

## Fish distributions along depth gradients of a sea mountain range conform to the mid-domain effect

Shane W. Geange, Amelia M. Connell, Philip J. Lester, Matthew R. Dunn and K. C. Burns

S. W. Geange (*shane.geange@vuw.ac.nz*), A. M. Connell, P. J. Lester and K. C. Burns, School of Biological Sciences, Victoria Univ. of Wellington, PO Box 600, Wellington, New Zealand. – M. R. Dunn, National Inst. of Water and Atmospheric Research Ltd (NIWA), Private Bag 14-901, Kilbirnie, Wellington, New Zealand.

Species richness often peaks in the middle of bounded geographic domains (e.g. latitude, altitude or depth). Hump-shaped richness distributions may be due to deterministic processes, such as adaptations to environmental variation. Alternatively, such distributions might also be due to stochastic process. The mid-domain effect (MDE) posits that hump-shaped richness distributions arise when species ranges are randomly arranged within the limits of the domain. We tested whether the MDE could account for the richness of bottom-associated (demersal) fishes between 200 and 800 m on the Chatham Rise, New Zealand. We quantified the depth distributions of 59 fish species from 1891 research trawl catches made between 1991 and 2007. Results showed a broad plateau of high species richness near the centre of the domain (between 300 and 700 m), which was consistent with expectations of the MDE. Further, empirical species richness was better explained statistically by predictions of the MDE than models incorporating additional abiotic predictor variables. Our results deviated from previous studies that identified a greater richness of fishes in warmer, shallower depths with higher primary production. However, our study was conducted entirely below the euphotic zone, at depths where gradients are relatively weak, suggesting that support for the mid-domain effect may increase across oceanic domains characterised by weak environmental gradients.

Species richness varies heterogeneously through space. Despite decades of study (MacArthur 1965, Pianka 1966, Rohde 1992, Rohde et al. 1993, Gaston 1996, Rex and Etter 1998, Brown 2001, Willig et al. 2003, Arita and Vázquez-Domínguez 2008), the processes regulating broad-scale patterns in species richness remain unclear. One possible explanation is that deterministic processes structure spatial variation in species richness. For example, regions with higher productivity may support greater population densities, which may in turn support more species (Currie et al. 2004). Areas with higher productivity might also promote more rapid generation times, which in turn elevate speciation rates (Allen and Gillooly 2006, Allen et al. 2006). Alternatively, spatial gradients in species richness might result from stochastic processes.

Across bounded geographic domains, species richness often peaks at the mid-point of the domain (Lees and Colwell 2007). Colwell and Hurtt (1994), and Willig and Lyons (1998) were among the first to recognise that humped-shaped richness distributions can be reproduced by randomly reshuffling species distributions within the hard boundaries of geographic domains. A mid-domain peak in richness is generated when there is increasing overlap of species ranges towards the centre of the domain because the extent of species ranges are bounded within the limits of the domain (Colwell and Hurtt 1994). Therefore, a peak in species richness might occur in

the centre of the domain independently of species interactions, environmental variation or evolutionary adaptation. Colwell and Lees (2000) termed this 'the mid-domain effect' (MDE), and suggested that it is a parsimonious explanation for heterogeneity in species richness across geographic gradients. A number of studies have found support for the MDE (Jetz and Rahbek 2001, Romdal et al. 2005, Dunn et al. 2007, Lees and Colwell 2007). Others report that MDE null models predict observed patterns in species richness poorly (Diniz-Filho et al. 2002, Hawkins and Diniz-Filho 2002, Smith and Brown 2002, McClain and Etter 2005, Kendall and Haedrich 2006).

Kendall and Haedrich (2006), and Smith and Brown (2002) investigated fish diversity across the geographic domain extending from the sea bottom to the sea surface and found that fish richness was greater in shallower waters than predicted by the MDE. These studies attributed patterns in species richness to higher productivity, increased temperatures and elevated food abundances in shallower waters (see also Connolly et al. 2003). Similarly, bathymetric gradients of species richness in polychaetes, cumaceans and bivalves have also been attributed to environmental factors such as productivity (Gage and Tyler 1991, Powell et al. 2003). However, it remains unclear how spatial gradients in fish richness might vary across oceanic domains characterised by weak or homogeneous environmental gradients.

We hypothesized that the spatial distribution of demersal fishes (i.e. those living on or near the seabed) on the Chatham Rise, a prominent bathymetric depth gradient (200–1000 m) in the southern Pacific Ocean, would conform to expectations of the mid-domain effect. The Chatham Rise is analogous to a terrestrial mountain chain (McCain 2005, Cardelús et al. 2006, Brehm et al. 2007) with the exception that it occurs at depths below where light can penetrate and support photosynthesis (~200 m). Therefore, there is no primary production in our sampling zone and organisms rely on energy inputs from vertically migrating mesopelagic organisms, and the fall of organic material, mostly detritus. We quantified the spatial distribution of 59 demersal fish species by sampling the bathymetric depth-distribution of fish in 1891 bottom trawls conducted between 1991 and 2007. The resulting data are then compared to null model simulations to test the prediction that species richness varies across the gradient according to the mid-domain effect. Finally, we incorporate abiotic predictors of species richness in an analysis to determine if the inclusion of these predictors better model empirical species richness than the MDE alone.

