

# **TESTING ENERGY BIODIVERSITY THEORIES ON MARINE FISHES**

by

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## ABSTRACT

Energy-based biodiversity hypotheses suggest that lower annual variation, higher cumulative, and higher minimum energy flux into an ecosystem should each support higher biodiversity. Satellite derived energy indices support these general hypotheses for terrestrial taxa. However, these hypotheses have not been broadly tested in marine systems. Here, we calculate five different marine versions of these energy indices with satellite data. These are photosynthetically available radiation, sea surface temperature, chlorophyll-a, primary production, and benthic flux of particulate organic carbon. We paired these five different marine proxies for energy indices to global fish species richness data in order to be the first study to test the three energy biodiversity hypotheses in the marine environment. Results indicated that for marine fishes, energy indices based on photosynthetically active radiation, sea surface temperature, primary production, and benthic flux of particulate organic carbon are broadly consistent with the three energy hypotheses. Our findings show that these biodiversity theories may be applicable in marine systems and indicate that fundamental underlying drivers of biodiversity on Earth are not limited by the marked differences between terrestrial and marine environments.

## **Chapter 1**

### **INTRODUCTION**

Global biodiversity conservation is a major concern among scientists, governments, and nongovernmental and intergovernmental organizations such as the United Nations, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), the Ocean Health Index, and the International Union for Conservation of Nature (IUCN). The United Nations Convention on Biodiversity released a framework document in January 2020 that calls for urgent changes and sets ambitious goals to “live in harmony with nature” by 2050, and includes the target for “Genetic diversity [to be] maintained or enhanced on average by 2030, and for 90% of species by 2050” (Convention on Biological Diversity 2020). Biodiversity is considered a critical resource for several reasons. Maintenance of biodiversity is associated with ecosystem stability (Pasari et al. 2013; McCann 2000) which can be explained as the “portfolio effect”: the more diversified assets are, the more resilient the entire system will be. Biodiversity loss has been found to degrade ecosystem services; for example, fisheries are more likely to collapse, water quality decreases, and ecosystems are less likely to recover from perturbations (Worm et al. 2006).

It is well documented that human actions are rapidly changing Earth’s climate, ecosystems, and species distributions (Kareiva et al. 2007; O. E. Sala and Jackson 2006; Brook, Sodhi, and Bradshaw 2008). Approximately 50% of the world’s forests have been removed, and converted into grazing or cropland (Millennium Ecosystem Assessment 2005). Some researchers have expressed recent loss of species as the 6<sup>th</sup>

mass extinction, as 322 species of terrestrial vertebrates have become extinct and 67% of monitored invertebrate populations showed decline in the last 500 years (Dirzo et al. 2014). More than 16,000 species of animals and plants are currently considered “threatened” by the International Union for Conservation of Nature (IUCN 2020). In the ocean, approximately one-third of fisheries stocks are overfished, 75% of coral reefs are threatened, and some of the richest regions of biodiversity are located in areas most affected by climate change (Kubiak 2019; Lauretta Burke et al. 2011; Ramírez et al. 2017). Additionally many economically important species have shifted their ranges both latitudinally and vertically in recent years in response to temperature changes. (Nye et al. 2009; US EPA 2016; Poloczanska et al. 2013; Oremus et al. 2020).

Because of the anthropogenic threats to marine biodiversity, it is important discover, monitor, and predict it. Marine biodiversity studies are challenging, due to the remoteness and inaccessibility of sample sites, the immense area, volume, and fluid nature of the oceans, and the movements of marine organisms. One- to two-thirds of the predicted 1 million total marine species have yet to be identified (Appeltans et al. 2012). Despite these issues, researchers have made progress in documenting marine diversity. For example, the Census of Marine Life was a 10-year (2000-2010) international ocean sampling effort which generated of over 45 million observations of marine species that are compiled into the Ocean Biogeographic Information System (OBIS), an open-access repository (Census of Marine Life 2010). The Census of Marine Life identified over 1200 new marine species (Penman, Pearce, and Morton 2011; O’Dor, Miloslavich, and Yarincik 2010; Ellis et al. 2011; Priede et al. 2013). This important work inspired the creation of the US Marine Biodiversity Observation

Network (MBON), co-sponsored by the US Integrated Ocean Observing System, NOAA, NASA, Office of Naval Research, and the Bureau of Ocean Energy Management. MBON is a collaborative network of scientists and resource managers that works to integrate existing data and novel studies to increase understanding of global biodiversity and ecosystem functions. They have made a variety of data available via an online portal (<https://mbon.ioos.us/>), which allows for comparisons between real-time and historical data, and across disciplines (physical, chemical, biological).

Comprehensive efforts to collect and standardize global biodiversity data facilitate the ability of researchers to develop models that predict biodiversity. For example, spatial regression analysis on the distribution of 13 marine taxonomic groups found that satellite-measured sea surface temperature was a significant predictor of the spatial richness distribution all groups, while yearly primary productivity (VGPM) was a significant predictor of a few taxa (non-oceanic sharks, pinnipeds, cetaceans, and euphausiids) (Tittensor et al. 2010). Additionally, machine learning has been used to create predictive models of terrestrial and ocean diversity based on several environmental factors as drivers, such as satellite-measured temperature, primary production (proxied by chlorophyll-a), sunlight, and topography/bathymetry (Gagné et al. 2020). This approach indicated that bathymetry (depth) is the strongest predictor of marine biodiversity, followed by water temperature and sunlight.

While various studies provide interesting insight on the statistical linkages between marine biodiversity and environment, they do not directly test existing biodiversity theories in the global marine environment, which is the focus of this manuscript. Here, we test three energy-related hypotheses that link energy to the

maintenance of biodiversity, and collectively refer to them in this study as the energy biodiversity hypotheses:

- 1) Available Energy Hypothesis
- 2) Environmental Stress Hypothesis
- 3) Environmental Stability Hypothesis

The Available Energy Hypotheses proposes that greater annual cumulative energy availability facilitates species richness, and it is supported by both *in situ* and *in vivo* studies. For example, the annual net primary productivity on islands around the world is positively related to resident bird diversity, predicting 70-80% of island bird richness (Wright 1983). In the lab setting, increasing food resources in *Drosophila* microcosm experiments yield both higher abundance of individuals and species richness in these flies (Hurlbert 2006). Secondly, the Environmental Stress Hypothesis proposes that higher minimum available energy facilitates higher species richness, by meeting the minimum physiological tolerance requirements of various species, allowing more species to persist. There is evidence that climactic tolerance can limit species distributions (Currie et al. 2004). For example, winter boundaries of North American bird species correspond to their metabolic needs. The Northern Boundary Metabolic Rate is 2 to 2.6x the Basal Metabolic Rate, indicating a physiological limit that determines a spatial range boundary for these species (Root 1988). In French lake fishes, increased mean annual air temperature facilitates species richness by allowing populations of species with specialized niches to persist (Mason et al. 2008). Lastly the Environmental Stability Hypothesis proposes that lower intra-annual variability of available energy facilitates richness. For example, strong seasonal changes can create resource bottlenecks. In Australia, annual dry seasons decrease food availability

(insects, nectar, and fruit) for bird species, and therefore decrease bird abundance and richness (S. E. Williams and Middleton 2008).

Terrestrial biodiversity researchers have investigated these three hypotheses to examine the effects of energy availability on terrestrial biodiversity, called the Dynamic Habitat Indices (Hobi et al. 2017; Radeloff et al. 2019). The DHIs were calculated (annual variation, cumulative, and minimum) for global terrestrial ecosystems with five different remote sensing proxies for energy. These include the Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Fraction of Photosynthetically Active Radiation absorbed by vegetation (fPAR), Leaf Area Index (LAI), and Gross Primary Productivity (GPP). These products were chosen because vegetation productivity is a proxy for food resource availability to animals, and productivity measures are known predictors of species richness (Mittelbach et al. 2001). NDVI and EVI are measurements of green land cover, or the photosynthetically active biomass in a given area (Tucker 1979). LAI is defined as the ratio of one-sided leaf area per unit of ground area, and fPAR is a related parameter as it is the fraction of Photosynthetically Active Radiation absorbed by that leaf area (Myneni, Nemani, and Running 1997). Finally, GPP is a calculation of actual production from photosynthesis, in milligrams of Carbon. Terrestrial GPP values are calculated by NASA using MODIS-Aqua and Terra data (RUNNING et al. 2004).

These terrestrial energy indices were compared to species richness maps for North American breeding bird species and to global ranges of amphibians, mammals, and resident birds species (Hobi et al. 2017; Radeloff et al. 2019). In the North America study, the relationship of richness of breeding birds in 6 functional guilds from the North American Breeding Bird Survey was compared to DHIs in 85



ecoregions. Univariate and multiple regression models showed that different functional guilds were better predicted by different energy proxies. GPP had the strongest relationship with the most guilds, but Leaf Area Index was most strongly associated with woodland bird species and grassland species were most strongly associated with fPAR. In the 2019 study, the energy proxies were calculated globally and compared to species range maps of amphibians, mammals, and birds. Through univariate and multiple regression models, the DHIs based on GPP correlate well with global species richness, predicting half to two-thirds of the distributions, depending on taxa. These studies showed agreement with the three hypothesized fundamental relationships of energy to diversity (negative relationship of variation to diversity, and positive relationships of cumulative and minimum energy to diversity). These results indicate support of the energy biodiversity hypotheses to elucidate the underlying mechanisms driving diversity on land. Theories linking energy and biodiversity are not inherently limited to terrestrial ecosystems, but these three hypotheses have not yet been tested in the global marine environment. Testing these hypotheses in the marine systems may indicate whether or not there are universal biodiversity drivers on Earth.

Terrestrial and marine ecology are sometimes considered to be incomparable, as these ecosystems have several important differences. The most basic difference is the density of the fluid medium. The greater density of water allows organisms in the oceans to be supported mid-water, which means they do not necessarily need to be associated with a hard substrate. This allows for the development of rich open water pelagic habitats and ecosystems. In contrast, most terrestrial taxa are highly associated with hard substrate. Due to the lower density of air, only some terrestrial species fly, and all of them eventually return to a hard substrate as part of their life history.

Another major difference in marine and terrestrial systems is the availability of water. Water is not limiting in marine systems like it is in terrestrial systems, where distribution of water is associated with biodiversity patterns of many plants and animals (Hawkins et al. 2003). The ocean ecosystem is considered to be much more “open”, as currents facilitate transport of materials such as nutrients, plankton, and larvae to relatively great distances compared to the terrestrial environment (Strathmann 1990; Denny 1993). Many marine taxa have larval offspring, which are subject to being driven spatially by physical water flows because of their small size and therefore low Reynolds number. Larvae dispersal of invertebrates and fish to great distances (on the order of 100 km) can lead to decoupling of offspring from adult habitats, in contrast to the limited dispersal of most terrestrial vertebrate animals (Shanks, Grantham, and Carr 2002; Waser and Jones 1983). The higher interconnectedness of ocean environments and greater distance of dispersal leads to lower endemism as compared to land. The smallest endemic areas in the ocean are on the order of 10s of km<sup>2</sup>, while on land endemic areas can be a few 100 m<sup>2</sup> (Boeuf 2011).

The temporal scales of physical and biological processes in terrestrial and marine systems are also vastly different (Steele 1991). In terrestrial systems, the primary producers are generally much longer lived (months-centuries) than in the marine systems (weeks-months), but the rate of change of change for physical atmospheric features is faster than that in the ocean (ex. weather fronts vs eddies) (Steele 1978; 1991). The effects of climate change also differ between the two environments, as the median rate of warming from 1960 to 2009 was three times faster on land than in the oceans (Burrows et al. 2011), but climate-driven leading edge

expansion of marine species ranges have been ~10x faster than terrestrial shifts (average of 72 km/decade for marine organisms) (Poloczanska et al. 2013).

Despite their differences, there are also important similarities between terrestrial and marine ecology. At the level of macroecology, there is a general decrease in diversity with increased latitude in both environments (Latitudinal Richness Gradient), indicating some base level of similar underlying functionality (Hillebrand 2004). In terrestrial and marine ecology, there are analogous community structures, like coral reefs and tropical rainforests where the rarity and dispersion of conspecifics is driven by predation by specialized natural enemies (Connell 1971). There are also analogies between taxa and functional groups of species. Out of the 31 currently identified animal phyla, 19 occur both in terrestrial and marine environments (Boeuf 2011), such as mollusks, arthropods, annelids, etc. Similar functional groups occur in both environments, including primary producers, consumers, and top predators. Some behavioral interactions are markedly similar, such as Dugong avoidance to predator Tiger sharks which is strikingly similar to Elk and Wolves (Wirsing and Ripple 2011).

While the marine environment is more subject to material and larval transport, it is not homogeneous. Just as the terrestrial environment has a variety of ecoregions with differing properties, the ocean also has bottom-associated ecoregions (reef, kelp forest, etc.) and open ocean ecoregions, also called biogeochemical/biogeographic provinces or seascapes (Oliver and Irwin 2008; Reygondeau et al. 2013; Kavanaugh et al. 2014). These regions can be classified using remote-sensed data, which highlights their dynamic boundaries. Marine community structures can follow seascape delineations, with some organisms such as sturgeon preferentially inhabiting their

seascape of choice (Gómez-Pereira et al. 2010; Breece et al. 2016; Montes et al. 2020). Furthermore, geographical speciation is common in the oceans as well as in terrestrial systems (Mayr 1954; Palumbi 1994; Dawson and Hamner 2003; Meyer, Geller, and Paulay 2005).

These factors indicate that marine organism distributions are influenced by regional environmental patterns, just as terrestrial ones are. However, while the fundamental environmental drivers of terrestrial diversity are water and energy (Currie 1991; Allen, Brown, and Gillooly 2002), water is a non-limiting resource in the marine environments, suggesting that energy may be especially important for marine biodiversity patterns. This reasoning leads us to hypothesize that energy biodiversity hypotheses may be broadly applicable in the marine environment. Indeed, there is evidence that energy in the form of temperature or primary production drives diversity patterns in the marine environment (Roy et al. 1998; Kerr and Packer 1999; Tittensor et al. 2010; Gagné et al. 2020). However the three biodiversity energy hypotheses have not been tested in the oceans, which is what we undertake within this study.

## Chapter 2

### METHODS

#### Fish richness

While biodiversity metrics can be calculated in a variety of ways, we decided to use species richness as the biodiversity metric for this study, which is defined by the sum of species within a given area. Global marine fish species richness was calculated from a database of fish species occurrence data with 55 km resolution, provided by collaborator / committee member Dr. Gabriel Reygondeau. To construct the database, he undertook several collection and cleaning steps. The name of each species was checked in the World Register of Marine Species (WoRMS) to identify any species synonyms. The occurrence and metadata for each species was amassed from *in situ* sampling efforts (Ocean Biogeographic Information System, the Global Biodiversity Information Facility, FishBase, International Union for the Conservation of Nature). The metadata included habitat designations (pelagic, demersal, etc) and the depth range of the species' occurrence. These steps resulted in occurrence maps for over 18,000 fish species, however some species occurrence was based solely on point observations, while other species have had their ranges defined by experts. *In situ* observed diversity is highly subject to sampling biases depending on the type of sampling gear and sampling effort. So, we decided to retain only the expert-defined range maps (4000 spp) for this study, which therefore represents the potential fish biodiversity per pixel.

