Do spatial scale and life history affect fish-habitat relationships?

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Abstract

1. Understanding how animals interact with their environment is a fundamental ecological question with important implications for conservation and management. The relationships between animals and their habitat, however, can be scale-dependent. If ecologists work at suboptimal spatial scales, they will gain an incomplete picture of how animals respond to the landscape. Identifying the scale at which animal-landscape relationships are strongest (the ‘scale of effect’) will improve our ability to better plan management and conservation activities.

2. Several recent studies have greatly enhanced our knowledge about the scale of effect, and the potential drivers of inter-specific variability, in particular life-history traits. However, while many marine systems are inherently multi-scalar, research into the
scale of effect has been mainly focussed on terrestrial taxa. As the scales of observation in fish-habitat association studies are often selected based on convention rather than biological reasoning, they may provide an incomplete picture of the scales where these associations are strongest.

3. We examined fish-habitat associations across four nested spatial scales in a temperate reef system to ask: (1.) at what scale are fish-habitat associations the strongest, (2.) are habitat elements consistently important across scales, and (3.) do scale-dependent fish-habitat associations vary in relation to either body size, geographic range size or trophic level?

4. We found that: (1.) the strongest fish-habitat associations were observed when these relationships were examined at considerably larger spatial scales than usually investigated; (2.) the importance of environmental predictors varied across spatial scales, indicating that conclusions about the importance of habitat elements will depend on the scales at which studies are undertaken; and (3.) scale-dependent fish-habitat associations were consistent across all life-history traits.

5. Our results highlight the importance of considering how animals relate to their environment and suggest the small scales often chosen to examine fish-habitat associations are likely to be suboptimal. Developing a more mechanistic understanding of animal-habitat associations will greatly aid in predicting and managing responses to future anthropogenic disturbances.

Key words: Australia, landscape ecology, reef fish, scale of effect, spatial grain.

Introduction

Understanding how species interact with the environment is a central tenet of ecology. However, the strength and direction of the relationships between animals and their environment can vary at different spatial scales (Wiens 1989; Miguet et al. 2016). For example, the abundance of beetles increases with the amount of forest cover but the strength of this effect varies markedly across spatial scales (Holland, Bert & Fahrig 2004). Consequently, elucidating the mechanisms driving species’ distributions is likely to critically depend on the scale at which the study is conducted, with important consequences for conservation. For example, environmental managers must often decide on the appropriate scales for siting protected areas, or for undertaking restoration efforts, to facilitate connectivity (McAlpine et al. 2016). If we have incomplete or misleading information about
the scales at which habitat is important, then these actions may not achieve their desired outcomes.

As the scale most appropriate for measuring associations between animals and the landscape is usually unknown, these relationships are best evaluated using multi-scale approaches (e.g. Graf et al. 2005; Meyer & Thuiller 2006; Grober-Dunsmore et al. 2008; Boscolo & Metzger 2009). The scale at which an ecological response (e.g., abundance) is most strongly related to the landscape structure (e.g., amount of habitat) can then be directly estimated. This is known as the scale of effect (Jackson & Fahrig 2012; Jackson & Fahrig 2015).

Determining the scale of effect will improve our understanding of the relationship between animals and their environment, and when this is scale-dependent. We might gain a very different picture of the relative importance of biotic or abiotic predictors of abundance if we work at one scale over another. Studies of the nesting behaviour of Brewer’s sparrow (Spizella breweri) illustrate this point – individuals select nesting habitats on the basis of shrub cover and height at landscape scales, but on the density of potential nest shrubs at smaller scales (Chalfoun & Martin 2007). Given the complexities of habitat selection behaviour, key relationships between animals and their habitats may be missed entirely by working at only one scale (Orians & Wittenberger 1991). As such, more studies are needed that examine the scale of effect across different landscapes and taxa so we can begin to better understand how and at what scales animals interact with habitats (Miguet et al. 2016).

The scale of effect likely varies among species, potentially due to differences in life-history traits (Miguet et al. 2016). The scale of effect is predicted to be positively correlated with home range size, body size, and dispersal ability, and to be larger for species at higher trophic levels (Miguet et al. 2016). Theoretical studies provide some support for these predictions, with average dispersal distance having a strong positive effect in models of simulated species (Jackson & Fahrig 2012) but these relationships may not be as strong in nature. For example, a recent quantitative review incorporating data from 583 species across a range of taxonomic groups found no convincing relationships between the observed scale of effect and 29 species traits (Jackson & Fahrig 2015). This lack of response could, in part, be due to many studies being conducted at suboptimal scales, further emphasising the need for more evidence on how and why relationships between animals and their habitats vary across different scales.

Research on the scale-dependence of animal-habitat associations has focused predominantly on terrestrial animals. For example, Jackson and Fahrig (2015) reviewed
multi-scale studies that reported relationships between abundance and landscape structure and found fewer than 10 relevant records for fish. Given the fundamental physical and biological differences between marine and terrestrial systems (Carr et al. 2003), we might expect different scales of effect. Marine systems are likely to be more demographically open, with greater dispersal rates and distances, and the scale of effect consequently may be larger for marine compared to terrestrial species. Thus, marine environments represent an interesting system to test the generality of this phenomenon.

