Disentangling the impacts of environmental change and commercial fishing on demersal fish biodiversity in a northeast Pacific ecosystem

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ABSTRACT: Conservation of marine biodiversity requires understanding the joint influence of ongoing environmental change and fishing pressure. Addressing this challenge requires robust biodiversity monitoring and analyses that jointly account for potential drivers of change. Here, we ask how demersal fish biodiversity in Canadian Pacific waters has changed since 2003 and assess the degree to which these changes can be explained by environmental change and commercial fishing. Using a spatiotemporal multispecies model based on fisheries independent data, we find that species density (number of species per area) and community biomass have increased during this period. Environmental changes during this period were associated with temporal fluctuations in the biomass of species and the community as a whole. However, environmental changes were less associated with changes in species occurrence. Thus, the estimated increases in species density are not likely to be due to environmental change. Instead, our results are consistent with an ongoing recovery of the demersal fish community from a reduction in commercial fishing intensity from historical levels. These findings provide key insight into the drivers of biodiversity change that can inform ecosystem-based management.

KEY WORDS: Biodiversity change · Environmental change · Groundfish · Ecosystem-based management · Marine spatial planning · Temperature · Fishing · Species richness · Community biomass

1. INTRODUCTION

Effective management of marine ecosystems requires an understanding of how species assemblages are responding to increasing rates of environmental change and impacts of human activities (Doney et al. 2012, Halpern et al. 2015, Smale et al. 2019). This is reflected in the current focus on ecosystem-based management, which emphasizes decisions that consider the full community of species present, their interactions with one another, and the environmental

conditions, as well as fisheries and other socio-economic factors (Long et al. 2015). Marine spatial planning, which strives to balance competing human demands with conservation goals in a spatially explicit way, is increasingly used as an approach to achieve ecosystem-based management (Douvere 2008, Frazão Santos et al. 2019). To facilitate the shift from traditional single-species-based management to the spatially explicit and multispecies approach needed for ecosystem-based management and marine spatial planning, monitoring and analysis of the

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community assemblage as a whole is required. In particular, there is a need to understand what factors determine the composition and diversity of the marine communities and how these communities are changing through time in response to ongoing environmental change and human activities.

In Canadian Pacific waters, the demersal fish community is a diverse assemblage of more than 100 species, many of which are targeted by commercial fisheries (DFO 2021). Demersal fish — often referred to as groundfish in the fisheries context (e.g. Anderson et al. 2019, DFO 2021) — occupy the continental shelf and associated slope in the Northern and Southern Shelf Bioregions. The distribution of the Northern Shelf Bioregion overlaps with the Pacific North Coast Integrated Management Area (PNCIMA; 1 of 5 priority areas for integrated ocean management planning in Canada). The goals and objectives of the ecosystem-based management framework outlined in the PNCIMA plan include: (1) maintaining the integrity of marine ecosystem structure, function, and resilience, and (2) improving our understanding of marine ecosystems in a changing marine environment (PNCIMA 2017).

There is considerable knowledge about the spatial and temporal variation of individual demersal fish species in Pacific Canada (Anderson et al. 2019), but there is limited understanding of how these patterns scale up to the community as a whole. The community is highly structured in space, corresponding to relatively static environmental conditions such as depth and seafloor substrate (Perry et al. 1994, Fargo 2012, Rubidge et al. 2016). However, knowledge of how the responses of species to changing climate and oceanographic conditions are impacting the community over time is lacking. Recent decades have seen an increase in extreme climatic events, including the marine heatwave that impacted the region from late 2013 to 2016 (Tseng et al. 2017). Periods of hypoxia are also increasing in frequency on the continental shelf (Crawford & Peña 2020), and there is evidence that these changes in temperature and dissolved oxygen may have caused local-scale shifts in population density of many species (English et al. 2022). However, it has yet to be determined how changes in other oceanographic conditions such as currents and primary production (Peña et al. 2019) may be impacting the demersal fish community. Understanding how this wide range of environmental variables combines to influence the distributions and dynamics of individual species is needed to provide an assessment of how environmental change is impacting the biodiversity and composition of the overall demersal fish community across space and time.

The demersal fish community in Pacific Canadian waters has long supported harvesting by commercial, recreational, and First Nations food and ceremonial fisheries (DFO 2021). Over the past decades, several spatial and non-spatial management interventions have been implemented in the commercial fishery with the goal of achieving a sustainable harvest. Individual transferable quotas, 100% at-sea observer coverage, and the deduction of discard mortality from quotas were implemented for the commercial trawl fishery over the period 1992–1997 (Turris 2000, Davis 2008) and for the longline and trap fisheries in 2006 (Stanley et al. 2015). Rockfish conservation areas (RCAs) that are closed to fishing that leads to substantial rockfish catch were established between 2004 and 2006 (Yamanaka & Logan 2010). Although RCAs are located in non-trawlable habitats (i.e. rocky reefs), their establishment may have indirectly impacted the composition of the demersal fish community in adjacent soft bottom areas, as many species are found in both habitats. In 2012, several additional measures were implemented to reduce habitat impacts of bottom trawling (Wallace et al. 2015). These included an ecosystem-based trawling footprint for the bottom trawl fishery, a measure co-led by the commercial industry and environmental groups, which limited commercial trawling to a subset of the region. Stock assessments have been completed for some species (16 species, 24 stocks, described by Anderson et al. 2021) that are targeted by the fishery. On average, stock status is estimated to have declined over the period of 1950 to around 2000, after which they stabilized, coinciding with the implementation of the management measures described above (Anderson et al. 2021). However, how these various management measures may have impacted the fish community as a whole, or if these measures resulted in conservation benefits for biodiversity, has not yet been examined.

Documented biodiversity changes in other marine regions provide an expectation for how the demersal fish community in Canadian Pacific waters may be changing. Multi-decade increases in species richness of benthic invertebrate and fish assemblages were observed in 8 of the 9 North American regions considered (Batt et al. 2017), but Canadian Pacific waters were not assessed, nor were the specific drivers of these increases. A meta-analysis of local-scale trends in marine species richness found that biodiversity losses are often associated with direct human impacts, while less impacted areas and those where

human impacts have been reduced are generally associated with biodiversity increases via range expansions, invasions, and population recoveries (Elahi et al. 2015). A related synthesis found that, in temperate regions, sea surface warming is often associated with increases in species richness and community abundance (Antão et al. 2020); however, non-climatic drivers of biodiversity change that could covary with warming, such as changes in fishing effort, were not assessed. Because individual species vary in their responses to change, measuring species richness alone can mask important changes to community composition (i.e. the identity and relative abundance of species) that could signal broader ecosystem changes (Hillebrand et al. 2018). Thus, richness is best interpreted in concert with assessments of the dynamics of the component species, as well as metrics such as species diversity (Jost 2006) that take abundance into account (Hillebrand et al. 2018).

Here we use a multispecies hierarchical model to estimate spatial and temporal changes in the biodiversity and composition of the demersal fish community in Canadian Pacific waters, based on fisheries-independent research trawl surveys over the period 2003 to 2018. We use this model to assess how a range of environmental variables, historical management measures, and commercial fishing pressure structure the composition of the community across space, and to determine which factors are responsible for driving changes in the community through time. Note that, from here on, we use the term species density, as opposed to species richness, to indicate that our measure of species number is standardized by area (i.e. the average area sampled by a survey trawl; Gotelli & Colwell 2011). With this analysis we test the following hypotheses: H1 — if the composition of the community is jointly structured by a suite of oceanographic conditions, then a model that includes relevant oceanographic variables will have greater predictive power than one that only includes depth and time. H2 — if changing environmental conditions and localized commercial fishing effort are the primary drivers of temporal changes in community composition, then changes in species occurrence and biomass should be predictable based on environmental covariates and measures of local fishing pressure. H3—if the 2013–2016 marine heatwave negatively impacted demersal fish, then species density, diversity, and community biomass should be lower in years when temperature is higher than average or oxygen is lower than average. H4 — if management interventions on the commercial fishery that preceded and coincided with the start of the research trawl surveys had a positive im-

pact on the community, then we predict overall increases in species density, diversity, and community biomass through time. While stock assessments focus on individual species of commercial or conservation interest, our analysis provides insight into the broader assemblage of species. Thus, our analysis can inform ongoing ecosystem-based management in this region by providing a unique understanding of the structure and functioning of the demersal fish community and how it is changing in response to ongoing environmental change.