To obtain the richness metric for this study, we summed the expert-defined fish ranges per pixel, for both the full species list (“all-fish”) and habitat subsets. The subsets were based on metadata for each species where it was available. Our “pelagic

group” (500 spp) included the metadata categories of Pelagic, Bathypelagic, Pelagic-Oceanic, and Pelagic-Neritic. Our “demersal group” (1642 spp) included the Demersal and Bathydemersal categories, and should be representative of fish that do not directly interact with surface energy signals. Our “reef fish group” included only reef fish shallower than 50 m (1274 spp) so it is representative of reef fish which likely do interact with surface energy signals. Because we excluded deep reef fish, we did not use the reef fish data in the offshore region tests described later.

### **Satellite data**

We calculated five different available energy proxies using data from NASA MODIS Aqua 9 km resolution, 8-day composite products (<https://oceandata.sci.gsfc.nasa.gov/directaccess/MODIS-Aqua/Mapped/8-Day/9km/>). Photosynthetically available radiation, sea surface temperature, chlorophyll-a, primary production via the Vertically Generalized Production Model (Behrenfeld and Falkowski 1997), and benthic particulate organic carbon flux were the proxies chosen as representations of available energy. These proxies can be sorted into two major groups, which are radiative/thermal energy (PAR and SST), and metabolic energy, which is stored within biological tissues (chlorophyll-a, primary production, and POC).

PAR is defined as the spectrum of visible light from 400-700 nm, which are the wavelengths that provide energy to the process of photosynthesis (McCree 1971; 1972). The MODIS Aqua PAR product utilizes Top-of-Atmosphere radiances in the 400-700 nm range and an algorithm originally designed for the SeaWiFS satellite (Frouin, Franz, and Wang, n.d.) (<https://oceancolor.gsfc.nasa.gov/atbd/par/>). PAR is

reported as a rate flux per day ( $E\ m^{-2}\ d^{-1}$ ), but each of the files represents an 8-day composite of data.

Temperature is generally not a direct energy source for organisms (Huston et al. 2003). However, it is positively related to respiration and primary production (Tait and Schiel 2013; Davison 1991; Clarke and Johnston 1996). Studies suggest that temperature is a driver of global diversity distributions (Latitudinal Diversity Gradient) (Currie 1991; J. R. G. Turner 2004; Gillman and Wright 2014), potentially due to physiological thermal tolerances of organisms (Currie et al. 2004). Remote sensed sea surface temperature is the thermal surface skin temperature of the ocean, less than 1mm of water thickness (Donlon et al. 2007; Wong and Minnett 2018) (<https://oceancolor.gsfc.nasa.gov/atbd/sst/>), but it is considered to be representative of the upper mixed layer of the ocean.

Chlorophyll-a concentration indicates the presence of primary producers and is commonly used to estimate the standing stock of algal biomass (Berkman and Canova 2007). Ocean chlorophyll can be calculated from an empirical relationship derived from *in situ* measurements of chlorophyll and blue and green remote sensing reflectances. The MODIS-Aqua chl-a product combines the OCX algorithm and Hu's color index (O'Reilly et al. 1998; Hu, Lee, and Franz 2012) ([https://oceancolor.gsfc.nasa.gov/atbd/chlor\\_a/](https://oceancolor.gsfc.nasa.gov/atbd/chlor_a/)).

Measurements of chlorophyll are a proxy for biomass, not necessarily primary production (carbon fixation rates), so ocean primary production was calculated using the Vertically Generalized Production Model (Behrenfeld and Falkowski 1997), which has an output of  $mg\ C\ m^{-2}\ d^{-1}$  and includes production vertically to the euphotic depth. The Aqua products used for this calculation were SST, PAR, Chl-a, and euphotic

depth (Lee et al. 2007), along with hours of daylight calculated by the R package “photobiology” (Aphalo 2015).

Particulate organic carbon (POC) is defined as suspended and sinking particles greater than or equal to 0.2µm, and is comprised of both allochthonous and autochthonous materials including live bacteria and detritus such as fecal pellets, dead cells, and shells (Kharbush et al. 2020). Sinking POC is the main export flux of surface primary productivity to the deep ocean, a mechanism known as the “biological pump”, which exports an estimated 4-12 Pg of Carbon per year to the deep ocean (Eppley and Peterson 1979; Laws et al. 2000; DeVries and Weber 2017). These particles are either sequestered in benthic sediments or become an important food source for pelagic or benthic heterotrophs (J. T. Turner 2015; Longhurst and Glen Harrison 1989). Here, benthic POC was calculated with surface calculations of POC (<https://oceancolor.gsfc.nasa.gov/atbd/poc/>) and the Martin Curve (Martin et al. 1987). The Martin Curve is an empirically derived power law equation with b parameter values specific to ocean basins:

$$\text{Flux at depth } Z = (\text{POC flux at 100 m}) * (Z/100)^{-0.82}$$

We made the assumption that the satellite-measured surface value of POC was equal to the 100 m flux. To calculate the global benthic flux of depths greater than 100 m, we used a global average of the b parameter of -0.82 (William M. Berelson 2001), and bathymetry values from the Global Multi-Resolution Topography Data Synthesis (<https://www.gmrt.org/>) as the Z parameter.

Because the fish richness dataset represents the average fish biodiversity conditions in the oceans over the full record of available data over time, the energy proxies needed to be transformed to average conditions as well. Average yearly energy



curves were created for each of the energy proxies by averaging the corresponding 8-day composite files over the available data (2003-2019). Importantly, as a year is not equally divisible by 8 days, the 46<sup>th</sup> time period is a 4- or 5- day composite and was excluded from each climatological year when the energy indices were computed. For each average energy curve, the coefficient of variation, cumulative, and minimum values were calculated. Because these data are satellite derived, they are intrinsically limited by seasonal availability of incident sunlight. Because of this, our analysis is limited between -50 and 50 degrees latitude to avoid areas in the polar regions which are often missing data.

Additionally, we considered the difference between coastal and open ocean spatial complexity. Coastal regions generally have higher environmental variability, while the open ocean has larger areas of similar environmental factors. For example, in coastal regions such as the Sea of Japan, surface ocean temperature and salinity correlation scales range from approximately 200-450km, and in Buzzards Bay, Massachusetts the chlorophyll scale is around 100 km and temperature scale is 250-340 km (Chu, Guihua, and Chen 2002; Jossart et al. 2020). In contrast, the scale of thermal signals in the tropical Pacific are up to 1500 km (Sprintall and Meyers 1991; White and Bernstein 1979; Molinari and Festa 2000), and sea surface salinity has homogeneous scales of more than 2000 km in the tropics (Tzortzi et al. 2016). Therefore, we defined a “shallow” and “offshore” spatial region and analyzed them separately. The shallow region is defined as the coastal regions with bathymetry < 200 m, while the offshore region is defined as ocean >500 km from the coast. We retained the 55 km grid size for the shallow region and rescaled the offshore region to a coarser

grid cell size of 550 km so that the grid cells in each region represent a rough average of 2 to 4 observations per homogeneous spatial unit of ocean.

### **Data matching and statistical analysis**

The fish richness and energy data maps were not initially generated on the same raster scale. In order to pair pixels of richness and energy data together spatially, the energy index datasets were interpolated (exponentially weighted average) to match the 55 km and 550 km grids. Once the energy index and fish data were matched to the same pixel scale, the raster data could be matched spatially 1:1 and plotted in x-y scale (2D density plots). Data were log<sub>10</sub> transformed (fish richness in all cases, and most of the energy data, see figures) to meet normality assumptions for statistical analysis (model II regressions – Ranged Major Axis method,  $n_{\text{permutations}} = 99$ ) (Legendre 2018). Model II regression was chosen as it minimizes the residuals in both the x and y direction, which is appropriate when there is uncertainty in both variables. This study uses measured environmental data as the x variable, not a controlled experimental condition, so Model II regression is appropriate. In the Ranged Major Axis method, the variables are standardized by their ranges, and then the sum square of lines perpendicular to the regression line are minimized. This method is appropriate for conditions where the scale and/or units of the variables differ, as is the case with the data in this study. The regressions were considered significant when  $p < 0.01$ . Additionally, Pearson correlation matrices were generated between all the energy proxies in the shallow and offshore region datasets.

## Chapter 3

## RESULTS

### Fish richness

When all of the fish ranges were summed to create the richness metric, global patterns in biodiversity can be observed (figure 1). In the shallow region (figure 1a), the latitudinal richness gradient can be seen, as highest richness is observed in equatorial regions, and decreases toward the poles. The offshore region (1b) highlights the pattern where highest richness is also generally found near to shore and decreases with increased distance from coast.

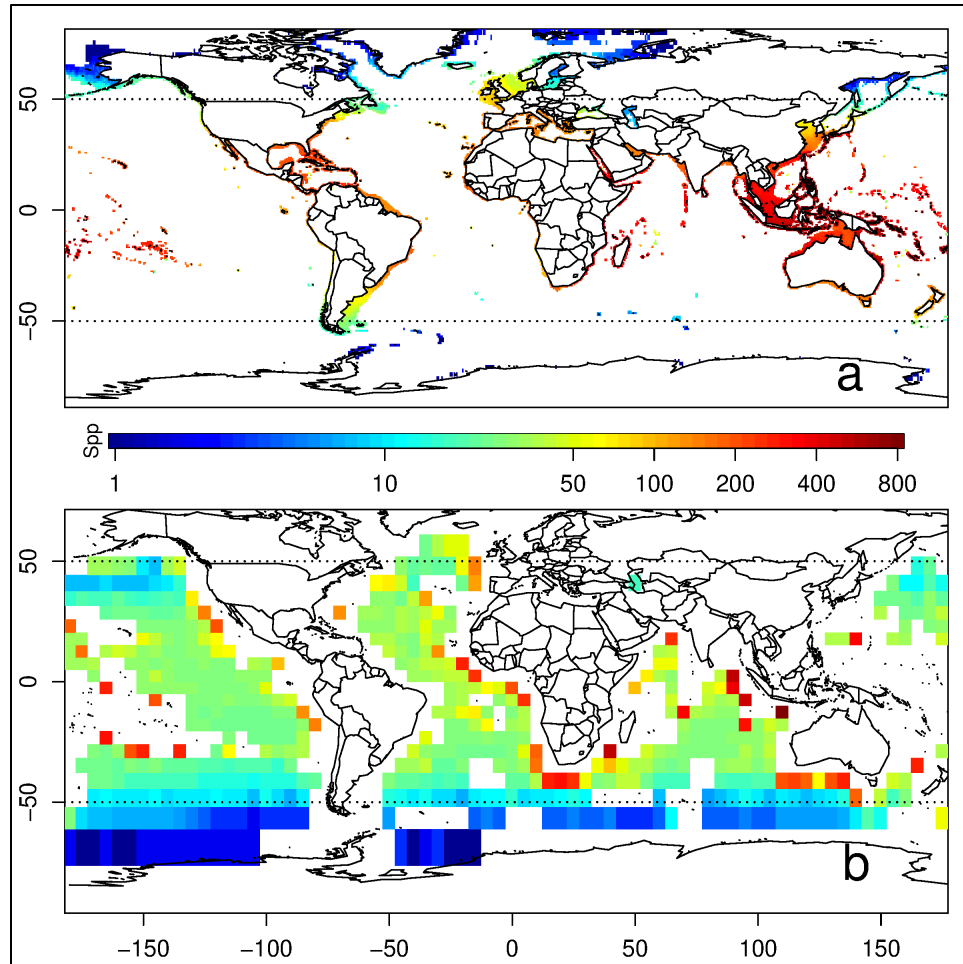


Figure 1 All-fish richness in the shallow (a) and offshore subsets (b). Black dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis. The global latitudinal richness gradient can be seen clearly in the shallow region, with higher species richness in low latitudes. Additionally highest richness is found in the coastal regions, with decreased richness offshore.

### **Satellite data**

For visualization purposes, the energy indices were plotted in Red-Green-Blue color scale, to visualize the spatial patterns of the energy indices. Variation in energy is plotted in red, cumulative in green, and minimum in blue. Figures 2 and 3 show PAR and benthic POC energy indices (see supplemental figures for the remainder of the energy figures). PAR is dominated by a latitudinal signal, where cumulative and minimum values are highest in low latitudes, and variation is highest in high latitudes. However other features like the intertropical convergent zones that are prone to persistent cloud cover display lower levels of cumulative and minimum PAR values. In contrast, the benthic POC map does not have an apparent latitudinal gradient, but rather a depth-driven pattern. Higher cumulative and minimum values occur in shallower areas, such as continental shelves and mid-ocean ridges. Highest variation in benthic POC is seen near river outflows, such as the Amazon River in South America and Congo in western Africa.

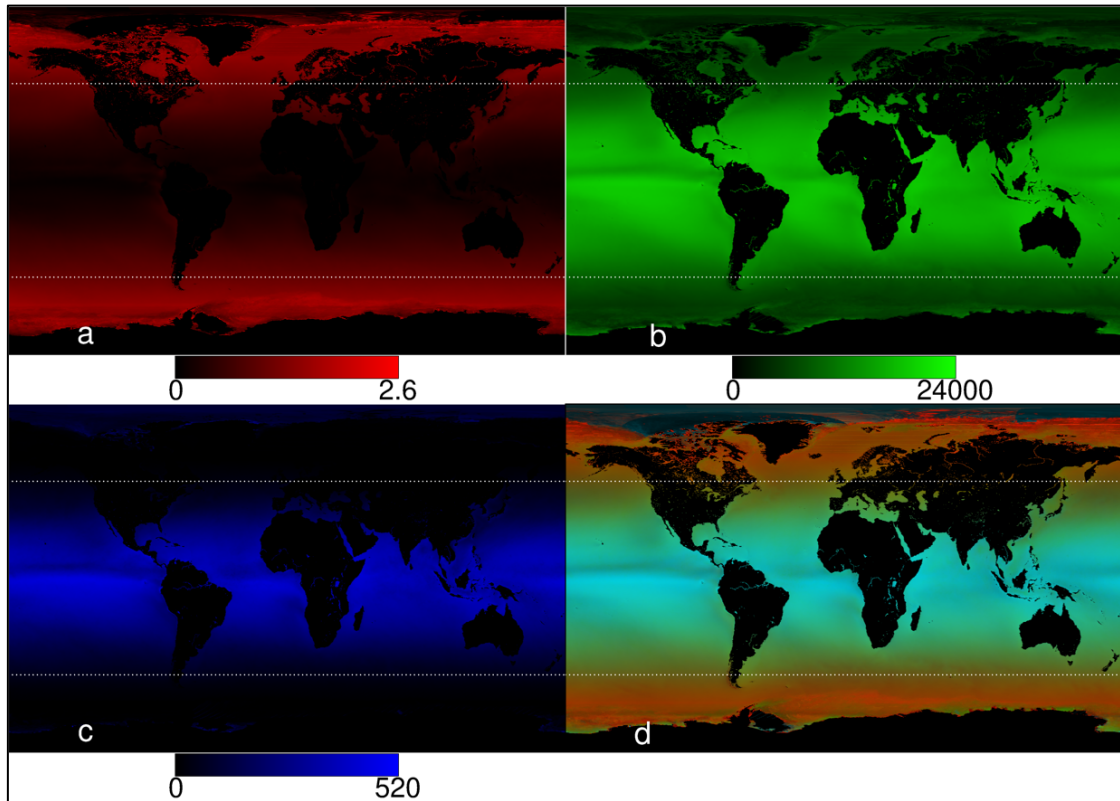


Figure 2 Energy indices calculated from Photosynthetically Available Radiation ( $\text{E m}^{-2}$ ). Annual variation in PAR (a) is highest in temperate and polar regions. Annual cumulative (b) and annual minimum (c) in PAR is highest in tropical and subtropical regions (b), although regions of high cloud cover are evident in equatorial regions. Combining these indices into a RGB representation shows where each of the different indices dominate the signal (d). White dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis.