Many marine habitats, especially coral reefs, are inherently multi-scalar (Sale 1998). Studies have examined how assemblage composition, in terms of the abundance of different taxonomic groups, might vary across spatial scales (e.g. Simonetta, Antonio & Lisandro 2005). There has also been extensive research on the determinants of the distribution and abundance of fish assemblages from small to ocean basin scales (Bellwood & Hughes 2001; Mora et al. 2003; Connolly et al. 2005). However, the focus has often been on identifying the relative importance of predictors measured at only one spatial scale, for example, fish assemblages in Australian estuaries were most strongly related to a mix of regional (coast type), estuary-wide (bar type), and local-scale factors (Valesini et al. 2014). Less work has aimed to understand how the relationship between fish and specific habitat variables might be scale-dependent e.g. at what scale is a particular environmental variable the best predictor of fish assemblages?

Reef fishes are ideal for testing for a scale of effect because there is abundant evidence that species richness, diversity and density are positively associated with habitat complexity (e.g. Choat & Ayling 1987; Connell & Jones 1991; Willis & Anderson 2003). Life-history traits are also known to contribute to inter-specific differences in responses to habitat. For example, fish-habitat associations vary based on size and trophic level (Choat & Ayling 1987; Anderson, DeMartini & Roberts 1989), and habitat structure can have scale-dependent effects on size (Nash et al. 2013; Nash et al. 2014). Marine fishes can also differ considerably in their dispersal abilities (Kinlan & Gaines 2003), which could influence the scales at which they associate with habitats.

Despite the evidence that reef fish are strongly habitat associated, and that these associations may differ among species based on their life-history traits, most studies examining abundance-habitat relationships are conducted at only very small spatial scales e.g., 25-50 m long transects (Choat & Ayling 1987; Anderson & Millar 2004), although this can be greater in studies of larger taxa (e.g. 1.5 km transects for three ray species: Vaudo & Heithaus 2013). This is a unit of measurement likely chosen due to convention or logistical
reasons, and does not mean that this spatial scale is where correlations are strongest between fish and habitat variables (Wiens 1989; Sale 1998). In fact, working at such small scales raises the possibility that many studies are gaining an incomplete picture of fish-habitat associations because they are not working at the scales at which these relationships are strongest.

Here we explore associations between nearshore rocky reef fishes and habitat in south-eastern Australia to answer three questions: (1.) at what spatial scales (100 – 1200 m) are fish-habitat associations the strongest (i.e. what is the scale of effect), (2.) are environmental predictors of fish assemblages scale-dependent, and (3.) do scale-dependent fish-habitat associations vary with life-history traits? We focussed on three life history traits – geographic range size, body size, and trophic level. Based on recent work (Miguet et al. 2016), we hypothesized that if fish-habitat associations are scale-dependent, we would observe larger scales of effect for larger species, those with larger geographic ranges, and those at higher trophic levels.

Materials and Methods

We worked at three locations (sites) along the coast of Victoria in south-eastern Australia (Fig. S1), collecting data between December 2007 and August 2008. Fish surveys were conducted using two standard methods, baited remote underwater video (BRUV) and underwater visual census (UVC), with characteristics of the underlying reef habitat also measured. We used this multi-method approach as BRUVs and UVCs provide different but complementary information about fish assemblages (Colton & Swearer 2010; Lowry et al. 2012). All surveys were conducted between 3.7 and 28 m depth. As these sites have similar species assemblages (Colton & Swearer 2012), and our sampling was conducted over a short temporal window at each site (Table S1), we combined surveys across all sites and sampling dates to look at overall fish-habitat associations.

Fish surveys

BRUV units were comprised of a Sony HC-series Handycam in an underwater housing mounted onto an aluminium frame. Bait, consisting of 400 g of crushed pilchards, was placed in a mesh pouch that was suspended from a PVC pipe 1.5 m from the camera lens. The unit was deployed and retrieved remotely onto or next to rocky reef, and was immersed for approximately 60 minutes, which has been shown previously to be an appropriate sampling duration (Colton & Swearer 2010). After deployment, the boat motored
away from the area. The footage was later viewed on a computer monitor and a commonly
used measure of relative abundance, MaxN, enumerated (e.g. Lowry et al. 2012). Videos
were watched in entirety, and MaxN calculated as the maximum number of each fish species
observed in any 1 frame/1 second interval.

UVC transects were conducted by an observer and buddy on SCUBA. The divers
took the water in the location in which a BRUV had been deployed and swam slowly
while the observer counted and identified fish in a 5 m wide belt transect. The direction of
each transect was chosen prior to the dive based on current velocity, presence of rocky reef,
and the ability of the boat to safely retrieve divers. Transect duration was limited by no-
decompression limits in dive tables and air supply. The observer looked in the water column
as well as through kelp and under overhangs for fishes, while the second diver, present for
safety purposes, remained behind the observer. Transect length was computed using the GPS
coordinates of diver entrance and egress points. BRUV and UVC methods, and the time
between sampling using the two methods at each location, are more fully described in Colton
and Swearer (2010). At least one day separated samples taken from a particular location
using the two methodologies to ensure they were independent.

