

# The birds and the seas: body size reconciles differences in the abundance–occupancy relationship across marine and terrestrial vertebrates

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Despite some fundamental differences in production processes and the ecology of consumer species on land and in the sea, further understanding of pattern and process in both biomes might be gained by applying common methods of macroecological analysis. We develop methods that reconcile apparent differences in abundance and occupancy for marine and terrestrial vertebrates, as exemplified by fish and birds. These recognize and take account of those aspects of the life history and ecology of marine and terrestrial animals that influence their abundance, distribution and trophic role. When abundance and occupancy are averaged within species over time we show that variation within a region is less for birds than fish, but when abundance and occupancy are averaged over space, the difference between birds and fish disappears. Further, we develop size rather than species-structured abundance–occupancy relationships for fish assemblages and demonstrate that patterns of intra-size class variation that are very similar to intraspecific variation in bird species, over both time and space. We argue that this result reflects the relative importance of body size and species identity respectively in determining trophic roles in marine and terrestrial environments. Selection of the appropriate analytical unit on land (species) and in the sea (size) helps to reconcile apparently divergent macroecological patterns, especially when these are driven by contrasting patterns of energy acquisition and use.

*'I argue that we should attempt to address the question of [ecological] generalizations capable of crossing the land-to-sea boundary' (Steele 1991a, p. 425).*

*'...a strong conceptual framework for comparing life in the marine realm with life on land has not been developed' (Dawson and Hamner 2008, p. 137).*

The exchange of ideas between marine and terrestrial ecology has largely been limited to a few targeted efforts (Steele 1991a, Beddington et al. 1994, Stergiou and Browman 2005). This reflects the 'wet' and 'dry' division of many facilities, journals, meetings and funding streams (Raffaelli et al. 2005, Menge et al. 2009, Webb 2009), a possible response by scientists to the physical and biological differences between systems. Although biophysical differences between marine and terrestrial systems can be overstated (Dawson and Hamner 2008), in terms of primary production and the ecology of consumer species these systems do differ fundamentally. The dominant primary producers in the sea are unicellular, motile, short lived and very responsive to short term changes in the physical environment while the dominant primary producers on land often provide structure, can grow in mass by many orders of magnitude and are often relatively unresponsive to short term environmental fluctuations.

Further, major groups of marine consumers (especially fish) tend to grow over many orders of magnitude in mass, change habitats and prey types with size, release large numbers of small pelagic eggs and provide no parental care while terrestrial vertebrate consumers have limited scope for growth, form long-term associations with habitat and provide their larger young with significant parental care.

One consequence of the differences between marine and terrestrial systems is that size rather than species identity accounts for most of the variation in the trophic roles of marine animals. Recognition of the significance of size led to the emergence of theory and applications that describe marine food web and system properties in terms of size composition (Kerr and Dickie 2001). Conversely, terrestrial food web theory focuses on species and on groups of species with similar trophic roles. The marine approach reflects the dominance of small primary producers in the marine environment, the relatively consistent relationships between predator and prey body sizes and the considerable scope for growth in many marine species, often exceeding five orders of magnitude in mass (Cushing 1975). Since many macroecological patterns and processes are a consequence of the energy demands and life histories of the species in a community (Brown et al. 2004) the development of theory

that is expected to apply to marine and terrestrial environments should therefore be informed by known differences in patterns energy acquisition and use. Consequently, terrestrial theory that is based on species having defined trophic roles may need to be revisited to account for the links between body size and trophic role in marine systems, so that cross-system comparisons can be made based on a common currency of 'trophic units'.

Here, we attempt to synthesise marine and terrestrial theory by developing a general approach for describing differences in the abundance–occupancy relationship for marine and terrestrial vertebrates. We work with fish and birds as they represent the life histories of the dominant marine and terrestrial vertebrates in the 10 g to 10 kg size range and because data with adequate spatial and temporal resolution are available. We focus on the abundance–occupancy relationship because it is one of the most general and robust macroecological relationships. Local population density and regional site occupancy are positively associated across species in the vast majority of habitats and taxonomic groups investigated to date (Blackburn et al. 2006). Simply put, locally common species are regionally widespread while locally scarce species are regionally rare. To account for the known links between body size and trophic role in marine systems we develop a new 'size-structured abundance–occupancy relationship' and show that accounting for differences in the trophic structure of marine and terrestrial systems can support the development and application of macroecological generalizations.

## Data

To investigate differences in abundance–occupancy dynamics in birds and fish, we use temporally and spatially replicated estimates of abundance and occupancy for each taxon. The temporally replicated bird data are for birds breeding on farmland in Britain from 1968 to 1999, as surveyed by the British Trust for Ornithology's Common Bird Census (CBC). Survey methods are described in Marchant et al. (1990), and the protocols used for estimating annual density and occupancy in Freckleton et al. (2006). Briefly, breeding birds on between 95 and 138 farmland sites throughout Britain, each measuring around 80 ha, were censused annually using a standard methodology. We consider only those 73 species recorded breeding at one or more sites in every year between 1968 and 1999. We use the species-specific estimates of mean and variance in local population density (averaged over occupied sites only) and regional occupancy (the proportion of surveyed sites occupied) given in Freckleton et al. (2006). This dataset excludes certain species (e.g. woodpigeon *Columba palumbus*, rook *Corvus frugilegus*) for which population size estimates were unreliable over some or all of the survey period due to very high abundances or colonial nesting habits.

The spatially replicated bird dataset is for breeding birds of Ontario (Bird Studies Canada et al. 2006, Cadman et al. 2009). This intensive survey of the avifauna of Ontario combined records of the presence or absence of breeding populations of species at a 10 km square resolution from 2001–2005, with estimates of the relative abundance of species obtained from ca 70 000 standardised point counts

throughout the province. We treated 47 regions of Ontario province, each with a typical area of around 1500 km<sup>2</sup>, as spatial replicates, estimating occupancy (the proportion of sampled 10 km squares in which breeding was considered either 'probable' or 'confirmed') and geometric mean abundance (mean number of individuals recorded across point counts in which that species was observed) separately for each species in each region. We excluded species which were recorded as breeding in fewer than 40 regions, and of those remaining we retained only those species for which we could estimate abundance (i.e. those which were recorded in at least one point count) in at least 35 regions. We also excluded colonial species such as laughing gull *Leucophaeus atricilla* and bank swallow *Riparia riparia*, as well as European invasive species (starling *Sturnus vulgaris* and house sparrow *Passer domesticus*), resulting in a final dataset of 81 species.

The temporally replicated fish data are for fishes of the Irish Sea. The Centre for Environment, Fisheries and Aquaculture Science (Cefas) 4 m beam trawl survey records the species, size and abundance of all fishes caught between August and October. Surveys have been conducted annually from 1988 to 2007 and are stratified by region and depth band. Between 95 and 176 trawl tows of 30 min duration are completed in each year, across between 14 and 31 standard ICES rectangles (boxes of 0.5° north–south and 1° east–west, area 3720 km<sup>2</sup> at 53°N). From each trawl, all individual fish >20 mm total length (TL) were counted, measured and identified, and abundances standardised to catch rates of individuals per hour trawl tow. More information is available in Parker-Humphreys (2004) and directly from Cefas (<www.cefas.co.uk>). Here, we exclude any taxon not identified to the species level, pelagic species that are not well sampled by the trawl, and any non-fish taxa. We also consider only those species that were recorded in at least 15 of the 20 annual surveys, resulting in a list of 59 species which together constitute 99% of the total catch (by numbers) across all years. Mean density for each species in a given year is calculated as the average catch rate of that species across all surveys in which it occurred. Regional occupancy is calculated at the level of standard ICES rectangle, with the occupancy for a species in a single year defined as the proportion of ICES rectangles sampled in that year in which the species was recorded.

