

RESEARCH PAPER



The relationship between geographic range extent, sea surface temperature and adult traits in coastal temperate fishes

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Editor: Jonathan Waters

Abstract

Aim: We use publicly available data to assess the influence of ocean basin, various biological traits and sea surface temperature on biogeographic range extent for temperate, continental shelf fish species spanning 141 families.

Location: Coastal waters of the temperate Northern Hemisphere.

Taxon: Teleost Fishes (Infraclass Teleostei).

Methods: We assess the relationship between species range extent and depth range, maximum body length, schooling behaviour and use of multiple habitats for 1,251 species of northern, temperate, continental shelf fishes in different basins (Atlantic vs. Pacific) and margins (east vs. west) using linear mixed-effect models with family and genus as nested random effects. We further assess the relationship between species range endpoint distribution and latitudinal temperature gradient using generalized linear models.

Results: We found strong positive relationships between the number of species northern range endpoints and the steepness of the latitudinal sea surface temperature gradient on the western margins of the Atlantic and Pacific Oceans, but no relationship on the eastern margins of these ocean basins. The strongest predictors of range extent in our global model are ocean basin/margin and depth range. Maximum body length, schooling behaviour and use of multiple habitats are also significant predictors of range extent in the global model. The factors influencing range extent differ by basin and margin.

Main conclusions: There are broad differences in patterns of species range extent and distribution of species ranges among basins/margins. These differences appear to be driven in part by variation in latitudinal water temperature gradient between basin margins. Our data suggest that sharp latitudinal temperature gradients may pose a barrier to dispersal and range expansion along the western margins of the Atlantic and Pacific Oceans, but not necessarily on the eastern margins. Our work also suggests that several post-settlement traits may be associated with range extent either globally or in some temperate basins.

KEYWORDS

adult traits, biogeography, range expansion, range extent, sea surface temperature, species distribution

1 | INTRODUCTION

Biogeographic range extent, or the area encompassed by a species' range, varies by orders of magnitude among species of marine fishes, yet despite decades of study the broad determinants of range size in marine fishes are largely unknown (Brown, Stevens, & Kaufman, 1996; Luiz et al., 2012; Victor & Wellington, 2000). Over 90% of marine fishes disperse pelagically as larvae adrift in the water column, and after establishing in a benthic habitat many species do not disperse throughout their adult lives (Leis, 1984). As many species disperse exclusively in their pelagic phases, some studies suggest that the amount of time a species' larva spend in the water column before settling, known as the pelagic larval duration (PLD), may correlate with range extent (Riginos & Victor, 2001; Shanks, Grantham, & Carr, 2003; Siegel, Kinlan, Gaylord, & Gaines, 2003).

Although a link between dispersal and range size may be intuitive, more recent research has not found evidence to support a clear relationship between PLD and range extent. In many tropical reef systems, where the majority of work on PLD and range size has occurred (Lester & Ruttenberg, 2005; Luiz et al., 2013; Mora et al., 2012), the distance between reefs is small enough that the larval durations of most reef fish are sufficient to colonize nearby reefs (Mora et al., 2012). It appears that only large, deep spans of ocean without suitable shallow reef habitat pose a significant barrier to dispersal for reef fishes with short larval durations. Recent studies suggest that PLD may only affect biogeographic range extent when there are significant barriers to dispersal, such as the East Pacific and Mid-Atlantic barriers, capable of filtering out species with shorter PLDs (Lessios & Robertson, 2006; Lester & Ruttenberg, 2005; Lester, Ruttenberg, Gaines, & Kinlan, 2007; Mora et al., 2012). While PLD may influence range size when ranges cross significant dispersal barriers, species living along continental coastlines will encounter few if any of these barriers. Therefore, data suggest there is a weak, inconsistent relationship between PLD and range size (Lester et al., 2007; Luiz et al., 2013; Shanks, 2009). As a result of these findings, ecologists have begun to focus on alternative mechanisms besides dispersal ability to explain the mechanisms limiting range extent (Luiz et al., 2012, 2013; Mora et al., 2012).

Successful colonization of habitat is a function of both dispersal ability and survival of juvenile fish post-recruitment (Marshall, Monro, Bode, Keough, & Swearer, 2010). Early post-settlement mortality varies widely among species in space and through time and can be a significant driver of population dynamics (Almany & Webster, 2006; Caley et al., 1996; Hixon & Beets, 1993; Victor, 1983). This suggests that traits aiding the survival of juvenile fishes may be important in allowing for the successful colonization of new areas, and thus, may be associated with range extent. In a global analysis on tropical reef fishes, Luiz et al. (2013) found a correlation between geographic range extent and traits that influence post-settlement survival such as schooling behaviour, maximum body size and nocturnal behaviour. Additionally, Luiz

et al. (2012) found a positive relationship between range extent and both maximum body size and use of multiple habitats along the continental coast of the western Atlantic. Other studies have shown that schooling behaviour may reduce predation on reef fishes (DeMartini, Anderson, Friedlander, & Beets, 2011; Sandin & Pacala, 2005), and fishes with large body sizes at adulthood may face less predation as juveniles (Munday & Jones, 1998) as a result of faster growth and larger juvenile body size (Murphy, Warren-Myers, Jenkins, Hamer, & Swearer, 2014). Furthermore, ecological generalists may be able to establish populations and persist in a greater number of habitats (Cassey, Blackburn, Sol, Duncan, & Lockwood, 2004), and generalists are less likely to be impacted by disturbance (Emslie, Pratchett, & Cheal, 2011; Emslie, Pratchett, Cheal, & Osborne, 2010; Feary, Almany, McCormick, & Jones, 2007; Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Each of these traits may increase probability of establishment post-settlement, ultimately leading to larger range size.

Collectively, these recent studies have given us a better understanding of the factors that influence range size in tropical reef fishes. However, the factors that influence range size may differ between temperate and tropical systems, and ecologists have not examined temperate systems in nearly as much detail (but see Leis et al., 2013; Lester et al., 2007). Temperate coasts often run largely from north to south along continental margins over large latitudinal expanses, whereas a great deal of tropical reef habitat is scattered among islands. Tropical basins contain large stretches of shallow, interconnected reef habitat with little temperature variation, punctuated by deeper, uninhabitable regions (Mora et al., 2012). Biogeographic barriers to dispersal in tropical seas are typically landmasses (such as the isthmus of Panama), large stretches of deep ocean uninhabitable to reef species (such as the East Pacific Barrier) or currents (such as the East Australia Current) (Cowman & Bellwood, 2013). Except for the Gulf of Alaska in the eastern Pacific, there are no land-based ("hard") barriers to dispersal along northern temperate coasts, although sharp latitudinal temperature gradients may pose a soft environmental barrier to range expansion. Along the western margins of the temperate Pacific and Atlantic, the Kuroshio current and Gulf Stream carry warm water offshore, resulting in abrupt changes in temperature across latitude where these currents move away from the coast. Such sharp temperature gradients are mostly absent along temperate eastern coasts and in tropical waters (Payne, Brown, Reusser, & Lee, 2012). For many species, these sharp latitudinal temperature gradients may pose barriers to dispersal, constraining their ranges. These currents may also limit range expansion by transporting larvae offshore, thereby reducing recruitment (Gaylord & Gaines, 2000). Therefore, we might expect species range endpoints to cluster around sharp temperature breaks in the western margins of the Atlantic and Pacific (Gaston & Chown, 1999; Tomašových, Jablonski, Berke, Krug, & Valentine, 2015).