## Material and methods

### Study area and sampling

Sampling was conducted on the Chatham Rise, which is one of New Zealand's most productive fishing grounds. The Chatham Rise is a prominent bathymetric ridge that extends approximately 500 nautical miles (926 km) east of the South Island of New Zealand, from Banks Peninsula to the Chatham Islands (Fig. 1). Compared to Hikurangi Trench to the north, and Bounty Trench to the south (both of which drop to below 3000 m), the Chatham Rise is relatively shallow, with extensive habitat at depths between 200 and 1000 m (although it rises to 50 m below sea level at the western end and to sea level at the Chatham Islands on the eastern end, and drops to below 2000 m when it meets the Hikurangi and Bounty trenches). The Subtropical Front, a zone of convergence between subtropical and subantarctic water masses, is permanently located on the crest of the Chatham Rise until it reaches the eastern end, where it dips south (Heath 1985, Bradford-Grieve et al. 1991). Relative to other offshore areas around New Zealand, primary productivity, benthic productivity and the productivity of zooplankton and mesopelagic fishes is high on the Chatham Rise (Bradford et al. 1991, Probert and McKnight 1993, Sullivan et al. 1993, Bradford-Grieve et al. 1997, 1999, McClatchie et al. 1997, Murphy et al. 2001, McClatchie and Dunford 2003, McClatchie et al. 2004).

Demersal fishes were sampled across a 200–800 m bathymetric depth-gradient on the Chatham Rise, which spanned 2° of latitude and 10° of longitude. Across this depth gradient, environmental conditions varied only weakly compared to shallower waters; pressure increases while temperature, productivity and environmental fluctuations decline relatively weakly with depth (Pickard and Emery 1982). Sampling took place during daylight hours in the austral summer on New Zealand Ministry of Fisheries funded annual trawl surveys,

undertaken by the National Inst. of Water and Atmospheric Research (NIWA). The gear and trawling methods followed Hurst et al. (1992). Briefly, 1891 bottom trawls were made between 1991 and 2007 (Table 1). The trawl used was a full-wing bottom trawl, which had a mean headline height of 7 m, a doorspread of 115 m, 100 m sweeps, a cod-end mesh of 60 mm and a 58.8 m ground-rope fitted with 500 mm steel bobbins (full specifications in Hurst and Bagley 1994). The sample design was two-phase stratified random, after Francis (1984). Phase-1 trawl stations were allocated from simulations based on catch rates from the previous three annual trawl surveys, after Bull et al. (2000). Phase-2 stations were allocated as required to achieve coefficients of variation below 20% for three common species (hoki *Macruronus novaezelandiae*, hake *Merluccius australis* and ling *Genypterus blacodes*). Each trawl was towed for approximately 3 nm at an over-ground speed of 3.5 knots (trawl methods are described further in Chatterton and Hanchet 1994). Each trawl catch (or sub-samples thereof) was sorted to species level, and species catch weight recorded along with the average depth and latitudinal and longitudinal position of each trawl.

### Rarefaction

The final dataset, comprising 1891 trawls made at depths between 200 and 800 m in January of each of the 16 sampling years (with the exception of 1991 and 1992 in which trawls were conducted in June and December, respectively) contained two sources of sampling bias: inter-annual bias (more trawls were conducted in some years than others: Table 1); and depth bias (more trawls were conducted at some depths than others: Table 1). We therefore conducted sample-based rarefaction to remove this sampling bias. For each of the 16 yr, we grouped trawls into one of six depth strata (200–299, 300–399, 400–499, 500–599, 600–699, 700–799 m: Table 1). To ensure sampling was spread evenly across years and depths, we randomly drew two trawls (the minimum number per depth category per year) from each combination of depth and year (i.e.  $n = 192$  trawls from the six depths over the 16 yr). We replicated this procedure 1000 times to calculate the average range for each species under uniform sampling in space and time. A large number of species were caught only occasionally and their rarity precluded credible estimates of their depth range. Therefore, we restricted our analyses to the 59 species (of a total 97 species sampled) that were sampled in ten or more trawls.

### Mid-domain effect

Using rarefied species range estimates, we calculated average species richness (total number of species) in 2 m bands across the 200–800 m depth gradient. We then compared empirical values of species richness against a null distribution as predicted by the mid-domain effect. We used RangeModel (Colwell 2008) to generate the null distribution based on 1000 randomizations of rarefied species ranges. Because our sampling did not cover the entire depth gradient across the latitudinal and longitudinal extent of the Chatham Rise, our geographic domain does not have strictly uniform hard boundaries. To address whether this attribute of the dataset