The spatially replicated fish data are for the coral reef fishes of the Lau Island group, Fiji. Full details of the census of the diurnally active reef fish communities across 13 islands are given in Dulvy et al. (2002). Briefly, all fish >8 cm fork length were recorded by SCUBA underwater visual census in 7 m radius point counts using a standard protocol. Fish were identified to species, and fork length visually estimated to the nearest 1 cm. We pool results across the second and third cruises described in Dulvy et al. (2002), from Sept–Nov 1999 and Feb–Mar 2000, excluding the cruise from Apr–May 1999 to minimise seasonal effects. The 13 islands have reef fronts of between ca 8 and 61 km, and we treated each island as a spatial replicate. We estimated the average population density and occupancy for each species within each island. Sampling within each island was stratified across different reefs, but here we simply consider all point counts within an island as replicate samples. The mean density of a species at a given island is, therefore, its average abundance across those

fish counts in which it was observed, and its occupancy is the proportion of fish counts in which it was recorded. There were between 18 and 96 fish counts on each island. Species recorded at fewer than 10 islands were excluded, resulting in a final list of 72 species, which together constituted 94% of all surveyed individuals.

### Expected differences between birds and fish in abundance–occupancy dynamics over space and time

Positive interspecific abundance–occupancy relationships have previously been observed in a range of fish and bird assemblages (Blackburn et al. 2006). However, although the interspecific relationship provides a useful link between local and regional scale population biology (Freckleton et al. 2005), its precise form can be significantly affected by differences between species in mean abundance, population status, or habitat preference (Freckleton et al. 2006, Webb et al. 2007). In general, considering the dynamics within species differing in such characteristics can greatly improve our understanding of interspecific patterns (Webb et al. 2007). Here, we explore how major differences in life history between birds and fish, particularly in terms of reproduction, dispersal and body size, may affect the details of the abundance–occupancy relationship.

Two key differences between birds and fish concern their reproductive strategies and their growth trajectory. Birds produce few large offspring each year which grow rapidly to a maximum size thanks to extensive parental care from one or more adult. In contrast, broadcast spawning fishes have a bipartite life cycle, producing thousands of larvae in order to bet-hedge over the productive but spatially-patchy planktonic juvenile habitat (Winemiller and Rose 1993), many of which die and the remainder grow continuously in an asymptotic indeterminate fashion. The consequences of this for abundance and occupancy are illustrated in Fig. 1. A generalised fish species is represented by individuals of different sizes, with large, reproductive individuals producing many small offspring, which disperse (often initially in the plankton) over a large area (Fig. 1A). High mortality as they grow in body mass over several orders of magnitude means that at any one time, a fish species will be represented by a mix of individuals of widely differing sizes feeding at differing trophic levels. In abundance–occupancy terms, this means that there will be an ontogenetic shift within species from high density, high occupancy small individuals towards low density, low occupancy large individuals (Fig. 1B). This leads us to predict that there will be high temporal variation in abundance and occupancy within fish species.

Birds, on the other hand, typically produce few offspring requiring a high degree of parental care, and birds are typically as large as they will ever be within their first year (Fig. 1D). For instance, Odum (2008) gives body mass data (in grams) for newly-fledged and adult females of 35 species of eastern North American bird. There is no detectable difference in mass between the newly-independent individuals and their parents (mean difference in  $\log(\text{mass}) = 0.021$ , 95% CI =  $-0.017$ – $0.059$ , paired  $t = 1.1271$ , DF = 34,

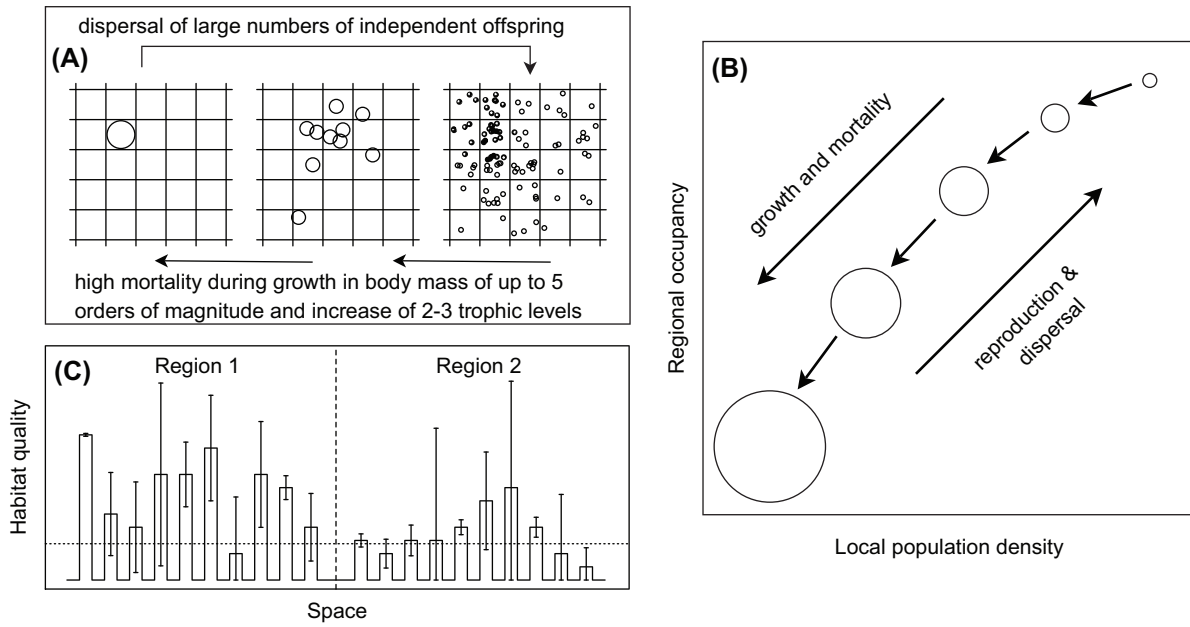
$p = 0.2676$ ). The high dependency of offspring on parental care is reflected in the generally low dispersal of most young birds: within species, typically the frequency distribution of natal dispersal distances is highly right-skewed (Paradis et al. 1998), with most individuals moving very little from the site where they were born. In consequence, the abundance and spatial distribution of a cohort of birds is likely to be much more constrained by that of the previous cohort, and temporal variation in population density and regional occupancy is expected to be less in birds than in fish (Fig. 1E).

These differences can also be envisaged in terms of distributions of habitat suitability. Freckleton et al. (2006) envisaged a landscape of habitat patches varying in quality, conceptually analogous to the earlier treatment of patchy marine habitats by MacCall (1990). A species can persist in a given patch only if the quality of habitat is sufficient for its birth rate to exceed its death rate. This results in a positive relationship between patch occupancy and the average population density within occupied patches (i.e. a positive abundance–occupancy relationship) if abundance is proportional to habitat quality (Freckleton et al. 2006). We extend this idea to consider variation in time and space. In marine systems (Fig. 1C), temporal variation of abundance (error bars) within habitat patches is expected to be relatively high, due to the tight coupling of physical and biological processes in the sea (Steele 1991a), leading to large variation in the regional occupancy of fish populations over short timescales. For example, it took just three years for the distributional extent of a marine fish (sand lance, *Ammodytes* spp.) to change as much as that of North American hardwood forest in 5000 post-glacial years (Steele 1991b; see Perry et al. 2005 for more recent examples of rapid changes in the distribution of fish species). In addition, the potential of juvenile fish to rapidly colonise new areas in the absence of adults (due to the frequent existence of a dispersive larval phase) may reduce inter-regional variation in abundance and occupancy.

In a typical terrestrial system (Fig. 1F), habitat quality will vary within a region, but differences will be more marked between regions, as major habitat types change (e.g. from primarily farmland to mainly forest). Within individual habitat patches, variation in habitat quality over time is likely to be relatively small compared to variation across patches within a region, and certainly compared to variation between regions. Even if overall the habitat quality within a region changes quite considerably over time, the rank order of patches is likely to remain relatively constant. As a consequence, both occupancy and population density will vary little over time for a given species within a given region, but variation between regions will be more marked. Thus, within regions common species will typically remain common, rare species will remain rare (Webb et al. 2007); but in different regions different species may dominate.

