The role of habitat complexity in shaping the size structure of a temperate reef fish community

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ABSTRACT: Understanding how habitat complexity shapes fish communities is necessary to predict the consequences of future habitat change. On temperate rocky reefs, the presence and characteristics of canopy-forming kelps and the architectural complexity, or rugosity, of the underlying rocky substratum are foundational elements of habitat complexity. However, it is not yet clear how these factors shape the size structure of rocky-reef-associated fish communities. Here, we use biomass spectrum models to evaluate how fish community size structure in high-latitude rocky-reef kelp forests is shaped by substratum rugosity and the degree of closure and density of the kelp canopy. We found that the presence of a closed kelp canopy was associated with an average 75% increase in overall fish biomass compared to open-canopy reefs. Furthermore, on the highest-rugosity reefs, the biomass of small fishes (32–64 g) was 800% higher than on the lowest-rugosity reefs, while large fish (1–2 kg) biomass was 60% lower. Consequently, biomass was more evenly distributed across body-size classes on high-rugosity reefs. By decomposing the biomass spectrum into total biomass and mean individual body mass, we found that higher kelp stipe densities also tended to be associated with larger fishes, but this effect was outweighed by the tendency for more small-bodied fishes with increasing rugosity. This study demonstrates how size-based analyses can give new insights into the ecology of temperate reef communities, and may be useful for tracking changes in kelp-associated assemblages in the coming decades with the maturation of marine protected areas, the recovery of sea otter populations, and changing climate.

KEY WORDS: Biomass size spectra · Community ecology · Coral reef · Ecosystem baseline · Energy flow · Foundation species

INTRODUCTION

Habitat structural complexity is profoundly important to ecological communities. Species abundance and richness are magnified in complex habitats through the provision of niches and environmental resources (MacArthur & MacArthur 1961, Tews et al. 2004), and increased habitat complexity can also lead to reduced predation and density-dependent competition (Shulman 1984, Hixon & Beets 1993, Beukers

& Jones 1998, Willis & Anderson 2003). However, the extent to which habitat complexity alters community size structure—the manner in which total community biomass is partitioned among body-mass size classes—remains unclear. Although community size structure has received very little attention on temperate reefs, it represents a promising avenue for understanding the community-scale effects of habitat characteristics as well as fishing and other drivers of change in marine ecosystems (Dulvy et al. 2004, Jen-

nings 2005, Wilson et al. 2010, Alvarez-Filip et al. 2011).

For many ecosystems, key determinants of habitat complexity are the presence and characteristics of foundation species—those that, by virtue of their structural or functional attributes, create and define ecological communities (sensu Dayton 1972, Ellison et al. 2005). On temperate rocky reefs, kelps—large brown macroalgae of the order Laminariales—are the primary foundation species (Dayton 1985, Stephens et al. 2006). The ecological importance of kelp forests is comparable to that of coral reefs in tropical waters (Beaumont et al. 2008, Smale et al. 2013, Steneck & Johnson 2014). Broadly, kelp forests 'fuel' coastal food webs by capturing inorganic carbon and making it available it to higher trophic levels (Dayton 1985, Dunton & Schell 1987, Duggins et al. 1989, Salomon et al. 2008, Krumhansl & Scheibling 2012), thereby increasing secondary production and consumer biomass both locally and across neighboring and distant habitats (Duggins et al. 1989). Thus, kelp cover can provide structural habitat (additional to the underlying substratum) and food (directly or indirectly), and typically gives rise to higher levels of biodiversity than are found in simple, unstructured habitats (Dayton 1985, Steneck et al. 2002, Stephens et al. 2006).