Habitat measurements

Habitat was measured along two 50 m transects (i.e., a 100 m sampling replicate) radiating out haphazardly from the location of a previous BRUV deployment. At 1 m
intervals along each transect, a diver measured the depth of the water column at the top of the
subacte using a depth gauge, recording minimum depth readings to minimize effects of
variable ocean swell. A second diver took photographs (using a Sony Cyber-shot 12.1
megapixel camera in an underwater housing) at 5 m intervals along the same transect tape,
placing a 1 m piece of white PVC pipe marked with 10 cm bands on the substrate
approximately perpendicular to the transect tape, and floating above the stick until its entirety
could be seen in the viewfinder.

The depth measurements were used to compute a contour distance (sensu
McClanahan & Shafir 1990) by solving Pythagoras’ theorem for the hypotenuse, with the
legs of the triangle equal to the 1 m distance separating depth measurements, and the
difference between two adjacent depth measurements. Rugosity was computed as the ratio of
contour distance to straight-line (transect) distance.

Habitat photographs were downloaded onto a computer and viewed using the program
CPCe (Kohler & Gill 2006). Using the Calibrate routine and the metre-stick, the length and
width of each photograph were measured. A grid of 5 x 10 cells was laid onto each photo and
a point randomly assigned within each cell. The substrate under each point was identified and
classified based first on whether it was abiotic or biotic, second on its physical attributes
(e.g., structure, height of vegetation), and third on the lowest level of taxonomic classification
possible (Table S2). The physical attributes described the type of substrate present, if any,
and the height that any biological matter extended above the benthos. Taxonomic resolution
was rarely possible beyond Class for animals, Family for macroalgae, and Genus for plants.
The habitat under the random point was assumed to represent the entire contents of the cell in
which it fell. The dimensions of each cell were computed based on the total length and width
of each photograph, and the number of points of each substrate type were multiplied by the
area of each cell and summed across the two 50 m transects to provide the total area covered
by each habitat type.

Data analyses

We conducted separate analyses exploring fish-habitat relationships for BRUV and
UVC datasets. The two datasets were paired to the habitat data based on the physical
proximity of replicate surveys using GPS coordinates, which meant that the matches were
slightly different. BRUV deployments were easily paired with habitat transects both because
the habitat transects originated from the site of a BRUV deployment, and because there was a
1:1 ratio of BRUV deployments to habitat transects (Table S1). Data from up to three habitat
transects were combined in order to be paired with data from a single UVC transect. The
amount of area covered by each habitat category (Table S2) was summed across the three
transects, and both depth and rugosity were averaged.

To explore the scale at which fish and habitat were most closely related, we
cumulatively aggregated habitat data to the ratios:

1. 1 BRUV: 1 Habitat = 100 m of habitat data
2. 3 BRUV or 1 UVC: 3 Habitat = 300 m of habitat data
3. 6 BRUV or 2 UVC: 6 Habitat: 600 m of habitat data
4. 12 BRUV or 4 UVC: 12 Habitat = 1200 m of habitat data

At each level of aggregation, we summed MaxN across all BRUV deployments, and summed
all habitat variables except for depth and rugosity, which were averaged. For the UVC data,
we computed a density for each species at each level of aggregation as the sum of the number
of individuals observed in n transects divided by the total area surveyed in n transects. We
summed rather than averaged data at each level of aggregation, as this represents the actual

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number of fish/total area of habitat cover observed for each replicate area at each scale.
(averaging would also likely result in stronger but spurious relationships between fish and
habitat as the precision of our measurements would be artificially overinflated).

Our intention was to implement a fully balanced design (Figure 1), which would have
resulted in the following levels of replication for BRUVs: \( n = 72 \) at 100 m (24 samples/site),
\( n = 24 \) at 300 m (\( n = 8 \) samples/site), \( n = 12 \) at 600 m (4 samples/site), and \( n = 6 \) at 1200 m (2
sample/site) and for UVCs the same level of replication at the three largest scales, as 300 m is
the smallest scale sampled. However, only 39 BRUV samples were collected at the 100 m
scale and 14 UVC samples at the 300 m scale due to factors outside our control (e.g. poor
weather, equipment failure, interactions with apex predators). Where surveys were missing,
we averaged data based on samples from the same site and spatial scale, assuming that the
following original data was available at each spatial scale: two x 300 m samples, three x 600
m samples, 6 x 1200 m samples for BRUVs. In total, we had 39 BRUV samples at 100 m, 14
at 300 m, 7 at 600 m and 5 at 1200 m. For UVCs, data aggregation at the 600 m scale
required that two samples were available at this scale at each site. Unfortunately, the missing
cells in our design meant that only two matches were available at two of the sites (Apollo
Bay and Barwon Heads) and none at the third (Wilson’s Promontory). We took the more
conservative approach of aggregating our data at the 1200 m scale rather than including the
600 m scale based on samples that were collected from non-adjacent areas at each site. For
UVCs at the 1200 m scale, we averaged data to infill missing cells if empirical data was
available from two of the four required samples. In total, we had 14 UVC samples at 300 m
and 6 at 1200 m.