2. METHODS

2.1. Demersal fish database

Our analyses are based on the Groundfish Synoptic Bottom Research Trawl Surveys that are conducted by the DFO for stock assessment research (Sinclair et al. 2003). The surveys are conducted between May and September and follow a random depth-stratified design with 2 km^2 sampling blocks throughout 4 regions (for map see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m689p137_supp.pdf): Queen Charlotte Sound (QCS), Hecate Strait (HS), West Coast Haida Gwaii (WCHG), and West Coast Vancouver Island (WCVI). Sampling was conducted in odd years since 2003 in QCS and 2005 in HS. QCS was also sampled in 2004. Sampling was conducted in even years starting in 2004 in WCVI and 2006 in WCHG. WCHG was also sampled in 2007. This analysis includes all survey years until 2018. Subsequent years were not included because we lack corresponding environmental covariates for these years.

We conducted our analysis on the cartilaginous and bony fish species caught in the surveys that were present in at least 15% of all trawls over the depth range in which they were caught. We defined this depth range as that which included 95% of all trawls in which that species was present. This cut off was used because the model failed to converge when rarer species were included in the analysis. We opted to use this depth coverage threshold rather than a raw count threshold to avoid excluding species that are always present in the deepest depths where we have fewer trawls (Fig. S2). The final dataset used in our analysis consisted of 57 species (Table S1). Although the surveys are best suited to sampling species found over soft substrates, they also catch species that are more associated with rocky substrates or the pelagic environment, and which may be better sampled by other methods. Nevertheless, many of these species

are caught frequently by the trawl research survey and so do form a component of the demersal fish community. Thus, we opted to keep them in our analysis if they meet our inclusion criteria because our model can still provide valuable inormation about their contribution to community dynamics and composition. However, to maintain transparency, we distinguish these species when presenting species-level data. Further details on the survey data used are provided in Text S1.

2.2. Spatiotemporal multispecies hierarchical model

We modeled the spatiotemporal dynamics of the demersal fish community using the Hierarchical Modeling of Species Communities (HMSC) framework and package (Tikhonov et al. 2021) in R v.4.0.2 (R Core Team 2021). This framework uses Bayesian inference to fit a multivariate hierarchical generalized mixed model (Ovaskainen & Abrego 2020). We modeled community dynamics using a hurdle model (Barry & Welsh 2002, Shelton et al. 2014), which consists of 2 sub models: a presence–absence model and a biomass model that is conditional on presence (referred hereafter as the conditional biomass model). For the presence–absence model, we modeled the presence of species j in trawl i as: $y_{ij} \sim$ Bernoulli $(\Phi(L_{ij}))$, using a probit link function with a cumulative distribution of $\Phi(L_{ij})$. For the conditional biomass model, we modeled the log biomass of species j in trawl i as: $y_{ij} \sim$ Normal(L_{ij}, σ^2). The symbol L_{ij} represents a linear predictor derived from the fixed and random effects in the model: $L_{ij} = L^F_{ij} + L^R_{ij}$. A full description of the HMSC model as well as details on model fitting and assessment are provided in Texts S2–S4.

2.2.1. Fixed effects — environmental covariates. As fixed effects in both models, we included oceanographic and bathymetric covariates that were previously identified as potentially influencing the distribution and abundance of demersal fish in this region (Nephin et al. 2020). We assessed the correlation between all variables in our model. Depth was highly correlated with temperature (−0.94) and oxygen (−0.83), and so we opted to use deviations for these 2 variables instead of their raw values (see Text S4 for details). These deviations represent positive or negative yearly anomalies of temperature or oxygen at a given location and so allow us to account for year-to-year variation associated with climate cycles (e.g. El Niño Southern Oscillation and the Pacific Decadal Oscillation). The highest correlation between the en-

vironmental variables used in our model was −0.46 (depth and primary production) (Fig. S3).

Our final list of environmental covariates included those that vary spatially but not temporally: bottom depth (log m), bathymetric position index (BPI), mean summer tidal speed (m s^{-1}; based on 3 h means), substrate muddiness, substrate rockiness, whether the trawl was inside or outside of the ecosystem-based trawling footprint, and survey region (QCS and HS vs. WCVI and WCHG); and covariates that vary in both space and time (Fig. S4): mean summer near-bottom temperature deviation (°C), mean summer near-bottom dissolved oxygen deviation (mmol m^{-3}), and mean summer cross-shore and along-shore current velocities near the seafloor (current velocity; m s^{-1}), mean summer depth-integrated primary production (primary production; gC m^{-2} d^{-1}), and local-scale (3 km^2) commercial fishing effort (log h km^{-2} yr^{-1}). Mean summer values represent the period from April to September, to correspond with the months in which the trawl surveys were conducted. We also included the linear effect of the year in which the trawl was collected. We used a third-order polynomial for bottom depth and a second-order polynomial for BPI to allow for species occurrences and biomass estimates to peak at intermediate values. We initially fit a second-order polynomial for depth but found that the symmetrical quadratic relationship with depth was a poor fit for many species and led to unrealistically high biomass estimates in the shallowest and deepest depths considered. All fixed effects were included additively without interactions, except for temperature deviation, oxygen deviation, and local-scale commercial fishing effort. Temperature and oxygen deviation were allowed to interact with the linear effect of bottom depth to allow the effect of warm vs. cold years (or high oxygen vs. low oxygen years) on species to vary with depth. Local-scale commercial fishing effort was allowed to interact with the trawling footprint. This allowed us to separate temporal changes in fishing effort that were due to the 2012 establishment of the ecosystem-based trawling footprint, compared to temporal changes in fishing effort in areas where fishing effort was permitted throughout the study period. To test for overfitting and to assess the importance of the environmental variables in the model, we also fit a second set of models that only included bottom depth, survey region, and year as fixed effects.

The substrate layers were obtained from a substrate model (Gregr et al. 2021), the oceanographic layers (bottom temperature, dissolved oxygen, tidal and circulation speeds, primary production) were obtained from a hindcast simulation of the British Co-

lumbia continental margin (BCCM) model (Peña et al. 2019), which is an implementation of the Regional Ocean Modeling System (ROMS) at a 3 km horizontal resolution (Haidvogel et al. 2008). Local scale commercial fishing effort was calculated from commercial fishing records. Further details on the environmental layers are provided in Text S4.

At the scale of the entire study region, there was a nearly linear decrease in commercial bottom trawl fishing effort through time, both measured as the total number of hours fished and as the total number of 3 km grid cells where any fishing occurred in a given year (Fig. S5). This 3 km scale was chosen to be small enough to capture areas where fishing effort is focused, while being large enough to smooth out smaller scale quasi-random variation in where the commercial effort occurred on any given year. Even so, this measure of local-scale fishing effort had high spatial variability from year-to-year and so the overall trend is much clearer when fishing effort is aggregated across the entire study region on a yearly basis (Fig. S5). However, because the decrease in coastwide commercial fishing effort was effectively linear, we elected to take a conservative approach and model these long-term changes using the fixed effect of year, rather than using the long-term coast-wide decrease in commercial fishing effort, as this makes clear the possibility that temporal trends may be due to factors other than changes in coast-wide fishing effort. We take this temporal decrease in coast-wide scale fishing effort into account in our interpretation of the temporal trends in the model.

2.2.2. Species trait data. HMSC uses a hierarchical structure to model how responses of species to the environmental covariates depend on species traits. As traits, we used maximum depth (log-transformed) and habitat preference (i.e. water column position or substrate association; Table S1) obtained from the rfishbase package (Boettiger et al. 2012). For maximum depth, we used the common deep depth trait from FishBase (Froese & Pauly 2016), when available. Otherwise, we used the maximum depth trait. We selected these 2 traits because we expected them to be informative of species depth and substrate type associations, which prior studies had identified as key determinants of the composition of the community (Perry et al. 1994, Fargo 2012, Rubidge et al. 2016). We included traits to improve model fit and convergence, rather than because we wanted to test specific hypotheses associated with traits, and so we chose not to extend our analysis to additional traits.

