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Relationship between abundance and range size in longline target species

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1 Executive summary

Changes in the spatial distribution of fish stocks is often ignored when considering the health of a population or examining the impacts of alternative fishery management strategies. Yet, reductions in the distribution of species with declines in abundance are evident across a diverse range of species, including birds, insects, mammals and fish. This phenomenon is particularly important for fisheries management where some stakeholders have limited ability to adapt to such effects, and would be acutely relevant to western and central Pacific Tuna fisheries, locally-based domestic fleets and the many artisanal and small-scale fishers.

Here, we first take an empirical approach to determine how abundance and spatial distribution of seven key tunas and billfish are related over a period of more than 50 years. We then create a simulation model of a spatially structured population to investigate the mechanisms that could drive the patterns observed in the empirical data.

We found that there was a positive relationship between abundance and range for all of the studied species, and that this relationship became more pronounced when focusing on areas of high local density. Simulation modelling highlighted that local densities of exploited mobile populations may not be related to local fishing mortalities when habitat quality varies within the stock range. In addition, the link between population abundance and range size is accentuated when individuals preferentially migrate to regions of high habitat quality within the range, especially if those areas are under heavier fishing pressure than habitats of lesser quality.

These findings reinforce the need for the inclusion of spatial dynamics in the consideration of target and limit reference points for mobile pelagics. Future work should more formally quantify the long-term population consequences of ignoring spatial population dynamics in fisheries management, as well as determine the potential of non-CPUE data sources to further elucidate the ecological mechanisms at play in the redistribution of population abundance under uneven spatial fishing mortality.

2 Introduction

Fisheries management often focuses on reference points derived from indicators of stock biomass or fishing intensity. Changes in the spatial extent of stocks are rarely assessed, but have potentially important management consequences. Dynamics in spatial occupancy could mean that some stakeholders get disproportionately affected by changes in stock biomass at the regional-level, even if the overall stock is at healthy levels. This is especially relevant to fisheries where stakeholders have access to limited areas within the stock range, such as the western and central Pacific tuna fisheries. In addition, dynamics in spatial occupancy can bias CPUE time-series by driving unaccounted for spatial changes in fleet dynamics (Carruthers et al., 2010; McKechnie et al., 2013) or by inflating CPUE indices in ways that are hard to standardize against (e.g. Rose and Kulka 1999).

A positive relationship between some metric of population abundance and geographic extent has been observed across many different species groups (fish, Fisher and Frank, 2004; Frisk et al., 2011; marine mammals, Hall et al., 2010; primates, Harcourt et al., 2005; birds, Blackburn et al., 1998; insects, Conrad et al., 2001; Sileshi et al., 2009; see Borregaard and Rahbek, 2010 for a review). This relationship is hard to document in practice because it requires detailed long-term series of both abundance and spatial extent for the population of interest (Zuckerberg et al., 2009). It appears logical, however, that such a relationship would exist as we know, by definition, that the species' range must be more extensive at high population abundance (Fig 1, blue point) than when the species is extinct (with a range size equal to zero) (Fig 1, red point). We refer to the trajectory between those two points as the *range-abundance relationship (RAR)*[3], and the shape it takes has key management implications for fisheries. For instance, the standing biomass of marine species fished at sustainable rates is typically expected to be close to 40% of the unexploited biomass, so range size at B_{MSY} could be unchanged compared to that at B_0 or have declined significantly (see Fig 1) depending on the shape taken by the RAR for the exploited species.

Mobility has been hypothesized by many authors to be a factor that should increase the strength of range-abundance relationships (Gaston and Blackburn, 2003). A related hypothesis is called 'density-dependent habitat selection' (DDHS, MacCall, 1990, derived from the Ideal Free Distribution *cf.* Fretwell and Lucas, 1969), whereby mobile individuals specifically select for higher quality habitat as defined by both intrinsic environmental characteristics (e.g. temperature, food, etc.) and the density of conspecifics, i.e. an 'effective' habitat quality. Under DDHS, high conspecific density increases competition for resources and reduces the effective habitat quality as perceived by individuals. Fishing could thus increase effective habitat quality in certain regions on the short-term by reducing competition for resources *via* the removal of competing individuals. The increased growth resulting from a reduction in population biomass is at the core of modern fisheries management, and DDHS, in effect, proposes a mechanism for that phenomenon to be enacted spatially.

Many species (Brown, 1984, but see Sagarin et al., 2006) experience higher habitat quality towards the middle of their range. It could thus be expected from DDHS that if range declines with biomass, the distribution of large pelagics should shift away from areas of lower quality (range 'edge') towards areas of higher quality (range 'core'). However, the spatial pattern of fisheries mortality in the Pacific could make it hard to discern this phenomenon from CPUE data since, for tropical tunas and billfish, fishing effort tends to be much more intensive in high quality habitat (the western equatorial zone) then in the range edges (high

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[3] The *intraspecific abundance-occupancy relationship (AOR)* is the technical term used in the ecological literature to refer to this concept, but because it tends to refers to mean density rather than total population abundance, we use the general term *range-abundance relationship* here to avoid confusion.

latitudes), such that the observed pattern of biomass change might not fit direct predictions from DDHS.

As part of the WCPFC Scientific Committee research plan (project 67; WCPFC 2013), this paper presents two independent approaches to explore relationships between range and abundance and spatial population dynamics in Pacific large pelagics. We first modelled the spatial distribution of seven longline target species based on 5×5 degree CPUE data to assess the relationship between abundance and spatial occupancy of stocks (section 3). Then, recognizing that multiple dynamics are at play in the generation of spatial patterns of abundance throughout the range, we simulated spatial population dynamics for mobile species to gain a better understanding of how core-edge habitat dynamics would be expected to affect local stock response to fishing, as well as identify conditions under which RARs can emerge (section 4).

3 Assessing range-abundance relationships from longline CPUE data

3.1 Methods

3.1.1 Description of datasets

1. We used monthly catch-and-effort aggregated 5×5 data (catch in individuals and effort in hooks) for the three main longline fleets operating in the Pacific: Japan, Korea and Chinese Taipei. We focused our analysis on the following longline target species: yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), albacore tuna (*Thunnus alalunga*), striped marlin (*Kajikia audax*), black marlin (*Makaira indica*), blue marlin (*Makaira nigricans*), and Indo-Pacific sailfish (*Istiophorus platypterus*). These species are all tropical except for albacore tuna and striped marlin which are temperate. Given sparse fleet and spatial coverage before 1960, data before that year were not included in the analysis.

2. A dataset of candidate explanatory oceanography variables was built. Monthly oceanography data from the Simple Ocean Data Assimilation (SODA) were selected based on their long-term temporal coverage (`http://www.atmos.umd.edu/~ocean/`, Carton and Giese 2008).[4] Temperature (at 25 meters and 215 meters), salinity (at 25 meters and 215 meters) and sea surface height data were spatially aggregated to match the CPUE dataset by averaging observations over 5 degree cells. Monthly values for the Southern Oscillation Index (SOI) since 1950 were obtained from the

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[4] We note that the model results for bigeye tuna use an older version of the oceanography database which was based on the GODAS oceanography model, but that we are in the process of updating it. The SODA dataset is now preferred because of its longer temporal coverage, but qualitative trends in model results remained the same for all species for which the switch in oceanography database was succesful.

Climate Analysis Section of the National Center for Atmospheric Research (`http://www.cgd.ucar.edu/cas/catalog/climind/soi.html`).

3.1.2 CPUE model

To assess changes in range size, we need an index of abundance that covers the entirety of the species' range. We used spatial and temporal splines (GAM) to model relative abundance on a 5×5 grid based on fishery and oceanography variables (see below). This statistical approach is essentially a hybrid between a typical fisheries CPUE standardization (Maunder and Punt, 2004) and a GAM-based species distribution model (Elith and Leathwick, 2009). The advantage of using splines is that the relationship of catch over space and time need not be linear or a complicated polynomial. The use of oceanographic variables provides additional explanatory power to predict abundance in cells where there is no fishing. The rationale of the approach is similar to that underlying the work in McKechnie et al. (2013), but here we are interested in modelling the geographic distribution of large pelagics rather than generating a single area-weighted abundance index.

Out of a set of candidate oceanography variables, we identified for each species the top two variables that explained on their own the highest proportion of variation, while being uncorrelated with each other (Pearson $p < 0.3$). The selected variables were used along with year, quarter, fisheries fleet and cell location (5×5 degree stratum) to predict CPUE using a semi-parametric approach implemented with the `mgcv` package in R (Wood, 2006; R Core Team, 2014). One of the key aspects of the model was an interaction between space and time. This interaction is key to capturing contrasting trends in abundance change in different parts of the range. Model selection was performed by defining a set of candidate models with (i) different combinations of oceanography variables and (ii) different structures for the interaction between space, time and fisheries fleet. The best model was selected to (1) maximize predictive power, (2) minimize temporal and spatial patterns in residuals, (3) minimize GCV (an index related to AIC) and (4) produce satisfactory diagnostics as assessed by the following plots: binned residuals (histogram, BR vs fitted), residuals vs explanatory variables, residual map for spatial autocorrelation, spatial variogram of residuals. The top-ranking model for each species was used to predict CPUE from 1960-2010 for each cell in the Pacific for the three fleets used in the analysis. The CPUE indices were then averaged over fleets to produce a fleet-standardized index of abundance by cell and time.