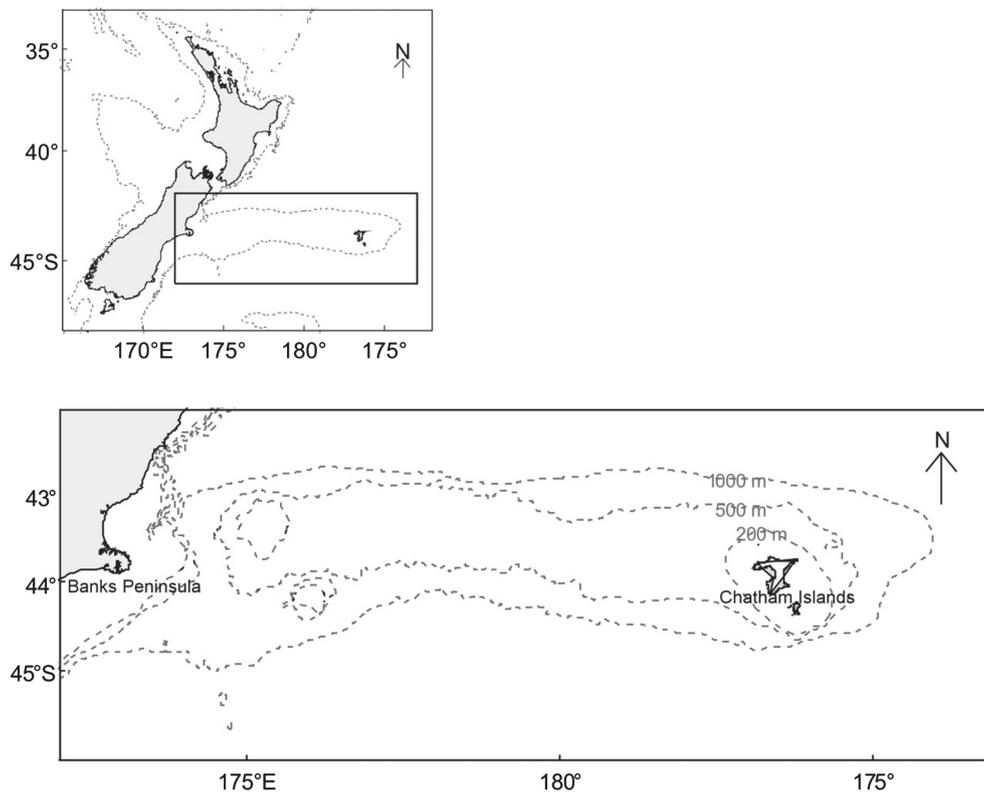


Figure 1. New Zealand with 1000 m depth contour, showing the relation of the Chatham Rise, dark rectangle, to the mainland (top). The Chatham Rise from Banks Peninsula on the left to the Chatham Islands on the right (bottom).

might influence results, we use two MDE null models, the ‘random mid-point’ null model which is compatible with soft boundary limitations; and the ‘spreading-dye’ null model which assumes hard boundaries. The random mid-point null model (Colwell and Lees 2000, Box 5) is a Monte Carlo approach whereby the empirical distribution of range sizes is sampled and each sampled range is placed on the domain at random, given the midpoint constraints imposed by the size

of the range. The spreading dye sampling null model (Jetz and Rahbek 2001) selects ranges at random, one at a time and without replacement, and then places them at random on the domain by choosing a range midpoint randomly from a uniform distribution spanning the domain. If the range lies fully within the domain, it is kept in that position. If a range extends beyond the domain limit, its initial random midpoint is shifted into the domain, the minimum distance necessary, so

Table 1. Number of 1891 trawls made between 200 and 800 m below sea level on the Chatham Rise, New Zealand, within each year/depth category. Each year trawls were conducted in January, except 1991 (June) and 1992 (December). Corresponding species richness pooled across trawls is shown in ( ). Note that no trawls were conducted in 1993.

Year	Depth (m)						Total
	200–299 m	300–399	400–499	500–599	600–699	700–799	
1991	17 (14)	23 (15)	70 (14)	33 (11)	23 (10)	12 (8)	178 (20)
1992	17 (14)	29 (19)	51 (15)	36 (11)	17 (8)	13 (9)	163 (24)
1994	23 (18)	33 (19)	47 (22)	37 (20)	17 (11)	7 (16)	164 (35)
1995	8 (20)	25 (23)	41 (23)	26 (21)	16 (20)	6 (23)	122 (42)
1996	12 (18)	19 (22)	33 (26)	11 (23)	10 (21)	4 (17)	89 (38)
1997	7 (20)	27 (26)	34 (27)	19 (21)	14 (23)	2 (20)	103 (38)
1998	3 (16)	26 (21)	25 (20)	23 (22)	10 (20)	4 (21)	91 (34)
1999	10 (16)	29 (24)	27 (25)	19 (18)	10 (19)	5 (24)	100 (35)
2000	12 (11)	27 (11)	51 (13)	20 (9)	15 (11)	3 (7)	128 (17)
2001	10 (12)	26 (13)	35 (12)	30 (15)	11 (9)	7 (10)	119 (19)
2002	6 (15)	28 (16)	36 (12)	22 (9)	6 (8)	9 (7)	107 (19)
2003	15 (11)	33 (13)	31 (12)	21 (10)	6 (8)	9 (9)	115 (17)
2004	10 (14)	18 (14)	40 (13)	23 (8)	13 (9)	6 (9)	110 (20)
2005	14 (12)	20 (16)	34 (11)	21 (8)	11 (11)	6 (6)	106 (20)
2006	8 (10)	20 (20)	31 (16)	20 (15)	9 (9)	8 (7)	96 (27)
2007	8 (17)	23 (18)	39 (24)	13 (12)	9 (12)	8 (8)	100 (37)
Total	180 (29)	406 (36)	625 (41)	374 (34)	197 (32)	109 (31)	1891 (97)

that its endpoint coincides with the domain limit. For both simulations, the output is the expected number of species in each band, with corresponding 95% confidence intervals.

We used two methods to test the predictive power of RangeModel. First, we calculated the proportion of bands in which observed values fell within the 95% confidence intervals around the null distribution. The resulting proportions are conceptually analogous to nonparametric correlation coefficients, with high values indicating a good fit of the observed data to MDE predictions. Second, we used Veech's (2000) displacement D test to compare the empirical and null species distributions. We use D in preference to the closely related Kolmogorov–Smirnov test, because D is more appropriate as a test for non-random structure in species richness when data is bivariate (e.g. species richness along spatial gradients) (Veech 2000). D is an index of how much the empirical curve differs from the null curve; high values of D indicate large differences between the observed and null curves (see Veech 2000 for details). The significance of the empirical D value is given as a p-value, calculated from the proportion of null D values greater than the real D value. P-values of <0.05 are considered significant, and would indicate that species richness patterns are inconsistent with expectations of the MDE.

Because some of the species ranges in our dataset were artificially truncated due to our sampling design (i.e. some species may commonly occur at depths shallower than 200 m, or deeper than 800 m), we also performed the above analyses on a reduced dataset containing 16 of the original 59 species (Supplementary material Appendix 1) whose ranges commonly occur between 200 and 800 m. Species ranges were determined using FishBase (< www.fishbase.org >) and published literature. For the 43 species removed, mean range size was 309 m (SE = 24; Supplementary material Appendix 1), with approximately half of the species (n = 22) having ranges encompassing > 50% of the soft domain limits imposed by the sampling design (Supplementary material Appendix 2).