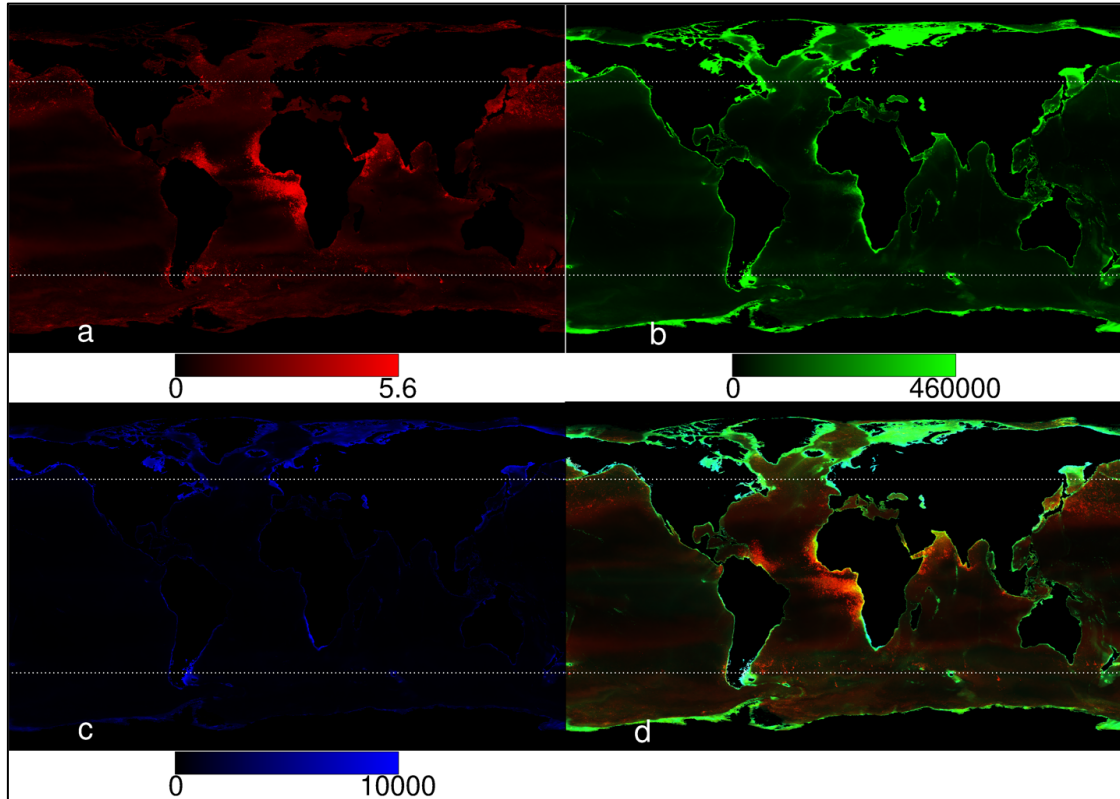


Figure 3 Energy indices calculated from benthic POC ( $\text{mg m}^{-2}$ ). Annual variation in benthic POC (a) is highest is seen near large river outflows (ex. Amazon and Congo) and monsoonal regions in the Indian Ocean. Annual cumulative (b) and annual minimum (c) in benthic POC both have their highest values in coastal regions. Combining these indices into a RGB representation show where each of the different indices dominate the signal (d). White dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis.

Correlation matrices were generated for all of the aspects of the energy proxies in the shallow and offshore region datasets (Figures 4 and 5). As mentioned previously, there are two groups of energy variables that are associated with each other (radiative/thermal and metabolic energy), and the energy proxies were found to generally correlated to each other within these groups. The first group are the PAR and

SST indices, which are mechanistically related through the radiative transfer theory. The second group are the Chlorophyll, VGPM, and benthic POC indices which are related through the production and export of organic matter. In the shallow region (Figure 4), PAR and SST are positively correlated in all three categories. Chlorophyll, VGPM, and benthic POC are also positively correlated to each other. Variation in VGPM is somewhat correlated to variation in PAR and SST, as both are inputs into the VGPM algorithm, but otherwise the two groups of energy proxies are not strongly correlated, indicating that they may be good independent energy proxies.

In the offshore region (Figure 5), PAR and SST are strongly correlated in the cumulative and minimum groups but not in variation. VGPM is positively correlated to variation in PAR and cumulative Chlorophyll (> 0.7), but all other correlations are relatively weak.

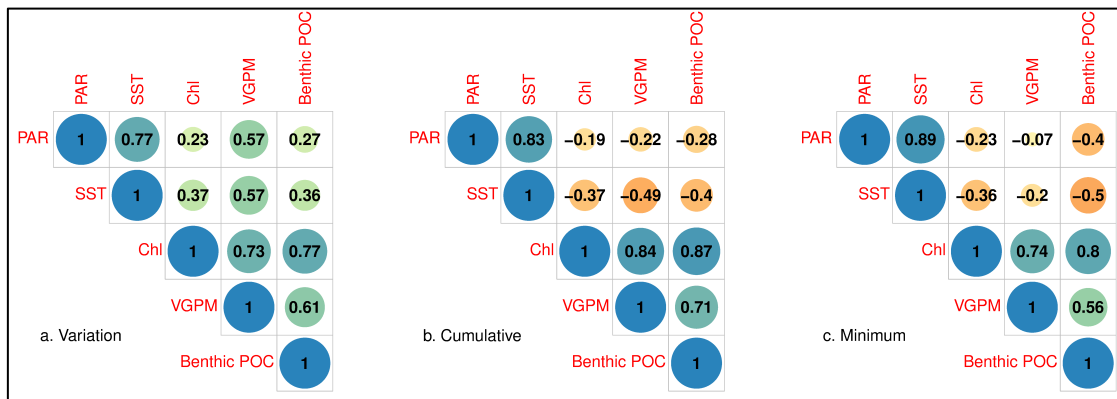


Figure 4 Correlation matrix (Pearson) of energy proxies in the shallow region dataset. PAR and SST are strongly positively correlated to each other, but not to the other proxies. Chlorophyll, VGPM, and Benthic POC are often positively correlated to each other. PAR and SST have slight negative correlation values to Chl, VGPM, and Benthic POC in the cumulative and minimum categories, and slight positive correlation in the variation category.

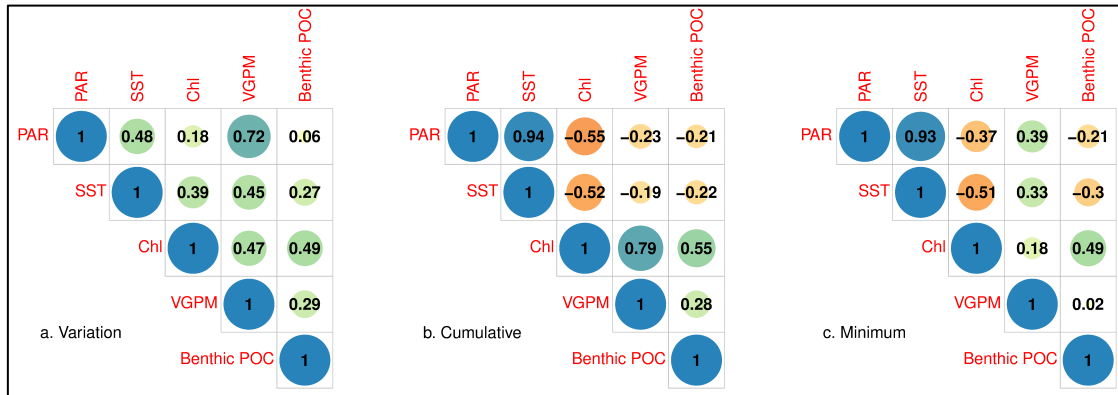


Figure 5 Correlation matrix (Pearson) of energy proxies in the offshore region dataset. The most highly correlated variables are PAR and SST in the cumulative and minimum categories. VGPM is positively correlated with variation in PAR and cumulative Chlorophyll. All other correlations are relatively weak.

### Data matching and statistical analysis

Pixels of fish richness data and energy index data were paired with Ranged Major Axis regression lines overlaid, to visualize the relationship between the variables. Figure 6 shows a set of examples using the PAR energy indices and the shallow region fish richness (all-fish). In each of these cases, the regression was significant ( $p$ -value  $< 0.01$ ). They showed a negative relationship of variation in energy to fish richness, and positive relationships of cumulative and minimum energy to fish richness, which are all in agreement with initial energy biodiversity hypotheses. This analysis was undertaken for each pair of energy index and fish richness subsets (see supplemental figures).



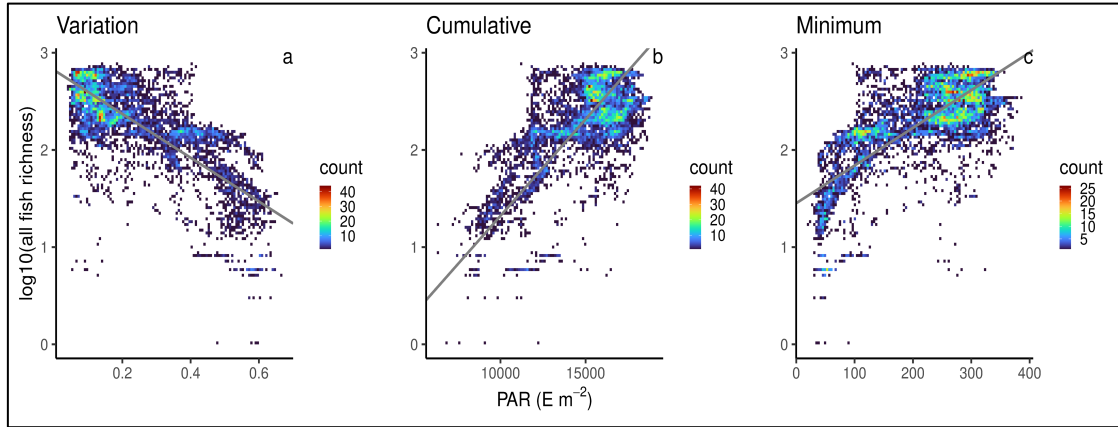


Figure 6 2D density plots of PAR energy vs all-fish richness (Shallow region). All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray, all p-values < 0.01.

Table 1 summarizes the results of all the combinations carried out with the shallow region subsets (reorganized to highlight fish groups in supplemental figures, table 3). PAR and SST both showed general agreement with the three biodiversity hypotheses for nearly all of the fish groups. Only the results for demersal fish versus variation in SST energy disagreed with the hypotheses. Chlorophyll and Benthic POC followed similar patterns to each other, where the cumulative and minimum results only followed the hypothesized results in the Demersal group. VGPM often agreed with hypothesized results in the variation and minimum energy categories. Reef fish results showed opposite patterns to the demersal fish, even though they are both bottom-associated organisms. In Chlorophyll, VGPM, and benthic POC, only the variation category followed hypothesized results, and cumulative and minimum energy showed significant negative regressions. Contrastingly, all three energy biodiversity hypotheses were followed for reef fish in the PAR and SST energy proxies.

Table 1 Summary of results from shallow region analysis (significance of model II regressions, Ranged Major Axis method). Green checkmarks indicate significant RMA regressions in agreement with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red x's indicate regressions that significantly disagreed with the hypotheses, and non-significant tests are marked as NS. PAR and SST most often support the hypotheses. Chlorophyll and benthic POC are less often correlated with richness, but notably seem to affect the deep fishes (Demersal group).

		Var	Cum	Min			Var	Cum	Min
PAR	All-fish	✓	✓	✓	SST	All-fish	✓	✓	✓
	Pelagic	✓	✓	✓		Pelagic	✓	✓	✓
	Demersal	✓	✓	✓		Demersal	✗	✓	✓
	Reef	✓	✓	✓		Reef	✓	✓	✓
Chl	All-fish	✓	✗	✗	Benthic POC	All-fish	✓	✗	✗
	Pelagic	✓	✗	✗		Pelagic	✓	✗	✗
	Demersal	✗	✓	✓		Demersal	✗	✓	✓
	Reef	✓	✗	✗		Reef	✓	✗	✗
VGPM	All-fish	✓	✗	✓					
	Pelagic	✓	✗	✓					
	Demersal	NS	✓	✓					
	Reef	✓	✗	✗					

Figure 7 shows an example of 2D plot results in the offshore dataset (PAR energy vs. all-fish species). Once again, this example shows significant results supporting all three of the energy biodiversity hypotheses. The summary of all of the offshore tests is seen in table 2 (reorganized to highlight fish groups in supplemental figures, table 4). Note that these offshore tests exclude reef fish, as our reef group did not include the deep reef fishes that would be found in the offshore region. Similarly to the shallow results, PAR and SST tests agreed with the biodiversity energy

hypotheses in most cases, except with demersal fish. VGPM followed the hypotheses in many cases with both surface and deep fishes. Chlorophyll and benthic POC only agreed with the hypotheses in the demersal group, with cumulative and minimum energy indices.

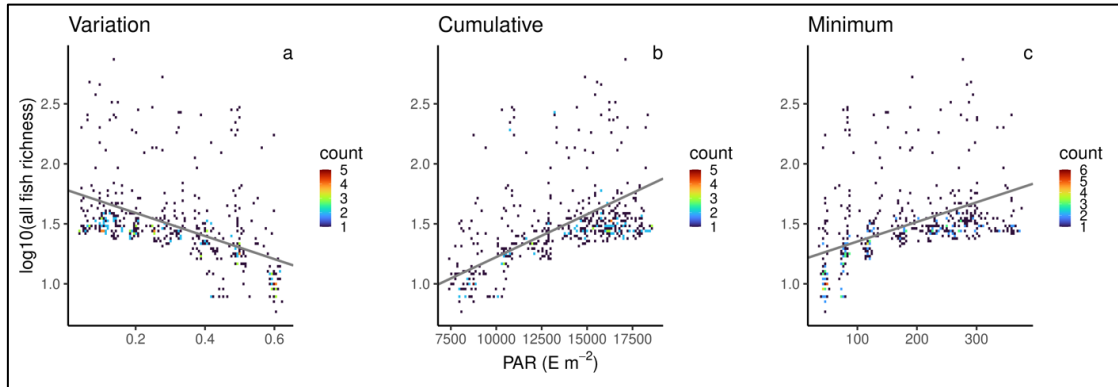


Figure 7 2D density plots of PAR energy vs all-fish richness (Offshore region). All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray, all p-values < 0.01.

Table 2 Summary of results from offshore region analysis (based on significance of model II regressions, Ranged Major Axis method). Green checkmarks indicate significant RMA regressions in agreement with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red x's indicate regressions that significantly disagreed with the hypotheses, and non-significant tests are marked as NS. PAR and SST show significance in agreement with the energy hypotheses in most cases. The surface signals of PAR and SST do not seem to affect demersal fish diversity where VGPM, Chl, and benthic POC do affect diversity of demersal fish.