We used both a log-normal and a delta log-normal approach to model CPUE, and retained for each species the one that performed better in terms of model diagnostics. For all species but the striped marlin, model diagnostics were better for the delta approach. See the appendix for a more detailed overview of model structure by species.

3.1.3 Estimation of range size

In order to estimate range size over time, predictions of relative abundance need to be converted to a time-series of presence-and-absences over cells, that is, we need to define a species-specific ‘detection threshold’ below which the species would be considered absent for the purposes of this analysis. The value of the detection threshold is expected to affect measured patterns of range change so we measured range size under low, medium and high detection thresholds. The low threshold tracks changes over time in the total distribution conservatively (as even cells with extremely low relative abundance are considered to be part of the range), while the high threshold tracks the changes in areas of high density within the range. These thresholds need to be species-specific as some of the study species are more common than others, such that a high detection threshold for a given species (e.g. blue marlin) might be a low detection threshold for another (e.g. albacore). To maintain a consistent methodology across species, we calculated thresholds based on the second year of lowest estimated total abundance for each species[5]. A year of low abundance was picked as a baseline to define the threshold levels so that we could track changes in range size for all years in the study time period: if the species is present under the defined threshold in a low abundance year, it should, by definition, also meet that threshold somewhere in the range in a year of higher abundance. For this year of low abundance, the 10th, 50th and 90th quantiles of cell-wise abundance were used as low, medium and high detection thresholds, respectively.

For each species-specific threshold level, range size was measured as the number of 5×5 cells in any given year where the species was present under the stated abundance threshold. The unit of area is degree^2, which overemphasizes cells in high latitudes, but our main goal here is to observe relative changes in occupancy over the range, not derive absolute measures of range size.

Relative abundance was calculated by summing predicted abundance across cells. We note that this is not a measure of absolute abundance. A comparison of estimated changes in abundance with stock assessments is included in Table 1.

3.2 Results/Discussion

3.2.1 Relationship between abundance and range size

Our abundance and range estimates were derived from CPUE which is notable for resulting in biases in abundance over time (Harley et al., 2001; Walters, 2003; Hampton et al., 2005). We thus focus our interpretation of the model’s results on qualitative trends and the shape of the relationship between relative abundance and range size, intead of making statements about absolute changes in abundance or range size. Relationship between abundance and

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[5] We picked the second lowest year to avoid extreme values in the year of lowest abundance, but the exact year chosen for the ‘low abundance’ years had no impact on qualitative trends.

range size for each of the seven study species were assessed from a model of spatial abundance for 1960-2010, as described in section 3.1. Except for albacore, predicted declines in relative abundance based on 5x5 CPUE data were comparable (within 15%) to those modelled in overlapping study periods of stock assessments (see Table 1), though black marlin and sailfish lacked conclusive stock assessments.

There were important declines in areas of high occupancy for both tuna and billfish since 1960, except for blue marlin (Figure 2, regions in dark red show cell abundances greater or equal to the 95th quantile of individual cell abundances predicted for the entire time-series). The distribution appears to contract towards distinct zones. These zones either consist of a single one around the equator (yellowfin and bigeye tuna), or one or two zones in sub-tropical latitudes (albacore tuna, striped marlin, black marlin, sailfish). Albacore tuna, which is the one species for which two distinct stocks have been identified in the Pacific (Montes et al., 2012), had important declines in spatial extent in the northern portion of its range only. Our methodology does not allow for the identification of causal mechanisms behind the observed changes, but fishing is a likely candidate, as all of these species have been directly or indirectly targeted by industrial fisheries at some point in the last 50 years and are currently under active management. The latest Pacific bigeye tuna assessment (Harley et al., 2014), for instance, estimates that the reduction in spawning potential from fishing has increased steadily since the 1960s to a level of more than 80% in the last few years. Long-term climatic cycles such as the Pacific Decadal Oscillation also have the potential to drive important fluctuations in population abundance following 15-25 years cycles or longer (Mantua and Hare, 2002; Chavez et al., 2003). Lastly, climate change is another likely candidate *via* changes in habitat conditions (e.g. ocean temperature). However, the latest modelling work on this question (Lehodey et al., 2010; Hazen et al., 2012) predicts a long-term shift in habitat that does not match the observed contraction.

Predicted relationships between abundance and range size were positive for all seven species (Figure 3). When a low detection threshold was used, the shape of the relationship was flat because cells retain a ‘presence’ status even though actual abundance is quite low (e.g. a ‘low’ detection threshold for yellowfin was 3 individuals per 100000 hooks or one fish for every 10 typical longline sets). Under such thresholds little change in measured range size occurs even if abundance decline in the cell has been steep and that the observed ‘presence’ may not be ecologically or commercially relevant. Using a higher detection threshold allows us to track changes in range size for areas where the species is more commonly present. For all three species of tuna, striped and blue marlin, the relationship is positive for high and medium detection thresholds. For yellowfin and bigeye tuna it is roughly positively linear, while for albacore, striped marlin and blue marlin it is positive but saturates at high abundances. For black marlin and sailfish range size is independent from abundance at high abundances, but declines quickly at lower values. Total abundance declines predicted for these two species were very steep (Table 1).

When we look at the number of cells that meet a minimum density value over time (Figure 4), compact zones of really high abundance are indicated by long tails in the distribution while thicker tails correspond to more even spread in abundance over the range. For instance, in Figure 4, cell count declines sharply from the first bin (i.e. the low density bin) for striped marlin, black marlin and sailfish, less steeply for albacore tuna, yellowfin tuna, and the decline is more gradual for bigeye tuna and blue marlin. When long tails disappear first as abundance declines, areas of high abundance tend not to be maintained even when declines in overall abundance are low. This was especially visible for albacore tuna and yellowfin tuna. Comparatively, bigeye tuna and blue marlin had areas of high abundance distributed over a larger proportion of the range (thick tails) and the disappearance of high density cells was more gradual.

3.2.2 Impact of mobility on measured RAR

One of the challenges in assessing empirically the effect of mobility on RARs is to obtain a measure of dispersal ability that can be used to compare between species (Gaston and Blackburn, 2003; Paradis et al., 1998). We did not attempt this in the current paper, but used population structure from genetics as a proxy instead. Albacore tuna, striped marlin and sailfish have the most pronounced regional structure of our focus species (Montes et al., 2012; Graves and McDowell, 2003) – indicating that they might tend to disperse less far than yellowfin, bigeye tuna, blue marlin and black marlin. There were however no obvious trend between this coarse metric of dispersal and the measured RARs for our study species. On the other hand no obvious time-lags were seen between changes in abundance and range extent, unlike for other less mobile species (Conrad et al., 2001), though no extensive analyses were undertaken to further verify this. It could be that the high mobility of large pelagics results in individuals regularly sampling a high proportion of their habitat such that equilibrium between abundance and range size is reached faster because of the high mixing rate within the range. This is explored further in the simulation work of Section 4.

3.2.3 Implications for management:

The status of stocks is often managed by estimating/modelling their current population dynamics, deriving a range of indicators, and comparing these to thresholds pre-defined by stakeholders as “acceptable” (e.g. compared to F_{MSY} or spawning biomass at MSY). Declines in range concurrent with biomass could bias estimates of stock abundance as CPUE indices usually implicitly assume that the spatial distribution of stocks is constant for the time spanned by the stock assessment (Swain and Sinclair, 1994). Biomass and fishing mortality indicators, while useful at the overall stock level, ignore features of fish populations that can impact stakeholders, for instance their spatial distribution. A change in the space occupied by a stock can affect fleets differentially depending on how mobile they are. In the Pacific for instance, domestic fleets may not have the same ability to track shifting stocks compared to distant-water fleets. In parallel, for stocks that cover multiple EEZs, like those of tuna and billfish, a contraction of the geographic range of target species could overtly affect some countries more than others even if overall stock levels are considered acceptable, because regional management systems are such that stakeholders can only legally access part of a species' distribution.

3.2.4 Caveats:

i. CPUE is not proportional to abundance The nature of CPUE data is such that it is often not proportional to abundance (Harley et al., 2001). CPUE can change for reasons independent of abundance, for instance if targeting for a given species is increased. This happened in the Pacific in the 1970s, when many longline industrial fleets started setting hooks deeper to increase the probability of catching deep-dwelling species like bigeye tuna (Ward and Hindmarsh, 2007). In the current case we used catch-and-effort data aggregated at a 5 degree resolution to maximize spatial and temporal coverage. This precluded us from explicitly accounting for changes in targeting since the variables used to predict targeting behaviour typically act at the much smaller scale of individual vessels (e.g. Hoyle et al. 2014). In order to minimize the effects of targeting while maintaining the wide spatial and temporal coverage afforded by the 5×5 coarser resolution CPUE data, we derived our indices of abundance from multiple fleets with different targeting practices over space and time, such that a single fleet's evolving targeting strategy should not drive the overall trend in abundance estimates in a cell. We also used oceanography data to predict rates of CPUE – in effect running a species distribution model with abundance data (Howard et al., 2014). This allowed us to fill gaps in the CPUE data so that behaviour in non-fished/sampled cells was explicitly modelled (Walters, 2003). We note, also, that many of the issues in CPUE data are parallel to the ones found in terrestrial biodiversity data used in studies of the geographic range, for instance spatial bias towards large cities and road, and highly diverse areas (Reddy and Dávalos, 2003; Dennis and Thomas, 2000).

ii. CPUE for target vs bycatch species: Two of the RARs for which the relationship is unchanging except at very low biomasses (black marlin and sailfish) were observed for billfish species which are typically not targeted by industrial longline fisheries, and for which really high declines in abundance between 1960-2010 were predicted from the model (Table 1). Catches for bycatch species are not as well reported as main target species, and this can preclude the production of conclusive stock assessments in some instances (e.g. sailfish, Hinton and Maunder, 2013). Because of the high uncertainty in the input indices of abundance, RARs derived here for these species should be interpreted with caution.