Differences in life history between fish and birds, and in the degree of coupling between physical and biological processes in terrestrial and marine systems, lead us to predict that species-level temporal variation in both abundance and occupancy within a region will be less in a bird assemblage than in a fish assemblage, and that the difference between

Generalised fish



Generalised bird

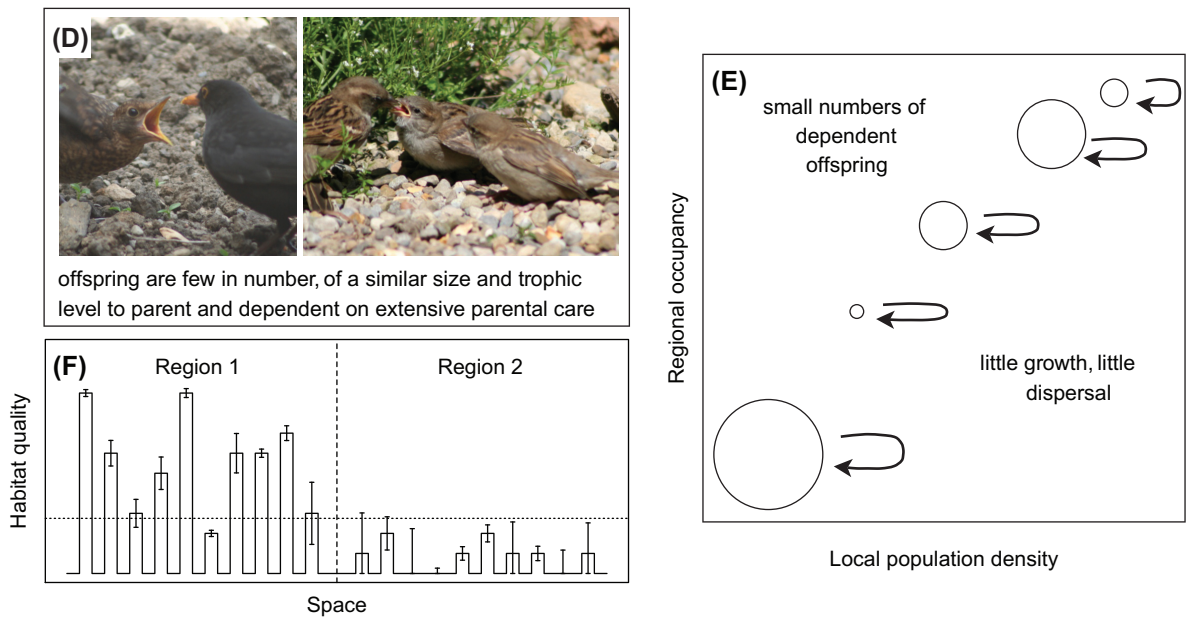


Figure 1. Generalised fish (A–C) and bird (D–F) abundance–occupancy dynamics. (A) Low density, low occupancy mature fish (large circle, left-hand panel) produce many small, dispersive offspring (small circles, right-hand panel). These offspring experience high mortality as they grow (middle panel). Overlaying these three panels results in a strong positive relationship between abundance and occupancy of individuals of different sizes within the same species (B; each point represents individuals of a similar body size, proportional to the size of the point). The relative proportions of individuals within a species at each ontogenetic stage will vary over time, leading to substantial temporal variance in both abundance and occupancy within species. This is illustrated in (C), which, following Freckleton et al. (2006) characterises a region in terms of a series of habitat patches differing in quality. Below the horizontal dotted line, habitat quality is insufficient for the species to persist, and so occupancy is simply the proportion of patches of a quality above this threshold; abundance is proportional to habitat quality. Here, we depict two regions, and the error bars illustrate a range of temporal variability of abundance within each habitat patch. High dispersal, for example due to broadcast spawning, means that offspring can colonise habitats that are not necessarily used by their parents, and so variation between regions is relatively low compared to variation over time within regions. Here, occupancy varies from 0.5–1 in region 1, and from 0.2–0.9 in region 2. (D). Birds typically produce few, highly dependent offspring, which rapidly attain a similar body size to that of their parents (for example the parent and fledgling blackbirds *Turdus merula* (left) and house sparrows *Passer domesticus* (right); photographs © T. J. Webb). Abundance is less tightly associated with body size, and species tend to remain in a similar region of abundance–occupancy space (E; each point represents a species, the size of the point is proportional to body size, and the arrows represent recruitment into the parental area of occupancy, at parental body size). Temporal variation of abundance within habitat patches will therefore be relatively low (F), and thus occupancy will also remain relatively stable over time within regions. Differences between regions may be quite substantial (F), as different species dominate in different habitats. Here, occupancy varies from 0.7–0.9 in region 1, and from 0–0.2 in region 2.