PAR	All-fish	Var	Cum	Min	SST	All-fish	Var	Cum	Min
	Pelagic	✓	✓	✓		Pelagic	✓	✓	✓
	Demersal	NS	NS	NS		Demersal	NS	NS	NS
Chl	All-fish	Var	Cum	Min	Benthic POC	All-fish	Var	Cum	Min
	Pelagic	NS	×	×		Pelagic	NS	NS	×
	Demersal	NS	×	×		Demersal	NS	×	×
VGPM	All-fish	Var	Cum	Min		All-fish	Var	Cum	Min
	Pelagic	×	✓	✓		Pelagic	×	✓	✓
	Demersal	×	✓	✓		Demersal	×	✓	✓

## Chapter 4

### DISCUSSION

Global biodiversity patterns are often described in terms of the latitudinal diversity gradient, which was first recognized in the early 1800s (Roy et al. 1998; Allen, Brown, and Gillooly 2002; Hillebrand 2004; Mannion 2020). In both terrestrial and marine ecosystems, species richness generally decreases with increased distance from the equator. Several explanations have been proposed for the underlying mechanisms driving the latitudinal diversity gradient. One explanation for higher diversity near the Equator has to do with the physical shape of the Earth and the species-area relationship. In general, larger areas of similar composition tend to contain higher species richness, (Preston 1962). Low latitudes on either side of the Equator represent a large contiguous environment, contrasted to higher latitude environments in the northern and southern hemispheres that have a smaller area due to the spherical shape of the Earth, leading to increased diversity in the tropics (Rosenzweig 1992; 1995). However, the general latitudinal pattern of species diversity is often disrupted by other environmental features, such as continental margins, topography / bathymetry, and aridity, indicating that environmental conditions and resource availability also play a large role in driving global diversity patterns.

Studies show that diversity of higher trophic level species in both terrestrial and marine environments can be correlated to aspects of available energy, which often have a latitudinal gradient (Mittelbach et al. 2001; Hawkins et al. 2003; Schipper et al. 2008; Rombouts et al. 2009; Radeloff et al. 2019; Saupe et al. 2019). Available energy can take several different forms and affect trophic groups differently. For example, radiation energy from the sun is used directly by photosynthetic organisms (PAR).

Hypothetically, higher PAR energy should be associated with increased diversity of photosynthetic primary producers. However, higher levels of PAR are not directly associated with higher diversity of terrestrial primary producers. Instead, variations in terrestrial plant diversity are associated with a combination of the factors of water availability and temperature (Currie 1991; O'Brien 1998; Francis and Currie 2003).

In addition to radiation energy, thermal energy (temperature and evapotranspiration), is often used as a proxy for available energy in biodiversity studies (Terent'ev 1963; Kerr and Packer 1999; Kerr and Currie 1999; Badgley and Fox 2000; Allen, Brown, and Gillooly 2002). These studies show that temperature is generally positively correlated with higher speciation. For example, higher thermal energy measurements of mean summer air temperature, annual potential evapotranspiration, and mean annual sea surface temperatures are associated with greater species richness in British breeding birds, North American *Epicauta* beetles, and eastern Pacific marine gastropods (respectively) (Lennon, Greenwood, and Turner 2000; Kerr and Packer 1999; Roy et al. 1998). Additionally, both radiation and thermal energy are significant drivers in global models of terrestrial and marine richness. For example, SST was the only significant driver of diversity across 13 marine taxa ranging from corals, zooplankton, fish, and mammals (Tittensor et al. 2010) and temperature and sunlight were in the top three important statistical predictors in both global terrestrial and marine biodiversity models (Gagné et al. 2020).

Here, we use fish richness to test whether the energy biodiversity hypotheses are supported when using PAR or SST as energy proxies in the marine environment. We found that the patterns in annual variation, cumulative, and minimum values in

PAR and SST meet the expectations of the energy biodiversity hypotheses. In our shallow region (Figure 1a), lower variation, higher cumulative, and higher minimum values in these energy proxies were associated with higher diversity in almost all of the fish groups (all-fish, pelagic, demersal, and reef), except in the case of SST variation in demersal fishes (Table 1). In our offshore region (Figure 1b), PAR and SST were also congruent with the energy biodiversity hypotheses in the all-fish and pelagic groups but were not significant in the demersal group (Table 2). These results show that radiative and thermal energy seem to be fundamentally related to global fish diversity and provide theoretical support to previous multivariate biodiversity studies (Tittensor et al. 2010; Zhang et al. 2019; Gagné et al. 2020). Energy proxies of PAR (Figure 2) and SST (Figure 8) energy indicate the general latitudinal patterns of these parameters, which may be an explanation for the general latitudinal pattern in species richness on Earth. There is a temptation to use latitude in biodiversity model development because it is powerful, but organisms don't sense latitude, they sense its correlates. Our results suggest that using an average cumulative measurement of sunlight or temperature as a latitudinally associated factor may be more appropriate instead.

Another form of energy that is widely investigated as a diversity driver is chemically stored metabolic energy (Hurlbert and Haskell 2003; Wright 1983; Balmford et al. 2001; Kaspari, O'Donnell, and Kercher 2000). This encompasses the energy in the form of fixed carbon that is stored within body tissues of all organisms. There are several different ways to estimate or quantify metabolic energy availability, including measurements of the standing stock of chlorophyll biomass, rates of primary production, or production of particulate organic matter. Indeed, primary productivity is

an important driver of terrestrial and freshwater diversity (Mittelbach et al. 2001; Hawkins et al. 2003). Meta analysis of 171 studies on the relationships between productivity and richness of terrestrial and aquatic plants, vertebrates, and invertebrates found there were often unimodal (“hump-shaped”) or positive relationships between these variables, particularly in cross-community analysis and on continental to global scales (Mittelbach et al. 2001). Individual studies show that NDVI can predict over 60% of North American bird richness, NPP is positively associated with island bird richness and has a unimodal relationship to African vertebrate richness (birds, mammals, snakes, amphibians, humans), and ground ant assemblages have a positive decelerating relationship with net aboveground productivity (Hurlbert and Haskell 2003; Wright 1983; Balmford et al. 2001; Kaspari, O’Donnell, and Kercher 2000).

Stored metabolic energy was also investigated in terrestrial studies with the three energy biodiversity hypotheses, in the forms of Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Fraction Photosynthetically Active Radiation absorbed by vegetation (fPAR), Leaf Area Index (LAI), and Gross Primary Productivity (GPP) (Hobi et al. 2017; Radeloff et al. 2019). The different energy proxies have varying predictive power in North American breeding bird guilds, but GPP is the strongest predictor of richness for most groups (Hobi et al. 2017). All three GPP metrics are predictive of the global ranges of amphibians, mammals, and resident birds species (> 60% predictive power) (Radeloff et al. 2019). Additionally, the cumulative energy proxy is the most important predictor of richness, followed by minimum and finally variation. Aside from prediction, inspection of the individual facets of these terrestrial analyses show agreement with



the three hypothesized fundamental relationships of energy to diversity (negative relationship of variation to diversity, and positive relationships of cumulative and minimum energy to diversity).

In this study, we tested the same three energy biodiversity hypotheses with analogous metabolic energy proxies in marine systems. These included chlorophyll biomass, primary productivity via the Vertically Generalized Production Model, and benthic flux of POC. These three energy sources were generally positively correlated to each other in the shallow region (0.56 to 0.87, Figure 4). In the offshore region, cumulative VGPM and Chlorophyll were positively correlated ( $> 0.7$ ), but all other correlations are relatively weak ( $\pm 0.5$ , Figure 5). The tests of these energy sources had similar patterns of results, which makes sense as they are generally correlated together. The variation hypothesis was most often supported. In our shallow region fishes (Figure 1a), variation in all three metabolic energy proxies (Chl (Figure 9), VGPM (Figure 10), and benthic POC (Fig 3)) support the hypothesis that lower annual variation in energy leads to higher species richness in the all-fish and pelagic groups. In the offshore region, the variation hypothesis is followed in primary production. The fact that the variation hypotheses is often supported in the marine metabolic energy proxies is a notable contrast to the terrestrial studies, where cumulative and minimum energy were found to be the strongest drivers of diversity. However cumulative and minimum metabolic energy were important in certain cases in the fish groups. In both the shallow and offshore region, cumulative and minimum hypotheses were significantly followed with the demersal fishes. In the all-fish and pelagic groups, the minimum hypothesis was supported with primary production energy (VGPM).

While the influence of the radiation and thermal energy sources are limited to the euphotic zone of the oceans, the metabolic energy sources affect both surface and deeper energy biodiversity. Photosynthetic organisms in the surface oceans transform radiative energy into metabolic energy (fixed carbon) via photosynthesis which supplies energy to the marine ecosystem. Organic carbon is further transformed into particulate organic carbon, including live bacteria and detritus such as fecal pellets, dead cells, and shells (Kharbush et al. 2020). Sinking POC exports an estimated 4-12 Pg of carbon per year to the deep ocean in the process known as the “biological pump” (Eppley and Peterson 1979; Laws et al. 2000; DeVries and Weber 2017), and is an important food source for pelagic or benthic heterotrophs (J. T. Turner 2015; Longhurst and Glen Harrison 1989).

In this study, we investigated the patterns of diversity in both surface-associated fish (pelagic group) and benthic-associated fish (demersal group). We expected that the demersal offshore fishes would not interact directly with surface energy signals (PAR and SST) (Table 2), but rather would be affected by the energy source of POC that sinks to the deep ocean. Our results support our expectation, as benthic POC was only in agreement with the cumulative and minimum hypotheses in the demersal group fishes in both the shallow and offshore region tests. The benthic POC energy map (Fig 3) shows higher cumulative and minimum POC values in shallower areas (continental shelves and mid-ocean ridges), as compared to the deep abyssal plain areas. Gagne et al 2020 demonstrated that ocean depth was a significant driver of their neural network model. Our results suggest that using depth in a model may actually be a proxy for benthic energy flux.

Interestingly, even though reef fish are substrate-associated like the demersal group, their results showed different patterns. The richness of reef fish follows all three energy biodiversity hypotheses in the cases of PAR and SST, but not in the metabolic energy proxies like the demersal fishes did. In chlorophyll, VGPM, and benthic POC, only the variation hypothesis was supported, and for cumulative and minimum energy we found significant negative regressions (opposite to the biodiversity hypotheses). These results may be due to the unique nature of reef systems. Reefs are found in oligotrophic waters, where nutrient limitations suppress planktonic algae growth and productivity, but corals are highly productive (Darwin 1976; Sammarco et al. 1999). This paradox is likely resolved by the fact that corals with their symbiotic zooxanthellae are highly efficient at uptake and recycling of nutrients (Wild et al. 2004; de Goeij et al. 2013). Overall coral reefs contribute an estimated 0.05% of global carbon fixation, much of which is recycled within the coral tissue itself, however approximately  $20 \times 10^{12}$  g of carbon per year is produced in excess and exported to the surrounding environments (Douglas 2009; Crossland, Hatcher, and Smith 1991). In this study, we only included surface-measured planktonic productivity, not benthic energy sources like coral. Potentially more detailed construction of the energy proxies including benthic energy sources on coral reefs would yield a better test of the energy biodiversity hypotheses in the case of reef fishes.

While outside the scope of this study, the energy biodiversity hypotheses should continue to be tested in the future with more marine richness data. First, there is currently only a subset of fish species which have expert-defined ranges (4000 spp). This study should be repeated with fish data as more comprehensive species range

maps are become available in the ocean. Second, this analysis could be expanded to many other groups of organisms, defined by either taxa or functional groups. For example, the response of marine mammal or reptile richness to environmental energy could be compared to their terrestrial counterparts, or the distributions of primary consumers or tertiary predators in both environments could be compared. It would also be interesting to investigate the response of organisms that are sessile (benthic invertebrates). As fish are mobile organisms, in many cases they could shift their range on a relatively short time scale in response to environmental conditions and food availability (Nye et al. 2009; US EPA 2016). However individual adults of sessile species can't escape local conditions as readily. Instead, their range shifts would depend on broadcast spawning and recruitment to suitable conditions, so they might have a slower response to changes in energy availability.

Under climate change, the energy proxies investigated in this study will likely change. Solar irradiance delivered to the top of Earth's atmosphere will continue following normal solar cycles (average  $\pm 1 \text{ Watt m}^{-2}$ ) (Lindsey 2021), but changes in cloud cover will affect the irradiance that reaches Earth's surface. Cloud cover is expected to decrease at low latitudes and increase in thickness at high latitudes (R. G. Williams, Ceppi, and Katavouta 2020), so the latitudinal pattern in the sunlight energy proxy will remain but the intensity of the gradient between low and high latitudes could increase. Cumulative and minimum values in sunlight will increase near the equator and decrease in low latitudes. Changes in cloud cover are predicted to contribute an overall warming effect in addition to greenhouse gas warming. The IPCC's Fifth Assessment report stated that over 90% of the heat from greenhouse gas emissions since 1970 had been absorbed by global oceans, causing rising

temperatures, and they predict 1-4°C ocean warming on average by 2100 (IPCC 2014). Predictions of the spatial variation in surface ocean warming are expected to partially depend on ocean circulation patterns. Upwelling of deep ocean water in the Southern Ocean is expected to have a dampening effect to the warming in that ocean area, in contrast to the more intense warming of the Arctic (Xie 2020). However meridional overturning is also expected to slow (Held and Soden 2006), so it is unclear how much Southern Ocean upwelling will be able to mitigate warming. Additionally, evaporation can dampen surface heating, so areas like the eastern Equatorial Pacific with low mean evaporation would warm relatively quickly (Xie et al. 2010). Overall the cumulative and minimum values of thermal energy would increase globally, with greater increases in the Arctic. Additionally, extreme El Nino events are also expected to become more frequent (Cai et al. 2014), leading to increased SST variation in the Equatorial Pacific.

In addition, the metabolic energy proxies are likely to change in distribution as well. Models disagree about the overall change in ocean primary productivity in the next 100 years, ranging from a global NPP increase of >30% to a decrease of >10% (Bopp et al. 2005; Schmittner et al. 2008; Tagliabue, Bopp, and Gehlen 2011). This lack of consensus is due to differences in model construction, in which environmental factors are considered. Photosynthesis increases with increased temperatures from 0 to 20°C, after which the rate of photosynthesis decreases with further increasing temperature (Hew, Krotkov, and Calvin 1969). So ocean areas that currently are relatively low temperature, such as high latitudes, would likely experience higher rates of photosynthesis as ocean warming progresses and sea ice retreats. However, increased temperatures in low latitude, tropical regions would likely cause decreased photosynthetic rates. Additionally, ocean primary productivity is driven by nutrient

availability via upwelling, and warming will likely cause stronger stratification at the tropics, further contributing to decreased productivity in those areas. Overall cumulative and minimum photosynthesis energy would therefore increase in high latitudes and decrease in low latitudes.