More generally, temperate marine species experience sharper changes in temperature across latitude and higher annual variation in temperature than tropical species. Stevens (1989) introduced the climatic variability hypothesis, arguing that patterns in



terrestrial diversity across latitude result from differences in annual temperature variation experienced by temperate and tropical species. Stevens (1996) later extended this hypothesis to explain patterns in bathymetric range extent across depth in marine taxa. Consequently, species adapted to broad temperature ranges may be expected (under the climatic variability hypothesis) to traverse gradients in temperature across both latitude and depth. In support of this hypothesis, several studies have found a positive relationship between range extent and depth range of marine fishes (Harley, Smith, & Moore, 2003; Smith & Gaines, 2003; Stevens, 1996). These results suggest that depth range and latitudinal range extent may not be causally linked, but that depth range should nonetheless be expected to correlate with latitudinal range extent. As habitat types and habitat diversity vary with depth (Macpherson & Duarte, 1994), species with large depth ranges may also be more likely to be ecological generalists (Luiz et al., 2013; Munday & Jones, 1998), capable of settling and establishing in a broader range of habitats.

Just as in tropical systems, juveniles of temperate species experience size-selective mortality due to predation (Murphy et al., 2014; Sogard, 1997). However, seasonal temperature variation is considerably greater in temperate systems than in tropical systems, and past studies suggest that juvenile fishes in temperate systems experience additional size-selective overwintering mortality not experienced by tropical species (Conover & Present, 1990; Henderson, Holmes, & Bamber, 1988; Oliver, Holeyton, & Chua, 1979; Sogard, 1997). As a result of both size-selective predation and overwintering mortality, larger species may have larger range extents in temperate systems. Specifically, because seasonal temperature variation is greatest along the western margins of the Pacific and Atlantic (Onogi et al., 2007), we might expect a stronger relationship between range extent and body size on the western margins of the Atlantic and Pacific compared to the eastern margins.

Here, we evaluate these predictions by modelling the relative effects that depth range, maximum body length, schooling behaviour and use of multiple habitats have on the range sizes of temperate fishes. We hypothesize that (1) sharp latitudinal temperature gradients not present in tropical oceans limit the range extent of temperate marine fishes and (2) post-settlement traits are associated with range extent in temperate marine fishes. Specifically, we expect a positive relationship between range extent and (2a) traits that reduce predation on juvenile fishes, such as schooling behaviour and body size and (2b) traits associated with greater habitat availability, such as depth range and use of multiple habitats. To evaluate whether traits examined in tropical systems (Luiz et al., 2012, 2013; Munday & Jones, 1998; Sandin & Pacala, 2005) also influence range extent for species along northern temperate coasts, we assess the relationship between range extent and post-settlement traits including depth range, maximum body length, schooling behaviour and use of multiple habitats for 1,251 northern temperate, shallow water, benthically associated species (Dataset S1). We also assess the relationship between species range distributions and coastal sea surface temperature encompassing their ranges (Dataset S2).

2 | MATERIALS AND METHODS

2.1 | Data acquisition

We focused our analyses on temperate fish species in the northern Atlantic and Pacific oceans. For the purposes of this analysis, we defined “temperate species” as those with at least part of their range in northern temperate latitudes. The data therefore included “bridge-species,” whose ranges include both temperate and tropical latitudes (Appendix S1: Figures S1 and S2). Based on initial inspection of species lists, there were insufficient data available from much of the southern temperate oceans, so we excluded these areas from our analysis. To standardize data collection, we included only species with data available in FishBase (Froese & Pauly, 2016). While information in FishBase was not exhaustive, data were generally reliable, and its consistent data fields provided a convenient way for us to standardize criteria for selection. We included only native bottom-associated marine fishes in the Infraclass Teleostei, whose minimum depth was no deeper than 100 m and maximum was no deeper than 1,000 m. While we did not use hard latitude limits to select species, the narrowest latitudinal ranges in which all species in the data occur are as follows: 28°–59° in the eastern Atlantic, 25°–52° in the western Atlantic, 28°–62° in the eastern Pacific and 24°–59° in the western Pacific (Appendix S1: Figure S1). We gathered data on each species whose range included part of a northern temperate coast (~10,000 sp.) using the packages “XML,” “stringr,” “RCurl” and “rfishbase” in R (Boettiger, Lang, & Wainwright, 2012; Lang, 2016, 2017; R Core Team, 2017; Wickham, 2017). We deemed species which inhabited two or more habitats to be occupants of multiple habitats. Habitats included: brackish water, the intertidal zone, soft mud or sand bottoms, and rocky reefs. We extracted depth and schooling information by matching strings in the “environment” and “biology” sections of each species’ summary page, respectively. For most species, FishBase provided maximum length in the form of total length, but occasionally provided only standard length. For these species, we estimated total length based on standard to total length conversion equations for the species, mean of the genus or mean of the family, as appropriate. In the few cases for which length conversion constants were not available at the family level, we multiplied standard length by 1.19 (the average of all conversion factors in our dataset) to estimate total length. We attempted to classify each species as diurnal or nocturnal and to gather pelagic larval duration data for each species, but as these data were only available for a small subset of species, we excluded these factors from our analyses.

We determined specific range endpoints from the FishBase range description for each species. If range data were vague (e.g., “Japan”), we attempted to supplement range data from field guides whenever possible. We used maximum linear distance (MLD) in km as a metric for geographic range extent. We defined MLD as the distance between the two farthest points in a species’ range on a line of constant bearing, or rhumb line, along the earth’s surface. We chose MLD because

it correlates well with other metrics of range extent, is informed by both the latitudinal and longitudinal range of a species, and has been used in other studies on range extent (Lester & Ruttenberg, 2005; Lester et al., 2007; Luiz et al., 2013; Mora et al., 2012). In our own data, we found that MLD along a rhumb line was highly correlated with other metrics of range extent, such as maximum great circle distance ($r = 0.98$). MLD was also highly correlated with latitudinal range, calculated by great circle distance ($r = 0.89$). We used the “geosphere” package in R to calculate MLD for each species (Hijmans, 2016a). We obtained range size information for 1,251 species (Appendix S2) and complete biological data for 782 species. Because some species had distinct ranges in different basins or along different margins of the same basin, these 1,251 species comprised 1,263 distinct observations, 793 of which had complete biological data.