We used R (R Development Core Team 2017) for statistical analyses, with all
recorded fish species included. We used the findCorrelation function from the caret package
to identify a set of 17 predictors that were not strongly correlated with each other (based on
Spearman’s correlation coefficient < 0.7; see Table S2 for list of all variables measured).

To determine at what spatial scales fish-habitat associations are the strongest
(Question 1), we used the BIOENV procedure (Clarke & Ainsworth 1993), which is a
dissimilarity-based method that can be used to identify the subset of explanatory variables
whose Euclidean distance matrix have the maximum correlation with community
dissimilarities, in our case, based on Bray-Curtis dissimilarity. BIOENV was implemented
with functions from the vegan and sinkr packages. We extracted the rho value for the best
model at each spatial scale as a measure of the strength of fish-habitat associations, with a
higher rho value indicating a stronger association between fish and habitat variables.
Because replication differed across spatial scales, stronger relationships could be expected at larger spatial scales where we had fewer samples. We therefore determined the strength of fish-habitat associations that would be expected based purely on the level of replication at each scale in the absence of any fish-habitat relationships, and then tested if our BIOENV results were stronger than this null expectation. To do so, we randomly re-sampled the original 39 BRUV samples of matching fish-habitat data collected at the 100m scale, to generate the full intended original data set (i.e. 72 samples). This dataset was split into two separate matrices, one containing the fish and another the habitat data, and the rows were randomly shuffled to remove fish-habitat associations in the 39 rows of original data. Matrices were then joined and the data aggregated by summing every 3, 6 and 12 rows of the simulated 100 m dataset to generate the null distributions of the 300m, 600m and 1200m scales. This process was repeated to generate 999 BIOENV models for each spatial scale, with the mean and 95% confidence intervals of the best model rho at each scale calculated across all simulations. We used a one sample t-test to compare if the rho for the best model based on our empirical data was significantly different than the rho values expected at each spatial scale based on the simulated data. If our observed rho was higher, it would indicate that fish-habitat associations are stronger than would be expected by chance, after accounting for differences in sampling effort. We also ran a power analysis for each spatial scale using the pwr.t.test function and extracted the effect size (Cohen’s d), which allows us to examine at spatial scale at which the difference between observed and empirical rho values was greatest. We also ran BIOENV models for the 300 m and 1200 m spatial scales using the UVC data. This comparison was included to examine consistency between the UVC and BRUV sampling techniques at these scales.

To assess if environmental predictors of fish are scale-dependent (Question 2), we calculated Pearson’s correlations between the abundance of each fish species and each habitat variable at each scale. We then converted all these correlations to absolute values (i.e. all negative correlations were multiplied by -1). We compared how the rank order of habitat variables varied between spatial scales based on this absolute Pearson’s correlation coefficient by calculating Kendall’s tau for all pair-wise correlations. Kendall’s tau is used to measure ordinal associations between two measured variables (in our case a pair of spatial scales), with a value of 1 when observations (in our case Pearson’s correlation coefficients describing fish abundance-habitat correlations) have identical ranks, and -1 when the ranks are fully different. Statistically significant (p<0.05) values indicate that ranks are not different between comparisons. We also compared the variables identified as being most influential in
the BIOENV analysis for each spatial scale based on our observed BRUV data, where we had four spatial scales to compare.

To test if scale-dependent fish-habitat associations vary with life-history traits (Question 3), we explored whether fish abundance-habitat relationships were consistent across three life-history traits: body size, trophic level, and geographic range size. We focussed on nine habitat variables identified as being important predictors across the four different spatial scales (see results), and calculated the Pearson’s correlation co-efficient between each fish species and each habitat variable at each spatial scale (i.e. for each fish species we had a measure of the correlation between its abundance and each habitat variable at each of the four spatial scales). We extracted the maximum recorded length and trophic level (five broad groups: carnivore, herbivore, omnivore, piscivore, planktivore) of all recorded species from the Fishes of Australia (fishesofaustralia.net.au) and FishBase (www.fishbase.org/) databases. We assume that maximum recorded lengths are a reasonable proxy of the average size observed for each species, at least in terms of relative differences, particularly given the error in estimating sizes visually underwater or from non-stereo BRUV deployments. Geographic range size was quantified using data in guidebooks (Kuiter 2000, Francis 2001, Gomon et al. 2008) and the GIS program DIVA (Hijmans et al. 2009). A grid of 1°x1° cells was overlaid upon a map of Australia and New Zealand. The geographic range size of a species was enumerated as the number of cells that a species’ range encompassed using only cells touching the coastline of either country. Range size and body length (total length, TL) were coded as categorical variables, with four groups within each variable corresponding to quantiles (for body length: 0-25% = 6-25cm, 26-50% = 25-40cm, 51-75% = 41-60cm, >75% => 60cm, for range size: 0-25% = 16-73.9 map cells, 26-50% = 74-90 cells, 51-75% = 90-103.3 cells, >75% = >104 cells).