4 Simulation of spatial dynamics for mobile species with changing habitat quality throughout the range

4.1 Methods

We used a spatial model with a grid layout where each cell has 8 neighbour cells (see Figure 5) and periodic boundaries[6]. Local populations dynamics in each cell follow a logistic model, that is, for each cell two main parameters are defined, the carrying capacity K and the *per capita* growth rate r. Local abundance at the next time step is then a function of abundance at the previous timestep, the expected population growth given how close abundance is to the carrying capacity, and fishery catches:

$$N_{t+1} = N_t + N_t \times r \times (1 - \frac{N_t}{K}) - F_t N_t \tag{1}$$

It is useful to break down the logistic part as it performs two roles: adding individuals (growth, reproduction, r_G thereafter) and removing individuals (natural mortality, r_M thereafter).

$$N_{t+1} = N_t + \underbrace{N_t \times r_G}_{growth} - \underbrace{N_t \times r_M \times -\frac{N_t}{K}}_{mortality} + \cdots \tag{2}$$

In the geographic range of a species we would expect growth and mortality rates to change throughout the range, and not necessarily jointly. As a simple example, reproduction by mobile animals might only occur in certain parts of the range, while mortality would be expected to occur throughout the range.

The r_G parameter allows us to introduce ‘core’, high quality habitats and ‘edge’, lower quality habitats in the model if r_G is set to higher values in designated core cells (see Figure 5). If r_M is set to the same value throughout the range, the lower r_G in edge cells results in slower growth for individuals in those cells, as well as a lower equilibrium biomass. This is representative of what is observed for many Pacific pelagics, which are only found in the edges of their range during the summer.

To add movement between cells we need to account for immigration and emigration:

$$N_{t+1} = N_t + N_t \times r_G - N_t \times r_M \times -\frac{N_t}{K} - F_t N_t + I_t - E_t \tag{3}$$

Immigration and emigration (dispersal) are often modelled as constant rates but in reality these rates are likely to be affected by both intrinsic factors like population density, and extrinsic factors like habitat quality. As a result we used various approaches to model dispersal rates and present these as scenarios:

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[6] When boundaries are periodic, cells at one edge of the grid send individuals to cells at opposite edges. This allows for a continuous distribution of neighbours *versus* reflecting boundaries where cells at the edge send back individuals to themselves.

1. *No dispersal:* Individuals do not move between cells. We know that this is not true for large pelagics but it serves as a useful baseline scenario to investigate whether and how within-stock mobility can change the predicted effects of fishing;
2. *Constant dispersal, no choice:* Individuals emigrate from their natal cell at a constant rate and move to neighbour cells in equal proportions (D_{pref} is set to 0 in equation 4 below);
3. *Constant dispersal, preferential movement:* Individuals emigrate from their natal cell at a constant rate, but they preferentially move to the neighbour cells where their effective growth is expected to be higher. Effective growth is a function of habitat quality as represented by r_G and density in the target cell N/K (see growth part of equation 2). The proportion of emigrating individuals that goes to a given neighbour cell Pn_i is defined as:

$$Pn_i = \frac{(r_{G,i} \times \frac{N_i}{K_i})^{D_{pref}}}{\sum\limits_{i=1}^{N=8} Pn_i^{D_{pref}}} \tag{4}$$

Note: We also modelled emigration from natal cell as a density-dependent process but as qualitative results were not impacted by this feature we only present scenarios 1 to 3.

Fishery mortality was implemented as a factor relative to population growth, since in logistic population models MSY occurs at $0.5r_G$. Low, medium and high fishing mortalities are then defined as below, equal to and greater than F_{MSY}, respectively. When there is population structure, the value of r_G in the core is being used to set the fishing mortality throughout the range. [7]

Simulations were run as follows: populations in all cells are allowed to reach equilibrium, and then fishing mortality is applied to cells based on pre-defined scenarios: (i) even throughout the range; (ii) on core cells only; (iii) on edge cells only. Once all cell populations have reached equilibrium local biomass under fishing, final equilibrium biomass values are extracted and used in scenario comparison. Qualitative trends in results were the same for grids of width 5 to 50 so we present results for a 5×5 for ease of interpretation.

4.2 Results and discussion

The simulation model of spatial population dynamics explored different scenarios of fishing mortality over the range and three scenarios of mobility: no movement between cells (baseline), even emigration between cells (migrating individuals spread evenly between neighbours), and preferred emigration between cells (migrating individuals preferentially move to cells with high effective quality, see Methods).

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[7] This means that if $r_{G,edge} < r_{G,core}$, a fishing mortality equal to F_{MSY} in the core will be high for edge cells as their F_{MSY} is lower than that of core cells.

4.2.1 No habitat structure, r is the same in the core and in the edges

When there is no spatial structure in habitat quality or fishing mortality, individuals cells reach the same equilibrium abundance independent of whether emigration occurs or not (Figure 6, top row).

If fishing mortality is present in the core only (Figure 6, middle row), core biomass will be lower compared to that of the edges, but if emigration is allowed individuals from the edges will migrate to the core, compensating for the decline in abundance due to fishing – even more so under preferential emigration. This is because fishing in the core reduces the N/K ratio in core cells, making effective habitat quality higher (since there is less competition) and individuals from edges will preferentially migrate to a core cell rather than an edge cell. In both emigration scenarios, even though the edges are not being fished, their residing biomass declines since they are now sending part of their biomass towards the core.

If fishing mortality is present in the edges only (Figure 6, bottom row), the opposite phenomenon occurs whereby biomass declines more in the edges than in the core. Core cells biomass still declines despite the absence of fishing, because core individuals are moving towards edge cells.

4.2.2 Core-edge habitat structure, r_G is higher in the core than in the edges, mortality r_M is constant throughout the range

When we add core-edge habitat structure (Figure 7) with a higher r_G in the core, and a fishing mortality set to F_{MSY} derived from core r_G values, equilibrium biomass for edge populations are lower than for core populations (simulating differences in habitat quality). When fishing is applied evenly throughout the range (top row), core populations have lower equilibrium biomass when there is dispersal between cells, although that decline is somewhat compensated when dispersal is preferential, as individuals from the edges move in greater proportions towards core cells since they have a better balance of r_G and N/K.

When only the core is being fished and there is movement between cells (Figure 7, middle row), the decline in the core will be lower when movement is preferential towards better habitat and edge cells will experience a decline in biomass even though they are not being fished themselves. A similar phenomenon occurs when only edge cells are being fished (Figure 7, bottom row), as individuals from core cells will move towards the edges since the lowered N/K will improve their effective habitat quality – but the decline in abundance for core cells will be minimal since the lower r_G of edge cells does not make them very attractive, even if competition is lower from a reduced N from fishing.

See Figure 8 for a summary of equilibrium fished biomass for the two dispersal scenarios compared to the no-dispersal baseline scenario.

4.2.3 Shape of the relationship between population abundance and range size

The relationships between population abundance and range size under the two dispersal scenarios were computed by calculating range extent (number of cells with $N > 0.05K$) and total population abundance (Figure 9). When there is no habitat structure in the range (core and edge have the same habitat quality), range size is unrelated to population abundance, except for very small values when the population is expanding at the start of the simulation. Because habitat quality is the same, the dispersal scenario has no effect on the measured RAR. As the difference in habitat quality between the core and the edges is gradually increased (Figure 9, left to right, top to bottom), the RAR starts to become increasingly linear, but this behaviour is much more pronounced under the scenario of preferential dispersal towards cells of higher quality.

5 Conclusion

We used 5×5 aggregated CPUE longline data from multiple fleets to derive range-abundance relationships for a set of seven target longline species. These relationships were positive for all species but became more pronounced when focusing on areas of higher mean density (high detection thresholds). The simulation model highlighted that such relationships are likely to emerge under relatively simple dispersal conditions as long as growth rate varies within the range – individuals only need to disperse between cells – but that the phenomenon is amplified if individuals preferentially move to high quality habitats. Furthermore, fishing over the range of a species where habitat quality is uneven, as is the case for large pelagics, can result in shifting patterns of dispersal between core and edge areas. These patterns might be possible to observe from otolith microchemistry, but the samples would have to come from periods of contrasting population abundance. Further work will aim to more formally quantify the long-term population consequences of ignoring spatial population dynamics in fisheries management, as well as determine the potential of non-CPUE data sources to further elucidate the ecological mechanisms at play in the redistribution of population abundance under uneven spatial fishing mortality.