To summarize, the objective of this study was to investigate whether three hypotheses relating energy to the maintenance of biodiversity are relevant to marine fish biodiversity. We found that the energy biodiversity hypotheses are broadly applicable to marine fishes. In general, lower variation, higher minimum, and higher cumulative energy had a relationship to greater fish richness. Our analysis is the first to investigate the underlying patterns of diversity in the global marine fishes from the perspective of the three energy biodiversity hypotheses, and with several types of energy proxies (radiation, thermal, and chemical/metabolic). We found that the radiation and thermal proxies (PAR and SST) supported all three hypotheses relating energy to fish richness in most cases (all-fish, pelagic, reef), except for the deeper dwelling fish group (demersal). These two latitudinally-associated proxies support the idea of energy sources as an explanation of the global Latitudinal Diversity Gradient. In the chemical/metabolic energy analysis, the hypotheses were followed in many cases, often in the variation and minimum energy tests, and including both surface dwelling and deep fishes in the case of primary productivity (VGPM). The hypotheses were less often supported with Chlorophyll or benthic POC as the energy source, with the important exception of the deep dwelling fish group (demersal group), usually in cumulative and minimum energy categories. Overall, this study shows that aspects of available energy support higher biodiversity in fish, as long as the energy source is matched to the environment inhabited by those species groups. These results support

the idea that energy is a fundamental underlying driver of biodiversity on Earth, not limited by the marked differences between terrestrial and marine environments.

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**Appendix**  
**SUPPLEMENTAL FIGURES**

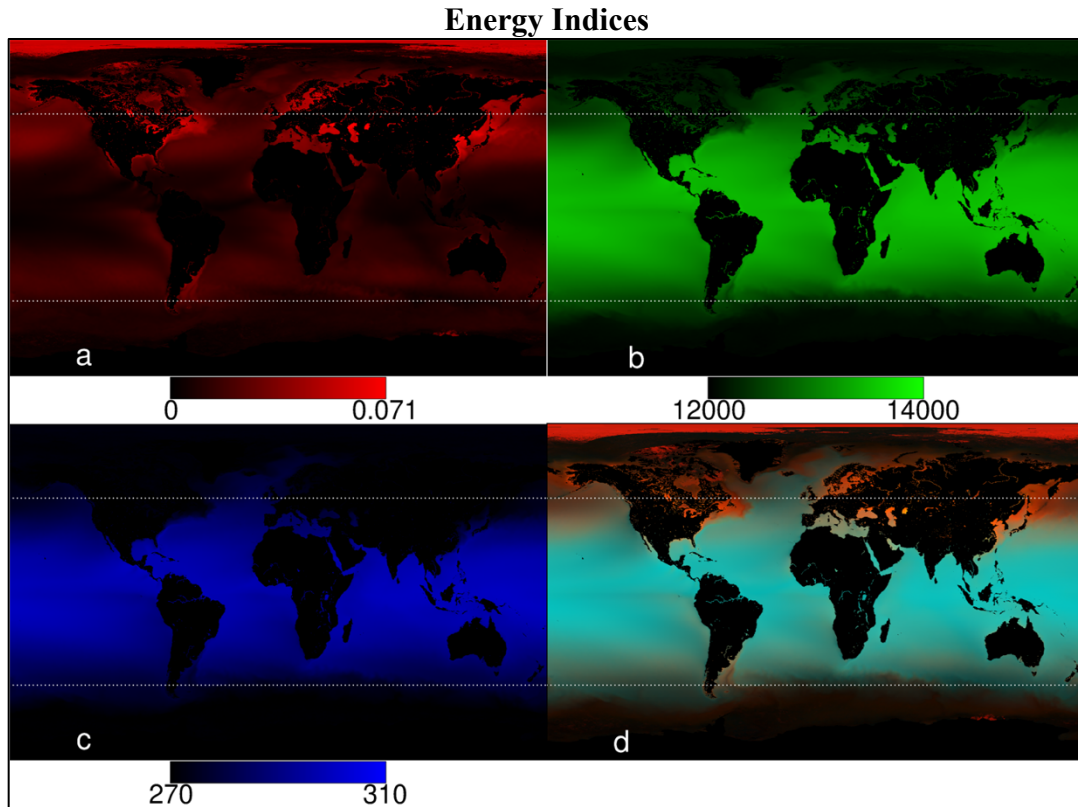


Figure 8 Energy indices calculated from SST (K). Highest variation in SST (a) is seen in the high northern latitudes and along coastlines in upwelling zones (ex. Peru), and in boundary currents (ex. Gulf Stream). Highest cumulative (b) and minimum (c) SST are seen at low latitudes. Combining these indices into a RGB representation show where each of the different indices dominate the signal (d). White dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis.

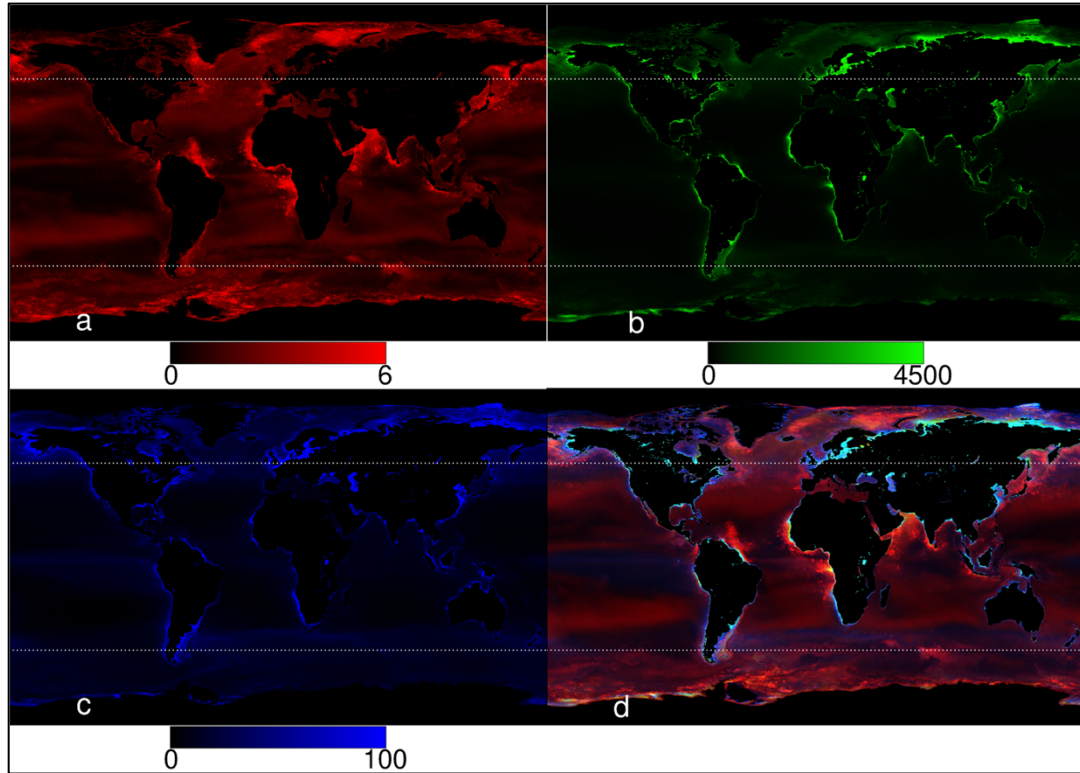


Figure 9 Energy indices calculated from Chlorophyll ( $\text{mg m}^{-3}$ ). These patterns are dominated by distance from coast. Highest annual variation (a), cumulative (b), and minimum (c) values are all found along coastlines. Higher variation is also seen at the edges of ocean basin gyres. Combining these indices into a RGB representation show where each of the different indices dominate the signal (d). White dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis.

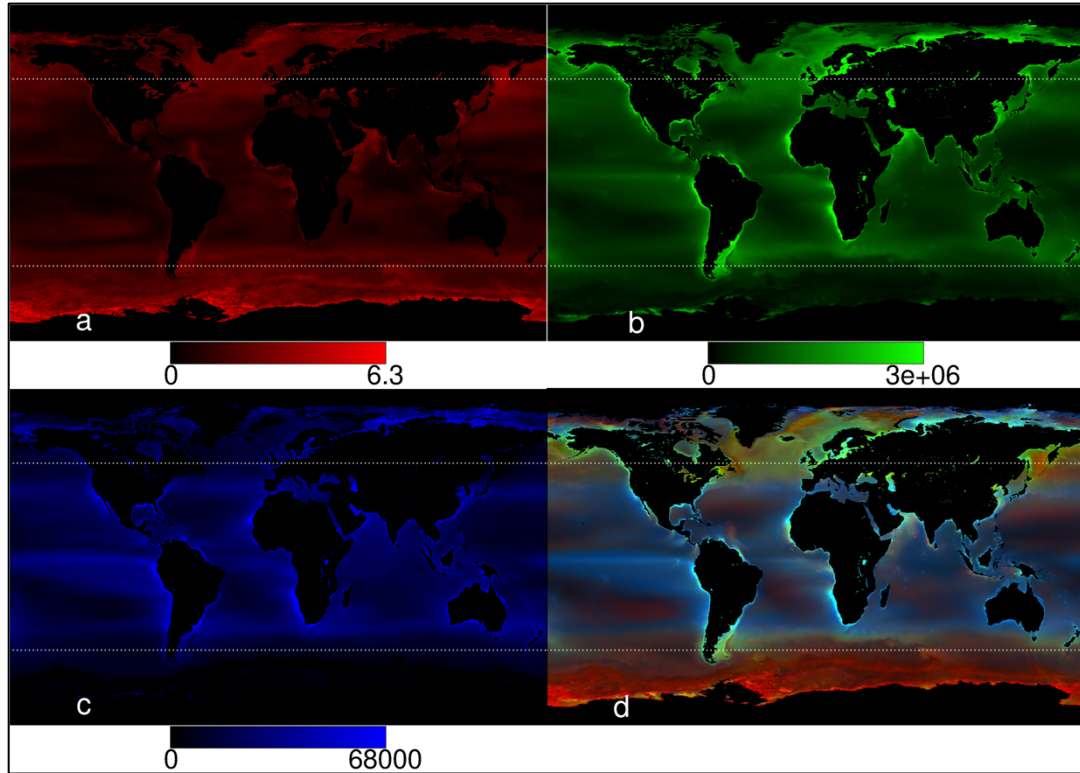


Figure 10 Energy indices calculated from primary production via VGPM ( $\text{mg C m}^{-2}$ ). Highest variation in VGPM (a) is seen at high latitudes. Highest cumulative (b) and minimum (c) values are found near coastlines, and Equatorial upwelling zones. Combining these indices into a RGB representation show where each of the different indices dominate the signal (d). Panel d highlights where oligotrophic centers of ocean gyres are visible (low cum and min, high var). White dotted lines indicate -50 to 50 degrees latitude, the extent of the dataset that was used in regression analysis.

### Results summary tables

Table 3 Results summary of the shallow region tests, organized by fish group (model II regressions, RMA). Green checkmarks indicate significant RMA regressions in agreement with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red x's indicate regressions that significantly disagreed with the hypotheses, and non-significant tests are marked as NS.

		Var	Cum	Min			Var	Cum	Min
All-fish	PAR	✓	✓	✓	Pelagic	PAR	✓	✓	✓
	SST	✓	✓	✓		SST	✓	✓	✓
	Chl	✓	✗	✗		Chl	✓	✗	✗
	VGPM	✓	✗	✓		VGPM	✓	✗	✓
	Benthic POC	✓	✗	✗		Benthic POC	✓	✗	✗
Demersal	PAR	✓	✓	✓	Reef	PAR	✓	✓	✓
	SST	✗	✓	✓		SST	✓	✓	✓
	Chl	✗	✓	✓		Chl	✓	✗	✗
	VGPM	NS	✓	✓		VGPM	✓	✗	✗
	Benthic POC	✗	✓	✓		Benthic POC	✓	✗	✗

Table 4 Results summary of the offshore region tests, organized by fish group (model II regressions, RMA) Green checkmarks indicate significant RMA regressions in agreement with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red x's indicate regressions that significantly disagreed with the hypotheses, and non-significant tests are marked as NS.

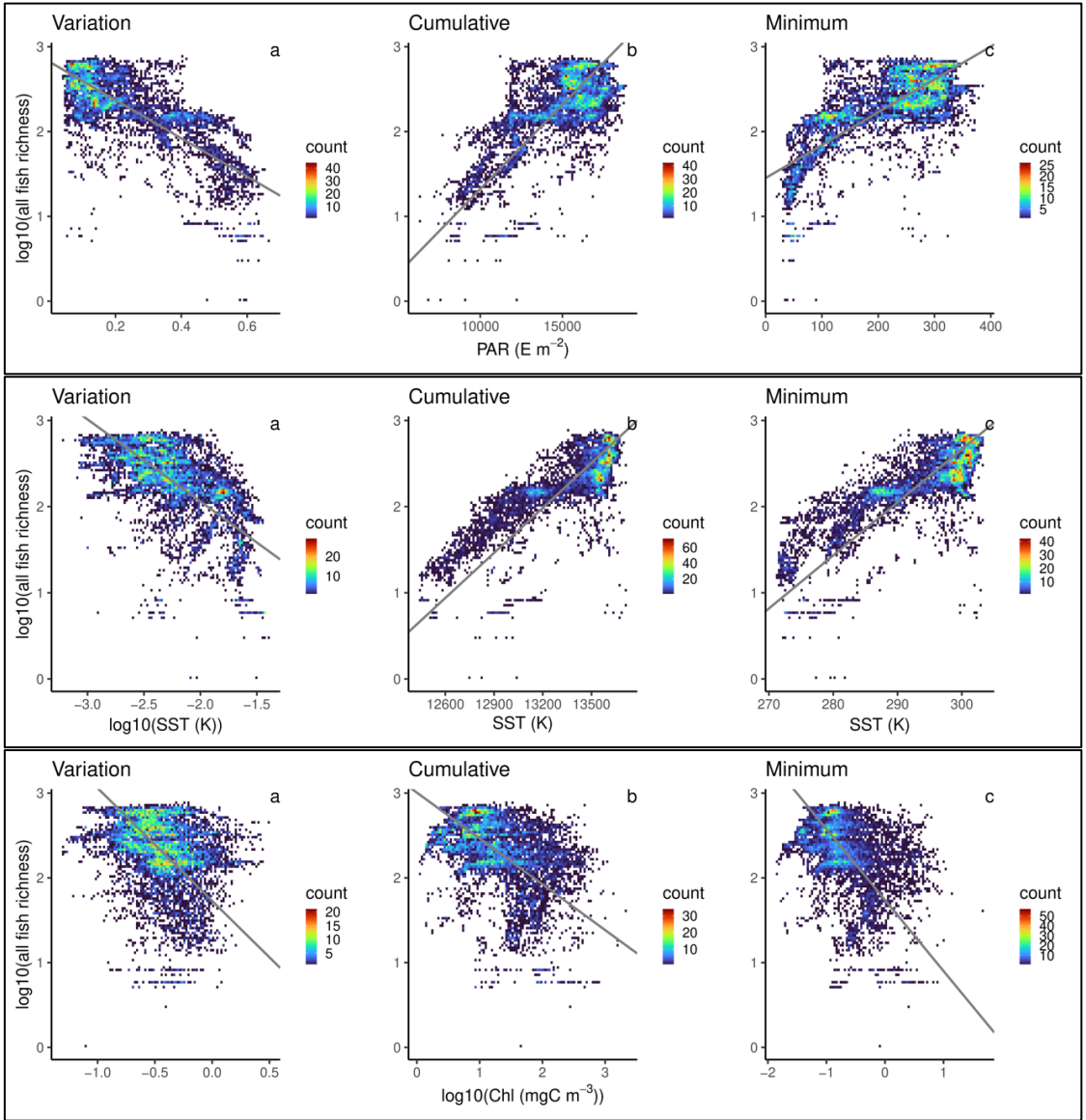
		Var	Cum	Min			Var	Cum	Min
All-fish	PAR	✓	✓	✓	Pelagic	PAR	✓	✓	✓
	SST	✓	✓	✓		SST	✓	✓	✓
	Chl	NS	×	×		Chl	NS	×	×
	VGPM	✓	NS	✓		VGPM	✓	NS	✓
	Benthic POC	NS	NS	×		Benthic POC	NS	×	×
Demersal		Var	Cum	Min					
	PAR	NS	NS	NS					
	SST	NS	NS	NS					
	Chl	×	✓	✓					
	VGPM	×	✓	✓					
Benthic POC	×	✓	✓						

**All results: shallow region**

Table 5 Correlation results (“r”) from the Model2 regression tests for the shallow region. Green shading indicates that the sign of the correlation agrees with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red shading indicates correlations with slopes that disagree with the hypotheses.