2.2.3. Random effects. We used random effects to model variation in the demersal fish community that is not associated with our fixed effects. This was done using a temporal random effect with a Gaussian Process prior with year of collection as the temporal coordinates. Further details on the structure of the temporal random effect and the priors used are provided in Text S2. We elected to include year as both a linear fixed effect and a Gaussian Process because such random effects are able to capture temporal trends over subsets of the time series but are not well suited to capturing overall linear trends (G. Tikhonov pers. com.). We initially fit the models using a latent spatial random effect (Gaussian random field) using the Universal Transverse Mercator (UTM) coordinates of the individual trawls. This spatial Gaussian random field had the same structure as the temporal random process, but with spatial coordinates instead of temporal coordinates. However, this model estimated a spatial length scale of autocorrelation of 0. Therefore, we elected to drop the spatial random factor and instead use the identity of the individual trawl as an independent and identically distributed (IID) random variable to account for co-occurrence patterns between species within each trawl, as this model is effectively the same, but runs much faster.

This model structure—spatiotemporal fixed effects, a temporally autocorrelated random effect, but no spatially or spatiotemporally autocorrelated random effects—allows us to estimate spatiotemporal changes in the demersal fish community that are associated with our environmental covariates as well as temporal trends in community composition that are common across the entire study region. However, because spatiotemporal random effects are not currently implemented in the HMSC framework, we cannot account for temporal trends that vary in space across our region but are not associated with our environmental covariates (e.g. Barnett et al. 2021). Thus, we focus our assessment of temporal change at the overall coast-wide scale. For details on model convergence and fit see Text S5.

2.3. Model estimates

2.3.1. Species level. The presence–absence model estimates the probability that a species is caught in an individual trawl. Comparing this value across the region gives us an indication of how widespread a species is. The conditional biomass model estimates how much biomass is expected in a trawl, if that species is caught in that trawl (i.e. conditional on presence). By multiplying these 2 estimates together, we get a non-conditional estimate of the biomass (here-

after referred to as biomass) that would be present in an average trawl.

2.3.2. Community level. For all estimates, we calculated species density as the sum of the estimated occurrence probabilities from the presence–absence model (Ovaskainen & Abrego 2020). We calculated community diversity as Hill-Shannon diversity, which is the exponent of Shannon diversity (Jost 2006), using the estimated biomass values for all species. This metric reflects the relative abundances of species in the community and gives greater weight to species when evenness is high. Community biomass was estimated as the sum of the estimated species biomass values. We calculated all metrics for all 1000 posterior draws of the model. We report the median value across this distribution except when otherwise indicated.

2.3.3. Variation partitioning. We used the Hmsc package (Tikhonov et al. 2021) to partition the variation explained by the fixed and random factors in the model. This estimates variance on a linear predictor scale by summing variance and covariances of predictor contributions within groups of predictors, but ignoring covariances across groups (Ovaskainen & Abrego 2020). For predictor groups, we used: tidal currents and mean summer current velocities together as currents, fishing effort and commercial fishing boundary as fishing, rocky and muddy substrate types as substrate, and all fixed and random year effects as time. This variation partitioning was done on each individual species, and we scaled the variation explained by each factor by the total variation explained in the model (i.e. Tjur R^2, or R^2). We estimated the overall community-level variation explained by taking the mean variation explained by each factor across all species.

2.3.4. Mapping community metrics across the region. To visualize spatial variation in the 3 community metrics, we estimated their mean value across all years over a 3 km^2 grid covering the spatial study extent. Grid cells were restricted to those that fell within the survey footprint and between 40 and 1000 m bottom depth, which covers 95.3% of the trawl depths (Fig. S2). To visualize which areas in the study region experienced the highest temporal variability, we calculated the temporal coefficient of variation for each of the community-level metrics across all years over the same 3 km^2 grid.

2.3.5. Predicting variation of the community across key environmental gradients. We quantified, post hoc, how the community varied across bottom depth —the spatial variable identified as explaining the most variation in community composition in the vari-

ation partitioning analysis. For this, we used the model to make conditional estimates for each of the 3 community-level metrics across the 40 to 1000 m depth gradient. For these conditional estimates, we used QCS and HS as the survey region, 2010 as the year (mid-year of the surveys), and held all other environmental variables at their mean value. We also made these estimates for each individual species, to understand which species were driving these community-level responses to bottom depth. To assess how temperature and oxygen anomalies have impacted the community, we repeated these estimates across the depth gradient for temperature deviations of −0.5 and +0.5°C (±1.9 SD) or for oxygen deviations of −20 and +20 mmol m^{-3} (±2.0 SD) (Fig. S6).

2.3.6. Predicting variation of the community through time. We used the model to make conditional estimates for the species- and community-level metrics across all years in the study at 5 bottom depths (40, 100, 200, 300, and 1000 m), chosen post hoc, to capture a range of depths that include the shallowest and deepest end of the depth range, as well as those where the model predicts species density, Hill-Shannon diversity, and biomass to be the highest. For these temporal conditional estimates, we set all environmental variables to their most likely value, given the year, based on a linear relationship (Ovaskainen & Abrego 2020), and with survey region set to QCS and HS.

We estimated the overall (i.e. non-depth-dependent) temporal trends for the individual species as the mean value of estimates at 40 bottom depth bins (equally spaced on a log scale from 40 to 1000 m), weighted by the proportion of 3 km^2 grid cells in the study region in each depth bin. We estimated the linear slope through time (i.e. change per year) for each species and for occurrence, conditional biomass, and biomass. We repeated this for each posterior draw to obtain the full posterior distribution of linear trends for each species and metric.

3. RESULTS

3.1. Spatial variation in community composition

Variables that were stationary through time but varied across space explained an average of 46.3% of the variation in species occurrences and 36.7% of the variation in conditional biomass (Fig. 1a). Of these temporally stationary variables, bottom depth explained the majority (35.4% of the species occur-

rence variation and 23.3% of the variation in conditional biomass). The random effect associated with the individual trawls explained 6.3% (8.1%) of the variation in occurrences (biomass). The other temporally stationary variables that explained variation in species occurrences (biomass) were BPI 2.1% (2.2%), survey region 0.9% (1.0%), and substrate 0.6% (1.1%). Note that these variation partitions are approximate because they do not account for covariation between variables, and so the summed variance explained by the individual component variables is not exactly equal to the variation explained by those variables when estimated as a single group (Ovaskainen & Abrego 2020). Species-specific parameter estimates for all spatial fixed effects are shown in Fig. S7.