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References

Billfish Working Group (2013). Stock assessment of blue marlin in the Pacific Ocean in 2013. Technical Report WCPFC-SC9-2013/SA-WP-09, WCPFC Scientific Committee, Pohnpei.

Blackburn, T. M., Gaston, K. J., Greenwood, J. J. D., and Gregory, R. D. (1998). The anatomy of the interspecific abundance-range size relationship for the British avifauna: II. Temporal dynamics. *Ecol Lett*, 1(1):47–55.

Borregaard, M. K. and Rahbek, C. (2010). Causality of the Relationship between Geographic Distribution and Species Abundance. *Q Rev Biol*, 85(1):3–25.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *Am Nat*, 124(2):255–279.

Carruthers, T. R., McAllister, M., and Ahrens, R. (2010). Simulating spatial dynamics to evaluate methods of deriving abundance indices for tropical tunas. *Can J Fish Aquat Sci*, 67(9):1409–1427.

Carton, J. A. and Giese, B. S. (2008). A Reanalysis of Ocean Climate Using Simple Ocean Data Assimilation (SODA). *Monthly Weather Review*, 136(8):2999–3017.

Chavez, F., Ryan, J., Lluch-Cota, S., and Niquen, M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, 299(5604):217–221.

Conrad, K. F., Perry, J. N., and Woiwod, I. P. (2001). An abundance-occupancy time-lag during the decline of an arctiid tiger moth. *Ecol Lett*, 4(4):300–303.

Davies, N., Harley, S., Hampton, J., and McKechnie, S. (2014). Stock assessment of yellowfin tuna in the Western and Central Pacific Ocean. Technical Report WCPFC-SC10-2014/SA-WP-04, WCPFC Scientific Committee, Majuro.

Davies, N., Hoyle, S., and Hampton, J. (2012). Stock assessment of striped marlin (Kajikia audax) in the Southwest Pacific Ocean. Technical Report WCPFC-SC8-2012/SA-WP-05, WCPFC Scientific Committee, Busan.

Dennis, R. L. H. and Thomas, C. D. (2000). Bias in Butterfly Distribution Maps: The Influence of Hot Spots and Recorder's Home Range. *Journal of Insect Conservation*, 4(2):73–77.

Elith, J. and Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu Rev Ecol Evol S*, 40:677–697.

Fisher, J. and Frank, K. T. (2004). Abundance-distribution relationships and conservation of exploited marine fishes. *Mar Ecol Prog Ser*, 279:201–213.

Fretwell, S. D. and Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor*, 19(1):16–36.

Frisk, M. G., Duplisea, D. E., and Trenkel, V. M. (2011). Exploring the abundance-occupancy relationships for the Georges Bank finfish and shellfish community from 1963 to 2006. *Ecol Appl*, 21(1):227–240.

Gaston, K. J. and Blackburn, T. M. (2003). Dispersal and the interspecific abundance-occupancy relationship in British birds. *Global Ecol Biogeography*, 12(5):373–379.

Graves, J. E. and McDowell, J. R. (2003). Stock structure of the world's istiophorid billfishes: a genetic perspective. *Marine And Freshwater Research*, 54(4):287.

Hall, K., MacLeod, C. D., Mandleberg, L., Schweder-Goad, C. M., Bannon, S. M., and Pierce, G. J. (2010). Do abundance–occupancy relationships exist in cetaceans? *J. Mar. Biol. Ass.*, 90(08):1571–1581.

Hampton, J., Sibert, J., Kleiber, P., Maunder, M., and Harley, S. (2005). Decline of Pacific tuna populations exaggerated? *Nature*, 434(7037):E1–E2.

Harcourt, A. H., Coppeto, S. A., and Parks, S. A. (2005). The distribution-abundance (density) relationship: its form and causes in a tropical mammal order, Primates. *J Biogeogr*, 32(4):565–579.

Harley, S., Myers, R. A., and Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Can J Fish Aquat Sci*, 58(9):1760–1772.

Harley, S. J., Davies, N., Hampton, J., and McKechnie, S. (2014). Stock assessment of bigeye tuna in the Western and Central Pacific Ocean. Technical Report WCPFC-SC10-2014/SA-WP-01, WCPFC Scientific Committee, Majuro.

Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S. A., Dunne, J. P., Costa, D. P., Crowder, L. B., and Block, B. A. (2012). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate change*, 3(3):234–238.

Hinton, M. G. and Maunder, M. N. (2013). Status of sailfish in the Eastern Pacific Ocean in 2011 and outlook for the future. Technical Report SAC-04-07c, IATTC Scientific Advisory Committee, La Jolla.

Howard, C., Stephens, P. A., Pearce-Higgins, J. W., Gregory, R. D., and Willis, S. G. (2014). Improving species distribution models: the value of data on abundance. *Methods in Ecology and Evolution*, 5(6):506–513.

Hoyle, S., Hampton, J., and Davies, N. (2012). Stock assessment of albacore tuna in the South Pacific Ocean. Technical Report WCPFC-SC8-2012/SA-WP-04, WCPFC Scientific Committee, Busan.

Hoyle, S. D., Langley, A. D., and Campbell, R. (2014). Recommended approaches for standardizing CPUE data from pelagic fisheries. Technical Report WCPFC-SC10-2014/SA-IP-10, WCPFC Scientific Committee, Majuro.

ISC Albacore Working Group (2011). Stock Assessment of Albacore Tuna in the North Pacific Ocean in 2011. Technical Report WCPFC-SC7-2011/SA-WP-10, WCPFC Scientific Committee, Pohnpei.

Lehodey, P., Senina, I., Sibert, J., Bopp, L., Calmettes, B., Hampton, J., and Murtugudde, R. (2010). Preliminary forecasts of Pacific bigeye tuna population trends under the A2 IPCC scenario. *Prog Oceanography*, 86(1-2):302–315.

MacCall, A. D. (1990). *Dynamic geography of marine fish populations.* Books in recruitment fishery oceanography. University of Washington Press, Seattle.

Mantua, N. J. and Hare, S. R. (2002). The Pacific decadal oscillation. *Journal of Oceanography*, 58(1):35–44.

Maunder, M. and Punt, A. (2004). Standardizing catch and effort data: a review of recent approaches. *Fish Res*, 70(2-3):141–159.

McKechnie, S., Hoyle, S. D., and Harley, S. J. (2013). Longline CPUE series that account for changes in the spatial extent of fisheries. Technical Report WCPFC-SC9-2013/SA-IP-05, WCPFC Scientific Committee, Pohnpei.

Montes, I., Iriondo, M., Manzano, C., Arrizabalaga, H., Jiménez, E., Pardo, M. Á., Goni, N., Davies, C. A., and Estonba, A. (2012). Worldwide genetic structure of albacore Thunnus alalunga revealed by microsatellite DNA markers. *Mar Ecol Prog Ser*, 471:183–191.

Paradis, E., Baillie, S. R., Sutherland, W. J., and Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *J Anim Ecology*, 67(4):518–536.

R Core Team (2014). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.

Reddy, S. and Dávalos, L. M. (2003). Geographical sampling bias and its implications for conservation priorities in Africa. *J Biogeogr*, 30(11):1719–1727.

Rose, G. and Kulka, D. (1999). Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (Gadus morhua) declined. *Can J Fish Aquat Sci*, 56:118–127.

Sagarin, R. D., Gaines, S. D., and Gaylord, B. N. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *TREE*, 21(9):524–530.

Sileshi, G., Hailu, G., and Nyadzi, G. I. (2009). Traditional occupancy-abundance models are inadequate for zero-inflated ecological count data. *Ecol Model*, 220(15):1764–1775.

Swain, D. P. and Sinclair, A. F. (1994). Fish distribution and catchability: What is the appropriate measure of distribution? *Can J Fish Aquat Sci*, 51(5):1046–1054.

Walters, C. (2003). Folly and fantasy in the analysis of spatial catch rate data. *Can J Fish Aquat Sci*, 60(12):1433–1436.

Ward, P. and Hindmarsh, S. (2007). An overview of historical changes in the fishing gear and practices of pelagic longliners, with particular reference to Japan's Pacific fleet. *Rev Fish Biol Fisher*, 17(4):501–516.

Wood, S. N. (2006). *Generalized additive models: an introduction with R*. Chapman & Hall/CRC, Boca Raton, 1st edition.

Zuckerberg, B., Porter, W. F., and Corwin, K. (2009). The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. *J Anim Ecology*, 78(1):172–181.