2.2 | Analyses of range endpoints

Because results from previous work suggests that temperature influences species ranges in northern temperate systems (Lester et al., 2007), we sought to evaluate the relationship between latitudinal temperature gradient and distribution of range endpoints for species in our data. To include this information, we used annual sea surface temperature maps obtained from NASA's Physical Oceanography Distributed Active Archive Center with a resolution of 0.011 degree latitude by 0.011 degree longitude to generate a map of average sea surface temperature between 1986 and 2016 (Chin, Vazquez, Armstrong, & Mariano, 2010). We cropped sea surface temperature maps to 24 nautical mile marine territory bands along each coast for which we had species distribution data (Flanders Marine Institute, 2016). We used the R packages “sp,” “rgdal” and “raster” to average temperature maps across years and crop the resulting map (Bivand, Keitt, & Rowlingson, 2017; Hijmans, 2016b; Pebesma & Bivand, 2005). We used 24 nautical mile shapefiles because they were the narrowest bands for which we could crop the sea surface temperature data without generating missing values. For each basin/margin, we extracted mean sea surface temperature at each degree of latitude from the cropped map of the basin/margin (Appendix S3, Dataset S2). Finally, we ran separate generalized linear models with a negative binomial error distribution for each basin regressing the number of species range endpoints in each degree of latitude against the temperature change in that degree of latitude and the number of species present in the data at that latitude. We used likelihood ratio tests to assess the significance of predictors, and adjusted for multiple comparisons using the Benjamini and Hochberg method (Benjamini & Hochberg, 1995; Neyman & Pearson, 1933).

2.3 | Analyses of range extent

Using the package “lme4,” we fit linear mixed-effects models with the square root of species range extent (MLD) in km as the response for the global dataset, western Pacific, eastern Pacific, western Atlantic and eastern Atlantic separately (Bates, Maechler, Bolker, & Walker, 2015). We accounted for differences due to basin (Atlantic

vs. Pacific) and margin (east vs. west) in the global model by including a single term with four levels: eastern Atlantic, western Atlantic, eastern Pacific and western Pacific, which we refer to here as basin/margin. We assessed the fit of competing generalized linear mixed-effect models with different error distributions (including negative binomial, Poisson and gamma), and linear mixed-effect models with different transformations (including log and square root) on the response, by examining residuals plots and assessing bootstrapped estimates of the skewness and kurtosis of the response (Cullen & Frey, 1999). We determined that a linear mixed-effects model with a square-root transformation on the response resulted in the best fit. In each model we fit depth range, maximum length, schooling behaviour, use of multiple habitats and all second-order interactions as predictors. We controlled for phylogeny by including family and genus as nested random effects (Luiz et al., 2012, 2013; Mellin, Huchery, Caley, Meekan, & Bradshaw, 2010).

We performed automated model selection by Akaike information criterion (AIC) on each basin/margin model using the “MuMIn” package (Barton, 2018; Burnham & Anderson, 2002; Zuur, Leno, Walker, Saveliev, & Smith, 2011). We did not consider the nested random effect of family and genus as a candidate for removal from any model. We assessed multicollinearity by calculating variance inflation factors (VIF) for each predictor before performing model selection. Based on VIF, we did not find any evidence for multicollinearity, except in the western Atlantic, which was remedied by excluding use of multiple habitats as a predictor from the western Atlantic model. We used likelihood ratio tests to evaluate the significance of model parameters, and adjusted p -values for multiple comparisons (Benjamini & Hochberg, 1995; Neyman & Pearson, 1933). To aid interpretation of model results, we assessed the relative support for each predictor by summing the AIC weights of all models including that term (Burnham & Anderson, 2002; McLean et al., 2016). We generated all figures using the package “ggplot2” in R (Wickham, 2009).

3 | RESULTS

3.1 | SST and range endpoint distribution

Adjusting for species richness gradients over latitude, latitudinal temperature gradient (i.e., temperature change across a given degree of latitude) is positively associated with northern range endpoint density (i.e., the number of species range endpoints per degree of latitude) in the western Pacific ($p < 0.001$) and Atlantic ($p < 0.001$), but not the eastern Pacific ($p = 0.446$) or Atlantic ($p = 0.779$, Figures 1 and 2). There is no significant relationship between southern range endpoint density and sea surface temperature gradient in any basin/margin (Figure 3).

3.2 | Patterns in range distributions

Species northern range endpoints appear to be more dispersed across latitude in the eastern margins of each basin than in the western margins, where latitudinal temperature gradients are steeper (Figure 1).