For each habitat variable, we ran a series of mixed effects models using the lmer package. The response variable in these models was the Pearson’s correlation co-efficient describing the absolute value of the correlation between fish abundance and each habitat variable as above, which was square-root transformed to improve normality. The first ‘null’ model we ran for each variable included only Scale, and we then added the three other predictors iteratively to look at all interactions between these variables and Scale (i.e., Scale with the other predictors individually and in combination). We compared the fit of models using the Akaike Information Criteria (Burnham & Anderson 1998). If scale-dependent fish-habitat associations vary with life-history traits, the most parsimonious model would include Scale and some combination of life-history traits (depending on which were most important).
In comparison, if scale-dependent fish-habitat associations are consistent across species with different life-history traits, then the most parsimonious model would include only the Scale term.

Results

Q1: At what spatial scales are fish-habitat associations the strongest?

Our results show that the strength of fish-habitat associations was stronger as spatial scale increased in the BRUV dataset (Fig. 2). We observed a similar trend in the Simulated dataset, showing that the BIOENV procedure produces stronger results with fewer samples. However, at 100 m, 600 m and 1200 m, the BRUV dataset best model rho was significantly higher than the simulated (one sample t-test for all scales, df = 998, p < 0.00001). At 300 m, the BRUV rho value was significantly lower than the simulated (one-sample t-test, df = 998, p < 0.00001). The 600 m scale was where the observed best model rho value was the most different to the simulated datasets (Cohen’s d = 2.95 at 600 m, d < 0.65 at all other scales), suggesting this is likely the scale where fish-habitat associations are the strongest. The UVC dataset provided comparable results in terms of increasing fish-habitat associations at larger scales: the best model rho at 300 m was 0.43 and at 1200 m was 0.77.

Q2: Are environmental predictors of fish assemblages scale-dependent?

We found evidence that environmental predictors of fish assemblages are scale-dependent, with the rank order of habitat variables significantly different at the 1200 m scale than the two smallest spatial scales (Table 1). The rank orders were also similar between the 600 m and 1200 m scales. In the BIOENV analysis, some variables were consistently in the best model (Table 2), indicating that they are important at multiple spatial scales: cover of *Carpoglossum confluens* (at all scales) and brown algae from the Family Cystoseiraceae (all scales except 1200 m). However, the importance of some environmental variables was scale-dependent: seven variables were in the best model at 600 m, more than at any other scales. Some variables were also only important at small (e.g. boulders at 100 m) and others only at larger scales (e.g. cover of sand at 600 m and 1200 m).

Q3: Do scale-dependent fish-habitat associations vary with life history traits?

For all predictors, the most parsimonious model based on AIC values included the scale term only (Table 3). This indicates that scale-dependent fish-habitat associations are consistent across species with different geographic ranges, body lengths, and trophic levels.
Question 1: At what spatial scales are fish-habitat associations the strongest?

We found that the strength of fish-habitat associations increased as the spatial scale at which these relationships were examined also increased. While we had fewer samples at larger spatial scales, our simulation model showed that the effect we observed was stronger than the increase in rho expected based on sample size alone. The rho value for the best model describing fish assemblages was highest at 1200 m but the fact that we observed the greatest difference between observed and simulated model results at 600 m suggests that this latter scale may be where fish-habitat relationships are strongest. A useful future step would be to sample the four different spatial scales with comparable levels of replication, which would allow this to be pinpointed more definitively. Ideally even larger spatial extents would also be considered, to remove the possibility that the true scale of effect is even larger than the scales we examined, which is often the case (Jackson & Fahrig 2015). Regardless, the range of scales we evaluated was still considerably larger than the scales at which fish-habitat associations are commonly studied i.e., 25-50 m transects (e.g. Choat & Ayling 1987; Anderson & Millar 2004). This suggests our understanding of fish-habitat associations in marine systems could be limited because we are not examining these relationships at the scales at which they are likely to be strongest.

At what scales then should marine ecologists work? In their recent review of scale-of-effect relationships in terrestrial organisms, Jackson and Fahrig (2015) found that biological reasoning was only used in 29% of studies to select scales. They propose that researchers should select scales based on expected scales of space use, ideally ranging from less than the home range of a species to greater than nine times the average dispersal distance (simulations suggest scale of effect is likely to be four to nine times the average dispersal distance: Jackson & Fahrig 2012). This could be difficult in marine systems as many benthic species can disperse hundreds of kilometres during the pelagic larval stage; at these very large scales their distributions are primarily driven by large-scale processes (e.g., currents and their associated temperatures; Figueira & Booth 2010). It thus may be more feasible to limit the selection of scales to those relevant to the movement of benthic life stages. However, if the true scale of effect is greater than 1200 m, this will prove challenging for conventional SCUBA-based survey methods and will necessitate further development of remote/autonomous technologies that can operate over larger scales than divers (Hussey et al. 2015). Furthermore, in such cases where average dispersal distances are considerable and
impractical to use, it might be possible to select more realistic scales based on the aims of the work (Jackson & Fahrig 2012). For example, if the goal is to provide information for managers, it might be acceptable to limit measurements to the scales at which management actions can be accomplished. However, if the goal is to identify the true scale of effect, researchers should be up front about their data and the limitations it places on the inferences they can make, as more informative relationships between animals and their environment might be observed at scales not considered within their study. Greater consideration of these factors will help in identifying the optimal scale at which to work in future studies of fish-habitat associations.