7 Figures

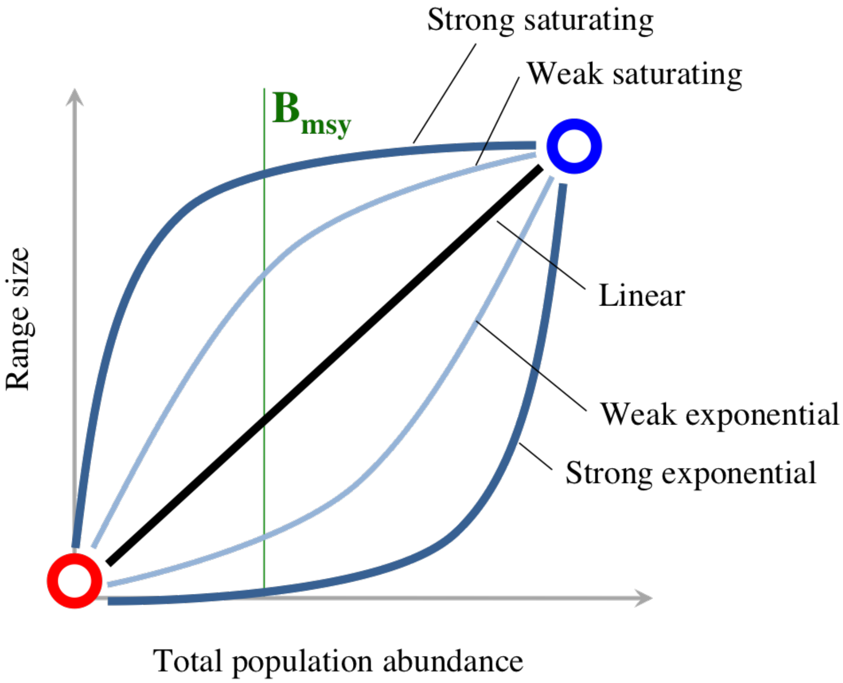

Figure 1: Diagram showing different shapes for the relationship between abundance and range size, and the size of the range at B_{msy} given these different shapes.

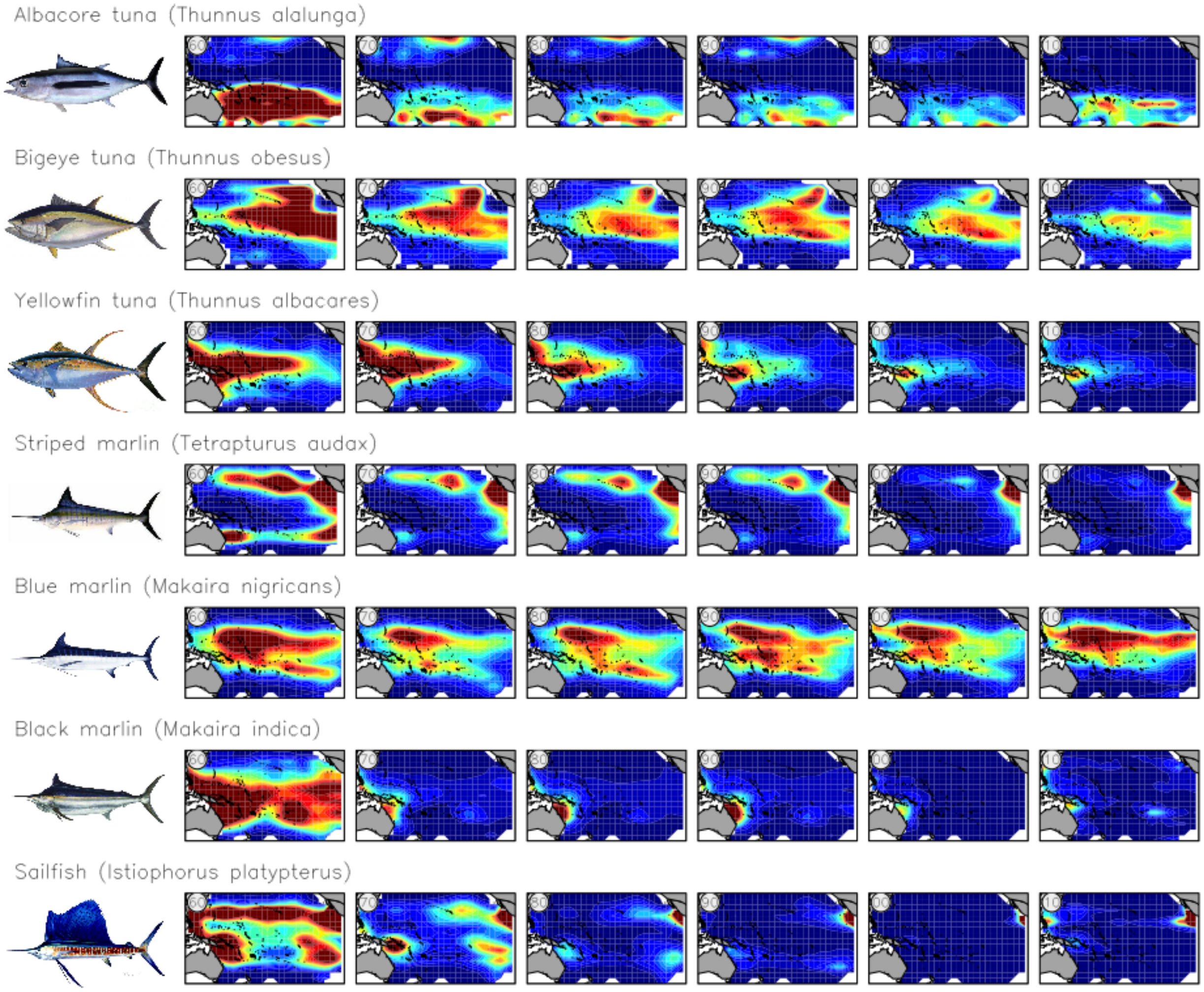

Figure 2: Predicted relative abundance (CPUE) over time for a set of seven target longline species (in rows). Predictions were made from a GAM oceanography model that included Japanese, Korean and Taiwanese longline CPUE data. Relative abundance within each species is shown for years from 1960 to 2010 in 10 years increments (in columns), going from dark blue (very low abundance, $\leq 2.5^{\text{th}}$ quantile of cell abundances predicted over the length of the time-series) to dark red (very high abundance, $\geq 95^{\text{th}}$ quantile).

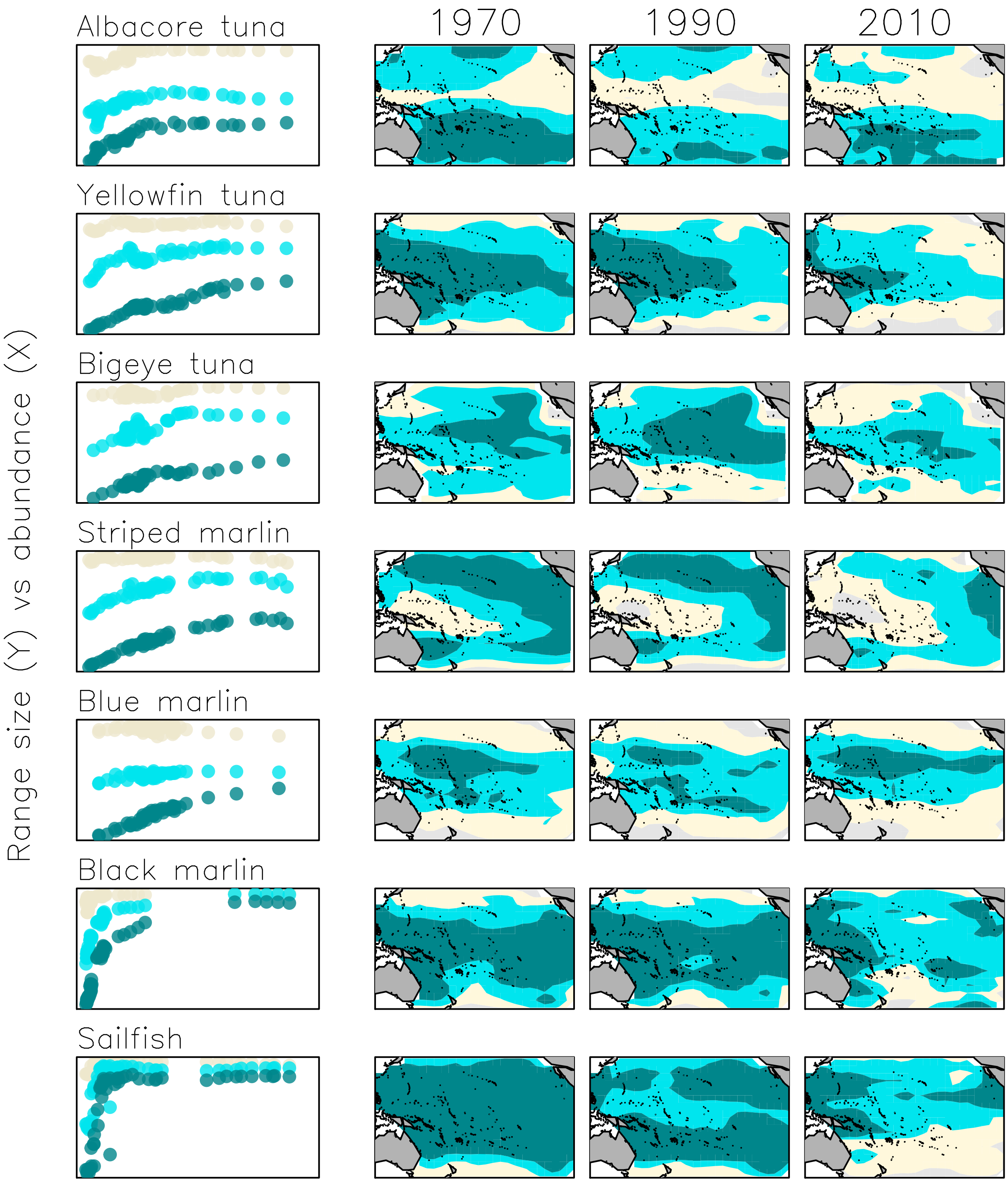

Figure 3: Range size as a function of low (beige), medium (light blue) or high (dark blue) detection thresholds for decades between 1970 and 2010. Threshold values were selected by species based on the second year of lowest abundance as described in the Methods.