A key question is whether there are general patterns in how fish community structure is shaped by habitat characteristics. Associations with kelp habitat vary widely among fish species and life stages (Jones 1988). Kelp facilitates the recruitment of larval fishes and provides key habitat for juveniles of many reef-associated species (e.g. Connell & Jones 1991, and reviewed by Carr & Syms 2006). Hence, numerous observational and experimental studies have found that the abundance and biomass of early life stages (recruits and young-of-the-year) of a wide range of reef-associated fish species increase with the presence and extent of kelp canopy (e.g. Choat & Ayling 1987, Anderson 1994, Levin & Hay 1996, Siddon et al. 2008). However, associations with kelp canopy for adult life stages are more variable among both species and locations. Studies focused on individual species or groups (defined based on trophic ecology or position in the water column) have found that the abundance of some species and groups is much greater in kelp forests than in comparable areas without a kelp canopy (e.g. Cowen 1983, Holbrook et al. 1990), while other species and groups are more abundant outside kelp forests (e.g. Choat & Ayling 1987, Jones 1988, Holbrook et al. 1990, Siddon et al. 2008). Fewer studies have examined patterns for

total community abundance and biomass, but results have been similarly mixed among those that have, with some studies reporting that total fish abundance and biomass are higher in the presence of a kelp canopy, and increase with increasing canopy density (Leaman 1980, DeMartini & Roberts 1990), while others report the opposite (e.g. Siddon et al. 2008).

The effects of substratum rugosity on reef fishes appear less variable than those that have been reported for kelp canopy, with more complex or higher-relief substrata supporting more fishes than less complex lower-relief substrata in terms of both abundance (Ebeling et al. 1980, Jones 1988, Cole et al. 2012) and biomass (Anderson et al. 1989). The inconsistent effects of kelp cover on fish community structure may be in part due to interdependence between the effects of kelp cover and substratum characteristics, with kelp becoming relatively less important with increasing substratum rugosity (or relief; Larson & DeMartini 1984, Choat & Ayling 1987, Anderson 1994). However, it is not clear how consistent this interdependence between the effects of kelp and substratum rugosity is. This is especially true for high northern latitude *Nereocystis lutkeana*-dominated kelp forests, which are much less well studied than more southern *Macrocystis pyrifera* forests (Springer et al. 2006). Understanding this interaction is particularly important for predicting the implications of global change, as key drivers of change (herbivory and climate) will affect kelp cover more dramatically and more rapidly than substratum rugosity.

The traditional approach for understanding the importance of habitat structure for temperate reef fish communities has been to study how the abundance of species (or groups of species) varies with habitat characteristics. This approach stems naturally from the concept of species niches, as the amount of niche space may be expected to depend on habitat structure. However, because responses to habitat characteristics vary widely between species (as described above), it is difficult to establish generalities and make predictions about how future changes in habitat are likely to affect fish community structure (Jones 1988). In contrast to these highly variable species-specific responses, fish community size structure appears to respond predictably to both habitat characteristics and overfishing, regardless of taxonomic composition (Jennings & Dulvy 2005, Alvarez-Filip et al. 2011).

Size spectra—relationships between body mass class and either total abundance in each size class (abundance spectra) or total biomass in each size class (biomass spectra) of individuals, irrespective of

species identity—provide an integrated picture of community size structure (Graham et al. 2005, Shin et al. 2005). Size spectra are often represented as linear regressions (with both size and biomass or abundance on log scales). The regression slope for such a biomass spectrum represents the relative dominance of small- versus large-bodied community members (Borgmann 1987, Kerr & Dickie 2001). Processes that give rise to relatively more small-bodied fishes lead to more negative/less positive biomass spectra slopes, while processes that result in relatively more large-bodied fishes generate more positive/less negative slopes. It is common practice to 'centre' the x-axis of size spectra by subtracting the mean of the size class midpoints. The intercept of a centred biomass spectrum then represents the 'height' of the midpoint of the regression line, which reflects the total biomass in the community (Daan et al. 2005).