**Question 2: Are environmental predictors of fish assemblages scale-dependent?**

Our results show that it is not only the strength of fish-habitat associations that differ across spatial scale, but also the relative importance of habitat variables. In particular, the rank order of habitat variables was different at the 600 m and 1200 m spatial scales in comparison with smaller scales, indicating that different variables are most important at these largest scales. Cover of the macroalgae *Carpoglossum confluens* was the only variable in the best model at all four spatial scales. This is consistent with previous work in the region showing that macroalgae can be important habitat for fish (*e.g.* brown macroalgae *Ecklonia radiata*: Fobert & Swearer 2017). These results suggest that some variables, especially cover of habitat-forming species like macroalgae are likely important across spatial scales. Other variables, however, were only important at some spatial scales, such as the cover of sand at the two largest scales. Similar variability in the importance of environmental predictors across spatial scales has been illustrated for other taxa. For example, the nest survival of birds from the Family Raillidae is dependent upon different environmental variables at the scale of territories (*e.g.*, water depth and vegetation density) and the scale of nests (*e.g.*, vegetation height) (Jedlikowski & Brambilla 2017).

Knowing which habitat elements animals are responding to, and at which spatial scales can help guide the implementation of conservation and restoration programs. If we inadvertently target habitat elements that are not the most important ones to animals, then restoration outcomes will be suboptimal. However, even if we restore the correct habitat elements, animals may not respond if these efforts are undertaken at the wrong spatial scale (Bond & Lake 2003). More detailed information about the scales of habitat association can help guide restoration efforts that are more biologically informed, rather than the spatial
extent being set by human perceptions of the scales that are most important or by economic
or social factors.

**Question 3: Do scale-dependent fish-habitat associations vary with life history traits?**

The species traits we analysed (body size, geographic range size and trophic level) did
not predict the scale-dependent responses by fish to the habitat variables we measured. Based
on Migeut *et al.* (2016), we hypothesized that larger species, those with larger geographic
ranges, and those at higher trophic levels would be associated with habitats at larger spatial
scales. Our results provide, to our knowledge, the first evidence that variability in the scale of
effect may in fact be only weakly related to differences in life-history traits in marine
systems, concordant with recent assessments for terrestrial animals (Jackson & Fahrig 2015).

It is possible that life-history traits truly are poor predictors of scale-dependent
responses to habitat but there are other explanations. First, many studies miss the true scale of
effect, and thus describe animal-habitat relationships at scales where they may not be
strongest (Jackson & Fahrig 2015). This raises the potential that the effects of life-history
traits might be stronger when tested at the optimal scale (i.e. where animal-habitat
relationships are strongest)—for example, if we were to examine fish-habitat associations at
larger scales than 1200 m. Second, the coarse resolution of available life-history trait
information might obscure effects. Relatively few of the species included in our study have
complete life-history information available. We were therefore reliant on sources of
information such as FishBase, which is a global system containing information on over
33,000 fish species. Although studying in detail the traits of all species in an assemblage is
likely to be impossible, collecting more detailed life-history information about a subset of key
species would allow more informative tests to be undertaken. For example, here we have
assumed that the maximum size, which was the only data available for all species, is a good
representation of the average size of species likely to be observed. However, maximum
recorded size could be an outlier, and not reflect the majority of fish found on a reef. Thus,
our approach is likely to be appropriate for comparing coarse differences (e.g., large vs. small
species) but more nuanced relationships might be detected with more detailed information
about size-frequency distributions for different species. Third, factors other than the life-
history traits we examined might be more important. Species traits are only one of five broad
categories of factors that influence the scale of effect, along with landscape variables and the
type of response (i.e., which things are measured), indirect rather than direct influences of the
landscape on habitat conditions, or the regional context of studies (Migueut *et al.* 2016). More
work is therefore needed to disentangle the relative importance of this broad range of potential influences.

It is also important to consider that neither method we used is especially good at surveying cryptic species (Willis 2001; Watson et al. 2005; Colton & Swearer 2010). These species are typically small and sedentary, and so are likely to respond to habitat at smaller scales. For example, the abundance and composition of cryptic fishes and habitat in New Zealand were strongly influenced by reef complexity when habitat was measured in 9 m$^2$ plots (Willis & Anderson 2003). Better sampling of cryptic species in the present study, however, is unlikely to change the conclusion that fish consistently respond most strongly to changes in habitat at larger scales given that cryptic species on these exposed reefs only comprise a minor fraction of the total assemblage. Regardless, measuring associations between fish and habitat at the assemblage level is likely to require a multi-scale approach (Meyer & Thuiller 2006) that incorporates scales of meters to kilometres as different components of the assemblage will respond to habitat variability across this range of scales.