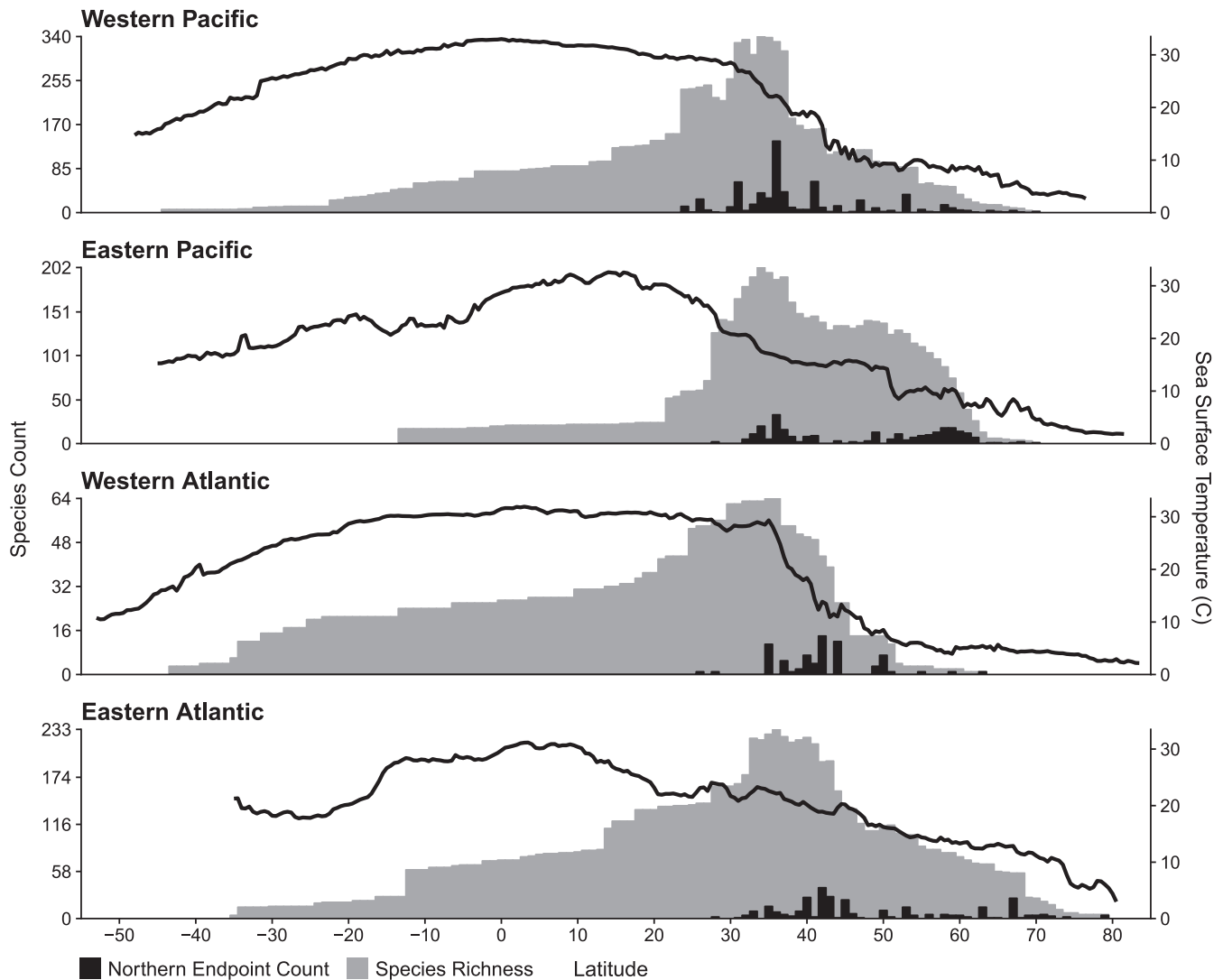


FIGURE 1 Bar chart showing fish species richness gradients and frequency distributions of northern species range limits, in grey and black respectively. Sea surface temperature is represented with a black line. Black bars represent the number of species whose northern range endpoint occurs in each degree of latitude. Species richness gradients represent only the species in the dataset, most of which have exclusively temperate ranges but some of which have ranges which extend beyond temperate waters

Northern range endpoints are heavily clustered around 42° in the western Atlantic and 36° in the western Pacific, the approximate latitudes where the Gulf Stream and Kuroshio current flow east off-shore respectively (Figure 2). In the eastern Atlantic, northern range endpoints peak at 42° and 70°, in the southern Bay of Biscay and in northern Norway respectively. The peak at 42° remains regardless of whether species endemic to the Mediterranean are included in the data. In the eastern Pacific, northern range endpoints peak around Monterey Bay at 36°, with a smaller and more gradual peak in the Gulf of Alaska at 58°.

In all basins/margins, large peaks in southern range endpoint density occur between 28° and 36°, with other peaks further south. Southern range endpoints peak at 30° in the western Atlantic and western Pacific, near northeast Florida and southern Japan. In the eastern Pacific, southern range endpoints peak in central Baja, at about 28°. In the western Pacific, there is an additional peak in southern range endpoint density around Taiwan

at 24°. The largest peak in southern range endpoints in the eastern Atlantic occurs at 36° (Figure 3). However, excluding species endemic to the Mediterranean, the largest peaks in the eastern Atlantic occur at 11° and 14°, the latitudes of Angola and Senegal respectively.

Basin/margin ($\chi^2(3) = 31.9, p < 0.001$) and depth range ($\chi^2(1) = 61.7, p < 0.001$) are the strongest predictors of biogeographic range extent in the global model, both with variable importance (RIV) metrics of 1. Mean range extent is similar in the eastern Atlantic ($4,562 \pm 123$ km) and western Atlantic ($4,610 \pm 348$ km), but much narrower in the eastern Pacific ($3,363 \pm 133$ km), and western Pacific ($2,451 \pm 93$ km, Figure 4). However, some of the difference in range extent by basin/margin is explained by other predictors in the model. Adjusted for other predictors in the model, species in the western Atlantic and eastern Atlantic have nearly identical range extent on average, while the average range extents of eastern and western Pacific species are 34 and 121 km narrower than the range extents of eastern Atlantic species respectively.

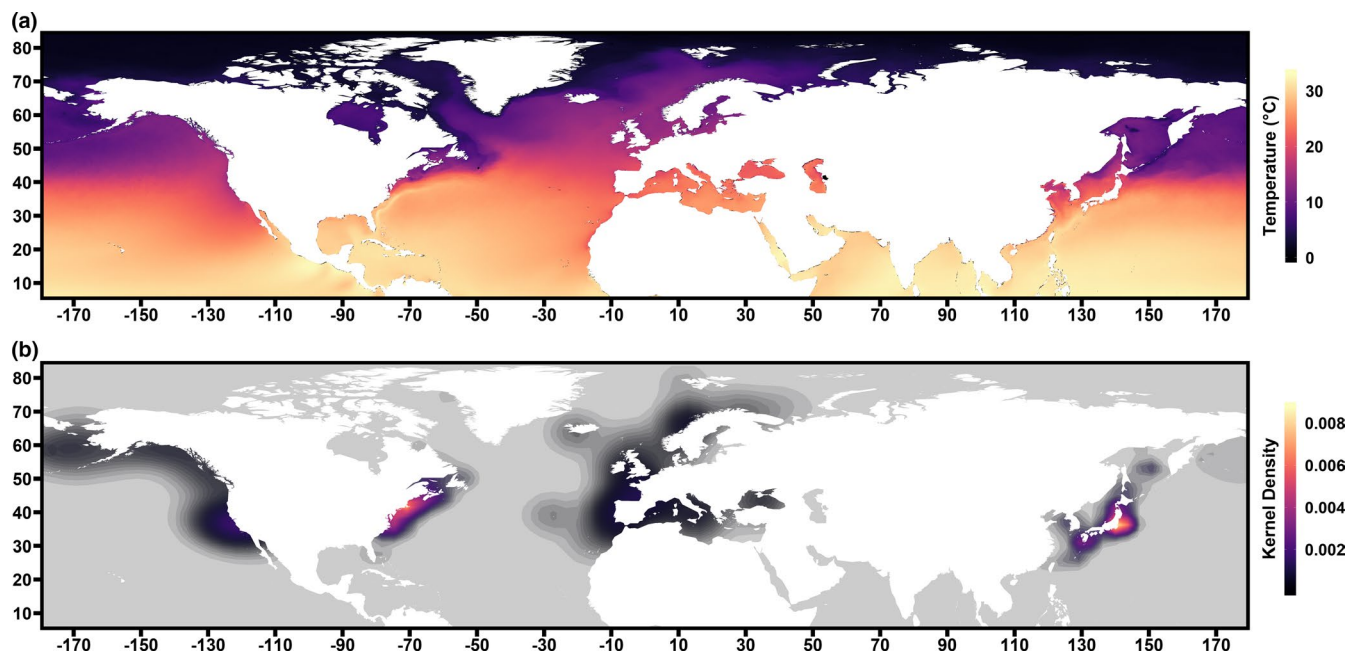


FIGURE 2 (a) Plot of mean annual sea surface temperature from 1985 to 2009. Plot generated from data available at NASA's Physical Oceanography Distributed Active Archive Center (Chin et al., 2010). (b) Heatmap of northern range endpoints of all species; warmer areas indicate greater relative density