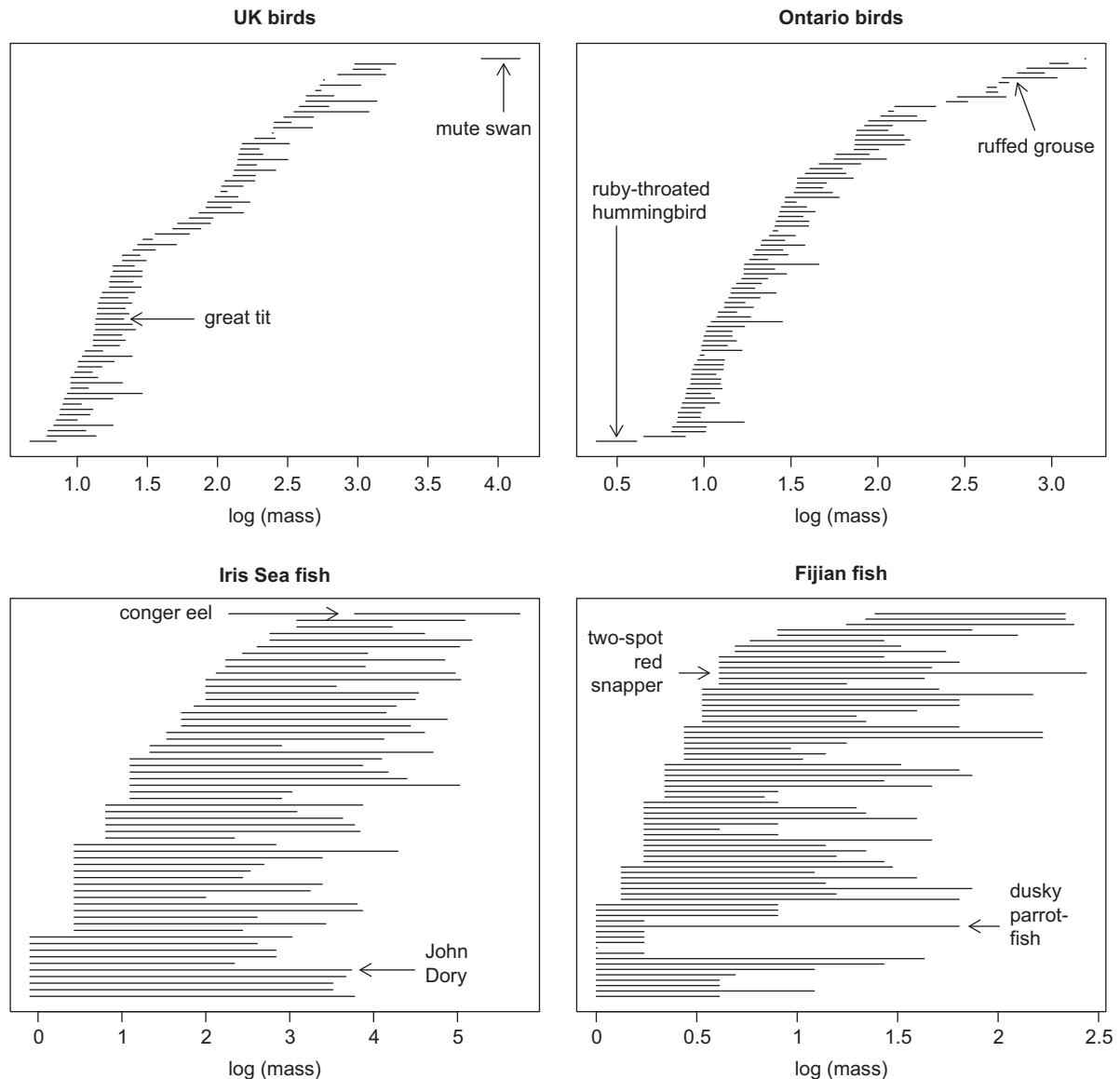


Figure 2. Size structure of the assemblages of UK farmland birds, Ontario birds, Irish Sea demersal fish and Fijian coral reef fish. Each horizontal line on each panel represents a single species, with the line extending from the minimum to maximum size recorded for that species. Bird size ranges are ranges in  $\log_{10}$  body mass taken from the literature (Dunning 2008), whereas in fish assemblages they are taken directly from the survey data. Because both surveys measured fish lengths, we convert these to a 'mass' scale using the approximation  $\text{mass} \propto \text{length}^3$ ; the numbers on the x-axis are therefore arbitrary, but for comparative purposes, an increase of one unit on all four plots is equivalent to a 10-fold increase in mass. Two exemplar species are identified from each assemblage. In the UK birds, the mute swan *Cygnus olor* varies between 7.6 and 14.3 kg ( $n = 94$ ); the smallest mute swans are  $> 5.7$  kg larger than the largest birds of any other species. 346 individual great tits *Parus major* vary in size by around 35%, from 15.75 to 21.5 g. In the Ontario birds, 107 ruffed grouse *Bonasa umbellus* varied in size from 498–566 g, whereas 584 ruby-throated hummingbirds *Archilochus colubris* varied from 2.4–4.1 g, with the largest hummingbird smaller than the smallest of any other species in this assemblage (the golden-crowned kinglet *Regulus satrapa*, with a minimum size of 4.5 g). In the Irish Sea fish, conger eel *Conger conger* with a length of up to 1770 mm were observed in the Irish sea survey ( $n = \text{ca } 219$ ), but the smallest individuals (390 mm, ca  $4.5 \times$  smaller on a linear scale, a difference of  $> 90$  fold on the 'mass' scale) were of a similar length to the largest John Dory *Zeus faber* (size range: 20–380 mm, a factor of 19 difference;  $n = 1098$ ). In the Fijian assemblage, the largest two-spot red snapper *Lutjanus bohar* of the 49 individuals observed was, at 65 cm,  $> 4$  times larger than the smallest (16 cm); likewise the largest dusky parrotfish *Scarus niger* was 4 times longer than the smallest (range: 10–40 cm,  $n = 15\,759$ ).

temporally and spatially replicated estimates of variation will be greater in birds than in fish. What is less clear is the extent to which this represents a fundamental difference in the structure and functioning of bird and fish communities. In

particular, although species identities may vary considerably over time and space in fish assemblages, is this reflected in similar variation in other ecological units, in particular body size classes?

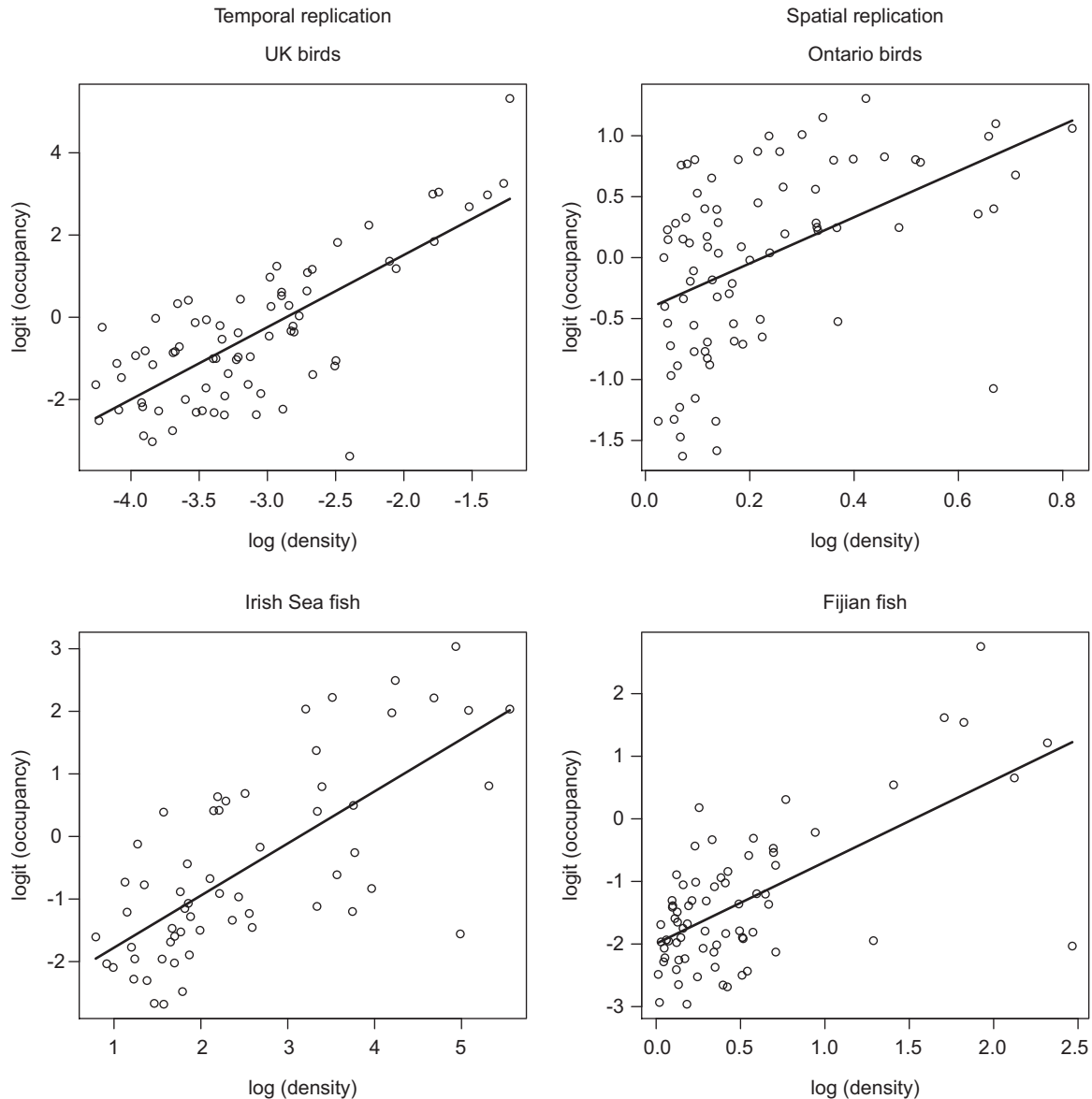


Figure 3. Interspecific abundance–occupancy relationships for UK farmland birds, Ontario birds, Irish Sea bottom dwelling fish and Fijian coral reef fish. Each point represents the local density and regional occupancy of a single species, averaged over time (UK birds and Irish Sea fish) or space (Ontario birds and Fijian fish). Fits of simple linear models of logit (occupancy) on log (density) are also shown (see Table 1 for details).

### Size structure in bird and fish communities

The scheme set out in Fig. 1 suggests that some of the difference in abundance–occupancy dynamics between birds and fish may be explained by differences in size structure of the animals in the samples (Fig. 2). The body sizes of all bird species in our two datasets were derived from data in Dunning (2008), taking minimum and maximum adult body masses (g) and combining data across the sexes where separate male and female masses were recorded. Body size data for both fish assemblages come directly from the datasets described above, as all individuals of every species were measured during the surveys. Analyses use size as recorded (total length for the Irish Sea fish, fork length for the Fijian fish), however for better comparison with the bird mass data in Fig. 2 we assume, based on principles of geometry and

empirical studies (Froese and Pauly 2010) that fish mass is approximately proportional to length<sup>3</sup>.

