months, resulting in a larger proportion of harvests occurring later in the year. However, biomass declines occurred concurrently with declines in fishing effort, signaling that changes in fishing behavior may have also been important. For instance, during periods of low Atlantic croaker abundance, the fish that were present in the Bay tended to be smaller-bodied overall (Bonzek et al., 2019). These smaller-bodied fish may have been less marketable, and therefore fishers would be expending less effort targeting them. In addition, during periods of high Atlantic croaker abundance, there were periods when the “market simply was not buying”, serving as another likely contributor to effort declines (L. Gillingham, VMRC, pers. comm., 2024). These market-driven factors may have resulted in declines in fishing effort during the spring and summer months, ultimately pushing the timing of Atlantic croaker harvests to later in the year and leading to reduced harvest compensation.

We incorporated the effect of declining effort into our analysis by relating effort declines to species harvest stability, finding that declining effort was associated with reduced stability. As noted previously, these effort declines may have originated from declines in Atlantic croaker abundance and body sizes, as well as from market dynamics during periods of high abundance. Given that Atlantic croaker and spot are for the most part harvested concurrently in the Bay (barring some seasonal exceptions for when these species are targeted individually) (R. J. Latour, pers. obs., 2023), declines in effort directed at Atlantic croaker could explain the declines seen in spot effort. In addition, declining effort may be attributable to declines in finfish fishery participation in Virginia waters that are associated with the changing demographics of the fleet, as evidenced by a decline in the number of younger participants in the fishery (White & Scheld, 2021). In response to these factors, fishery participants may be tempted to switch to other fisheries and marine-related industries that may be more profitable and with greater promise of future reliability in harvest, including but not limited to the growing aquaculture industry, as well as fisheries for blue crabs (*Callinectes sapidus*) and hard clams (*Mercenaria mercenaria*) (White & Scheld, 2021).

Like many fishes inhabiting temperate ecosystems, the life histories of Atlantic croaker, spot, and striped bass involve a seasonal migratory phase wherein fishes seasonally move into and out of inshore habitats from the continental shelf (Buchheister et al., 2013; Murdy & Musick, 2013). Importantly, the peak abundances of these species in VA waters are typically seasonally compensatory, implying that their harvest dynamics may also be seasonally compensatory, and that this compensation would stabilize the harvest portfolio. We found evidence for this effect, although the positive contribution of seasonal species compensation to harvest asynchrony was overwhelmed by the negative effect of species statistical averaging as discussed previously. This finding suggests that seasonal species compensation was and is not effective in stabilizing within-year harvests in the face of fewer fish in the Bay year over year. Such biomass declines among fished species may challenge the capacity for Bay fishers to diversify among finfish species, since these fisheries have historically operated inshore (Kirkley, 1997) where the diversity of viable alternative finfish targets is limited and where gear types are different from those used offshore (Kirkley, 1997), limiting the ease of diversifying spatially to offshore targets.

However, one diversification opportunity that may prove important for providing stability to commercial fishers in the Bay that would also not require leaving the Bay to fish is the emerging blue catfish (*Ictalurus furcatus*) fishery. Blue catfish is an invasive species whose abundances have increased dramatically in Bay tributaries in recent years, and in VA waters, harvests of blue catfish have exceeded those of striped bass since 2015 (Fabrizio et al., 2021). The governments of Maryland and Virginia have recently put forth legislative efforts supporting the development of a commercial fishery around this species (Senate Joint Resolution 4, 2021; Blue Catfish Processing, Flash Freezing, and Infrastructure Grant Program, 2023).

The substantial yield of blue catfish in Bay tributaries in recent years demonstrates the increasing importance of this fishery and raises a limitation of the presented analysis. First, the Bay is home to several species of finfish and invertebrates that are not considered within this study. For instance, beyond blue catfish whose low abundances in the Bay mainstem were inconsequential during our study period (2002–2018), the Bay supports relatively enormous blue crab fisheries that, at a regional scale, are valued at $80–$100 million USD annually (Scheld et al., 2021). Additionally, in the MD portion of the Bay mainstem, the pelagic Atlantic menhaden (*Brevoortia tyrannus*) is the second most valuable finfish after striped bass, the harvests of which were valued at ~$700,000 USD annually over the study period. While we focused our analyses on fishes that were well-sampled in ChesMMAP bottom trawl surveys and so excluded these important species, if comparable biomass estimates can be made to those presented here, then it would be reasonable to include these species in a future analysis.

Similarly, our analyses were geographically constrained to ensure the overlap between commercial harvest data and the ChesMMAP survey. Future work should consider expanding this approach to Bay tributaries and their associated commercial and recreational fisheries. Lastly, we assumed a unidirectional relationship between species abundances and species harvests, although harvesting will certainly influence the population dynamics of harvested species (Arlinghaus et al., 2017; Moore et al., 2021). Future work should explore these bidirectional dynamics, but doing so here is beyond the scope of this paper.