The utility of size-based analyses, and particularly size spectra, for assessing the state of marine ecosystems is becoming increasingly widely recognised (Jennings 2005, Shin et al. 2005, Petchey & Belgrano 2010, Trebilco et al. 2013). The strength of the size-based approach, and size spectra in particular, is that it provides a quantitative and integrated picture of community structure that is readily comparable across systems (Petchey & Belgrano 2010, Trebilco et al. 2013). Thus, the approach has the potential to enable comparison across systems of widely differing diversity and species composition (e.g. Bianchi et al. 2000). A further benefit is that the size-based approach connects to a rich and rapidly developing body of theory on energy flow and community metabolism that provides expectations for size spectrum slopes based on the way that energy moves through communities via size-based predator–prey interactions (Brown & Gillooly 2003, Jennings 2005, Trebilco et al. 2013). Hence, size-based analysis can provide insights into food web structure and function that complement and extend those from traditional species-based analyses (Jennings 2005). To our knowledge, the effects of habitat structure on community size structure on temperate reefs have not yet been quantified.

Here, we take a size-based approach to examine the importance of both *Nereocystis* canopy characteristics and substratum rugosity for the structure of a temperate reef fish community. Specifically, we ask how the slope and intercepts (midpoint heights) of community biomass spectra vary with *Nereocystis* canopy cover and stipe density, as well as with substratum rugosity. We also consider total community biomass and mean individual body mass, which are 2

simple and informative summary metrics of size structure (Dulvy et al. 2004, Shin et al. 2005). We quantitatively test the community-scale effects of habitat structure by simultaneously considering the importance of substratum rugosity and kelp cover. In addition to providing insight into how habitat shapes community size structure in our study system, we hope that this analysis will help advance temperate reef community ecology by connecting it to the rapidly developing literature on how size-based energy flows shape community structure and function (Petchey & Belgrano 2010, Yvon-Durocher & Allen 2012, Trebilco et al. 2013).

MATERIALS AND METHODS

Study area

We conducted this study on temperate nearshore rocky reefs off the northwest coast of British Columbia (BC), Canada, within and around the Gwaii Haanas National Marine Conservation Area Reserve and Haida Heritage Site, Haida Gwaii (formerly the Queen Charlotte Islands; Fig. 1). On this part of the
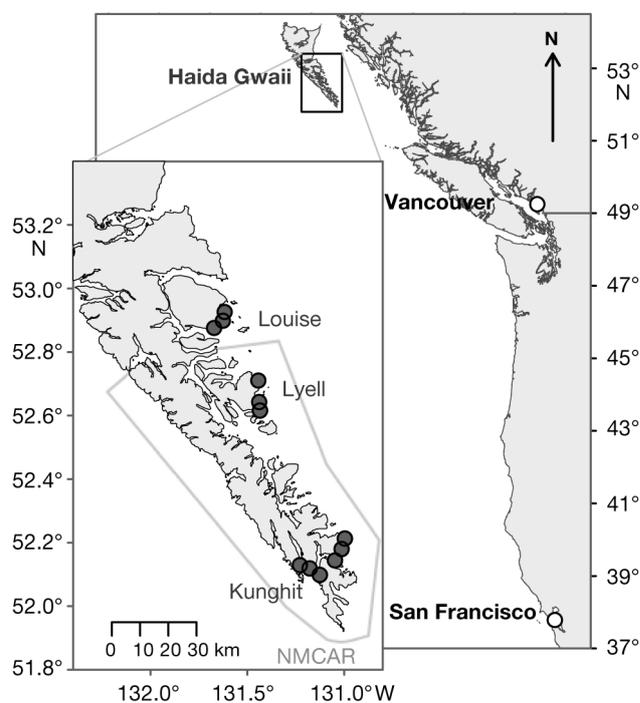

Fig. 1. Research sites (●) on the northwest coast of British Columbia, Canada, within and around the Gwaii Haanas National Marine Conservation Area Reserve and Haida Heritage Site at the southern end of the island archipelago of Haida Gwaii. A total of 12 rocky reef sites were nested within 4 areas (n = 3 sites per area)

Pacific Coast, kelp forests dominate rocky substrata in shallow waters on all but the most exposed shores (Springer et al. 2006, Steneck & Johnson 2014), and we restricted our surveys to areas with hard substrata. The annual kelp *Nereocystis luetkeana* (hereafter *Nereocystis*) is the dominant canopy-forming subtidal kelp species around Haida Gwaii. Understory kelps are comprised of a variety of other species from the order Laminariales.