At any given time each fish species in a region tends to be represented by individuals that vary more in size than the individuals of a given bird species, notwithstanding the size selectivity of the sampling (mesh size) and census (animals < 8 cm excluded) methods. Typically, sampled individuals of an Irish Sea fish species vary in mass by around 3.2 orders of magnitude, those of a Fijian fish species by around 1.2 orders of magnitude (Fig. 2); this compares to approximately 0.2 orders of magnitude of variation in mass within species in both bird assemblages. Across such a size range, it is expected that the trophic roles of species will change considerably because feeding in most marine fishes is strongly size based and the average relationship between predator and prey size in marine fishes is typically between 10<sup>2</sup> and 10<sup>3</sup>: 1

Table 1. Interspecific abundance–occupancy relationships for the four assemblages, and inter-size class abundance–occupancy relationships for the two fish assemblages. n refers to the number of species or size classes included in each analysis. Slopes are of the linear models of logit(occupancy) on log(density) illustrated in Fig. 4 (species-level analyses) and Fig. 7 (size-class analyses), and all are highly significantly positive ( $p < 0.00001$  in all cases). Also shown are the  $R^2$  values for the same models.

Assemblage	n	Slope $\pm$ SE	$R^2$
UK birds	73	1.76 $\pm$ 0.185	0.56
Ontario birds	81	1.90 $\pm$ 0.387	0.23
Irish Sea fish			
species	59	0.83 $\pm$ 0.110	0.50
size class	11	1.74 $\pm$ 0.155	0.93
Fijian reef fish			
species	72	1.30 $\pm$ 0.184	0.42
size class	11	3.05 $\pm$ 0.309	0.92

(Cushing 1975). This implies that the smallest sampled individuals of a given fish species could be feeding one trophic level below those of larger individuals.

Bird species do, on the other hand, exist as coherent trophic entities, with all individuals of a given species attaining a similar size and fulfilling a similar ecological role. At the same time, trophic interactions are less size structured. For instance, in the UK farmland bird assemblage the largest species which feeds primarily on vertebrate prey (the buzzard *Buteo buteo*) is smaller than eight herbivorous, invertebrate-feeding or omnivorous species (diet information from BWPi 2006).

Woodward et al. (2005) discuss the effects that the kinds of ontogenetic shifts in body size we see in fish (Fig. 2) will have on the analysis of trophic interactions and therefore on macroecological relationships. In particular, analyses at the level of the species, although they can provide a useful overall summary of the system on land, may be inappropriate to capture the individual size-based pattern of energy flow and dynamics in the sea. As Raffaelli (2005, p. 61) puts it, ‘...the Latin binomial of... the herring *C[lupea] harengus*, does not exist as a trophic entity, but as a particle continuously changing in size, interacting with other such particles which we also conveniently label with Latin binomials, which have no trophic reality for the herring’.

### Interspecific abundance–occupancy relationships in birds and fish

Interspecific abundance–occupancy relationships are shown for all four systems in Fig. 3. In each case, density and occupancy is estimated for each species as the mean of the annual estimates (for the UK birds and the Irish Sea fish) or the mean across spatial units (regions for the Ontario birds and islands for the Fijian fish). The relationships are approximately linearised by a logit transformation of proportional occupancy (i.e. log(proportion occupied sites / proportion unoccupied sites)), and a log transformation of density. All four relationships are highly significantly positive, with density explaining between 23 and 56% of the variance in occupancy (Table 1). These four assemblages thus provide further support for the generality the positive abundance–occupancy relationship in macroecology (Blackburn et al. 2006): in each case, locally

common species are regionally widespread, locally rare species are regionally scarce.

### Intraspecific variation in abundance and occupancy

We use the multiple estimates of both density and occupancy for each species in each assemblage to expand our view of the interspecific abundance–occupancy relationship to incorporate intraspecific variation. Rather than fitting separate intraspecific models (Webb et al. 2007), we consider the variance of each species in bivariate ‘abundance–occupancy space’. We calculate the 95% CI of both log (density) and proportional occupancy for each species over time (for the British birds and the Irish Sea fish) or space (for the Ontario birds and the Fijian fish), constraining occupancy CIs to lie between 0 and 1. In Fig. 4, we plot each species as a polygon, centred on its mean density and occupancy, with linear dimensions defined by the density and occupancy confidence intervals described above. The immediate impression is that there is considerably more variation in abundance and occupancy in the spatially varying datasets compared to the temporally replicated ones. Within the temporally replicated systems, birds appear to vary less than fish in both dimensions, with bird species existing as more distinct entities in abundance–occupancy space than do fish species.

To provide a quantitative comparison of variation across abundance and occupancy dimensions in each dataset, we first consider the area spanned by the density and occupancy axes in each panel of Fig. 4 as a ‘constraint space’. For each species, we then calculate a ‘proportional abundance–occupancy area’, as the proportion of this total available abundance–occupancy space covered by its abundance–occupancy polygon. A species spanning the entire range of observed densities and occupancies would thus have an abundance–occupancy area of 100%; in each panel of Fig. 5 areas of 1% and 0.1% are also illustrated. The distribution of proportional abundance–occupancy areas across species is shown for each assemblage in Fig. 5. To test for differences between taxa (birds vs fish) and replication (temporal vs spatial), we fitted a linear model of proportional abundance–occupancy area (logit transformed) as a function of taxon, replication and their interaction. Overall this model explained 54% of the variation in abundance–occupancy area, and the interaction between taxonomic group and mode of replication was highly significant ( $F_{1,281} = 54.9$ ,  $p < 0.00001$ ). Temporal variation in abundance and occupancy was much lower than spatial variation in birds, but this difference was less pronounced in fish (Table 2, Fig. 5).

### The size-structured abundance-occupancy relationship

To combine the species-based, macroecological approach inherent in abundance–occupancy relationships with a size-based approach suitable for marine fish, we develop a ‘size-structured abundance–occupancy relationship’. As an alternative to taxonomic classification, we placed each individual fish from the Irish Sea survey into 10 cm length classes, grouping all individuals  $> 100$  cm together to result in 11 size classes. For the Fijian reef fish, we used