In the present analysis, we have provided novel insights into how species asynchrony relates to harvest asynchrony to stabilize commercial fishing harvest portfolios. In a system like MD where the dominant fishery target was seasonally closed to harvesting, we showed that harvest asynchrony arose due to the diversification of harvests occurring during the closure, and that this diversification stabilized the within-year harvest portfolio overall, but harvest stability was not associated with the stability of portfolio value. In VA, declines in the biomass of target species in the Bay played a key role in how within-year species asynchrony related to harvest asynchrony. With biomass declines came a greater evenness of population variabilities that was associated with declines in harvest compensation, and a coincident decline in effort that was associated with declines in species harvest stability. In addition, declines in harvest compensation and species harvest stability created a negative trend in the stability of the harvest portfolio in Virginia, although periods of high portfolio stability were associated with high portfolio value stability.

Understanding how stability arising from ecosystem processes contributes to the stability of dependent social-ecological systems has the potential to unlock novel management strategies that leverage these stabilizing features while concurrently conserving biodiversity.

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## Figures

A diagram of a system stability

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*Figure 1*. Conceptual model describing the generalization of a stability partitioning framework originally applied in an ecological context (Thibaut & Connolly, 2013), and extended to consider the asynchrony partitioning method introduced by Zhao et al. 2022. Variables connected by “” indicate a multiplicative relation between those variables, where their product is given by the variable indicated with an arrow.

A map of the ocean

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*Figure 2*.Map of Chesapeake Bay and its location along the east coast of the United States (inset). The light blue area refers to the area of the ChesMMAP survey falling within waters managed by the state government of Maryland (MD), and the light orange area the area falling within the management jurisdiction of Virginia (VA). The black line denotes the boundary between MD and VA waters.

A group of graphs showing different types of data

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*Figure 3*. Within-year time series of commercial fishing harvests in Maryland (top, a) and Virginia (bottom, b), where each line corresponds to a different year. Vertical lines correspond to the months where biomass indices for each species were estimated.

A collage of graphs

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*Figure 4.* Within-year time series of modeled species biomasses in Maryland (top, a) and Virginia (bottom, b), where each line corresponds to a different year. Note the change in y-axis scales between species.

A diagram of a patient's flow

Description automatically generated with medium confidence

*Figure 5.* Linked path diagrams showing the relationships between asynchrony in the community (red) and harvest portfolio (green) in MD (top) and VA (bottom) waters. Variables connected by an “” indicate a multiplicative relation between those variables, the product of which is given by the variable following the arrow. Statistical relationships were modeled using SEMs, the hypothesized paths of which are shown in the black boxes: dark blue arrows indicate positive relationships (P < 0.05), red arrows negative, double-headed black arrows correlated errors, and dotted grey lines no relationship. Numbers next to paths show standardized coefficients. See Table 1 for definitions of terms.

A graph of different types of graphs

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*Figure 6.* The relationship between the harvest compensation effect (CPEHarvest) and the seasonal harvest ratio (SHR) in MD (bottom left; R2 = 0.64). Also shown are harvest time series from Maryland during years when the SHR was highest (right; 2012) and lowest (top; 2009). Red shaded areas show the months during which the striped bass fishery was closed.

A graph of different colored lines

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*Figure 7.* Time series of annual biomass (a) and harvests (b) in the Virginia and Maryland regions of the Chesapeake Bay mainstem between 2002-2018.

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*Figure 8.* Interannual time series of annual species statistical averaging (a, SAESpecies), species compensation effects (b, CPESpecies), harvest statistical averaging (c, SAEHarvest), and harvest compensation effects (d, CPEHarvest) in Virginia. Trend lines are from linear models shown with 95% confidence intervals (see Table S4 for details).

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*Figure 9.* Species-specific time series of the weighted-average month of harvest in Virginia, where weights are given by monthly harvests. A positive linear trend indicates that the timing of harvests shifted to be later in the year, and a negative trend, earlier.

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*Figure 10*. Time series of total annual fishing trips across months (a) and total harvest per trip (b) in the Virginia portion of Chesapeake Bay. The across-species annual average number of trips is used in VA SEM 1, shown in Fig. 5.

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*Figure 11*. Time series of portfolio harvest stability in Maryland (a) and Virginia (b). Virginia portfolio harvest stability declined significantly over the study period (P < 0.001), as shown by the trend line with 95% confidence interval.

Table 1. Definitions of asynchrony and stability terms, their abbreviations, and general mathematical formulas.

|  |  |  |  |
| --- | --- | --- | --- |
| ***Term*** | ***Abbreviation*** | ***Formula*** | ***Description*** |
| Total harvest stability (all months) |  |  | The stability of total harvests across all species and months. |
| Total harvest stability (5 months) |  |  | The stability of total harvests across all species during the five months when biomass estimates are available. |
| Species harvest stability |  |  | The inverse of weighted-average harvest variability across species. We calculated this index for the five months when biomass estimates are available. |
| Asynchrony |  |  | A measure of the stabilizing effects of compensation and statistical averaging; either among harvests of multiple stocks or among the biomass dynamics of multiple species . |
| Statistical averaging effect |  |  | The enhancement of harvest or community stability following independent fluctuations among species harvests  or population dynamics. |
| Compensation effect |  |  | The enhancement of harvest or community stability following negatively correlated dynamics among species harvests or population dynamics . |















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