3.3 | Life history trait models

After adjusting for basin/margin, maximum length ($p = 0.016$, $RIV = 0.92$), depth range ($p < 0.001$, $RIV = 1$), schooling behaviour ($p = 0.038$, $RIV = 0.76$) and use of multiple habitats ($p = 0.0014$, $RIV = 0.987$, Table 1) are all significantly positively associated with range extent in the global model, but there are no significant interactions. Factors associated with range extent differ when we examine data by basin and margin. Depth range is significant and highly important ($RIV > 0.98$) in models for the eastern Atlantic, western Pacific and eastern Pacific (Figure 5). Maximum length is included in only the eastern Pacific and Atlantic models but is significant and has high relative importance ($RIV > 0.94$) in each. The effects of both depth range and maximum length (adjusted for other predictors) in the global and basin models are relatively slight; a one standard deviation increase in either predictor is associated with an increase in range extent of less than 80 km in each of these models (Table 1, Figure 5).

Schooling behaviour is retained in all models except for the eastern Pacific but is not significant in any and is of consistently lower importance than depth range and maximum length. Even adjusted for differences due to family and genus, schooling species in the western Atlantic tend to have substantially larger range extents, so the absence of a significant relationship in the western Atlantic may be due to the relatively low sample size for the basin ($n = 43$) (Table 1, Figure 5). About 23% of species in the western Atlantic dataset were marked as schoolers, compared to 3%, 8% and 9% in the Western Pacific, eastern Pacific and eastern Atlantic respectively. Use of multiple habitats is included only in the western Pacific model but is significant and highly important ($RIV = 0.94$). It was not considered in the western Atlantic due to multicollinearity. In the western Pacific, use of

multiple habitats is associated with a roughly 80 km increase in range extent, adjusted for other predictors (Table 1, Figure 5). Of the species in the eastern Atlantic, eastern Pacific and western Pacific, 31%, 7% and 20% are identified as using multiple habitats respectively.

The only interaction retained in any model is that between depth range and maximum length. It is significant in the eastern Pacific and has moderate relative support ($p = 0.047$, $RIV = 0.7$), while in the eastern Atlantic it is nonsignificant and has weak relative support ($p = 0.102$, $RIV = 0.52$, Table 1). In the eastern Pacific, the relationship between maximum length and range extent is more positive for species with larger depth ranges, but the (nonsignificant) interaction between depth range and maximum length is reversed in the eastern Atlantic.

4 | DISCUSSION

In our global model, basin/margin appears to be the strongest predictor of range extent in temperate marine fishes. In the western Atlantic and Pacific, our analysis indicates that sharper changes in temperature over latitude are associated with a greater number of species northern range endpoints. There is no such relationship on the eastern margins of each ocean basin or for southern range endpoints along either side of the Pacific or Atlantic. In the western Pacific and Atlantic, range endpoints peak near the areas where the Kuroshio current and Gulf Stream turn offshore and flow east (Figure 2a) and taper off gradually towards lower latitudes. As water in each of these currents moves offshore, temperature changes abruptly across narrow stretches of latitude. By comparison, the temperature gradients resulting from the southward movement of currents along the eastern margins of the Atlantic and Pacific basins

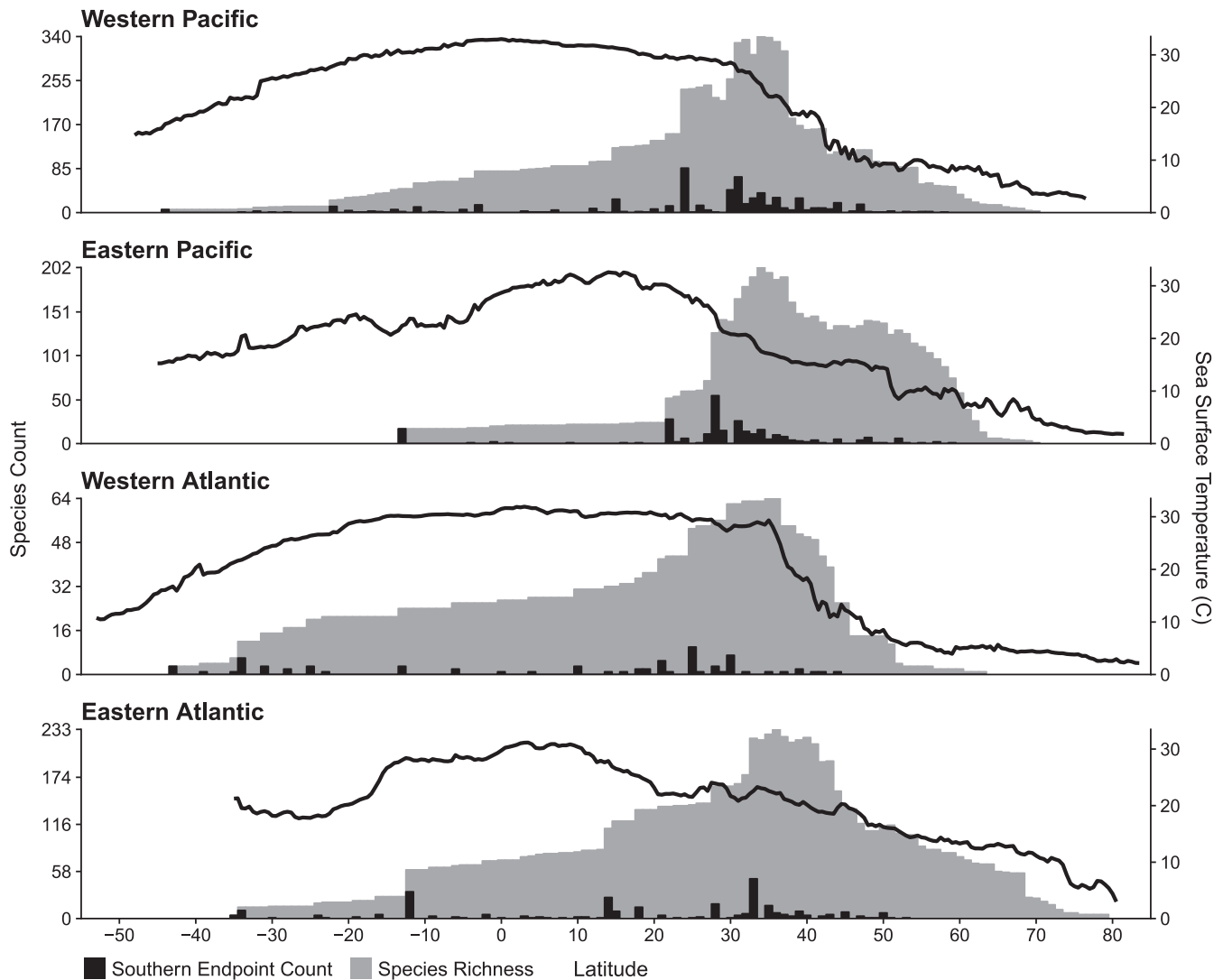


FIGURE 3 Bar chart showing teleost fish species richness gradients and frequency distributions of southern species range limits, in grey and black respectively. Sea surface temperature is represented with a black line. Black bars represent the number of species whose southern range endpoint occurs in each degree of latitude. Species richness gradients represent only the species in the dataset, most of which have exclusively temperate ranges but some of which have ranges which extend beyond temperate waters