### Abiotic predictors of species richness

Fish species richness may change according to variables such as temperature, pressure and primary productivity. Estimates of sea surface productivity are available for our study site, but unfortunately, we have no data regarding the relationship between surface productivity and food availability at depths such as 700 m for any specific sampling location. Given site-specific sea currents, upwelling and advection, it is unlikely that surface productivity would directly correlate with food availability at the same location. Therefore, here we analyse only temperature and pressure. Temperature and pressure were estimated at depth for 282 of our 1891 bottom trawls (conducted in Austral summers between 2004 and 2007). To obtain estimates of temperature for all of our replicates, we used the predicted mean fit from a linear regression between collected depth and temperature data to assay temperature for each of the 2 m bands in our MDE analysis. For each of these bands, we also calculated pressure  $P_{atm}$  as:

$$P_{atm} = \frac{P_o + p \times g \times h}{101300} \quad (1)$$

where  $P_o$  is atmospheric pressure at the ocean surface (taken as 101325 Pa),  $p$  is liquid density (taken as 1025 kg m<sup>-3</sup>),  $g$  is gravitation acceleration (taken as 9.81 m s<sup>-2</sup>), and  $h$  is depth (m).

To determine if temperature and/or pressure explains variation in empirical species richness better than predictions of the MDE alone, we conducted two sets of analyses; the first used forward stepwise multiple regressions; and the second used information-theory approaches. We used forward stepwise multiple regression to establish the importance of temperature and pressure as explanatory variables of empirical species richness. Stepwise multiple regression is used here to find a set of independent variables that together provide a 'best' fit to empirical species richness by minimizing the sum of squared residuals. The initial model began with no independent variables, and added each of the independent variables (MDE predictions, temperature and pressure) one at a time if they met the criterion of statistical significance ( $p < 0.05$ ). We conducted four forward stepwise regressions, two for each dataset (the full dataset containing 59 species, and the reduced dataset containing 16 species). The first used temperature, pressure and the random mid-point MDE null model as independent predictor variables. The second used temperature, pressure and the 'spreading dye' MDE null model as independent predictor variables.

Information-theory approaches were carried out in SAM (Rangel et al. 2010). We conducted multiple linear regression with AIC-based model selection to evaluate the importance of temperature, pressure and MDE predictions as explanatory variables of empirical species richness. As with the forward stepwise multiple regression above, we conducted two analyses for each dataset.

### Results

Over the 16 yr of sampling, among-year variation in the number of species caught ranged between 17 (2000 and 2003) and 42 (1995; Table 1), with a mean of 28 (SE = 2.2). The number of species caught in each of the six depth categories ranged between 29 (200–299 m) and 41 (400–499 m; Table 1), with a mean of 34 (SE = 1.1). In total, 97 species were sampled from the 1891 trawl catches, and consisted of demersal, benthopelagic, and occasional benthic and pelagic species. The species included alfonosinos (Berycidae); dogfishes (Squalidae); dories (Zeidae); ghost sharks (Chimarridae); hakes (Merlucciidae); ling (Ophidiidae); morid cods (Moridae); oreos (Oreosomatidae); rattails (Macrouridae); scorpionfishes (Scorpaenidae); scampi (Nephropidae); squid (Loliginidae); stargazers (Leptoscopidae) and warehou (Centrolophidae; Supplementary material Appendix 1). Of the 97 species sampled, 59 were present in 10 or more trawls, representing 99.6% of the total depth range by year sampled occurrences.

The mean range size of the 59 species included in the rarified dataset was 309 m (SE = 21; Supplementary material Appendix 1). Approximately half of the species (n = 30) had ranges encompassing > 50% of the soft domain limits imposed by the sampling design (Supplementary material Appendix 2). Species richness was greatest at 324 m (38 species) and lowest at 215 and 790 m (5 and 1 species, respectively) (Fig. 2a). For the reduced dataset containing 16 species,