Investigating the scale of effect in marine ecosystems

Several recent papers have greatly enhanced our theoretical understanding of how and why relationships between animals and landscape structure vary across different scales (Jackson & Fahrig 2012; Jackson & Fahrig 2015; Miguet et al. 2016). Interestingly, these have focussed exclusively on terrestrial species. For example, Jackson and Fahrig (2015) conducted a meta-analysis to determine if ecologists were selecting the optimal scales at which to work but did not include fish. Testing theories in a wide range of contexts is a key component for building a general predictive understanding of ecology (Rotjan & Idjadi 2013; Borer et al. 2014). This is especially important given that terrestrial and marine ecologists often conduct work in isolation (Menge et al. 2009).

There are good reasons to believe that marine and terrestrial systems differ in ways that influence animal-habitat associations and the scales at which those associations occur. For example many marine species are more demographically open, with greater dispersal rates and distances, leading to population structures at larger spatial scales (Carr et al. 2003). As a consequence, we might predict the scale of effect to be greater, on average, in marine systems. Our research provides some support for this notion, but more explicit comparisons are needed between the scale of effect in terrestrial and marine systems to improve general understanding of how all animals interact with their environments.
Working at optimal scales to improve ecological understanding and guide conservation

Our study suggests that we may have missed the true scale of effect even though we examined fish-habitat associations at a range of spatial scales, including ones much larger than routinely considered. If we had conducted our study at only the smallest spatial scale examined, we would have gained a different picture of fish-habitat associations, such as which environmental predictors were most important. Studies of the spatial scale at which landscape structure influences biological responses is in its infancy (Miguët et al. 2016). More multi-scale studies are needed that examine biota-habitat relationships to determine where these are strongest, especially in aquatic habitats. In particular, a greater consideration of how and why researchers select spatial scales at which to work is important. Although our focus has been on marine fishes, similar scale-dependent habitat relationships occur in other aquatic taxa (e.g. freshwater fish: Crook et al. 2001), indicating that this message has implications for a wider audience than simply marine fish ecologists.

Studies documenting the scale of animal-habitat relationships provide fundamental information about the ecology of species. However, such studies also have important applied implications about how we mitigate anthropogenic disturbances to the environment. Human impacts are widespread, and increasing throughout the world’s oceans (Halpern et al. 2015). To ameliorate these effects, efforts are underway to protect and restore habitats. Two of the questions facing managers who implement protected areas, be they terrestrial or marine, is how to site them to facilitate connectivity (through movement of larvae and/or adults) and how large they need to be in order to sustain populations. It is crucial that management decisions are based on knowledge of how animals rather than humans perceive and respond to the environment (Van Dyck 2012). If our human perceptions poorly match how animals perceive the environment, conservation and management actions are likely to fail (Hale et al. 2015; Hale & Swearer 2017). Our results suggest that marine fish may respond to their environment at larger scales than previously considered, and highlight the importance of considering the scale at which species relate to their environment (Wiens 1989; Sale 1998) when making management decisions. Failure to do so may hinder our efforts to manage anthropogenic disturbances in the ocean. Consequently, developing a more mechanistic understanding of marine animal-habitat associations will greatly improve our ability to protect and manage marine resources and to predict how ecosystems will respond to further environmental change.

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Authors’ contributions
MC and SS designed the study, and MC collected all data. MC, PP and RH conducted statistical analyses. All authors contributed critically to drafting the manuscript and gave final approval for publication. Comments from three anonymous reviewers improved earlier versions of the manuscript.

Data Accessibility
All fish abundance (UVC and BRUV) and habitat data associated with this study have been deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.819236j (Hale et al. 2018).

References


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Table 1 Changes in the rank order of importance of environmental predictors of fish assemblages across spatial scale. Kendall’s tau describes the degree to which the rank order of habitat variables (described in Table S2) is concordant (or not) between pairs of spatial scales. * indicates statistical significance (p < 0.05).

<table>
<thead>
<tr>
<th>Scale (m)</th>
<th>100</th>
<th>300</th>
<th>600</th>
<th>1200</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td></td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>0.71*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>0.40*</td>
<td>0.37*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>0.19</td>
<td>0.25</td>
<td>0.52*</td>
<td></td>
</tr>
</tbody>
</table>

Table 2 The environmental variables identified as the best predictors of fish assemblage composition using the BIOENV procedure across four spatial scales.