are much more gradual (Payne et al., 2012), and range endpoints along the eastern margins show no relationship with latitudinal sea surface temperature gradient (Figures 1 and 2). These results are consistent with the hypothesis that sharp latitudinal temperature gradients pose a barrier to dispersal and range expansion along the western margins of the Atlantic and Pacific Oceans.

Our study supports the conclusions of several other studies that have shown that Rapoport's rule, which holds that species latitudinal range extent is positively associated with latitude, does not generally apply to marine systems (Gaston & Chown, 1999; Mora & Robertson, 2005; Rohde, 1996; Rohde, Heap, & Heap, 1993; Smith & Gaines, 2003; Tomašových et al., 2015). Because species at higher latitudes experience greater seasonal variation in temperature, Rapoport's rule predicts that these species will also be better able to withstand latitudinal variation in temperature (Stevens, 1989, 1996). However, water temperature varies little across latitude and across seasons in tropical marine systems, so

the climatic variability hypothesis invoked to explain Rapoport's rule predicts that even tropical species with narrow thermal tolerances can inhabit large stretches of latitude. Accordingly, tropical marine species display larger range extents than temperate species, on average (Tomašových et al., 2015). Our dataset includes species whose ranges extend into the tropics; we find mean range extent is highest for species whose latitudinal range midpoints are in lower latitudes (Appendix S1: Figure S1), which is consistent with the results of previous studies and with the expectation of the climatic variability hypothesis applied to marine systems (Jones, Caley, & Munday, 2002; Tomašových & Jablonski, 2017; Tomašových et al., 2015, 2016). The climatic variability hypothesis predicts that the equatorward range limits of temperate species adapted to broader temperature ranges should be less impacted by abrupt temperature changes than the poleward range limits of tropical and subtropical species adapted to narrow temperature ranges. Given that our analyses pertain only to species occurring

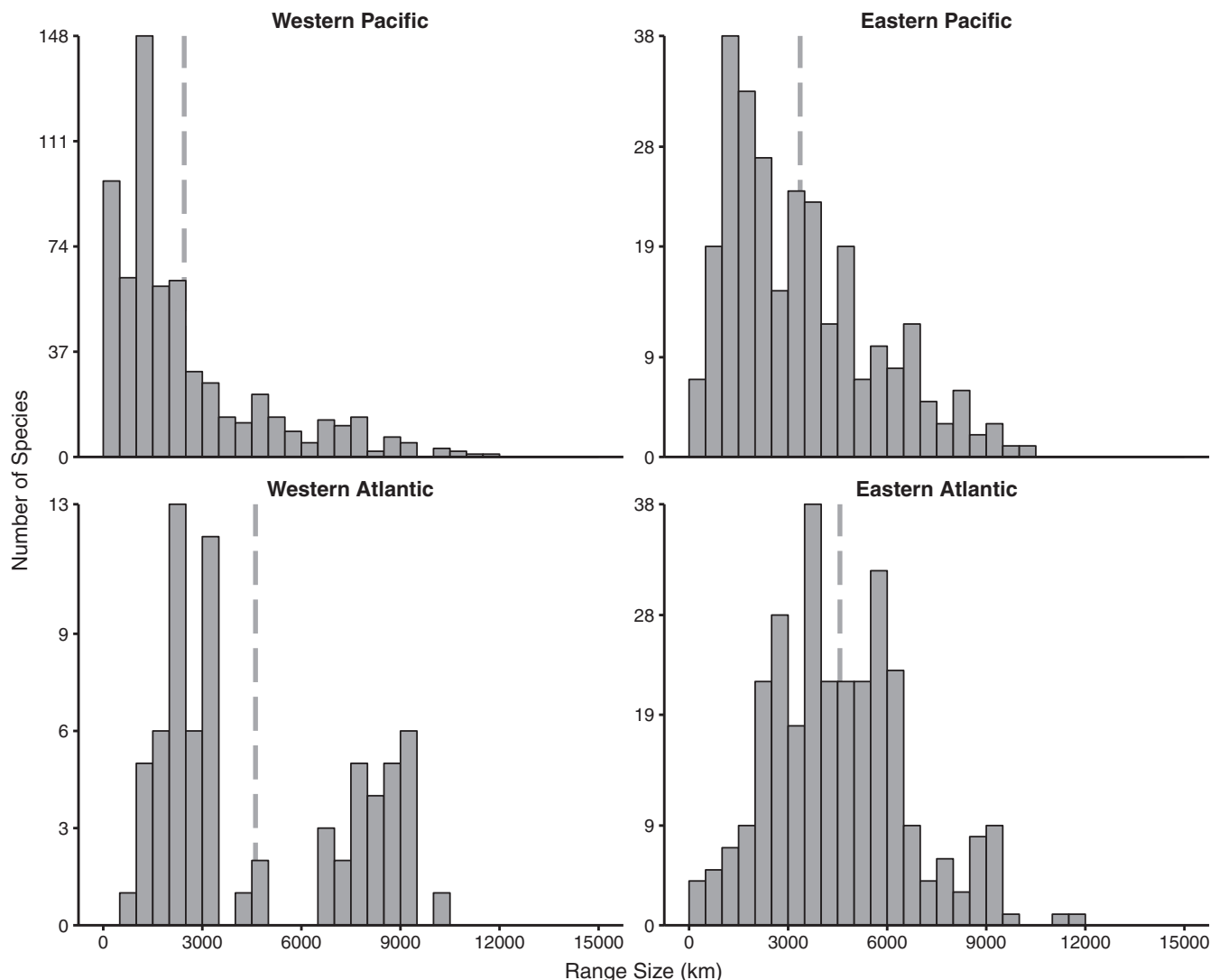


FIGURE 4 Frequency distributions of teleost fish species biogeographic range extent, measured as the maximum linear distance between any two range endpoints in a species range. Mean range extent, denoted by a dashed line, is greatest in the eastern Atlantic (4,794 km), followed by the western Atlantic (4,435 km), eastern Pacific (3,424 km) and finally western Pacific (2,478 km)

in northern temperate latitudes, the absence of a correlation between species southern (equatorward) range endpoints and latitudinal temperature gradients in our data is also in agreement with the climatic variability hypothesis. Overall, our results suggest that while Rapoport's rule cannot be applied generally to marine systems, the climatic variability hypothesis used to explain Rapoport's rule in terrestrial systems may also help to explain large-scale biogeographic patterns in marine systems.