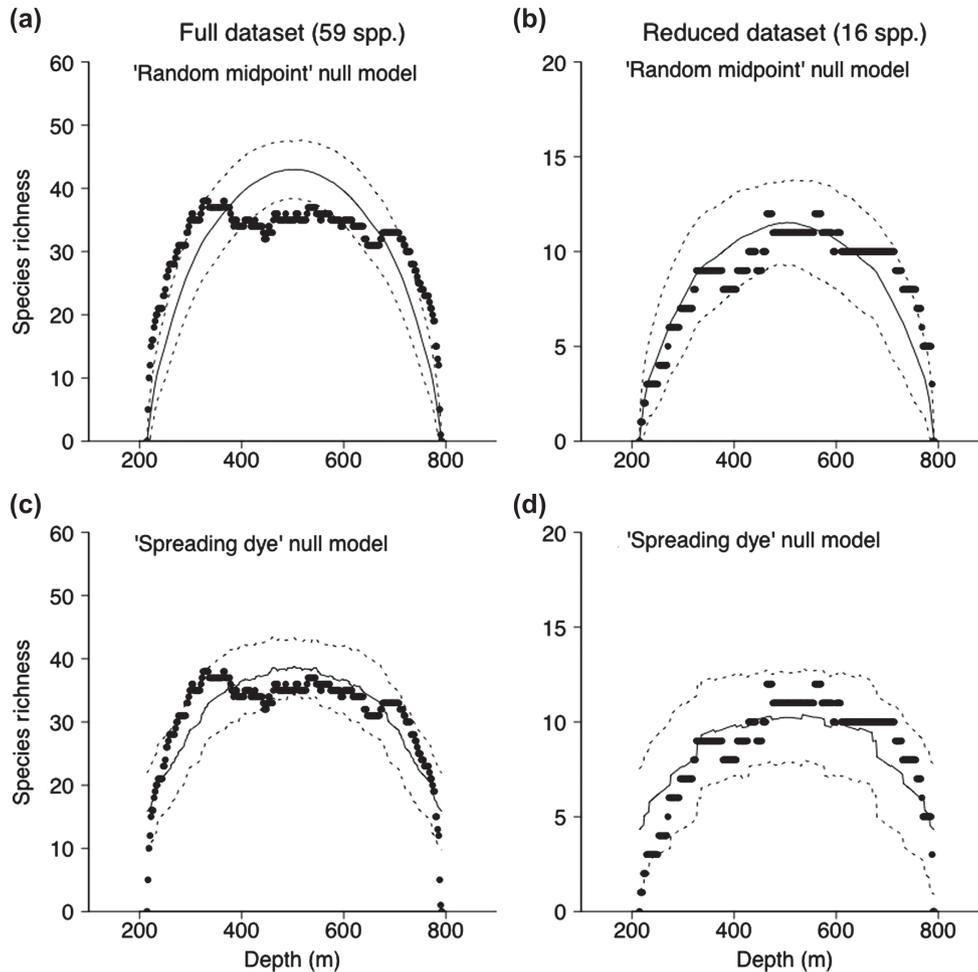


Figure 2. Comparisons between observed values of species richness (black dots) and expected values of species richness generated by the mid-domain hypothesis (solid lines bounded by 95% CI's, as indicated by broken lines). Null model predictions are derived from the random mid-point null hypothesis (panels a and b) and the Spreading dye null hypothesis (panels c and d) using 100 randomizations of the rarified depth ranges of 59 species demersal fish species found on the Chatham Rise, New Zealand (panels a and c), and for 16 of those 59 species whose ranges commonly occur between 200 and 800 m below sea level (panels b and d).

mean range size was 311 m (SE = 3; Supplementary material Appendix 1). Six of the 16 species had ranges encompassing > 50% of the soft domain limits imposed by the sampling design (Supplementary material Appendix 2). Species richness was greatest between 558 and 570 m (12 species) and lowest at 214 and 792 m (0 species) (Fig. 2b).

For the dataset containing all 59 species, the observed pattern in species richness was not well predicted by the random mid-point null model. The proportion of empirical data points falling within the 95% confidence intervals of the MDE was 0.393 (Fig. 2a). Veech's (2000) displacement test confirmed that patterns of species richness differed significantly from expectations of the random mid-point null model ( $p < 0.001$ ). Although the random mid-point null model was inconsistent with MDE predictions, the 'spreading-dye' null model did successfully predict the observed pattern of species richness. The proportion of empirical data points falling within the 95% CI of the MDE was 0.941 (Fig. 2c). Results from Veech's (2000) displacement test indicate that the shape of the empirical species richness curve did not differ significantly from predicted values generated by the spreading-dye null model ( $p = 0.164$ ).

The random mid-point null model predicted the observed pattern of species richness when the analysis was restricted to the 16 species whose ranges commonly occur between 200 and 800 m depth. The proportion of empirical data points falling within the 95% confidence intervals of the MDE was 0.937 (Fig. 2b). Results from Veech's (2000) displacement test indicate that the shape of the empirical species richness curve did not significantly differ from predicted values generated by the random mid-point null model ( $p < 0.309$ ). The spreading-dye null model also successfully predicted the observed pattern of species richness. The proportion of empirical data points falling within the 95% CI of the MDE was 0.979 (Fig. 2d). Results from Veech's (2000) displacement test indicate that the shape of the empirical species richness curve did not significantly differ from predicted values generated by the spreading-dye null model ( $p = 0.471$ ).

Temperature differed by < 4°C across the gradient. Temperature was negatively correlated with depth ( $R^2 = 0.601$ ,  $p < 0.001$ ). For a 100 m increase in depth, temperature decreased by 0.6°C. For a 100 m increase in depth, pressure increased by 9.3 atm. Forward, stepwise multiple regression models indicated that temperature and pressure did

not provide a better explanation for empirical species richness than predictions of the MDE alone (Table 2, Fig. 3). All four final models were highly significant (59 spp. 'random-midpoint'  $R^2 = 0.782$ ,  $F_{3,286} = 341.8$ ,  $p < 0.001$ ; 59 spp. spreading-dye  $R^2 = 0.725$ ,  $F_{3,286} = 251.2$ ,  $p < 0.001$ ; 16 spp. 'random-midpoint'  $R^2 = 0.927$ ,  $F_{3,286} = 1213$ ,  $p < 0.001$ ; 16 spp. spreading-dye  $R^2 = 0.893$ ,  $F_{3,286} = 794.2$ ,  $p < 0.001$ ). However, they included the MDE predictors; temperature and pressure were unimportant in all four models.

Using AIC-based model selection, all possible multiple linear regressions with temperature, pressure and MDE predictions were considered as explanatory models. In all cases, three models were indistinguishable from one another ( $\max\Delta AIC < 3$ ). All three models included MDE predictors, and these models emerged as the best explanations for empirical species richness: 1) MDE predictions and temperature; 2) MDE predictions and pressure; and 3) MDE predictions, temperature and pressure. AIC was substantially lower ( $\min\Delta AIC > 6$ ) for these models than for any other single variable models, or a combination of temperature and pressure. Whilst the models fitted using AIC indicated empirical species richness patterns were best described by MDE plus either a temperature or pressure predictor, in all cases the best individual predictor was MDE. Presumably, the addition of a temperature or pressure predictor explained some residual patterns in species depth preference.