Fish	Energy	var_r	cum_r	min_r
All-fish	PAR	-0.747	0.671	0.698
	SST	-0.582	0.812	0.806
	Chl	-0.276	-0.408	-0.378
	VGPM	-0.567	-0.395	0.105
	POC	-0.365	-0.402	-0.381
Pelagic group	PAR	-0.638	0.597	0.580
	SST	-0.375	0.708	0.669
	Chl	-0.049	-0.110	-0.109
	VGPM	-0.372	-0.067	0.396
	POC	-0.079	-0.127	-0.127
Demersal group	PAR	-0.057	0.127	0.030
	SST	0.099	0.139	0.109
	Chl	0.269	0.249	0.210
	VGPM	0.017	0.354	0.517
	POC	0.466	0.407	0.383
Reef	PAR	-0.808	0.699	0.761
	SST	-0.644	0.885	0.862
	Chl	-0.346	-0.456	-0.413
	VGPM	-0.588	-0.498	-0.044
	POC	-0.472	-0.500	-0.474





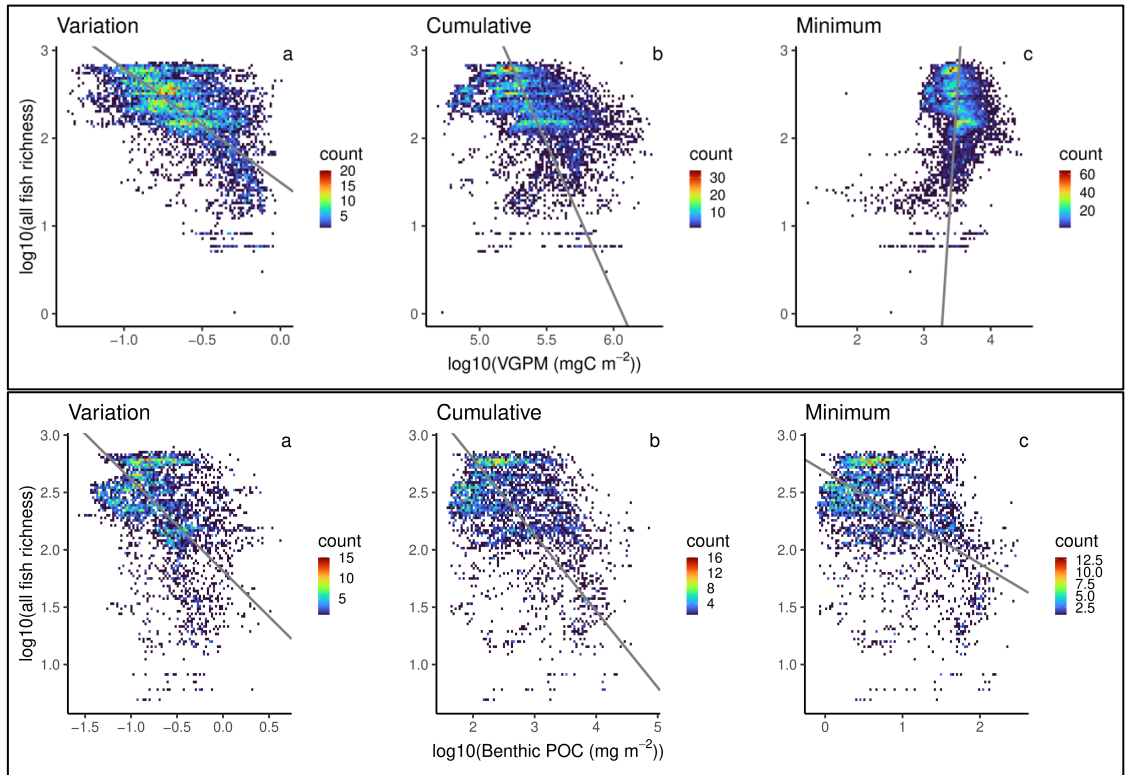
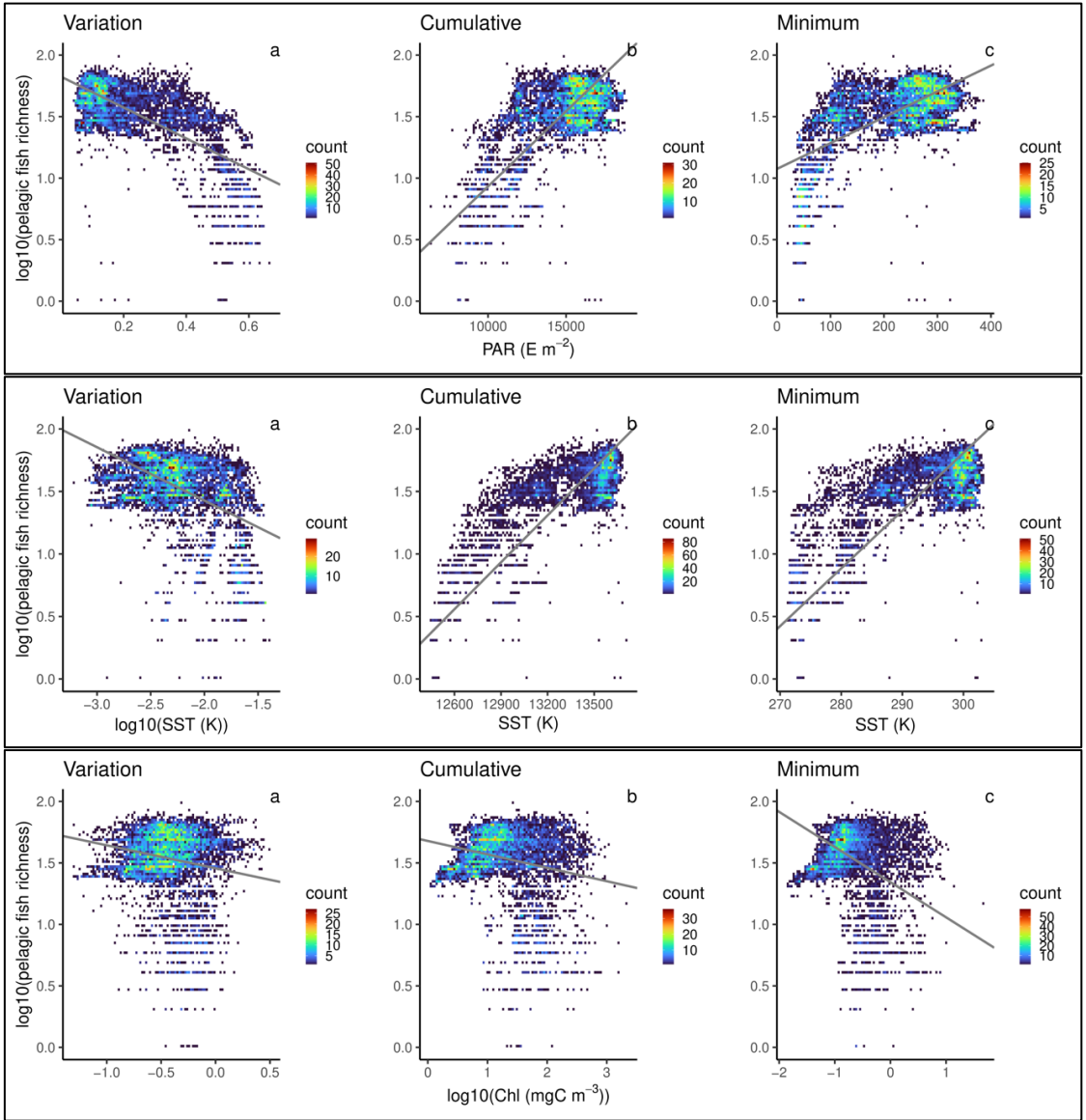


Figure 11 2D density plots of energy groups vs all-fish richness (Shallow region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



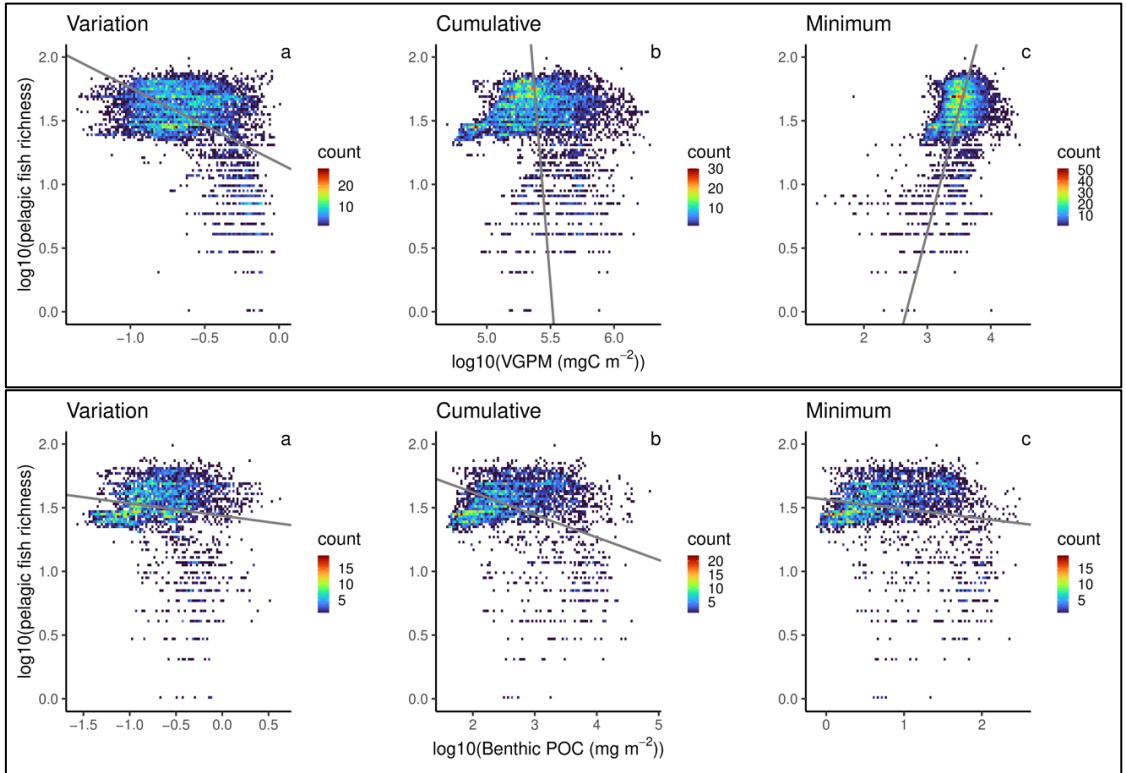
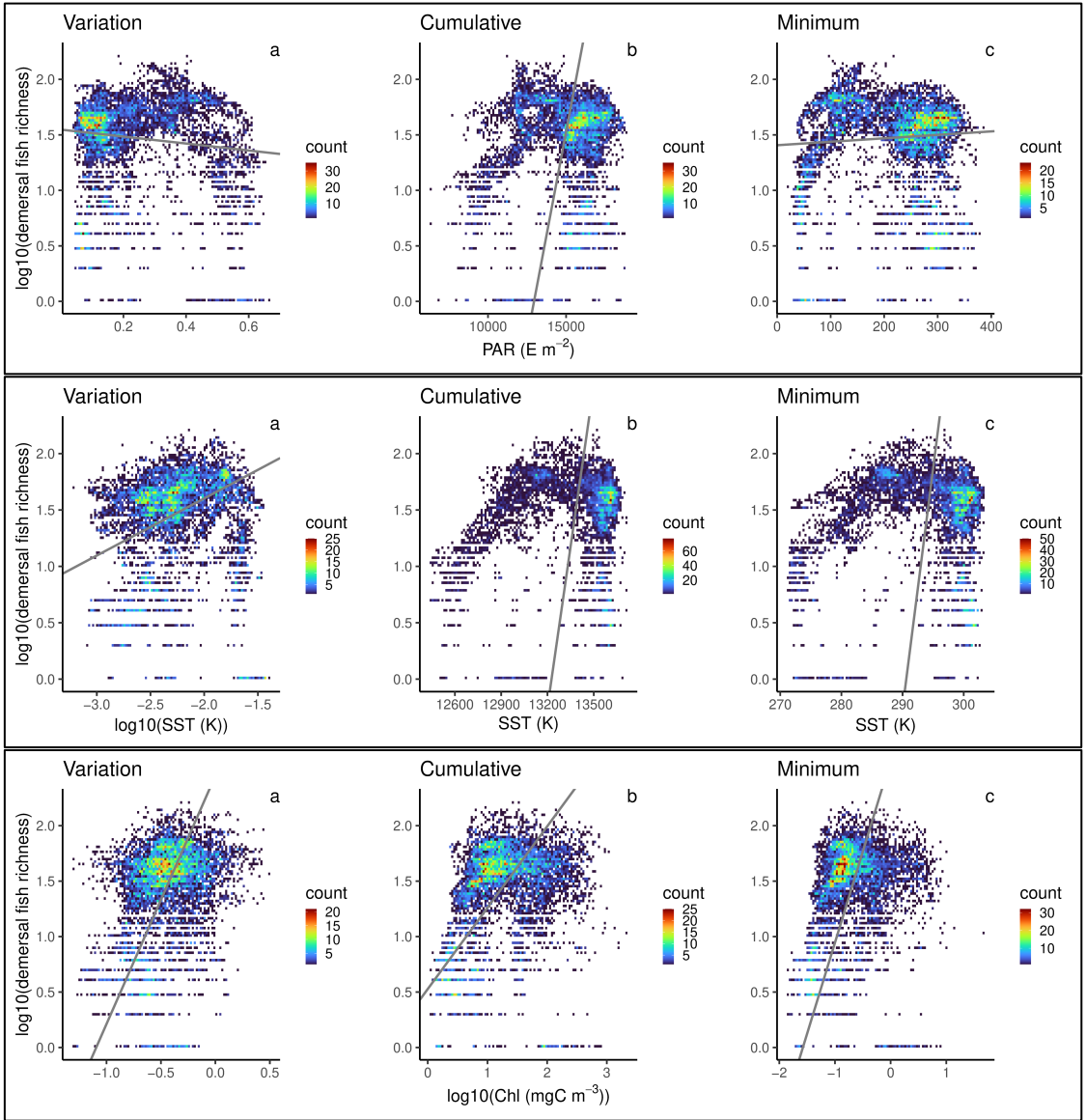


Figure 12 2D density plots of energy groups vs pelagic group fish richness (Shallow region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