Of the traits considered in this study, depth range is the strongest predictor of range extent in the global model and is retained in every basin model besides the western Atlantic, suggesting that depth range may generally correlate with geographic range extent (Table 1, Figure 5). Both the mean and the annual range in temperature vary across gradients of both depth and latitude, so there are many possible explanations for this pattern. It is possible that species observed across a large depth range may be more likely to have large latitudinal range extents due to increased habitat availability or may be able to escape latitudinal gradients

in sea surface temperature by occupying different depths along their latitudinal range. Alternatively, depth range and latitudinal range may both be related through a third trait, as species adapted to broad temperature ranges may be able to traverse large gradients in both depth and latitude (Harley et al., 2003). Finally, the observed relationship between depth range and range extent may result partly from sampling constraints, as rarely observed species are unlikely to have been sampled over a large range of depths. Whatever the drivers, our study suggests that bathymetric and geographic range are generally correlated.

Larger individuals should experience reduced predation and overwintering mortality, suggesting that juveniles of larger species may be able to survive and colonize new habitat more effectively and therefore may have larger range sizes (Conover & Present, 1990; Luiz et al., 2013; Munday & Jones, 1998; Murphy et al., 2014; Sogard, 1997). We see some support for this hypothesis in our analyses: there is strong evidence ($RIV > 0.9$) for a positive relationship between maximum length and range extent in the global, eastern

TABLE 1 Results of AICc-based model selection for global and basin-level models

	Term	Coefficient	SD	RIV	χ^2	df	<i>p</i> adj.
Global	Basin/margin	—	—	1.00	32.7	3	<0.001
	Depth Range	6.15	199.4	1.00	61.6	1	<0.001
	Max Length	2.09	35.4	0.92	5.8	1	0.028
	Multiple Habitats	5.86	—	0.99	10.2	1	0.0038
	Schooler	5.92	—	0.76	4.3	1	0.0503
Pacific							
East	Depth Range	8.61	210.7	1.00	61.2	1	<0.001
	Max Length	3.41	34.7	0.94	4.9	1	0.0438
	Depth Range Max Length	3.12	—	0.70	4.6	1	0.0472
West	Depth Range	6.09	153.0	1.00	19.0	1	<0.001
	Multiple Habitats	8.84	—	0.94	6.4	1	0.0228
	Schooler	13.75	—	0.79	3.4	1	0.0737
Atlantic							
East	Depth Range	3.22	220.5	0.99	8.1	1	0.0099
	Max Length	4.88	39.8	1.00	16.1	1	<0.001
	Schooler	5.94	—	0.67	3.0	1	0.0882
	Depth Range Max Length	-1.35	—	0.53	2.8	1	0.0954
West	Schooler	16.05	—	0.79	3.8	1	0.0642

Note: Only predictors retained following model selection are shown. For continuous predictors, coefficients are the change in square-root range extent predicted from a one standard deviation increase in the predictor, which are reported in the "SD" column. For binomial predictors, coefficients are the change in square-root range extent predicted for species for species that school or use multiple habitats. RIV represent the relative variable importance of each term based on AIC weights for candidate models containing that term. *p*-Values lower than 0.05 are considered significant and are bolded.

Pacific and eastern Atlantic datasets (Table 1, Figure 5). However, maximum length is not included in models for either the western Atlantic or western Pacific, where seasonal temperature gradients are steepest and thus overwintering mortality is expected to be higher for juvenile fishes. As a result, the mechanism linking the apparent relationship between range extent and body size is unclear. Some research suggests that physiological constraints can negate the survival advantages of larger body size in juvenile fishes (Sogard, 1997). We speculate that latitudinal temperature gradients along the western margins of both basins create hard physiological limits such that the advantage of size, if one exists, is overridden.

Ecological generalists may have better establishment success in a greater range of habitats (Cassey et al., 2004), and may be more resilient to local disturbance as they are adapted to a variety of conditions (Emslie et al., 2010, 2011; Feary et al., 2007; Wilson et al., 2006). In basins/margins where "soft" environmental biogeographic barriers (barriers other than impassible landmasses, such as offshore currents or strong temperature gradients) constrain species ranges, we might expect traits associated with ecological generality to be associated with larger range extents (Cowman & Bellwood, 2013; Luiz et al., 2012). The effect of use of multiple habitats, one measure of ecological generality, is significant and highly important at the global scale and in the western Pacific, but we did not consider it in the western Atlantic due to multicollinearity. Proportionally fewer

species are marked as using multiple habitats in the eastern Pacific compared to the eastern Atlantic and western Pacific, so differences in statistical power may influence these results.

Several studies suggest that species that school experience lower predation risk (DeMartini et al., 2011; Luiz et al., 2013; Sandin & Pacala, 2005). Recently settled juveniles capable of finding and schooling with conspecifics or other species may have better establishment success, and adult schooling behaviour may increase range size by increasing resilience of local populations. In our analyses, schooling behaviour was positively associated with range extent in the global model and every basin model except for the western Pacific (Table 1, Figure 5). However, schooling behaviour was only weakly significant and moderately important in each of these models, although differences in the prevalence of schooling behaviour among basins/margins may affect these results. Without adjusting for differences due to family and genus, western Atlantic schooling species have ranges that are roughly 3,000 km larger, on average (Figure 5). Our results suggest that schooling behaviour may be a generally associated with larger range extent in marine fishes, and, unsurprisingly, species closely related to schooling species tend to also school.