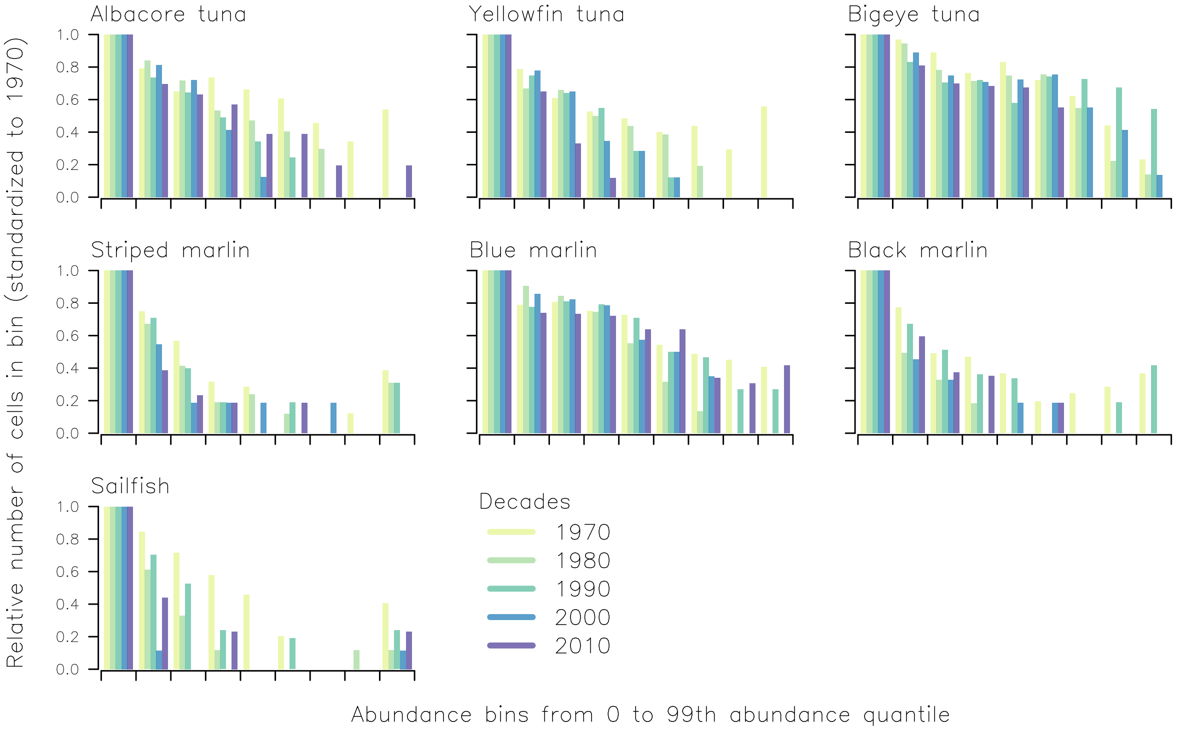

Figure 4: Relative changes in the distribution of abundance over ten year intervals from 1970 to 2010. Histogram bins were defined as even intervals from 0 to the 99th quantile of abundance (cells above this value were grouped in the last bin). Cell counts in each bin were logged to highlight distributions in the tails, and standardized according to bin count in 1970. Counts for each decade by bin are represented as adjacent vertical bars going from yellow (1970) to purple (2010).

Table 1: Comparison of relative trends in abundance from fitted 5×5 CPUE in the current study with recent stock assessment predictions when available

Species	Predicted % of biomass left, this study	Stock assessment*
Yellowfin tuna	18.2%	23.8% of adult biomass left, 1960-2010, (Davies et al., 2014)
Bigeye tuna	29.6%	21.4% of adult biomass left, 1960-2010, (Harley et al., 2014)
Albacore, south of equator	25.5%	≈54.5% left, 1960-2012, (Hoyle et al., 2012)
Albacore, north of 10N	17%	≈ 90% left, 1970-2010, (ISC Albacore Working Group, 2011)
Striped marlin, South-west Pacific	13.7%	≈31.6% of unfished biomass, (Davies et al., 2012)
Blue marlin	60.4%, 1960-2010, 92.6%, 1970-2010	63.6%, 1971-2011, stock biomass left, (Billfish Working Group, 2013)
Black marlin	6.2%	No stock assessment
Indo-Pacific sailfish	4.9%	Unconclusive stock assessment, (Hinton and Maunder, 2013)

* matching years, baseline or reference scenario and total biomass used unless otherwise specified

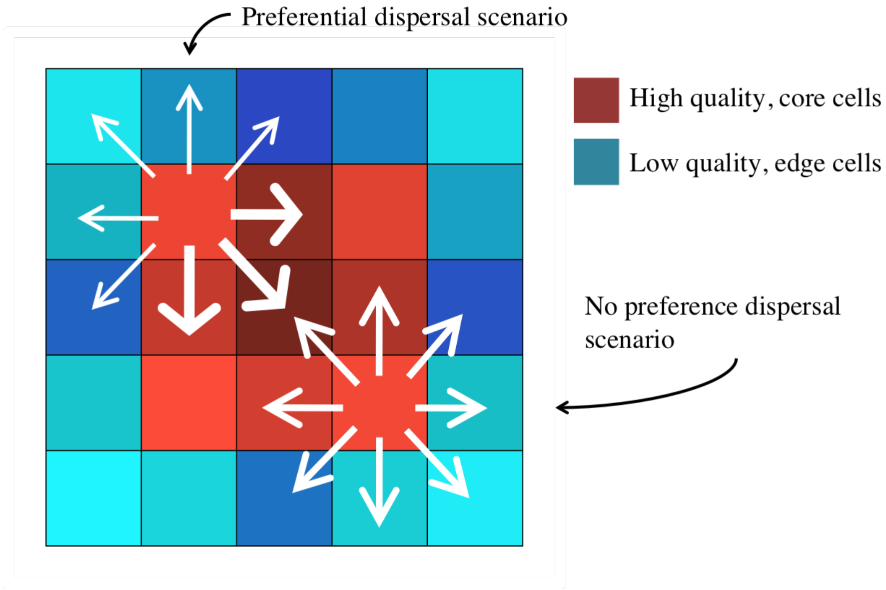

Figure 5: Sample cell layout with core-edge habitat structure (core cells in reds have higher habitat quality, edge cells in blues have lower habitat quality). Under the no preference dispersal scenario (bottom right), emigrating individuals move to all 8 neighbour cells in equal proportions. Under the prefered dispersal scenario (top left), emigrating individuals move to the 8 neighbour cells with a heavier proportion towards high quality cells (here the 'quality' depends on the cell habitat type only (colour), but in the model it is a function of cell quality and conspecific density).