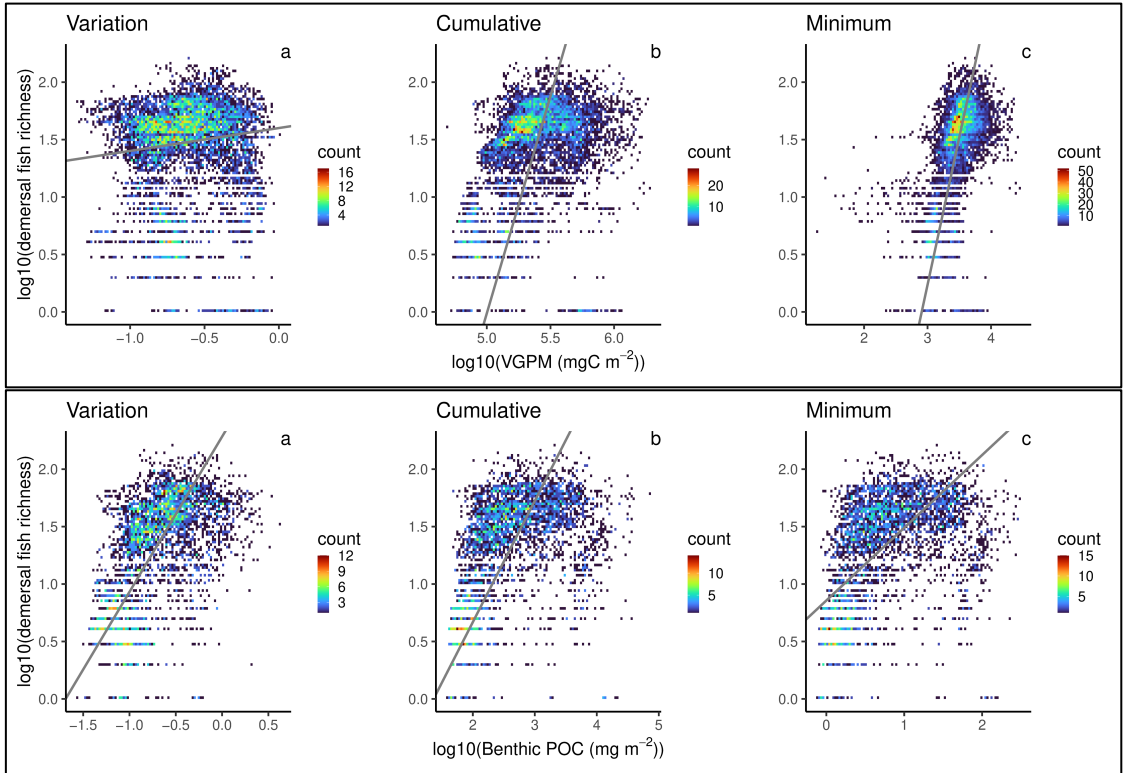
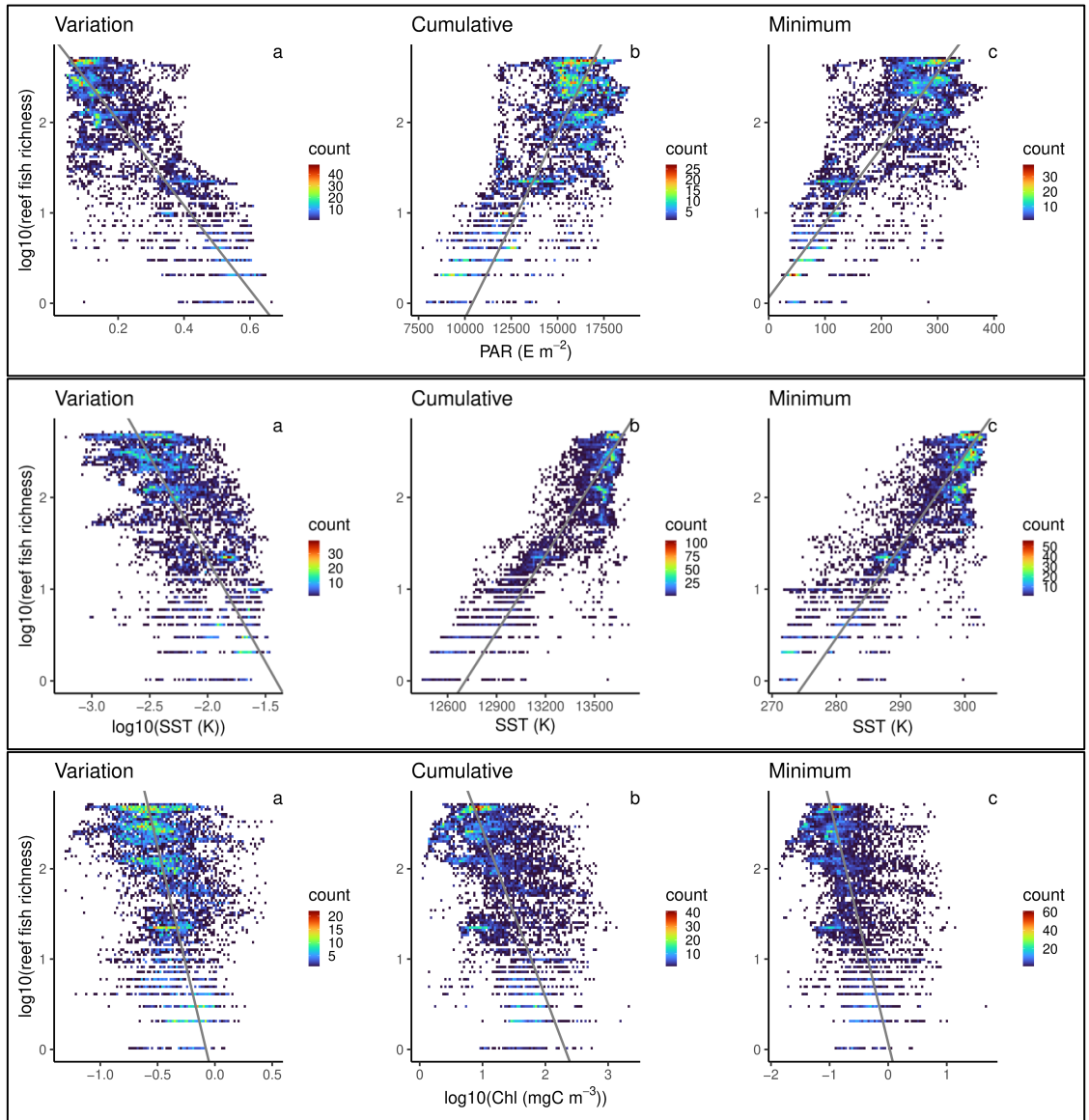


Figure 13 2D density plots of energy groups vs demersal group fish richness (Shallow region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



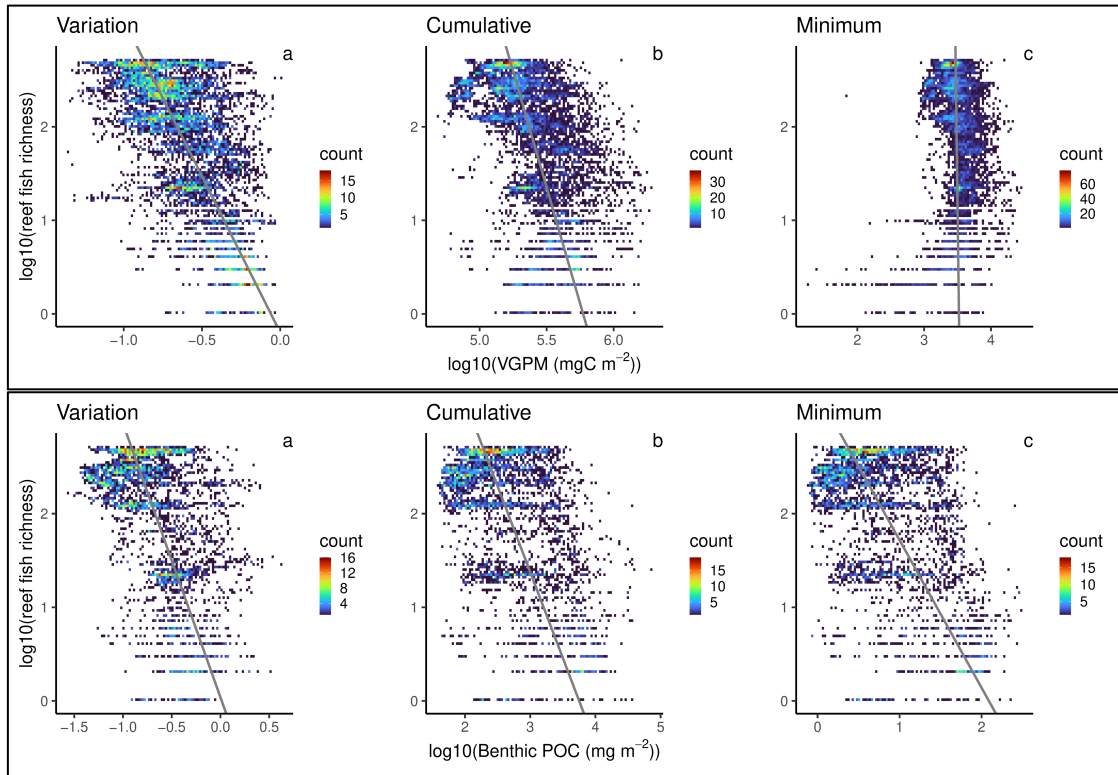


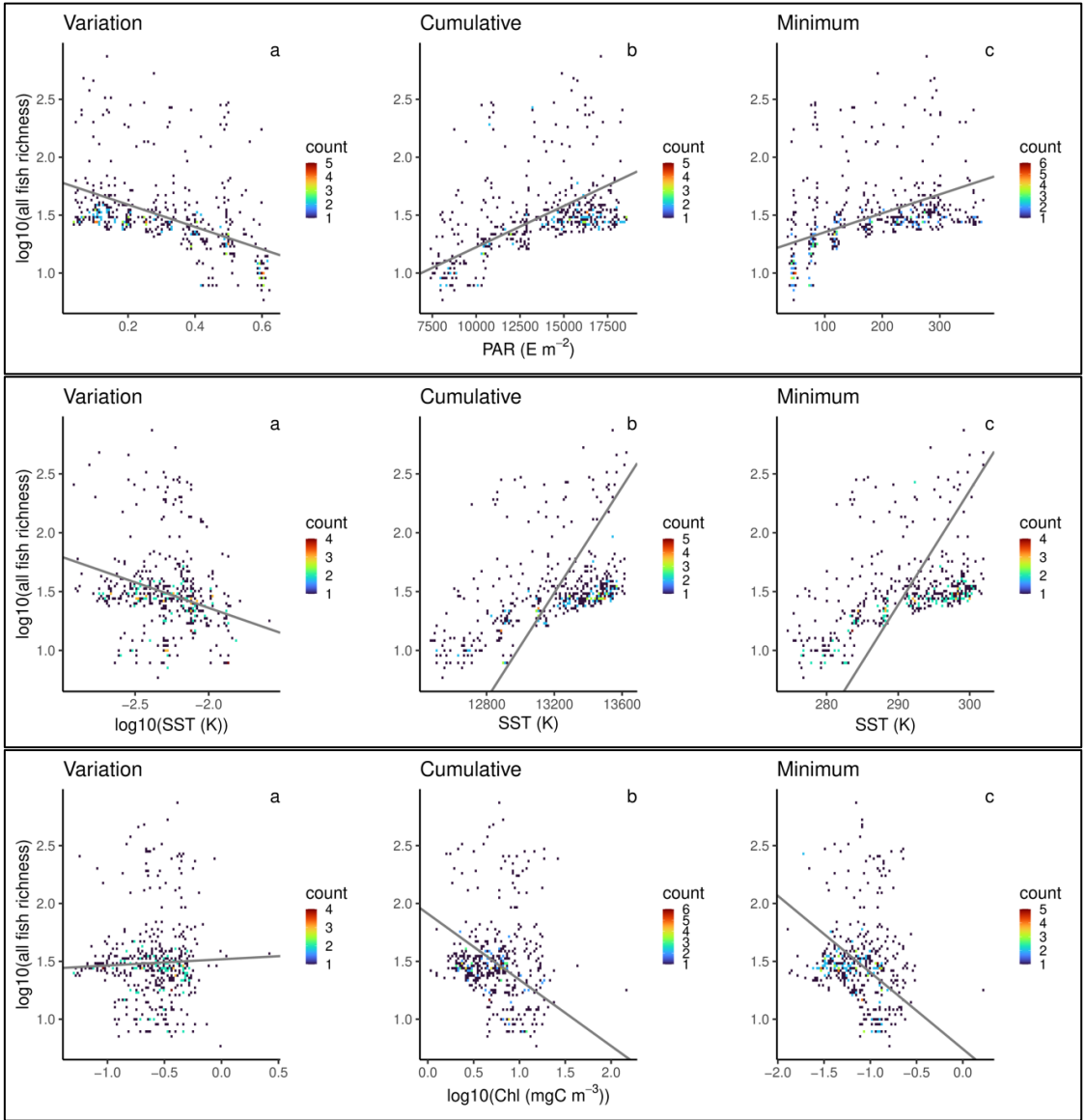
Figure 14 2D density plots of energy groups vs reef fish richness (Shallow region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



**All results: offshore region**

Table 6 Correlation results (“r”) from the Model2 regression tests for the offshore region. Green shading indicates that the sign of the correlation agrees with the energy biodiversity hypotheses: negative slopes for variation, and positive slopes for cumulative and minimum. Red shading indicates correlations with slopes that disagree with the hypotheses.