Historically, sea otters *Enhydra lutris* were the dominant predator of invertebrate grazers on the BC coast, but they were extirpated from BC by the fur trade early in the 1900s (Kenyon 1969, Gibson 1988, Fedje & Mathewes 2011). As for most areas on the Pacific Coast where urchin predators have been removed, in BC this led to the formation of extensive sea urchin barrens, and a kelp zone that is largely restricted to shallow depths affected by wave turbulence (Watson & Estes 2011). Sea otters have not yet returned to southern Haida Gwaii; hence this pattern typifies the sites we surveyed, with kelp being replaced by barrens below an average depth of 8.9 ± 0.46 m below chart datum.

Underwater visual census of kelp-forest fish size and abundance

Fish communities were visually surveyed using belt transects at 12 sites: 3 sites in each of 4 areas (Louise, Lyell, Kunghit East and Kunghit West) in southern Haida Gwaii (Fig. 1). Surveys were undertaken in the summer (between late June and early August) each year from 2009 to 2012, with the majority of sites surveyed every year (a full description of the survey protocol is provided in Trebilco et al. 2014). Belt transects were 30 × 4 m and laid parallel to shore, with the ends of each transect separated by a minimum of 5 m. Replicate transects were surveyed at each site in each year (n = 4 in 2009, n = 6 in 2010–2012), and split evenly between 'deep' and 'shallow' strata (tide-corrected depth of 12.0 ± 1.3 and 7.7 ± 1.1 m below chart datum, respectively).

For each transect, an individual SCUBA diver deployed a plastic transect metre tape while swimming forward at an approximately constant speed (Watson et al. 1995). Conspicuous fishes present in the sampling area on the bottom and in the water column to a height of 4 m above the bottom were recorded. Groups excluded from the census because they are cryptic include: blennies, gobies, sculpins, and gunnels (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m532p197_supp.pdf for a species

list). Count time was not standardized as it depended on fish abundance and habitat characteristics. The size (total length) of each individual fish counted on transects was visually estimated to the nearest centimetre. To ensure accuracy of length estimates, observers were trained by estimating the size of known-length objects underwater (following Bell et al. 1985, Polunin & Roberts 1993). Additionally, observers carried a 'reference pole' (an 80 cm length of PVC, labeled with centimetre increments, and mounted at the end of a 1.5 m pole, as per Frid et al. 2013) which was used to both directly measure fish where possible and benchmark visual estimates. Individual weights were calculated from lengths using species-specific length–weight conversions from FishBase (www.fishbase.org).

Measurement of habitat covariates

We quantified key habitat characteristics including depth, substratum rugosity, and 2 measures of *Nereocystis* canopy cover. Depth was recorded at the start of each fish transect, and transects were deployed following a constant depth contour. Recorded depths were subsequently tide-corrected to chart datum, which in Canada is based on the lowest low water large tide.

We measured rugosity by contouring a 3 m length of fine-link chain (1 cm links) to the reef parallel to the transect tape, then calculating the ratio between the length of the chain (3 m) and the distance along the transect line between the start and end points (following Risk 1972). We took 3 randomly stratified rugosity measurements per transect at each site in one year, and the means of these measurements were calculated for each site/depth stratum combination.