3.2. Spatial diversity and biomass variation

Species density was estimated to vary spatially from 5.4 to 20.2 per area sampled by the average trawl across the study extent, with a median value of 13.2 (Fig. 2a). Highest species density was estimated at mid depths (16.0 around 210 m), with relatively low numbers of species estimated in the shallowest (9.9 at 40 m) and deepest waters (8.2 at 1000 m; Fig. 2d). Hill-Shannon diversity was estimated to vary spatially from 1.2 to 17.1 across the study extent, with a median value of 11.1 (Fig. 2b). The highest diversity (11.5) was also estimated at mid depths, but the diversity peak extended from around 100 to 200 m. Similar to species density, relatively low Hill-Shannon diversity was estimated in the shallowest (6.3 at 40 m) and
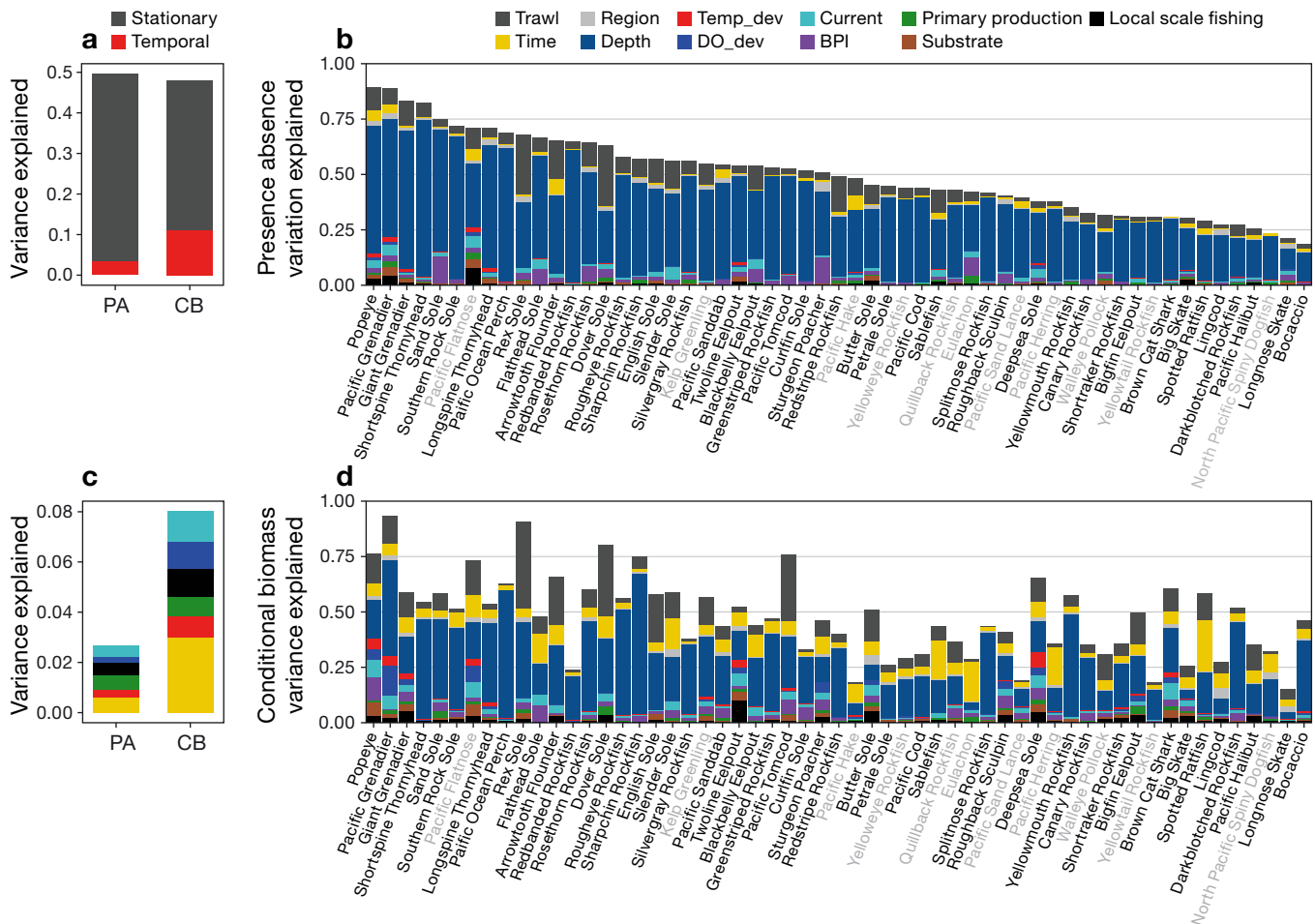

Fig. 1. Variation explained by the presence–absence (PA) and conditional biomass models (CB). (a) Total variation explained by the temporally stationary and temporally varying variables together in each model. (b,d) Variation explained for each species by the fixed and random effects in the (b) presence–absence and (d) conditional biomass models. Variables that capture similar aspects of the environment are grouped. (c) Variation explained by each of the temporally varying variables on average in the 2 models. Species in (b) and (d) are arranged on the x-axis from highest to lowest variation explained in the presence–absence model. Names of species that are unlikely to be well sampled by the trawl (i.e. pelagic-neritic, rocky substrate-associated, benthopelagic, bathypelagic) are shown in grey. Note that rougheye rockfish refers to the rougheye/blackspotted rockfish complex
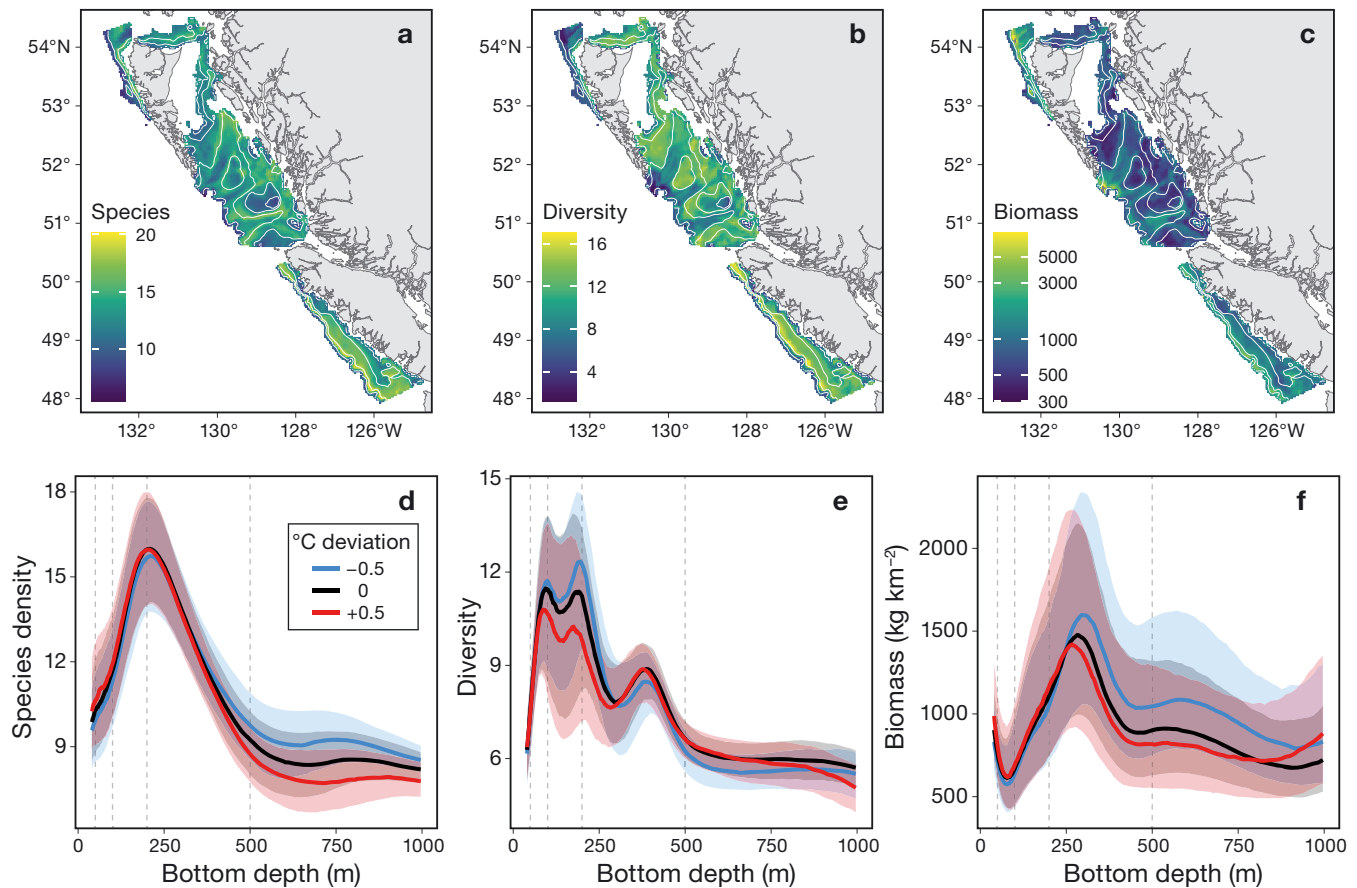
Fig. 2. Estimated variation in (a,d) species density, (b,e) Hill-Shannon diversity (effective number of species), and (c,f) community biomass across (a,b,c) the study region and (d,e,f) bottom depth. Contour lines correspond to seafloor depths of 50, 100, 200, and 500 m. (d,e,f) Lines show the median estimated value and the bands show the 50% credible interval. The vertical dashed lines correspond to the depth contours in (a,b,c). See Fig. S10 for individual species depth curves and Fig. S9 for an estimate of how oxygen deviations alter how community-level metrics vary with depth. Fig. S11 shows a continuous estimate of the community-level metrics across the range of temperature deviations in the study

deepest waters (5.7 at 1000 m; Fig. 2e). Community biomass was estimated to vary spatially from 321 to 5407 kg km^{-2} across the study extent, with a median value of 908 (Fig. 2c). The highest biomass was estimated at mid depths (1476.8 kg km^{-2} at 280 m; Fig. 2f). Biomass was estimated to be lower in the shallowest areas (903 kg km^{-2} at 40 m) and deepest bottom depths (721 kg km^{-2} at 1000 m).