Fish	Energy	var_r	cum_r	min_r
All-fish	PAR	-0.432	0.435	0.402
	SST	-0.171	0.485	0.475
	Chl	0.015	-0.118	-0.122
	VGPM	-0.210	0.094	0.316
	POC	0.034	-0.096	-0.140
Pelagic group	PAR	-0.637	0.681	0.616
	SST	-0.275	0.715	0.709
	Chl	-0.043	-0.296	-0.284
	VGPM	-0.395	0.049	0.470
	POC	-0.022	-0.256	-0.304
Demersal group	PAR	0.106	-0.125	-0.125
	SST	0.152	-0.094	-0.110
	Chl	0.214	0.296	0.241
	VGPM	0.214	0.322	0.150
	POC	0.251	0.307	0.257



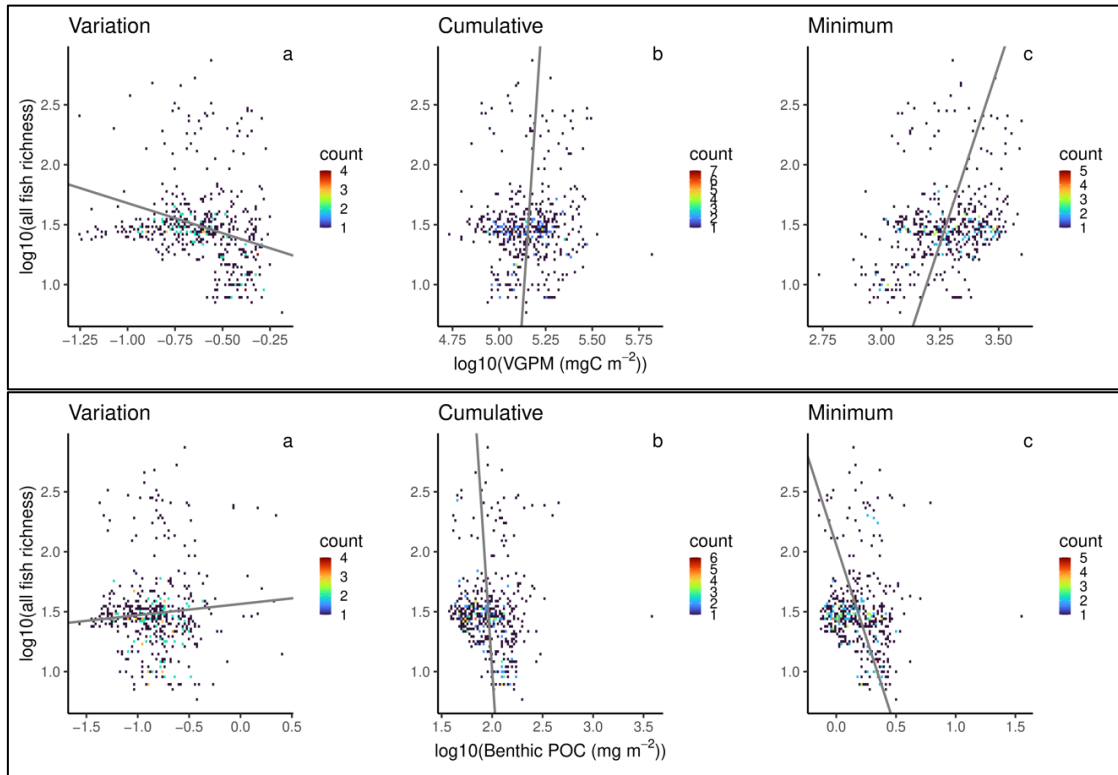
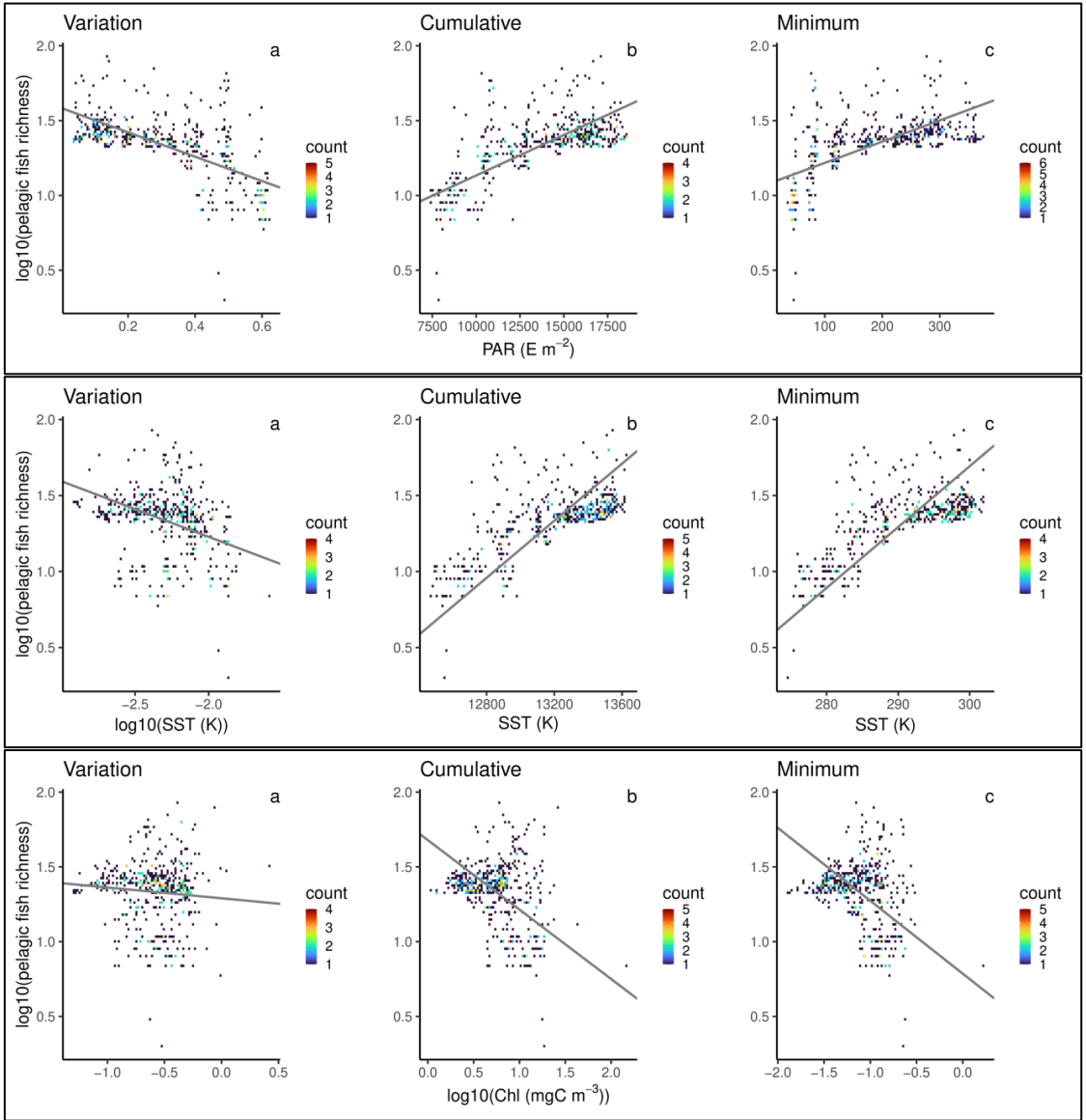


Figure 15 2D density plots of energy groups vs all-fish richness (Offshore region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



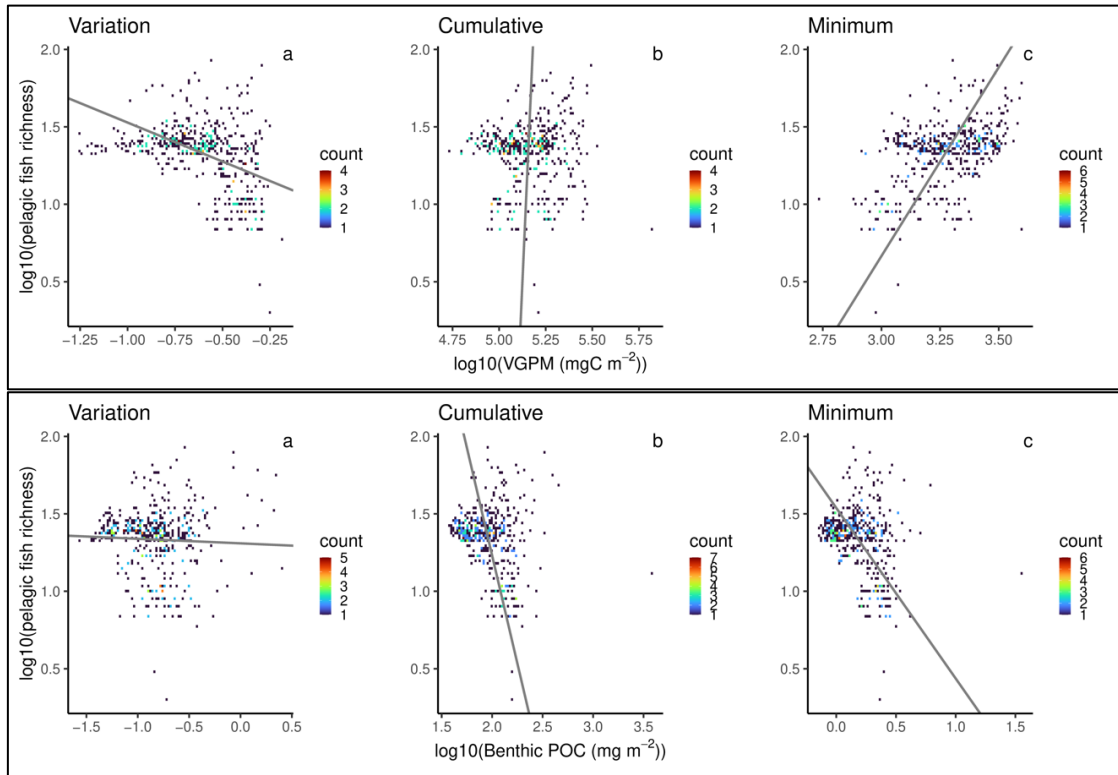
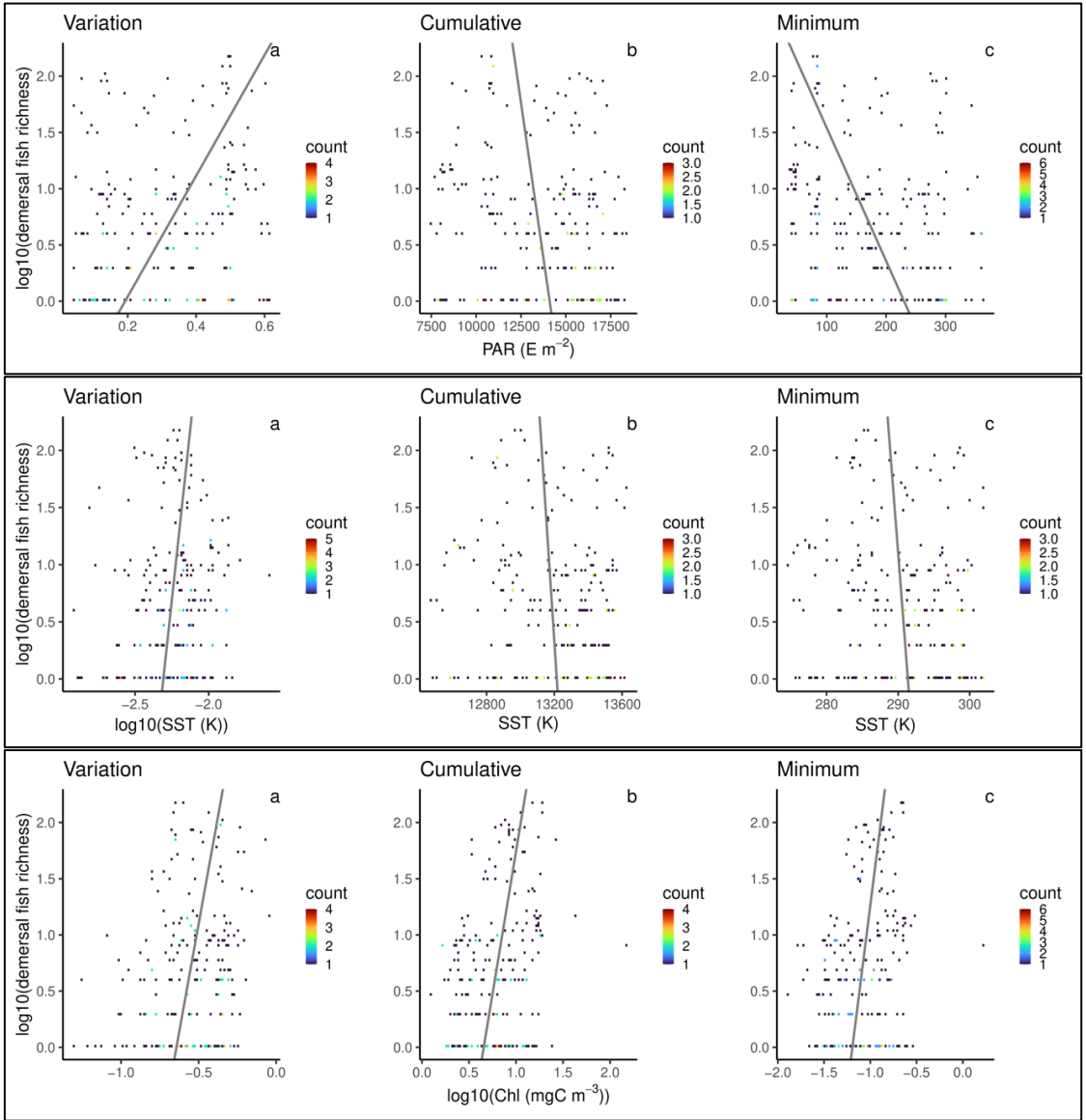


Figure 16 2D density plots of energy groups vs pelagic group fish richness (Offshore region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray



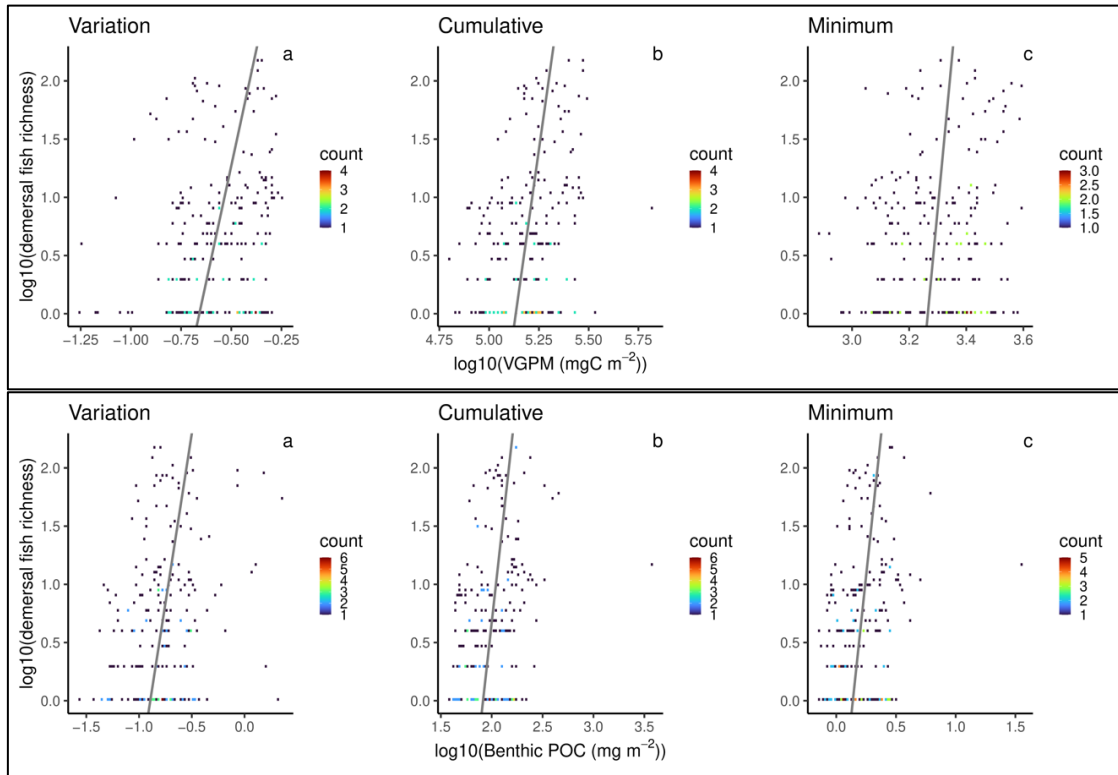


Figure 17 2D density plots of energy groups vs demersal group fish richness (Offshore region). By row, the energy groups are: PAR, SST, Chlorophyll, VGPM, and Benthic POC. All data were limited -50 to 50 degrees latitude. Ranged Major Axis regression lines shown in gray