## Discussion

Results from our analyses were consistent with the hypothesis that spatial variation in the richness of deep-sea, demersal fishes is structured by geometric constraints. We detected a

Table 2. Summary of forward stepwise multiple regression of species richness versus MDE predictions, pressure and temperature. MDE null model predictions are derived from the random mid-point null hypothesis and the spreading dye null hypothesis using 100 randomizations of the rarified depth ranges for 59 demersal fish species found on the Chatham Rise, New Zealand (full dataset), and for 16 of those 59 species whose ranges commonly occur between 200 and 800 m below sea level (reduced dataset).

	Estimate	SE	p
Full dataset (59 spp.) random mid-point null model			
Intercept	373.952	718.826	0.604
MDE	0.514	0.016	< 0.001
Pressure	-2.083	4.131	0.615
Temperature	-31.693	64.068	0.621
Full dataset (59 spp.) spreading-dye null model			
Intercept	417.892	807.433	0.605
MDE	0.835	0.031	< 0.001
Pressure	-2.400	4.640	0.605
Temperature	-36.601	71.966	0.611
Reduced dataset (16 spp.) random mid-point null model			
Intercept	75.474	163.159	0.604
MDE	0.798	0.014	< 0.001
Pressure	-0.381	0.938	0.685
Temperature	-6.846	14.542	0.638
Reduced dataset (16 spp.) spreading-dye null model			
Intercept	130.917	197.907	0.509
MDE	1.307	0.029	< 0.001
Pressure	-0.725	1.137	0.524
Temperature	-12.125	17.639	0.491

broad plateau of high species richness near the centre of the domain, between 300 and 700 m, which is consistent with MDE predictions of randomly overlapping spatial distributions of the study species. Further, empirical species richness was better explained by predictions of MDE models than by either temperature or pressure.

The results of this study are inconsistent with several previous studies on fish communities. Kendall and Haedrich (2006) determined that observed patterns in the species richness of bottom-dwelling fishes in Faroe-Iceland Ridge, Denmark Strait, southern New England and northern Gulf of Mexico regions generally declined with depth. There is also indirect evidence that bathymetric patterns of richness for gastropods, bivalves and polychaetes in the western North Atlantic differs substantially from MDE expectations (Pineda and Caswell 1998, McClain and Etter 2005). On the other hand, Bellwood et al. (2005) showed that spatial variation in coral reef richness in shallow waters of the Indo-Pacific was consistent with the MDE.

Smith and Brown (2002) found that diversity of pelagic fish species in the north-west Pacific Ocean decreased sharply with depth, with more than half of the species occurring between 0 and 300 m. The authors therefore rejected the MDE hypothesis and suggested that productivity, temperature and food availability structure spatial patterns in fish distributions deterministically. A key difference between the present study and previous work on depth distributions of pelagic fish is that the geographic domain in our study system lies below the euphotic zone, reducing temperature and productivity gradients. Temperatures throughout the depth range of this study varied by only 4–7°C each year, while Smith and Brown (2002) reported a range of approximately 18°C at their study site in the North Pacific. Strongly correlated with this range in temperatures, they reported a 500-fold increase in plankton biomass in surface waters relative to their deepest sites (Smith and Brown 2002). This large variation in food availability likely influences consumer biomass and/or richness. Therefore, in the absence of strong variation in primary productivity, temperature and other environmental conditions, geographic constraints may primarily determine patterns of species richness on areas of the Chatham Rise that lay below the euphotic zone; however, in areas that extend into the photic zone we may expect the relative impact of the MDE to be disrupted by other drivers of species richness (e.g. primary productivity or temperature).

Our sampling did not cover the entire depth gradient across the latitudinal and longitudinal extent of the Chatham Rise, so our geographic domain did not have strict uniform hard boundaries. The shallowest portion of the Chatham Rise that was sampled in this study was approximately 200 m; however, it rises to 50 m below sea level at its western end, and up to sea level at the Chatham Islands on its eastern end, and drops below 3000 m into the Hikurangi and Bounty trenches. Consequently, the depth ranges of many species in our dataset were artificially truncated. To compensate for this we performed a similar analysis on a reduced dataset in which species whose ranges did not commonly occur between 200 and 800 m depth were omitted. The results from this analysis were concordant with the original results, with empirical species richness consistent with MDE predictions.