3.3. Temporal variation in community composition

Temporally varying variables together explained an average of 3.3% of the variation in species occurrences and 11.1% of the variation in conditional biomass (Fig. 1a). Time (fixed and random effects combined) explained 0.6% of the variation in occurrences but explained 3.0% of the variation in biomass

(Fig. 1c). The other temporally varying variables that explained variation in occurrence (biomass) were primary production 0.6% (0.8%), commercial fishing effort 0.5% (1.1%), current velocities 0.4% (1.2%), temperature deviation 0.3% (0.8%), and dissolved oxygen deviation 0.3% (1.1%). Reflecting this low amount of variation explained by the temporally varying environmental factors, many species-specific coefficients had credible intervals that overlapped zero (Fig. S8).

3.4. Temperature and oxygen anomalies and their influence on the community

Year-to-year near-bottom temperature and oxygen deviations over the study period resulted in relatively small changes in the composition of the community

based on the low amount of variation explained (Fig. 1). Temperature anomalies were estimated to have had minor impacts on species density, while warmer than average conditions were associated with decreases in Hill-Shannon diversity and community biomass, although in all cases, there was high overlap across the credible intervals (Fig. 2a–d). Negative oxygen anomalies were also associated with a decrease in species density, Hill-Shannon diversity, and community biomass, although there was high overlap in the credible intervals and the strength of this relationship varied by depth (Fig. S9). The strongest predicted responses to oxygen anomalies occurred at around 200 m depth, where the model predicted that an increase of 20 mmol m^{-3} of oxygen would increase all 3 community level metrics.

3.5. Temporal diversity and biomass variation

The model estimated that species density has increased gradually over time (Fig. 3a), with notable increases at all but the deepest depths (e.g. +3.1 species between 2003 and 2018 at 200 m). Although the estimated increases in species density are generally smaller than the 50% credible intervals in any given year, there is a consistent positive shift in the posterior distribution through time, which is consistent with an overall increase in species density despite the high spatial variability (Fig. 2a). These temporal changes in species density are reflected in the spatial patterns of variability (Fig. 3d), where the model estimated low temporal variation in species density in the deepest areas off the continental shelf, but shallower areas, in particular the area east of Haida
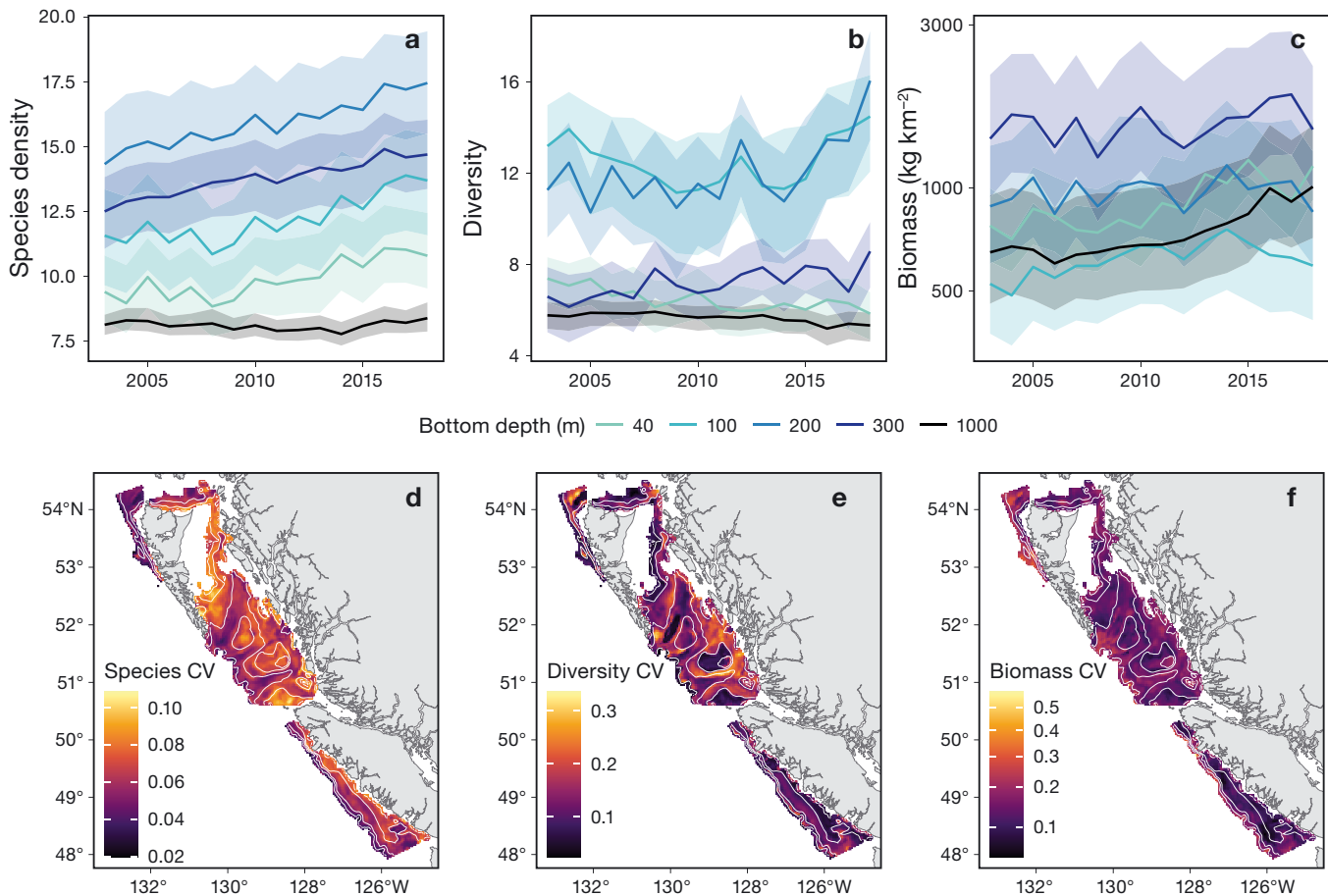

Fig. 3. Estimated temporal variation in (a,d) species density, (b,e) Hill-Shannon diversity (effective number of species), and (c,f) community biomass. (a,b,c) Estimated time series at 5 representative bottom depths (40, 100, 200, 300, and 1000 m), which capture the maximum variation in estimated species density and diversity (Fig. 2). Lines show the median estimated value and the bands show the 50% credible interval. The y-axis for (c) is log transformed to emphasize temporal variation at depths with low biomass. (d,e,f) Coefficient of variation (CV) for each 3 km^2 grid cell across all years in the study. Contour lines correspond to seafloor depths of 50, 100, 200, and 500 m. Note, the color scale in (f) is square-root transformed

Gwaii, were estimated to have been much more variable through time.

The model did not estimate the same gradual increase in Hill-Shannon diversity as it did for species density (Fig. 3b). Instead, temporal changes in diversity depended on depth, with the only notable temporal change in the 5 bottom depths considered occurring at 100 and 200 m. At these depths, diversity has fluctuated through time and has increased markedly since 2014 (e.g. +5.30 at 200 m). These temporal changes in diversity are reflected in the spatial patterns of variability (Fig. 3e), where temporal variability in diversity was estimated to be highest at bands that correspond to these depths on the continental shelf.

The model estimated moderate increases in community biomass at most depths over this time period (Fig. 3c) with the greatest increases occurring at the deepest depths (+361.02 kg km^{-2} between 2003 and 2018). This is reflected in the highest temporal variation in community biomass estimated in the deepest areas, off the continental shelf (Fig. 3f).