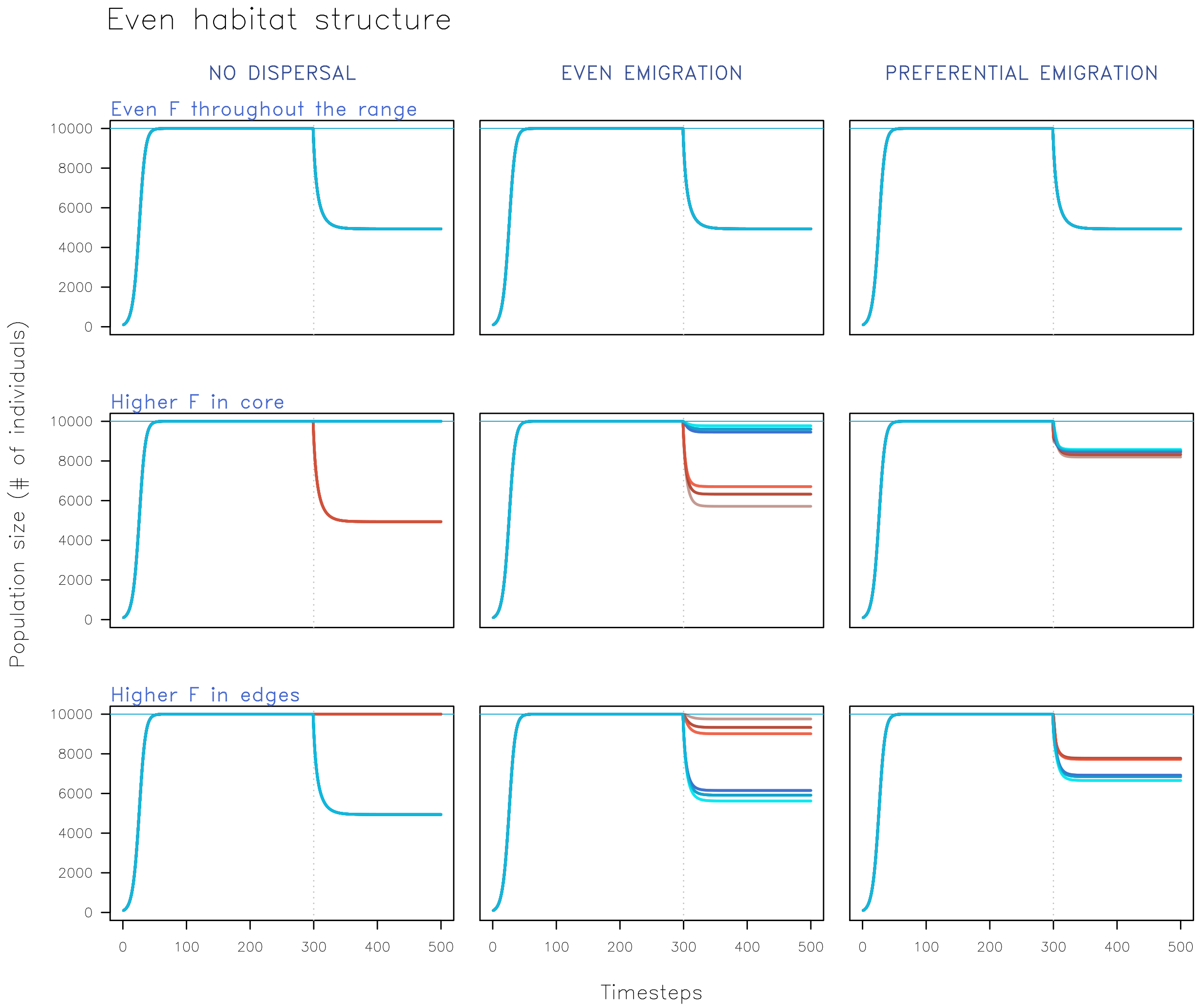

Figure 6: Time-series of population abundance given an even structure of habitat quality in the range. Three different patterns of fishing mortality in the range are shown: even fishing mortality throughout the range (top), fishing mortality in the core only (middle), fishing mortality in the edges only (bottom). The resulting trends in population abundance are shown for three dispersal scenarios: no dispersal (left), even emigration to all neighbours (middle), preferred emigration to neighbours with higher quality habitat, as defined by r_G and the density of conspecifics. Core cells are in reds, edge cells are in blues, but their r_G parameter is set to the same value; the start of fishing is indicated with a dashed line.

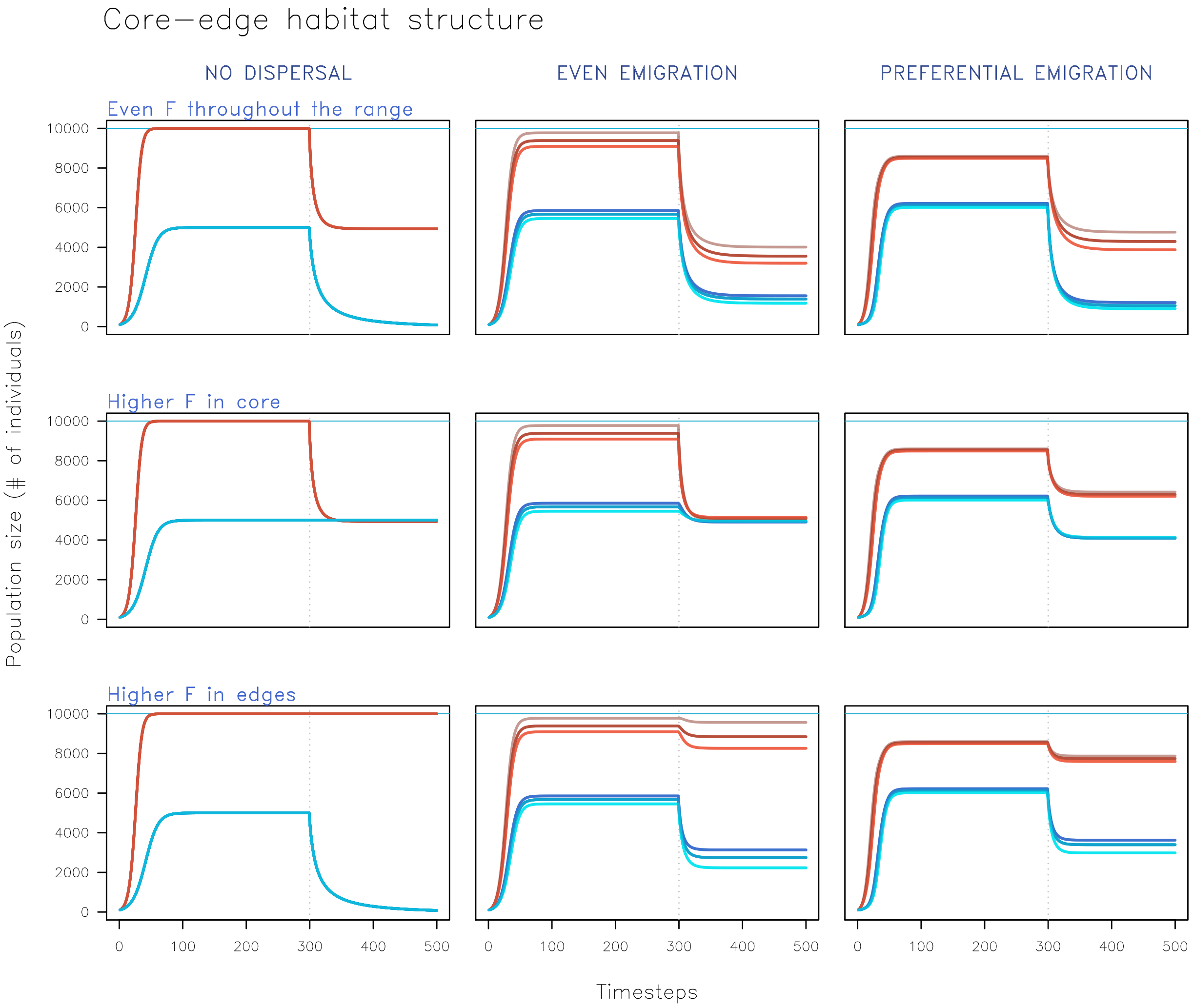

Figure 7: Time-series of population abundance given a core-edge habitat quality structure in the range. Three different patterns of fishing mortality in the range are shown: even fishing mortality throughout the range (top), fishing mortality in the core only (middle), fishing mortality in the edges only (bottom). The resulting trends in population abundance are shown for three dispersal scenarios: no dispersal (left), even emigration to all neighbours (middle), preferred emigration to neighbours with higher quality habitat, as defined by r_G and the density of conspecifics. Core, high quality cells are in reds, edge, low quality cells are in blues; the start of fishing is indicated with a dashed line.