The 2 measures of *Nereocystis* canopy cover recorded were a visually assessed transect-scale score for canopy extent (1 = closed canopy, 0.5 = fragmented canopy, 0 = no canopy), and a site-scale measurement of *Nereocystis* stipe density. Transect-scale canopy cover scores were recorded during the visual surveys described in the previous section (with the canopy being scored as closed if the whole transect had canopy cover, and fragmented if parts of the transect had no canopy cover). Site-scale *Nereocystis* stipe density was estimated by counting all *Nereocystis* stipes >1 m length along a single 2 m wide transect, perpendicular to shore, running from the deepest extent of the kelp bed to the shore at a haphazardly chosen point approximately at the middle of

the span of the fish transects (refer to Trebilco et al. 2014 for further detail). *Nereocystis* stipe density was then calculated in stipes m^{-2}. These transects were completed for 25 of the 37 unique combinations of site and year in the dataset. The 2 measures of *Nereocystis* cover quantify different characteristics of the kelp canopy and are not strongly correlated (Fig. S1 in the Supplement). Stipe density describes the overall density of the bed for each site, while canopy cover scores reflect the absolute cover on the transects surveyed within each site. We checked for multicollinearity among habitat covariates using variance inflation factors (VIF; Zuur et al. 2013). All VIF scores were <3, indicating that multicollinearity is unlikely to be a problem in this analysis.

Data subsetting for modeling

We narrowed the size fraction of reef fishes used for analysis to the range of body sizes that can be surveyed effectively with underwater visual transects (Ackerman 2000, Graham et al. 2005). Biomass spectra for reef fish are not expected to be linear when smaller size classes are retained because underestimation of abundance and biomass in small size classes causes the size spectrum to 'tail off' and become humped. One reason that biomass at small body sizes is underestimated by visual surveys is that a large proportion of small fish tend to be hidden in shelter such that they are not available to count. Another is that other taxa (e.g. invertebrates such as crustaceans and gastropods) are likely to share a substantial proportion of the trophic resources and comprise some or all of the biomass at small body sizes (meaning that a linear spectrum would only be expected if they were also included). This underestimation has been empirically demonstrated on coral reefs using rotenone poisoning to examine what is missed in visual surveys on coral reefs (Ackerman et al. 2004). Similarly, in the North Sea shelf ecosystem, invertebrates have been shown to make up an increasing fraction of the smallest size classes when sampled using appropriate trawl and grab gears (Jennings & Dulvy 2005), and it is common practice to exclude size classes that are not sampled effectively by fishing gears in fitting size spectra.

To circumvent these issues, we first excluded fish <5 cm, and then used the modal mass of fish >5 cm (32 g) as the lower size cut-off for inclusion in analyses, assuming that this was the minimum size that was surveyed effectively (following Ackerman et al. 2004) (Fig. 2A). We also excluded 3 fish larger than
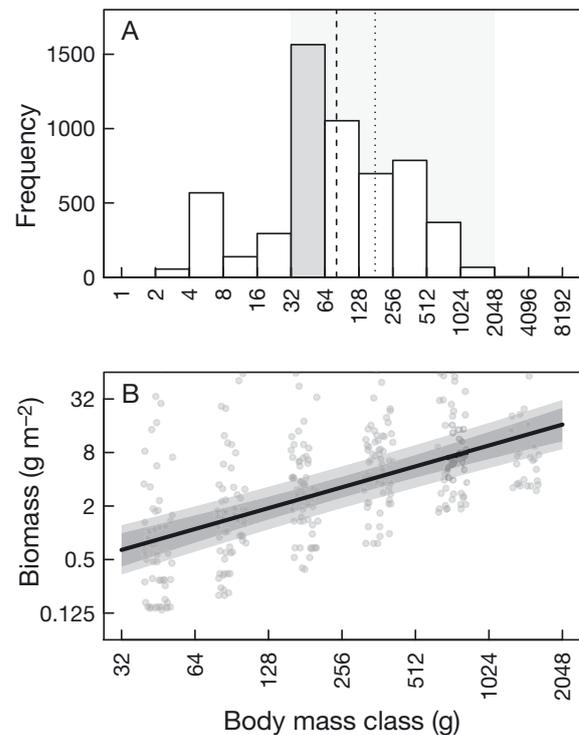