3.6. Temporal species-level changes in occurrence and biomass

The model estimated a wide range of temporal trends for the individual species (Figs. 4 & S16), but in general, increases in occurrence and biomass were more common than decreases. The estimated increases in species density through time (Fig. 3a) were due to the fact that the majority (61.4%) of species were estimated to have increased in occurrence, while only 8.8% of species were estimated to have decreased (Figs. 4 & 5A). Among the species that are well sampled by the research trawl survey, spotted ratfish, sand sole, and flathead sole showed the largest increases in estimated occurrence, while lingcod, Pacific sanddab, and longnose skate showed the largest estimated decreases.

Likewise, the increases in estimated community biomass were associated with increases in 45.6% of species, while only 10.5% of species were estimated to have decreased in biomass. Among the species that are well sampled by the research trawl survey, flathead sole, butter sole, and roughback sculpin showed the largest increases in estimated biomass, while bocaccio, lingcod, and longnose skate showed the largest estimated decreases. The estimated increase in Hill-Shannon diversity at 100 and 200 m from 2014 to 2018 was largely driven by a decline in biomass of arrowtooth flounder (Fig. 5b), which con-

tributes by far the largest biomass to the community at this depth. Coupled with increases in other species, most notably sablefish, this resulted in a community with a more even composition in recent years compared to before 2014. While arrowtooth flounder was also estimated to have decreased at other depths (e.g. 300 m), it is not as dominant at these depths and so these estimated declines did not have as large an impact on Hill-Shannon diversity.

4. DISCUSSION

Our goal was to determine the factors that structure the demersal fish community in the northeast Pacific to understand how this community is changing across space and time. As hypothesized (H1), the composition and diversity of the community was highly structured by spatial variation in environmental conditions. However, this variation was primarily driven by conditions associated with bottom depth, whereas other variables explained only a small fraction of the spatial compositional variation. Contrary to expectations (H2), temporal changes in the community over the past 2 decades do not appear to have been driven primarily by changes in the environmental conditions considered or by localized fishing effort. In particular, our analysis suggests (H3) that the temperature anomalies associated with the 2013–2016 marine heatwave did not result in large scale changes in the composition or diversity of the community as a whole. Instead, the main signal of temporal change is a gradual increase in species density and biomass over the past 2 decades that corresponds to documented increases in other marine regions in North America (H4; Batt et al. 2017). As this increase is not associated with environmental changes or localized fishing effort in our model, it is likely a reflection of an ongoing recovery of the community associated with the spatial and aspatial conservation management initiatives that were implemented on the commercial fishery between the late 1990s and early 2010s, but which could not be directly accounted for in our model. Together, these findings provide an understanding of the current state of the demersal fish community and how it is changing in response to environmental change and commercial fishing intensity.

In this region, bottom depth is clearly the most important predictor of community composition. Depth explained the majority of the explained variation in the model (Fig. 1), and the model with only bottom depth, survey, and year as fixed effects had almost as
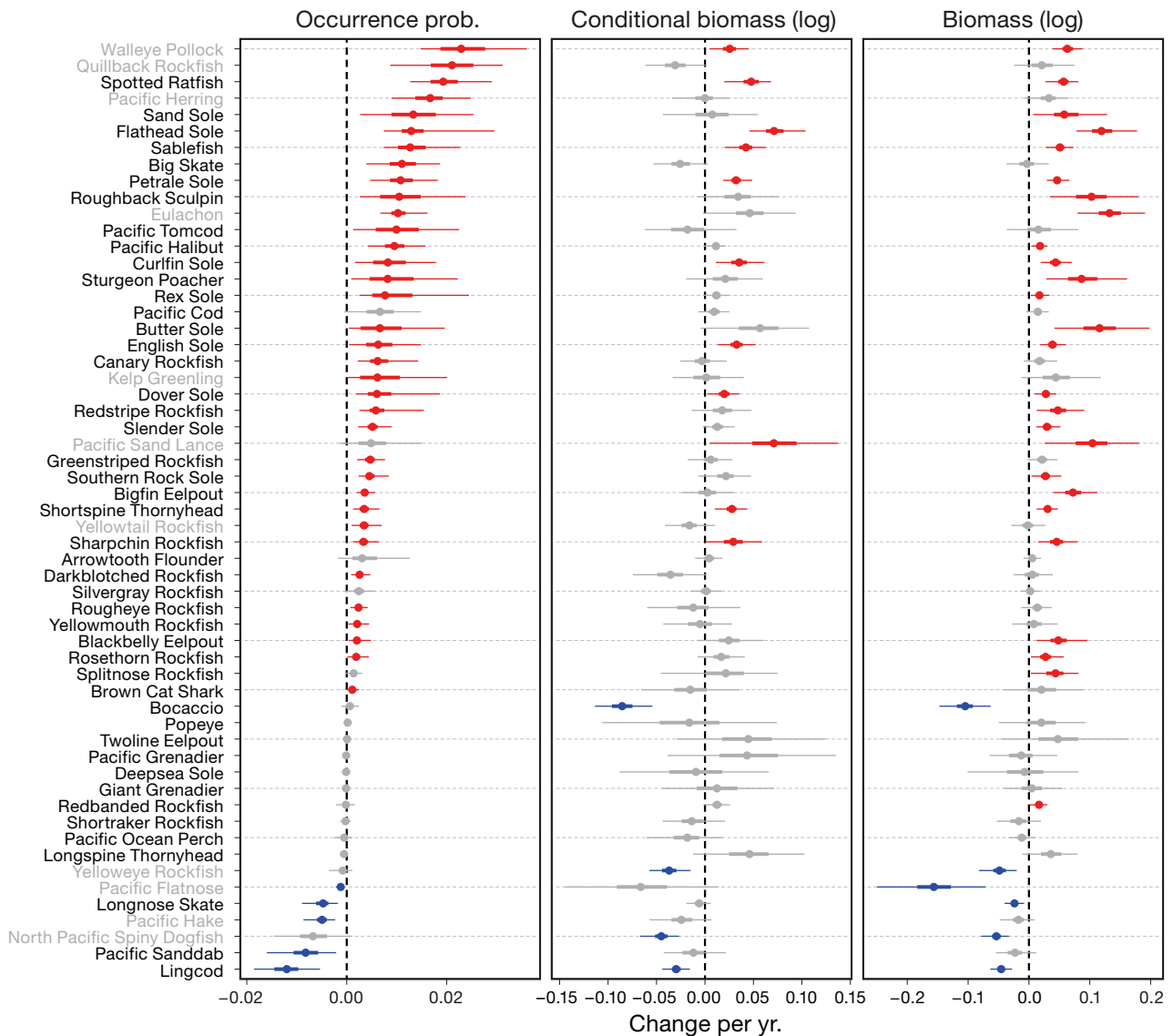
Fig. 4. Linear temporal trends of occurrence probability, conditional biomass (kg km^{-2}), and biomass (kg km^{-2}) for all species. Points show the median estimated coefficient, thick (thin) horizontal lines show the 50% (95%) credible interval. Species are arranged on the y-axis from largest increases (red) to largest decreases (blue) in occurrence. Estimates where the 95% credible interval overlaps 0 are shown in grey. Names of species that are unlikely to be well sampled by the trawl (i.e. pelagic-neritic, rocky substrate-associated, and benthopelagic) are shown in grey. Note that rougheye rockfish refers to the rougheye/blackspotted rockfish complex

much predictive power as our full model (Fig. S13). This aligns with previous observations in this region (Perry et al. 1994, Fargo 2012, Rubidge et al. 2016), and the general understanding that species ranges are constrained by depth (Froese & Pauly 2016). Our study region includes both the continental shelf and slope, and thus spans more than 1000 m of depth. Therefore, it is not surprising that the majority of the variation in our dataset was associated with this variable. It is, however, important to remember that depth itself is unlikely to be the causal factor in struc-

turing the community. Rather, it is likely that the distribution and abundance of fish are determined by a combination of variables that are correlated with depth such as temperature, dissolved oxygen, and pressure (Brown & Thatje 2015). The high correlation between bottom depth, temperature, and dissolved oxygen is the reason we included temperature and dissolved oxygen as yearly deviations at the 3 km^2 scale, rather than as raw values. Such correlations should not affect our ability to estimate the composition of the community within the time span for which

Fig. 5. Time series of median estimated (a) species occurrences and (b) biomass at 5 representative bottom depths (40, 100, 200, 300, and 1000 m). (Solid lines) Species that were estimated to have increased in occurrence regionally during study period; (Dashed lines) species with no estimated directional occurrence trend; (dotted lines) species with estimated declines in occurrence. Species are ordered in the legend from greatest increase in estimated occurrence to greatest decrease in estimated occurrence. Only species with an estimated biomass that exceeds 20 kg km^{-2} in at least 1 year at that depth are shown. See Fig. S12 for species with less biomass. Credible intervals are omitted for clarity. Note that rougheye rockfish refers to the rougheye/blackspotted rockfish complex

we have observed data (Urban 2019), as is the focus of our study. However, separating out the influence of depth-associated variables will be critical to make predictions about how the community may respond to environmental changes in the future (Brown & Thatje 2015).