There are several other factors that may affect range extent that we do not consider here, which include abiotic factors such as habitat distribution and availability (Lessios & Robertson, 2006; Mora et al., 2012) and traits such as pelagic larval duration, larval rafting behaviour and

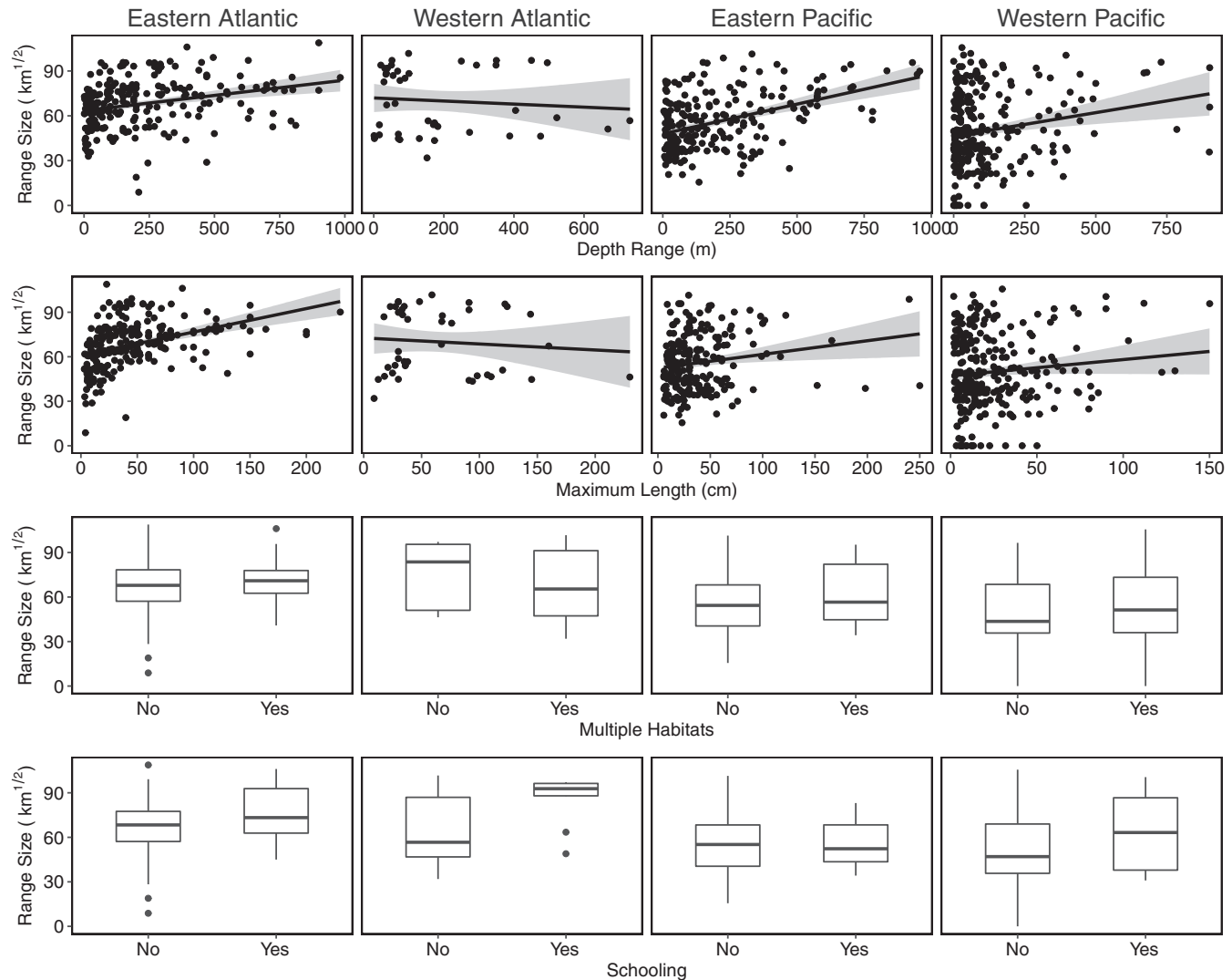


FIGURE 5 Bivariate plots of square-root range extent and traits of teleost fish examined in this study: depth range, maximum length, use of multiple habitats and schooling behaviour

nocturnal activity (Highsmith, 1985; Luiz et al., 2012, 2013; McCauley, Hoffmann, Young, & Micheli, 2012). There are also ecological processes that may affect range extent for which we have little or no information, such as priority effects, interspecific competition, predation and mutualisms. Priority effects, in which the prior recruitment of a species diminishes the recruitment success of other species (Almany, 2003; Shulman et al., 1983), may reduce the probability that a species will colonize new areas and may thus diminish the relationship between species traits and range extent. Interspecific competition can reduce local recruitment, abundances and species geographic range extent (Bonin, Boström-Einarsson, Munday, & Jones, 2015; Forrester, 2015; Robertson, 1996; Woodland, 1999). Although these processes may obscure biogeographic patterns, our study suggests that species range extent is related to abiotic factors such as latitudinal temperature gradients and traits such as depth range, maximum length and schooling behaviour.

While using published data from FishBase allowed us to compile an extensive dataset on species ranges and biology across global temperate oceans, data quality and availability varies among species. We attempted to remedy this problem by supplementing range data

from field guides for species which had vague range data in FishBase, but all biological correlates are based solely on data obtained from FishBase. Biological and biogeographic data from online databases vary in quality, and range data may be inaccurate due to misidentification of species, inaccurate georeferencing of species observations and biased sampling that favours more populated regions (Anderson, 2012; Maldonado et al., 2015). Because we lacked sufficient biological data for many species, we included substantially more species in our sea surface temperature analysis compared to our analysis of the relationship between range extent and adult traits. Additionally, there were fewer species that met our criteria in the West Atlantic than in the other basins/margins, reducing statistical power in the western Atlantic; this small sample problem was exacerbated by exclusion of species without complete biological data. Despite these limitations, data from FishBase produced compelling patterns in species range sizes and distribution. Future studies on similarly large groups of species with more detailed biological information may be needed to elucidate general rules and patterns in species range extent.

Our results suggest there are broad differences in average range extent and distribution of species ranges among basins/margins, and that these differences may be due in part to variation in latitudinal temperature gradient between basin margins. In addition, while there are some basin/margin-level idiosyncrasies in our results, the data we present also indicate that several post-settlement traits identified in previous work are associated with range extent at the global or within-basin scale. As these traits are also correlated with range size in tropical regions, our results suggest that post-settlement survival may influence range much more generally than once believed. Collectively, these results shed additional light on the factors that control species ranges in marine systems.

ACKNOWLEDGEMENTS

We thank the California Polytechnic State University, San Luis Obispo Biological Sciences department for their support, as well as Dr. Scott Chamberlain, Dr. Andrew Schaffner and Dr. Ryan Walter for their guidance regarding data analysis.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY

Species range extent, range endpoint distribution and sea surface temperature data are available in the supplemental materials. Data DRYAD DOI: <https://doi.org/10.5061/dryad.8n4pn0b>

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BIOSKETCH

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Author contributions: B.I.R. conceived the study; B.I.R., M.C.G. and S.M.H. designed the study; M.C.G. and S.M.H. gathered the data; M.C.G. analysed the data and generated the figures; M.C.G. led the writing, with contributions from B.I.R. and S.M.H.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Goodman MC, Hannah SM, Ruttenberg BI. The relationship between geographic range extent, sea surface temperature and adult traits in coastal temperate fishes. *J Biogeogr.* 2019;00:1–13. <https://doi.org/10.1111/jbi.13595>