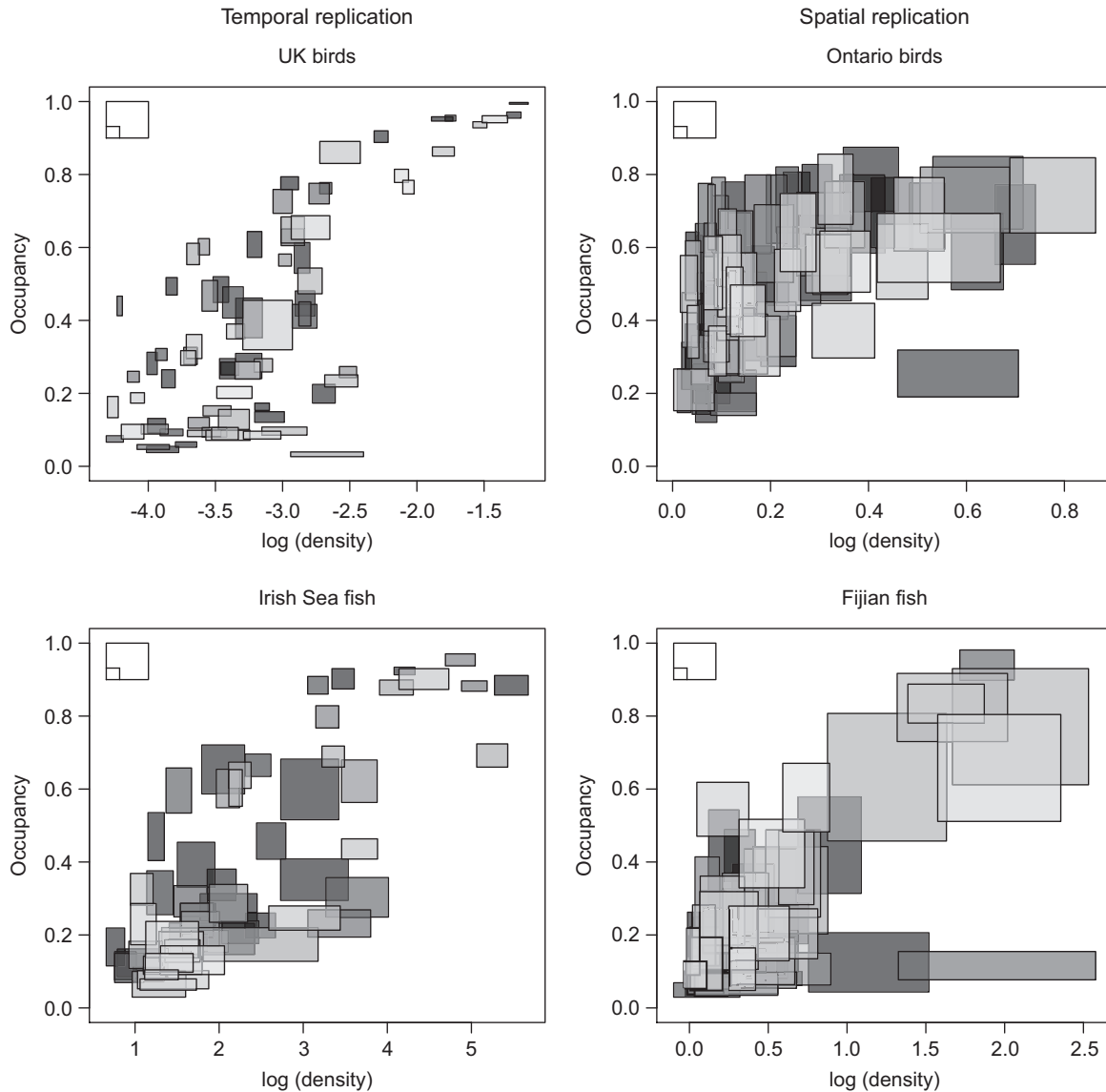


Figure 4. Intraspecific variation in density and occupancy presented in interspecific ‘abundance–occupancy space’ for UK farmland birds, Ontario birds, Irish Sea demersal fish and Fijian coral reef fish. Each polygon represents a species, and is centred on the mean density and occupancy of that species; its dimensions correspond to the 95% CI of density and occupancy over time (UK birds and Irish Sea fish) or space (Ontario birds and Fijian fish). In each panel, the box in the top left corner depicts an area of 1% (large box) and 0.1% (small box) of the abundance–occupancy area spanned by both axes.

5 cm length classes, grouping all individuals > 60 cm which again resulted in 11 distinct size classes. We then treat these classes in the same way as species in the previous interspecific analyses (Fig. 3): in each year (for Irish Sea fish) or each island (Fijian reef fish), for each size class the proportion of sites occupied and mean population density at these occupied sites was calculated. These were then averaged across all years or islands, producing ‘inter-size class abundance–occupancy relationships’ (Fig. 6, top panel). As before, we fitted linear models of  $\text{logit}(\text{occupancy})$  on  $\text{log}(\text{density})$ , both of which were highly significantly positive (Table 1). Size class population density explains > 90% of variation in size class occupancy in both fish assemblages (Table 1). It is also clear (Fig. 6, top panel) that small individuals tend to be common everywhere, whereas large large individuals are both regionally scarce and locally rare.

Analogs of intraspecific dynamics can also be applied to size classes. As before, we calculated 95% CIs of both  $\text{log}(\text{density})$  and proportional occupancy for each size class over time (for the Irish Sea fish) or space (for the Fijian reef fish). This intra-size class variation is shown in the bottom panels of Fig. 6. These polygons appear to be significantly smaller than those representing the dynamics of fish species (Fig. 4), an impression strengthened when the distributions of polygon proportional areas are compared between species and size classes (Fig. 5).

We used linear models to investigate this statistically. First, considering only fish assemblages, we fitted a model of  $\text{logit}(\text{proportional abundance–occupancy area})$  as a function of grouping factor (species or size class) and replication (temporal or spatial), including the interaction between these two factors. The second smallest size class in the Irish



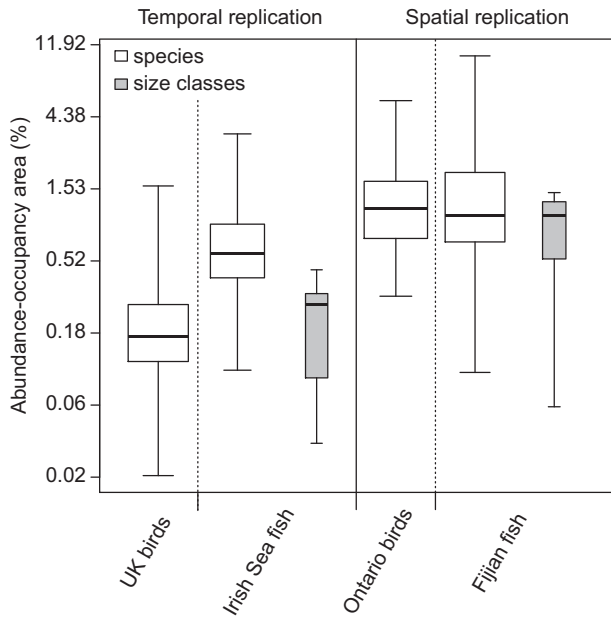


Figure 5. The distribution of the proportion of total available abundance–occupancy space taken up by bird and fish species or size classes. For each assemblage, the horizontal bar is the median percentage, the box is the interquartile range, and the whiskers extend to the data extremes. The width of each box is proportional to the number of species or size classes in that assemblage. Abundance–occupancy areas have been logit-transformed, but for ease of interpretation labels on the y-axis have been back-transformed to percentages. The second smallest size class in the Irish Sea fish assemblage has an area of 0 (occupancy = 1 in all years), and is excluded from this figure because 0 cannot be logit-transformed (see text for more details). For all datasets, open bars represent species-level analyses; for the fish datasets, shaded bars represent size-class analyses. The assemblages to the left of the solid vertical line are temporally replicated, those to the right are spatially replicated.

Sea assemblage has an abundance–occupancy area of 0 (proportional occupancy is 1 in all years), which is problematic because it cannot be logit-transformed. We thus assigned this size class an arbitrarily small area (three standard deviations below the mean area of all logit-transformed proportional areas). This results in a logit(proportional abundance–occupancy area) of 8.79, equivalent to 0.015% of the abundance–occupancy plot area, compared to the observed

minimum area across all other species and size classes of 0.021%. An alternative approach – excluding this size class – does not qualitatively affect our conclusions, indeed quantitative effects are very small.

There was no significant interaction between grouping factor (size vs. species) and replication (temporal or spatial) ( $F_{1,149} = 3.67$ ,  $p = 0.0572$ ), although there is a trend for the difference between species- and size-based grouping to be greater in the temporally-replicated Irish Sea data than in the spatially-replicated Fijian assemblage (Table 2). Removing the interaction, both main effects were highly significant (grouping:  $F_{1,150} = 24.3$ , replication:  $F_{1,150} = 27.0$ ,  $p < 0.00001$  in both cases). Species have larger abundance–occupancy areas than size classes, and abundance–occupancy areas are smaller in the temporally replicated assemblage than the spatially replicated one (Table 2).

Finally, we compared bird species with fish size classes by fitting a model of logit(proportional abundance–occupancy area) as a function of grouping (bird species or fish size classes), replication (temporal or spatial) and their interaction. The interaction between grouping and replication was not significant ( $F_{1,172} = 2.66$ ,  $p = 0.1049$ ); removing the interaction, both grouping ( $F_{1,173} = 5.50$ ,  $p = 0.0201$ ) and replication ( $F_{1,173} = 281.9$ ,  $p < 0.00001$ ) were significant. For both bird species and fish size classes, abundance–occupancy areas are considerably higher in the spatially replicated assemblages than in the temporally replicated assemblages (Table 2). There is no difference in abundance–occupancy areas between temporally replicated fish size classes and bird species, whereas abundance–occupancy areas in the spatially replicated assemblages are somewhat larger for bird species than for fish size classes (Table 2).

### Body size, abundance and occupancy in bird and fish communities

Taking species-level averages over time or space in all four assemblages considered here, we find strong support for a positive interspecific abundance–occupancy relationship in each case (Fig. 3, Table 1). Given that this relationship is among the most general patterns in ecology (Gaston et al. 2000), this is perhaps not surprising, and it illustrates how simple species-level analyses are useful for documenting broad patterns regardless of whether the system in question

Table 2. Estimated mean (with 95% CI) proportion of the abundance–occupancy plot area occupied by bird and fish species and fish size classes. Estimates in the same row may differ across columns as they are derived from fitted models with logit(proportional abundance–occupancy area) as the response. For ease of interpretation, model estimates are back-transformed into percentages. In the description of the model, taxon refers to a comparison between birds and fish, replication is a comparison between temporal and spatial studies, and grouping compares species-level with size class-based analyses.