While bottom depth was predictive of compositional differences over broad spatial scales, variables such as substrate type, ocean currents, primary production, and the bathymetric position index were important for predicting differences in community composition across habitats that occur at similar depths. This is reflected in the consistent reduction in predictive power when variables other than bottom depth, survey, and time were removed from the models (Fig. S13). Although the amount of variation explained by non-depth-associated variables appears relatively small in contrast to the large degree of community turnover across the depth gradient (Perry et al. 1994, Fargo 2012), non-

depth-associated variables are important in determining the composition of the community at local scales. That temporally varying environmental variables explained more variation in biomass than occurrence suggests that environmental change is having larger impacts on abundances than on the distribution of species. Still, our analysis suggests that increases in species occurrences over the time period considered have resulted in an overall increase in species density. These estimated temporal changes in species density at any given location are much smaller than the estimated spatial differences in species across the depth gradient, which is why temporal variables explain much less variation in occurrences compared to the spatial variables (Fig. 1a). Together, these results suggest that spatial environmental changes drive community turnover, while temporal environmental changes are driving year-to-year fluctuations in biomass as well as long-term changes in species density.

The overall increase in species density and community biomass that we documented over the duration of the study period (Fig. 3) is consistent with increases seen in other marine regions in North America (Batt et al. 2017). Increases in species density in other regions have been attributed to 3 potential drivers: (1) range shifts due to changing environmental conditions, (2) colonization of invasive species, or (3) population recoveries associated with reduced human impacts (Elahi et al. 2015).We consider these drivers in the following paragraphs.

Our analysis suggests that the increase in demersal fish species density over the period of 2003–2018 is unlikely to be primarily driven by changing environmental conditions. We found evidence that species have responded to changes in temperature, oxygen, primary production, and ocean currents (see also English et al. 2022), but these variables only explained a subset of the temporal variation in the community (Fig. 1c). Furthermore, the estimated increases in species density and community biomass were largely linear (Fig. 3) and so do not match the non-linear fluctuations in environmental conditions over this time period (Fig. S4). Changes in environmental conditions largely followed the regional climate cycles, such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation, that are a dominant source of environmental variation in the North Pacific and are known to influence recruitment of many demersal fish species (King et al. 2001, King & McFarlane 2006). While year-to-year changes in primary productivity, mean summer temperature, and oxygen did influence the occurrence and biomass of many species (see also English et al. 2022), our findings suggest that contrary to our expectation, the 2013–2016 marine heatwave only resulted in moderate changes in the diversity and biomass of the community (Fig. 2d,e,f; Litzow et al. 2020). In addition, our estimated increases in species density are not due to the establishment of non-native species, as we excluded rare species from our analysis. The researchers responsible for conducting the survey trawls have also confirmed that the species in our analysis have been consistently identified and that the estimated increases in species density are not likely due to improvements in taxonomic identification.

After ruling out environmental change and invasive species, we propose that the most likely driver of the increases in species density and overall community biomass has been the overall reduction in commercial fishing intensity over the past 2 and a half decades. Over our study period (2003–2018), there has been a 59% decrease in the total number of hours fished via bottom trawl, a 58% spatial reduction in the extent of area that has been fished, and a 43% decrease in total catch via bottom trawl by the commercial fishery (Fig. S5). Furthermore, most species in the community have seen a decrease in discarded biomass (i.e. bycatch; 45 of 57 species), landed biomass (32 of 57 species), or total biomass (i.e. landed plus discarded biomass; 45 of 57 species) by the bottom trawl commercial fishery over this period (Fig. S14). There does not appear to be any association between these decreases and the estimated changes in species density and biomass in our model (Fig. S15). However, this is not surprising, because decreased catch by the commercial fishery could be associated with decreased fishing pressure, in which case the population should increase, or with a decrease in abundance of the species. Distinguishing such trends in the commercial catch data requires a formal stock assessment and is beyond the scope of our study. Nevertheless, the fact that we see a decrease in biomass harvested in the commercial fishery is consistent with our hypothesis that decreasing fishing pressure is the likely driver of the increases in species density and community biomass.

These reductions in fishing intensity likely reflect the management interventions that were implemented during this period (Wallace et al. 2015), as well as socioeconomic factors in the region. As outlined in our methods, we opted not to include these coast-wide aggregate measures of fishing effort in our model and instead include localized fishing effort, from which these coast-wide measures are derived. However, local-scale fishing effort explained only a small fraction of the temporal variation in the community, and when there was a relationship between species biomass and local fishing effort, it was often positive, suggesting that fishers are targeting areas where they expect to find high biomass. Likewise, areas inside of the ecosystem-based trawling footprint tended to have higher biomass than areas where fishing was excluded. This footprint was established as a voluntary measure by the commercial trawl fishery, and areas where fishing was previously concentrated tended to be included within the footprint (Wallace et al. 2015). Notably, the overall reduction in the spatial extent of the fishery does not appear to be primarily associated with the implementation of the footprint, as the decline in fishing extent has been continuous over the study period (Fig. S5b). Thus, it is likely that the spatial reduction is due to the reduction in overall hours fished, with the remaining effort being concentrated in areas that are known to be most productive. The overall in-

creases in species density are mostly associated with the linear temporal fixed effect and this is consistent with decreased fishing intensity at the coast-wide scale, along with the associated management interventions.

That the negative association between fishing effort and species occurrence is stronger at the coast-wide scale than at the local scale likely reflects the fact that fish populations are mobile and connected across space. Thus, they are likely responding to fishing at a broader spatial scale than that at the specific locations that are trawled. This indicates that areas that are fished may be seeing increases in species density and biomass that are due to reductions in fishing pressure elsewhere in the region. This aligns with evidence that suggests that areas without fishing, such as marine protected areas, generally increase the abundance and diversity in adjacent regions through spillover effects (Di Lorenzo et al. 2020). Our conclusion that a reduction in commercial fishing intensity is responsible for the increase in species density and community biomass also aligns with the finding that in regions where fisheries are intensively managed, stocks tend to be above target levels or in the process of rebuilding (Hilborn et al. 2020). Our study corresponds with a period that immediately followed the implementation of management interventions that are thought to have stabilized groundfish stocks in Pacific Canadian waters, which were previously estimated to have declined from 1950 to around 2000 (Anderson et al. 2021). In this context, it seems likely that the increases in density and more moderate increases in community biomass are the beginning of an ongoing recovery of the community associated with reduced fishing pressure, although it should be noted that some species are still declining. While we lack a historical reference for demersal fish biodiversity in this region, the status of individual stocks is still below historical levels (Anderson et al. 2021) and we expect the same to be true for species density and community biomass.