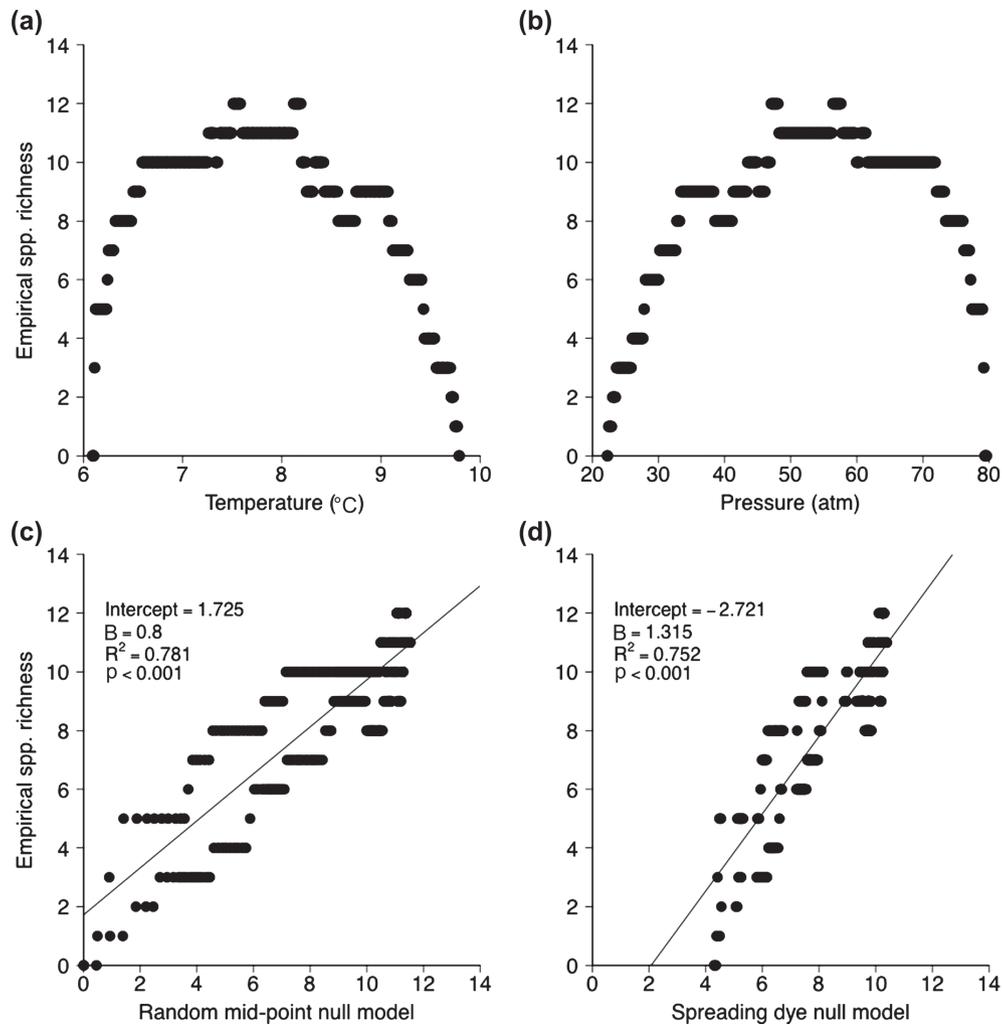


Figure 3. Correlations between empirical species richness for 16 species of demersal fishes commonly found between 200 and 800 m on the Chatham Rise, New Zealand, and: (a) temperature (an abiotic predictor of species richness); (b) pressure (an abiotic predictor of species richness); (c) mid-domain predictions of species richness utilizing the random mid-point null model; and (d) mid-domain predictions of species richness utilizing the ‘spreading dye’ null model. Where fitted, solid lines indicate predicted mean fits from significant linear correlations. Although not shown here, similar correlations were found for the full dataset containing 59 demersal fish species.

Our results are inconsistent with previous New Zealand studies. Leathwick et al. (2006) found that the species richness of demersal fish in oceans around New Zealand was greatest between 900 and 1000 m below sea level, with moderately high richness between 400 and 1100 m. Species richness was greatest in waters with high surface concentrations of chlorophyll a, and in zones where water bodies of contrasting origins mixed. Species richness was lower in waters that were cooler than expected given their depth (Leathwick et al. 2006). Similarly, McClatchie et al. (1997) found that species richness on the Chatham Rise was greatest between 500 and 1000 m, and was associated with current intensification and regions of enhanced surface phytoplankton pigment concentration. These two studies suggest that although our results might be explained by relatively invariant environmental conditions, they could also be influenced by an unmeasured underlying productivity gradient.

Sampling attributes such as the relatively small geographic domain and somewhat soft boundary limits may explain differences between this study and most previous work (Smith and Brown 2002, Kendall and Haedrich 2006).

Alternatively, geographically constrained fish distributions might also result from relatively homogeneous environmental conditions across the depth gradient. Future work in other oceanic regions that are devoid of obvious environmental heterogeneity is needed to test the hypothesis that the relative importance of stochastic effects in determining spatial patterns in species richness increases in the absence of strong environmental gradients. Our analysis of the distribution of demersal fishes along a depth gradient on the Chatham Rise supports this hypothesis, and is consistent with expectations of the MDE.

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## References

Allen, A. P. and Gillooly, J. F. 2006. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. – *Ecol. Lett.* 9: 947–954.