Replication	Assemblage	Model		
		Taxon × replication	Grouping × replication	Bird species vs fish size classes
Temporal	UK birds	0.17 (0.14–0.22)		0.17 (0.14–0.22)
	Irish Sea fish			
	species	0.60 (0.43–0.85)	0.60 (0.27–1.31)	
	size class		0.15 (0.07–0.31)	0.15 (0.08–0.29)
Spatial	Ontario birds	1.17 (1.00–1.37)		1.17 (1.00–1.37)
	Fijian reef fish			
	species	1.12 (0.88–1.41)	1.12 (0.65–1.92)	
	size class		0.61 (0.36–1.01)	0.61 (0.38–0.96)

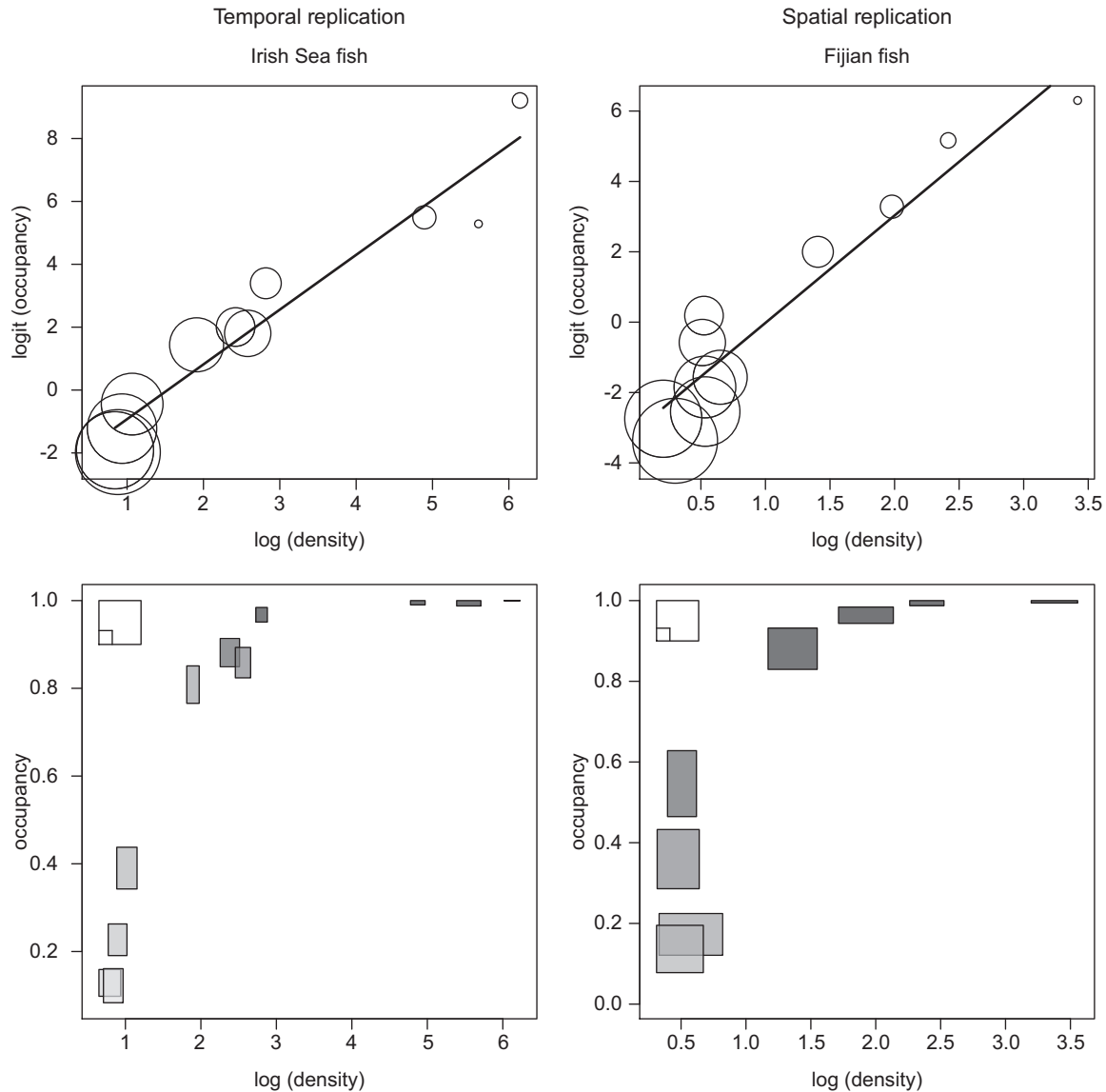


Figure 6. Inter-size class abundance–occupancy relationships (top panel) and intra-size class variation in density and occupancy presented in inter-size class abundance–occupancy space (bottom panel) for Irish Sea demersal fish and Fijian reef fish. Each point in the top two figures represents the local density and regional occupancy (averaged over time or space) for fish of any species that are of a given body size. The size of each point is proportional to the body size that it represents. The polygons in the bottom two figures represent the variance (95% CI) in local density (width of polygon) and regional occupancy (height of polygon) for fish within each size class over time or space in the two assemblages. The box in the top left corner of these figures depicts an area of 1% (large box) and 0.1% (small box) of the abundance–occupancy area spanned by both axes.

is marine or terrestrial (Smith et al. 2008, Witman and Roy 2009). Indeed, the temporal dynamics of interspecific summary statistics have previously been used in both birds and fish to detect interesting human-driven changes in these communities (Fisher and Frank 2004, Webb et al. 2007). Nevertheless, species-level summaries conceal considerable variation within species, and understanding these intraspecific processes can greatly increase our understanding of community-level abundance–occupancy dynamics (Freckleton et al. 2005, 2006, Webb et al. 2007).

By considering intraspecific variation in abundance and occupancy, we find strong support for our prediction that temporal variation within a region will be less in a bird assemblage than in a fish assemblage (Fig. 4, 5). This is in

keeping with Steele's (1991a) argument that marine systems are inherently more variable than terrestrial systems at decadal timescales due to the tight coupling of physical and biological processes in the sea. However, it is worth noting that the UK bird assemblage studied here has in fact been the subject of substantial conservation concern, precisely because the CBC and similar surveys have documented significant changes in the abundance and distribution of various species (Greenwood 2003). This has been caused by the rapid and extensive rates of habitat modification over the period of monitoring (Chamberlain et al. 2000, Greenwood 2003) and Webb et al. (2007) show how these temporal changes have left a macroecological signature on the abundance–occupancy relationship in this community. Steele