<table>
<thead>
<tr>
<th>Scale (m)</th>
<th>Habitat variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>Algae &gt; 10 cm tall</td>
</tr>
<tr>
<td></td>
<td>Boulder</td>
</tr>
<tr>
<td></td>
<td><em>Carpoglossum confluens</em></td>
</tr>
<tr>
<td></td>
<td>Coralline algae</td>
</tr>
<tr>
<td></td>
<td>Cystoseiraceae</td>
</tr>
<tr>
<td>300</td>
<td><em>Carpoglossum confluens</em></td>
</tr>
<tr>
<td></td>
<td>Cystoseiraceae</td>
</tr>
<tr>
<td></td>
<td><em>Ecklonia radiata</em></td>
</tr>
<tr>
<td>600</td>
<td><em>Carpoglossum confluens</em></td>
</tr>
<tr>
<td></td>
<td>Coralline algae</td>
</tr>
<tr>
<td></td>
<td>Cystoseiraceae</td>
</tr>
<tr>
<td></td>
<td><em>Ecklonia radiata</em></td>
</tr>
<tr>
<td></td>
<td>Encrusting macroalgae</td>
</tr>
<tr>
<td></td>
<td>Macroalgae of unknown length</td>
</tr>
<tr>
<td></td>
<td>Sand</td>
</tr>
<tr>
<td>1200</td>
<td><em>Carpoglossum confluens</em></td>
</tr>
<tr>
<td></td>
<td>Sand</td>
</tr>
</tbody>
</table>

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Table 3 AIC values from linear mixed effects models testing the strength of fish-habitat associations across spatial scales (“Scale”), and if these scale-dependent habitat associations vary according to three life-history traits: geographic range (“Range”), body size (“Length”) and trophic level (“Diet”). Bold values indicate the model with the lowest AIC score.

<table>
<thead>
<tr>
<th>Model</th>
<th>Boulder</th>
<th><em>C. confluens</em></th>
<th>Coralline algae</th>
<th>Algae (&gt; 10 cm tall)</th>
<th><em>Cystoseira</em>ae</th>
<th><em>Ecklonia</em> radiata</th>
<th>Sand</th>
<th>Encrusting macroalgae</th>
<th>Macroalgae (unknown length)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scale</td>
<td>-75.43</td>
<td>-42.17</td>
<td>-65.02</td>
<td>-56.62</td>
<td>-37.47</td>
<td>-97.56</td>
<td>-40.10</td>
<td>-71.35</td>
<td>-53.95</td>
</tr>
<tr>
<td>Scale*Range</td>
<td>1.26</td>
<td>24.47</td>
<td>0.97</td>
<td>7.21</td>
<td>22.30</td>
<td>-21.67</td>
<td>31.02</td>
<td>1.52</td>
<td>13.00</td>
</tr>
<tr>
<td>Scale*Diet</td>
<td>-11.17</td>
<td>9.29</td>
<td>11.16</td>
<td>16.05</td>
<td>17.90</td>
<td>-20.37</td>
<td>30.36</td>
<td>-19.21</td>
<td>7.51</td>
</tr>
<tr>
<td>Scale*Length</td>
<td>-15.82</td>
<td>20.47</td>
<td>7.47</td>
<td>-0.30</td>
<td>22.53</td>
<td>-22.58</td>
<td>32.01</td>
<td>-5.56</td>
<td>5.92</td>
</tr>
<tr>
<td>Scale<em>Range</em>Diet</td>
<td>119.26</td>
<td>131.81</td>
<td>135.43</td>
<td>109.42</td>
<td>129.37</td>
<td>122.41</td>
<td>151.13</td>
<td>106.31</td>
<td>129.52</td>
</tr>
<tr>
<td>Scale<em>Range</em>Length</td>
<td>159.51</td>
<td>183.68</td>
<td>159.70</td>
<td>134.92</td>
<td>183.62</td>
<td>137.10</td>
<td>178.56</td>
<td>170.71</td>
<td>167.98</td>
</tr>
<tr>
<td>Scale<em>Diet</em>Length</td>
<td>84.51</td>
<td>126.55</td>
<td>131.73</td>
<td>128.55</td>
<td>138.97</td>
<td>97.29</td>
<td>140.22</td>
<td>112.59</td>
<td>110.82</td>
</tr>
<tr>
<td>Scale<em>Range</em>Length*Diet</td>
<td>258.20</td>
<td>282.65</td>
<td>262.60</td>
<td>254.75</td>
<td>266.40</td>
<td>254.99</td>
<td>282.36</td>
<td>266.69</td>
<td>275.45</td>
</tr>
</tbody>
</table>
Figures

**Figure 1** Schematic illustrating how fish abundance and habitat data were aggregated. The ruler represents a habitat survey, the video camera a BRUV fish survey, and the SCUBA diver a UVC fish survey. Background shading indicates the scale of aggregation at each site.

**Figure 2** Model fit (rho) of best model from BIOENV analysis examining fish-habitat relationships across spatial scales based on simulated data (Simulated), and empirical data collected using baited remote underwater video (BRUV). For the Simulated data, the mean (and 95% confidence interval) is presented based on 999 simulations. Sample sizes for the spatial scales are n = 39 at 100 m, n = 14 at 300 m, n = 6 at 600 m, and n = 5 at 1200 m.
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