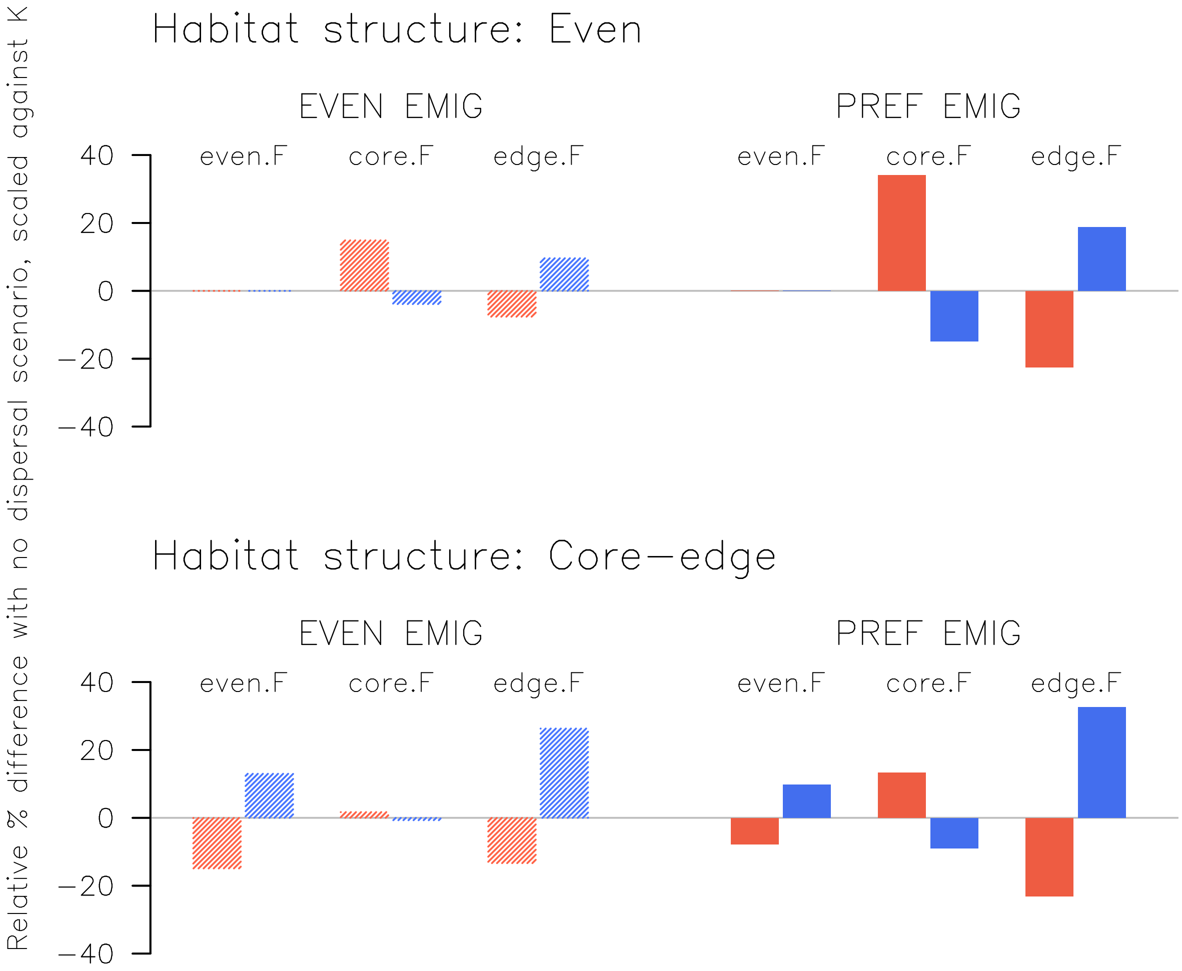

Figure 8: Comparison of equilibrium biomass under fishing for dispersal scenarios even emigration (left panel, dashed bars) and preferred emigration (right panel, full bars), compared to the baseline no-dispersal scenario, for core cells (red) and edge cells (blue).

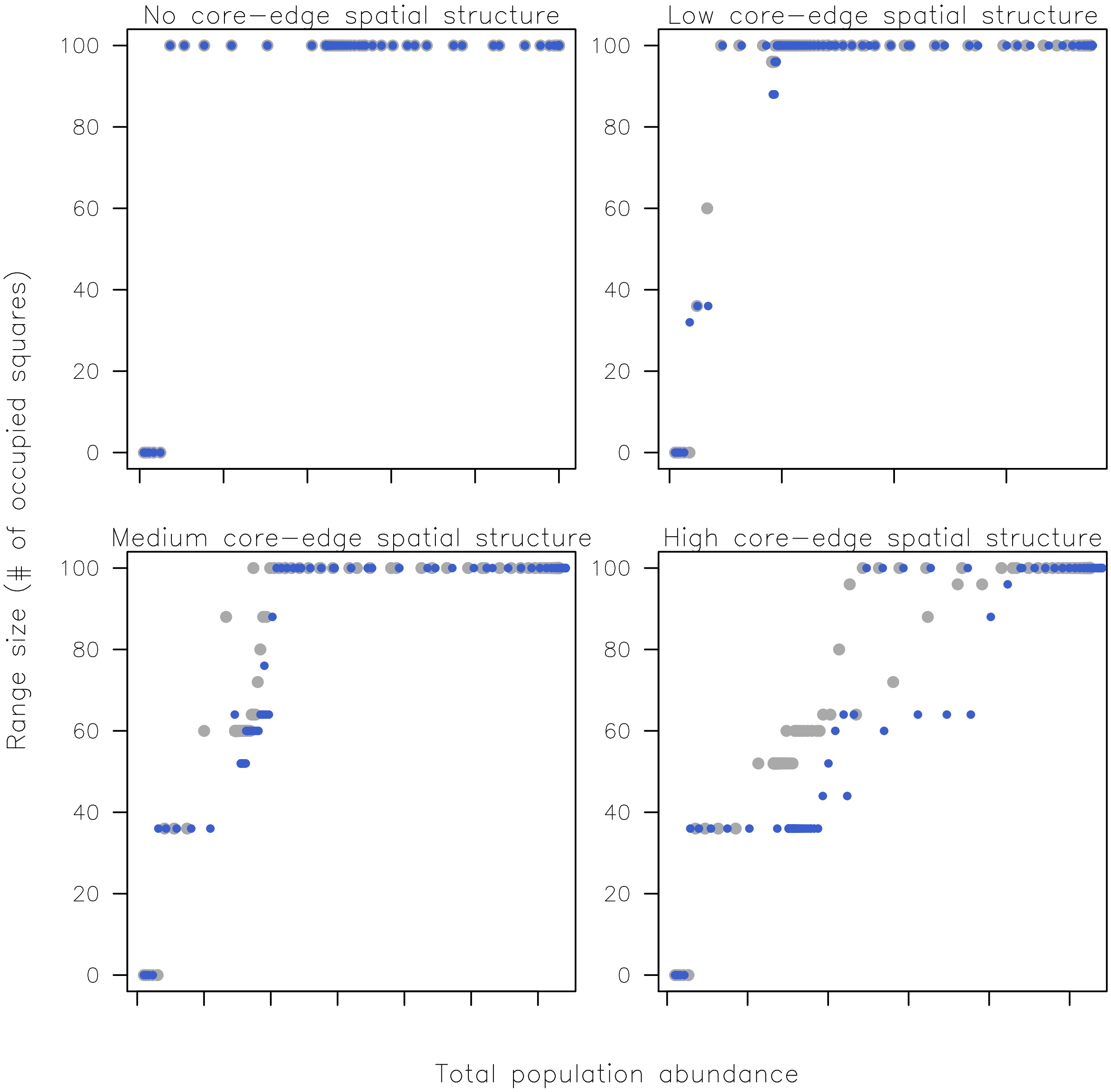

Figure 9: Range-abundance relationship under two dispersal scenarios: even movement throughout the range (grey points); preferential movement towards cells with better effective habitat (blue points).

8 Appendix

Description of semi-additive GAM models with oceanography variables

For each species two error distributions were tested to predict CPUE, and the one that performed the best in terms of model diagnostics was retained. In the first instance CPUE was modelled as log-normal with a small constant added so that the natural logarithm can be taken ($c = 0.01$):

$$\begin{aligned} &ln(CPUE + c) = \\ &f(\text{year, quarter, lon, lat, oceanography variable 1, oceanography variable 2}) + \text{intercept} + \epsilon \end{aligned} \tag{5}$$

where f is a semi-parametric additive predictor.

In the second instance a delta-lognormal (hurdle) model was used in which the probability of obtaining a positive catch and the catch rate when catch is non-zero are modelled separately.

$$Pr(Y = y) = \begin{cases} \omega, & \text{y=0} \\ (1 - \omega)f(y), & \text{y} > 0 \end{cases} \tag{6}$$

ω is the probability of obtaining zero catch and is modelled using a binomial distribution with a logit or clog-log link. $f(y)$ is the catch rate when catch is non-zero and it is modelled using a log-normal distribution with an identity link (but no constant added, $c = 0$). In both cases we used the same model structure to estimate the binomial and positive components in the model as in equation 5. This assumes that the same explanatory variables drive the occurrence of positive catch rates and their magnitude, although the relative importance of these variables may vary between the binomial and positive component.

Table 2: Final model structure retained for each species

Species	Model type	Binomial link	Model structure*
Albacore tuna	DeltaLN	Logit	s(temp215,by=as.factor(yy5i),k=20) + s(salt025,k=20,by=as.factor(yy5i)) + as.factor(flag)*as.factor(dec) + as.factor(qtr) + s(lond,latd,k=80) + s(yy, by=as.factor(latd),k=12)
Bigeye tuna	DeltaLN	Logit	s(temp215,by=as.factor(yy5i),k=20) + s(salt215,k=20,by=as.factor(yy5i)) + as.factor(flag)*as.factor(dec) + as.factor(qtr) + s(lond,latd,k=80) + s(yy, by=as.factor(latd),k=12)
Yellowfin tuna	DeltaLN	Logit	s(temp025,salt215,by=as.factor(yy5i), k=30) + as.factor(flag)*as.factor(dec) + as.factor(qtr) + s(lond,latd,k=80) + s(yy, by=as.factor(latd), k=12)
Striped marlin	Log-normal	—	s(salt215, k = 15) + s(temp025, k = 15) + s(lond, latd, k = 40) + qtr + flag * dec + s(yy, by = as.factor(latd), k = 15)
Blue marlin	DeltaLN	Logit	s(temp215,by=as.factor(yy5i),k=20) + s(salt025,k=20,by=as.factor(yy5i)) + as.factor(flag)*as.factor(yy5i) + as.factor(qtr) + s(lond,latd,k=80) + s(yy,by=as.factor(latd),k=12)
Black marlin	DeltaLN	Logit	s(temp215,k=20) + s(salt025,k=20) + as.factor(flag)*as.factor(dec) + as.factor(qtr) + s(lond,latd,k=30) + s(yy, by=as.factor(latd),k=15)
Indo-Pacific sailfish	DeltaLN	Clog-log	s(temp025, salt215, by=as.factor(yy5i), k=30) + as.factor(flag)*as.factor(dec) + as.factor(qtr) + s(lond,latd,k=80) + s(yy, by=as.factor(latd),k=12)

*Variable abbreviations: tempX, saltX are temperature and salinity at X meters, respectively; yy, yy5i, dec are year, 5 year interval, and decade; qtr is quarter; flag is fisheries fleet; lond and latd are longitude and latitude 5×5 degree cell; $s(...)$ indicates a spline was fitted, with k being a parameter controlling the spline flexibility.