Our results are in contrast to the expectation (Hillebrand et al. 2018) and evidence from a global meta-analysis (Blowes et al. 2019) that suggests that temporal changes in ecological communities are more likely to be reflected in temporal turnover rather than changes in species density. The predominant signal of temporal change in our analysis is the overall increase in species density, driven by increased probability of occurrence in the majority of species, while there is little temporal change in the identity of species present (Fig. 5a). In addition, Hill-Shannon diversity is estimated to have remained largely con-

stant through time in our region (Fig. 3), which indicates that the relative abundance of species in the community is remaining relatively constant, even as occurrence is increasing. The exception being at depths of 100 to 200 m where Hill-Shannon diversity is estimated to have increased since 2014 as the result of a substantial decline in arrowtooth flounder and increases in other species, in particular sablefish at 200 m. This decline in arrowtooth flounder is concerning, as we discuss below, but does not represent a case of community turnover as this species still comprises 15.2% of the community biomass at 200 m depth, even after the recent declines (Fig. 5b). We suspect that this divergence from Hillebrand et al. (2018) and Blowes et al. (2019) may be because community change here is hypothesized to be a signal of recovery from historically intense bottom trawling rather than changes in environmental conditions. Bottom trawling is a relatively indiscriminate harvesting method and would have reduced population sizes of species across the community (Pedersen et al. 2017), although spatial variation in fishing effort may impact some species more than others. In contrast, changing environmental conditions is likely to cause greater compositional turnover by favoring some species over others (Doney et al. 2012, Thompson et al. 2020). This highlights that expectations for biodiversity change should differ depending on the hypothesized driver of change. Furthermore, given the lack of a pre-exploitation reference, our results do not reflect an increase in biodiversity from an unperturbed state (Cardinale et al. 2018). Rather, they are consistent with an ongoing recovery from a historical decrease in biodiversity that predates the start of our survey data.

Although we found that changes in mean summer temperature and dissolved oxygen did not result in large changes in the composition and diversity of the demersal fish community over the time span of our study, temperature and oxygen deviations were associated with changes in occurrence and biomass for many species (Fig. S8). Thus, it is likely that the community may be sensitive to the changes in climate that are projected over the coming decades (IPCC 2013, see also English et al. 2022). Our model is not appropriate for projecting species and community responses to future conditions because we only estimate responses of species to temperature and oxygen deviations across a period of 15 yr. Models that are better suited to this goal predict considerable community reorganization and biodiversity change under future conditions (Cheung et al. 2009, Morley et al. 2018). Our results highlight the need to con-

sider both climatic and non-climatic drivers of biodiversity change when assessing the impact of climate change. Whereas Antão et al. (2020) found that recent warming is often correlated with increases in species density in temperate marine communities, including in North Pacific waters, their analysis did not consider fishing. Over the time span included in our study, the majority of temperature change was due to year-to-year variability resulting from climate cycles (e.g. El Niño and the Pacific Decadal Oscillation), rather than overall climate warming. Because the overall increases in species density and community biomass are not closely correlated with changes in seafloor temperature, it seems unlikely that they are driven primarily by climate warming. Continued monitoring and consideration of the impacts of climate change will be critical to sustainably managing marine communities, and accounting for other drivers of biodiversity change, such as fishing, will be essential for these efforts.

Modeling all species together in a single analysis provides unique insight into the individual species dynamics responsible for community-level changes. Many of the species that are responsible for the increased species density and community biomass are flatfish (Fig. 4), which, compared to other species in the community, tend to reach reproductive maturity at an earlier age (Froese & Pauly 2016) and so may have rebounded faster when fishing intensity was reduced. However, while increases in occurrence and biomass were estimated for most species, this is not universal and a number of species were estimated to have decreased during this time (Fig. 4). Of concern are the decreases estimated for arrowtooth flounder, North Pacific spiny dogfish, lingcod, yelloweye rockfish, and Pacific flatnose (Fig. S16). The decline in arrowtooth flounder since 2014 is similar to observed declines in the Gulf of Alaska (Spies et al. 2019). These declines are associated with an increase in targeted commercial fishing effort associated with the emergence of new markets following the development of processing techniques (Anderson et al. 2019, Spies et al. 2019). A stock assessment for arrowtooth flounder is underway in British Columbia, but this species was assessed as not being subject to overfishing in the Gulf of Alaska (Spies et al. 2019). North Pacific spiny dogfish, while widespread in the region, were estimated to be declining in biomass and this may reflect their sensitivity to fishing as a long-lived and slow-to-mature species (Froese & Pauly 2016). The estimated declines in lingcod occurrence are variable and relatively moderate, but they indicate that further assessment may be warranted, particularly as the last stock assessment was done nearly 10 yr ago (DFO 2012). Yelloweye rockfish is a conservation priority (Gale et al. 2018) and has high cultural significance (McGreer & Frid 2017) and is listed as threatened under the Canadian Species At Risk Act (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2020). The estimated decline in biomass for yelloweye rockfish is consistent with recent assessments (Keppel & Olsen 2019, Cox et al. 2020, DFO 2020b). Pacific flatnose is rarely caught in the trawl surveys (75 occurrences) and so our estimates of change for this species are relatively uncertain. However, the posterior distributions for occurrence and biomass change are negative in our analysis (Fig. 4), indicating that this species may warrant further assessment. The estimated decrease in bocaccio biomass over the study period also corresponds with documented trends in the region (Anderson et al. 2019). However, a recent recruitment event for bocaccio has resulted in increases in occurrence and biomass (DFO 2020a), which is evident in our model. Similar increases in recent years are also estimated for quillback rockfish, sablefish, and Pacific sanddab, although Pacific cod is estimated to have decreased since 2016 (Fig. S16). Our analysis complements formal stock assessment by providing information that can be used to prioritize species for stock assessment. Furthermore, because our analysis is not limited to species of commercial and conservation interest, it provides an indication of the trends for species for which stock assessments are not conducted.

Our community-level analysis provides a general understanding of the spatial and temporal factors that structure the demersal fish community. However, our analysis has some limitations that are important to keep in mind when assessing our results. First, species that are not well sampled by the trawl surveys may not be accurately estimated by our model. Second, because our model did not include spatiotemporal random effects, we likely underestimated spatiotemporal variability in the region. However, our model should provide a reliable estimate of the overall spatial and temporal patterns that are our focus of inference. Finally, it is not possible to know at which spatial and temporal scales environmental factors and commercial fishing impact the species. The spatial and temporal scales of our environmental data were chosen to align with the spatial resolution of the trawl surveys and the time of year in which the surveys are conducted. However, it is likely that mismatches in the spatial and temporal scales of our fixed effects and the relevant ecological processes may have limited our ability to assess their influence on the community. Despite these caveats and limita-

tions, our model should be well suited to capturing how the community is structured in space and how it is changing through time.

This analysis provides key insight into the current state of the demersal fish community in Canadian Pacific waters and spatial outputs that can inform ongoing marine spatial planning and ecosystem-based management initiatives. With regard to the specific objectives outlined in the PNCIMA ecosystem-based management framework (PNCIMA 2017), our analysis: (1) establishes a baseline understanding of the diversity and functioning (i.e. biomass) of the demersal fish community and how it varies across time and space, and (2) provides an estimation of how this community is responding to ongoing environmental change and fishing pressure. Our spatial estimates of species density, diversity, and biomass can be used to identify areas that are of high conservation value. Identifying high conservation value areas is needed for the development of a marine protected area network in the region, which is a key focus of the PNCIMA plan (PNCIMA 2017). However, we caution against basing decisions only on these metrics, as areas with low species density may also be critical habitat for particular species. Our finding that bottom depth, and variables associated with depth, are the primary factors that determine the composition and spatial turnover of the community (Perry et al. 1994), suggests that the full depth range in the region should be represented in protected areas in order to cover the habitat of all species (see Martone et al. 2021). Within a given bottom depth strata, focus should be placed on maximizing other aspects of environmental heterogeneity such as substrate type, circulation, and tidal currents, as well as bathymetric features such as canyons and ridges. It is encouraging to see that the species density and biomass of the community appears to be increasing following the implementation of management interventions that were aimed at controlling commercial fishing intensity. However, this recovery appears to be ongoing, and evidence suggests that biomass of many species is still likely below historical levels (Hilborn et al. 2020). The same is likely true for species density, and the implementation of ecosystem-based management initiatives, including those based on marine spatial planning (Douvere 2008, Frazão Santos et al. 2019), should have additional benefits in terms of the health and sustainability of the demersal fish community (Folke et al. 2004, Isbell et al. 2017, Loreau et al. 2021). While our analysis suggests that environmental changes experienced over the past 15 yr did not result in large-scale changes in the community,

this is unlikely to be the case in the future, given the accelerating rates of change projected by climate models (Cheung et al. 2009, e.g. IPCC 2013, Morley et al. 2018). Because of this, effective ecosystem-based management approaches will be critical for preserving the biodiversity of the demersal fish community and the abundance of its component species, many of which are integral to the socioeconomic health of the region.

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