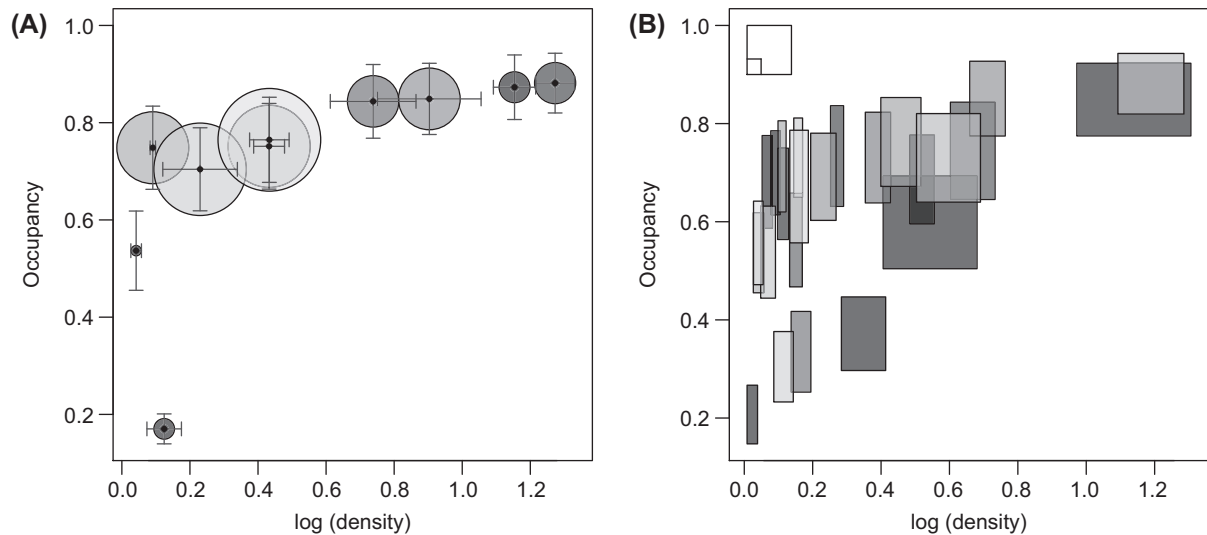


Figure 7. (A) Inter size-class abundance–occupancy relationship for Ontario birds. All individuals were classified into one of 10  $\log_2$  size classes based on the mean body mass for each species, and the occupancy and mean population density of each size class was calculated for each region. The solid black symbols indicate the mean values for density and occupancy across regions for each size class, and the error bars represent 95% CIs in each dimension. The shaded symbols are proportional to body size: larger symbols represent larger birds. (B) Feeding guild-based abundance–occupancy relationship for Ontario birds. Each species was classified into one of 25 feeding guilds following the scheme of De Graaf et al. (1985). These guilds combine information on diet and feeding method; for instance, the alder flycatcher *Empidonax alnorum* is classified as an insectivore: air sallier, and the American crow *Corvus brachyrhynchos* as an omnivore: ground forager. The population density and occupancy of each feeding guild was estimated for each region; the polygons are centred on the mean of each variable across regions, and their dimensions represent the variance (95% CI) across regions in local density (width of polygon) and regional occupancy (height of polygon). The scale box depicts an area of 1% (large box) and 0.1% (small box) of the abundance–occupancy area spanned by both axes.

(1991a) argues that such rapid, spatially-extensive human impacts on terrestrial ecosystems are making them behave more like oceanic systems, where ecological and physical processes occur at similar scales. Thus, the temporally-replicated bird assemblage that we consider display unusually high levels of temporal variability; and yet temporal variability in the distribution and abundance of fish species is still significantly greater (Fig. 4, 5).

When abundance and occupancy are averaged over space, rather than time, the difference between birds and fish disappears (Fig. 4, 5). This supports our prediction that the difference between spatial and temporal variation will be less in fish than in birds. It should be recognised, however, that the Ontario birds were surveyed across a wide range of habitats including boreal forests, wetlands, and arable farmland, whereas the Fijian reef fish were all sampled on reasonably similar regions of coral reef. If birds were sampled only in similar habitats across regions, it is likely that spatial variance would be somewhat less than that recorded here.

The second major difference between birds and fish that needs to be considered in analyses of abundance and occupancy concerns their contrasting life history strategies. In particular, there are large differences in body size structure between birds, with determinate growth and little size structure in trophic interactions, and fish, with indeterminate growth and strongly size-structured trophic interactions (Fig. 1). A corollary of this fundamental difference is the consequent differences in reproduction and dispersal, with birds producing a small number of big, dependent offspring (which tend to remain largely in their natal area) and fish typically producing large numbers of small, independent offspring.

Thus, in our assemblages, bird species are represented by individuals of approximately the same size, whereas the same species of fish may be represented by individuals differing markedly in size (Fig. 2). Both bird surveys target adult birds only, and the fish surveys exclude small individuals, so if Fig. 2 was to cover the full size range of each species all lines would extend further to the left. However, the general pattern would hold, with lifetime growth in mass of  $\leq 1$  order of magnitude for birds and of up to five orders of magnitude for fish. This means that ecological interactions such as competition and predation are more consistent in birds but will vary in fish as a function of body mass. Consequently, size classes provide a more coherent ecological grouping for fish than species identity.

When we construct size-structured abundance–occupancy relationships for both fish assemblages, we find patterns of intra-size class variation very similar to intraspecific variation in birds over both time and space (Fig. 5, 6). Importantly, this link between abundance, occupancy and body size provides a means to understand how changes in size composition, such as those predicted by existing size-based models (Duplisea et al. 2002, Blanchard et al. 2005, Shin et al. 2005), might influence regional patterns of occupancy.

Such size structuring is not apparent in bird communities. To illustrate this, we assigned all individual birds in the Ontario dataset to size classes, assuming that all individuals of a given species attain the mean size for that species, which we obtained from Dunning (2008). Ten size classes were defined on the basis of  $\log_2$  body mass (i.e. size class 1 was for species with a mass of 2–4 g, size class 2 for species of 4–8 g, and so on). Abundance–occupancy statistics for each of the 47

regions of Ontario were then calculated on the basis of these size classes, ignoring species identity. Figure 7A shows that, as predicted in Fig. 1E, there is no consistent ordering of birds of different sizes in abundance–occupancy space, and that the confidence intervals of size classes in both density and occupancy dimensions frequently overlap. Thus, a size-structured approach to avian macroecology is not justified.

We have ignored any life history differences within either the bird or the fish assemblages. However, our results suggest several potentially interesting comparisons. For instance, range sizes of teleost fish are larger in egg producing species than live-bearers (Goodwin et al. 2005), a difference hypothesised to be due to the greater colonisation potential of dispersive offspring. Similarly, marine invertebrates with dispersive larval phases tend to have larger geographic ranges (Jablonski 1986), with consequences for abundance–occupancy relationships (Foggo et al. 2007). Differences in body size also affect the spatial distributions of many marine species (Webb et al. 2009). This suggests that there may be a continuum between ‘pure bird’ and ‘pure fish’ abundance–occupancy dynamics, with the degree to which patterns are driven by species-level or size-class level processes differing across different taxonomic or functional groups.

Of course, other classification schemes may make sense in some instances. In birds, for example, although body size is less informative than species identity (Fig. 7A), it is possible to categorise individuals in other ways. An obvious candidate is feeding guild: we might expect birds feeding on similar resources to have similar abundance–occupancy dynamics, regardless of specific identity. Certainly, classifying the Ontario birds into feeding guilds, using the scheme of De Graaf et al. (1985) produces a sensible distribution of entities in abundance–occupancy space (Fig. 7B). The resulting abundance–occupancy polygons are smaller on average than the species-level polygons (averaging 0.84% of the abundance–occupancy area, cf. 1.17% for species-level polygons; linear model on logit-transformed proportions,  $F_{1,104} = 4.7$ ,  $p = 0.0325$ ). Intriguingly, the guild-based abundance–occupancy areas for Ontario birds do not differ from the size-based Fijian areas ( $F_{1,34} = 1.0$ ,  $p = 0.314$ ), suggesting that such an analysis may make a sensible starting point for an ecological exploration of avian abundance–occupancy relationships. In general, we suggest that consideration of the effects of different life history strategies (e.g. determinate vs indeterminate growth, broadcast spawning vs brooding) on patterns of temporal and spatial variation in abundance and occupancy may help to determine the appropriate level of ecological organisation at which to study any particular group of species.

In conclusion, making sensible comparisons between different systems greatly benefits the search for general understanding of the processes structuring communities (Steele 1991a, Dawson and Hamner 2008). Our analyses show that it is possible to go beyond simple summaries across species to generate predictions about intraspecific variation in macroecological variables in different taxa and under different sampling regimes. Clearly, the four extensive surveys that we have analysed differ considerably in methodology, spatial extent, and taxonomic scope, all of which may influence the abundance–occupancy relationships. Nevertheless, we believe that the major differences between birds and fish are real, and can

best be explained through consideration of the appropriate ecological ‘units’ (species or size class) for analysis. Choice of these units can profoundly affect interpretation of differences between systems, and Raffaelli’s (2005) ‘curse of the Latin binomial’ will affect all analyses of species with indeterminate growth coexisting in strongly size-structured networks, in which body size rather than specific identity dominates in determining ecological role. Comparing similar functional units on land and in the sea may help to reconcile apparently divergent macroecological patterns that are underpinned by patterns of energy acquisition and use.

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