- Allen, A. P. et al. 2006. Kinetic effects of temperature on rates of genetic divergence and speciation. – *Proc. Natl Acad. Sci. USA* 103: 9130–9135.
- Arita, H. T. and Vázquez-Domínguez, E. 2008. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. – *Ecol. Lett.* 11: 653–663.
- Bellwood, D. R. et al. 2005. Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. – *Ecol. Lett.* 8: 643–651.
- Bradford, J. M. et al. 1991. Phytoplankton biomass in relation to surface hydrography of southern New Zealand and possible effects on the food chain. – *N. Z. J. Mar. Freshw. Res.* 25: 133–144.
- Bradford-Grieve, J. et al. 1991. Advances in New Zealand oceanography, 1967–1991. – *N. Z. J. Mar. Freshw. Res.* 25: 429–441.
- Bradford-Grieve, J. M. et al. 1997. Size-fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. – *N. Z. J. Mar. Freshw. Res.* 31: 201–224.
- Bradford-Grieve, J. et al. 1999. Pelagic ecosystem structure and functioning in the subtropical front region east of New Zealand in austral winter and spring 1993. – *J. Plankton Res.* 21: 405–428.
- Brehm, G. et al. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. – *Global Ecol. Biogeogr.* 16: 205–219.
- Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. – *Global Ecol. Biogeogr.* 10: 101–109.
- Bull, B. et al. 2000. Proposed survey design for the Southern Plateau trawl survey of hoki, hake and ling in November–December 2000. – Ministry of Fisheries, Wellington.
- Cardelús, C. L. et al. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. – *J. Ecol.* 94: 144–156.
- Chatterton, T. D. and Hanchet, S. M. 1994. Trawl survey of hoki and associated species in the Southland and Sub-Antarctic areas, November–December 1991 – (TAN9105). – Ministry of Fisheries, Wellington.
- Colwell, R. K. 2008. RangeModel: tools for exploring and assessing geometric constraints on species richness (the mid-domain effect) along transects. – *Ecography* 31: 4–7.
- Colwell, R. K. and Hurr, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. – *Am. Nat.* 144: 570–595.
- Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – *Trends Ecol. Evol.* 15: 70–76.
- Connolly, S. R. et al. 2003. Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. – *Ecology* 84: 2178–2190.
- Currie, D. J. et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. – *Ecol. Lett.* 7: 1121–1134.
- Diniz-Filho, J. A. F. et al. 2002. Null models and spatial patterns of species richness in South American birds of prey. – *Ecol. Lett.* 5: 47–55.
- Dunn, R. R. et al. 2007. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. – *Global Ecol. Biogeogr.* 16: 305–312.
- Francis, R. I. C. C. 1984. An adaptive strategy for stratified random trawl surveys. – *N. Z. J. Mar. Freshw. Res.* 18: 59–71.
- Gage, J. D. and Tyler, P. A. 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. – Cambridge Univ. Press.
- Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms and implications. – *Trends Ecol. Evol.* 11: 197–201.
- Hawkins, B. A. and Diniz-Filho, J. A. F. 2002. The mid-domain effect cannot explain the diversity gradient of Nearctic birds. – *Global Ecol. Biogeogr.* 11: 419–426.
- Heath, R. A. 1985. A review of the physical oceanography of the seas around New Zealand – 1982. – *N. Z. J. Mar. Freshw. Res.* 19: 79–124.
- Hurst, R. J. and Bagley, N. W. 1994. Trawl survey of middle depth and inshore bottom species off Southland, February–March 1993 (TAN9301). – Ministry of Fisheries, Wellington.
- Hurst, R. J. et al. 1992. Standardisation of hoki/middle depth time series trawl surveys. – MAF Fisheries Greta Point Internal Report 194, Wellington.
- Jetz, W. and Rahbek, C. 2001. Geometric constraints explain much of the species richness pattern in African birds. – *Proc. Natl Acad. Sci. USA* 98: 5661–5666.
- Kendall, V. J. and Haedrich, R. L. 2006. Species richness in Atlantic deep-sea fishes assessed in terms of the mid-domain effect and Rapoport's rule. – *Deep-Sea Res. Part I* 53: 506–515.
- Leathwick, J. R. et al. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. – *Mar. Ecol. Prog. Ser.* 321: 267–281.
- Lees, D. C. and Colwell, R. K. 2007. A strong Madagascan rainforest MDE and no equatorward increase in species richness: reanalysis of the missing Madagascan mid-domain effect, by Kerr, J. T., Perring, M. & Currie, D. J. (*Ecol. Lett.* 9: 149–159, 2006). – *Ecol. Lett.* 10: E4–E8.
- MacArthur, R. H. 1965. Patterns of species diversity. – *Biol. Rev.* 40: 510–533.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. – *Ecology* 86: 366–372.
- McClain, C. R. and Etter, R. J. 2005. Mid-domain models as predictors of species diversity patterns: bathymetric diversity gradients in the deep sea. – *Oikos* 109: 555–566.
- McClatchie, S. and Dunford, A. 2003. Estimated biomass of vertically migrating mesopelagic fish off New Zealand. – *Deep-Sea Res. Part I* 50: 10–11.
- McClatchie, S. et al. 1997. Demersal fish community diversity off New Zealand: is it related to depth, latitude and regional surface phytoplankton? – *Deep-Sea Res. Part I* 44: 647–667.
- McClatchie, S. et al. 2004. Acoustic backscatter and copepod secondary production across the Subtropical Front to the east of New Zealand. – *J. Geophys. Res.* 109, doi: 10.1029/2000JC000751.
- Murphy, R. J. et al. 2001. Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. – *N. Z. J. Mar. Freshw. Res.* 35: 343–362.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. – *Am. Nat.* 100: 33–46.
- Pickard, G. L. and Emery, W. J. 1982. Descriptive physical oceanography, an introduction. – Pergamon Press.
- Pineda, J. and Caswell, H. 1998. Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. – *Deep-Sea Res. Part II* 45: 83–101.
- Powell, S. M. et al. 2003. The deep-sea demersal fish fauna of the northern Gulf of Mexico. – *J. Northwest Atl. Fish. Sci.* 31: 19–33.
- Probert, P. K. and McKnight, D. G. 1993. Biomass of bathyal macrobenthos in the region of the Subtropical Convergence, Chatham Rise, New Zealand. – *Deep-Sea Res. Part I* 40: 1003–1007.
- Rangel, T. F. et al. 2010. SAM: a comprehensive application for spatial analysis in macroecology. – *Ecography* 33: 46–50.
- Rex, M. A. and Etter, R. J. 1998. Bathymetric patterns of body size: implications for deep-sea biodiversity. – *Deep-Sea Res. Part II* 45: 103–127.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. – *Oikos* 65: 514–527.
- Rohde, K. et al. 1993. Rapoport's rule does not apply to marine Teleosts and cannot explain latitudinal gradients in species richness. – *Am. Nat.* 142: 1–16.

- Romdal, T. S. et al. 2005. The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. – *Ecology* 86: 235–244.
- Smith, K. F. and Brown, J. H. 2002. Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. – *Global Ecol. Biogeogr.* 11: 313–322.
- Sullivan, C. W. et al. 1993. Distributions of phytoplankton blooms in the Southern Ocean. – *Science* 262: 1832–1837.
- Veech, J. A. 2000. A null model for detecting nonrandom patterns of species richness along spatial gradients. – *Ecology* 81: 1143–1149.
- Willig, M. R. and Lyons, S. K. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. – *Oikos* 81: 93–98.
- Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. – *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.

Supplementary material (Appendix E7231 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–2.