Fig. 2. (A) Frequency of fish >5 cm surveyed in log$_2$ body mass bins and (B) the site-scale community biomass spectrum for kelp forest fishes. Shaded bar in (A) represents the modal size class, with dashed and dotted lines representing the median and mean masses of surveyed fish, respectively. Shaded region denotes the size range for (B), as included in models. Points in (B) are jittered (randomly offset) on the *x*-axis so that individual points can be seen. Shaded bands indicate 95% confidence intervals incorporating uncertainty in the fixed (dark band) and random (light band) effects, respectively

2048 g from the analysis and used 2048 g as our upper cut-off to ensure that all size classes in the analysis were well represented in our data (Fig. 2A). On average, the cut-offs we chose resulted in 95% of the total fish biomass observed at sites being included in the analysis (median of 99%), while fish smaller than 32 g comprised an average of 3% (median 1%) of the total biomass surveyed at sites. We kept this range of body sizes consistent for all models to maximize the comparability of results.

Only the subset of 25 site/year combinations for which *Nereocystis* density data were obtained were included in models including *Nereocystis* density as a predictor. All other models used data from all sites and years. For all models, we aggregated data across transects within depth strata. Depth and kelp canopy cover score were recorded for individual transects, so we took the averages across transects within each combination of site, depth stratum and year. As

described above, *Nereocystis* stipe density was a site-level average, while rugosity was averaged across transects within depth strata at each site. In exploratory analyses, we fitted models that included both stipe density and canopy cover together (for sites at which stipe density was recorded). The direction and magnitude of parameter estimates for these models were consistent with models in which the 2 kelp predictors were considered separately, hence we only present results for the separate models here.

Statistical analysis

We fit linear mixed-effects models to examine how substratum rugosity, kelp canopy cover and stipe density, and depth stratum explain each of the 3 key aspects of community size structure considered—community biomass spectra, average individual body mass and total biomass (Table 1). All models were fitted using the R package lme4 (Bates et al. 2013), and all analyses were conducted using R version 3.0.2 (R Development Core Team 2013). For each set of models, we evaluated 2 subsets, one using transect-level canopy cover score as the predictor for *Nereocystis*, and the other using site-level *Nereocystis* stipe density.

Model structure

For community biomass spectra, we assigned individual fish to 6 mass classes (i.e. 32–64, 64–128, 128–256, 256–512, 512–1024 and 1024–2048 g). We then summed all biomass in each bin to the bin midpoints (M) for each depth stratum within each site,

and divided by total area surveyed to give biomass (B) per unit area (g m^{-2}) within each size class. We centred the body mass class midpoints (M) about zero by subtracting the mean of the log bin midpoints prior to model fitting to remove correlations between the slope and intercept (Daan et al. 2005), and so that these 'heights' provide a metric of total community biomass that is comparable between size spectra with different slopes. We then modeled biomass spectra with $\log_2 M$ as the predictor and $\log_2 B$ as the response.

To evaluate the effects of kelp canopy and substratum rugosity on the slopes of biomass spectra, we included interaction terms between each covariate and the bin midpoints M. A 3-way interaction term between rugosity, the kelp covariate and M was also included in each model to assess whether the effects of rugosity and kelp on biomass spectra slopes were interdependent. The non-interactive effect of each covariate gives its effect on biomass spectra intercepts (or 'height', as M was centered around 0).

Total biomass and mean body-size models had total biomass ($\Sigma(B)$) and mean body size ($\overline{M}$), respectively, as the response variables. To assess whether the effects of kelp canopy and substratum rugosity on these aspects of size structure are interdependent, we included interaction terms between rugosity and the kelp covariate (Table 1).

In all models, we accounted for the spatially and temporally nested structure of the data by including both year and site nested within area (Louise, Lyell, East Kunghit, West Kunghit) as crossed random effects. The random structure allowed the intercept to vary randomly with year in all models. The intercept also varied randomly with site nested within area for total biomass and mean body-size models,

Table 1. Saturated models. In biomass spectrum models, M is the midpoint of each body mass class. The notation (1|x) implies that the intercept varies randomly with the predictor, while (1 + M|x) implies that both slope and intercept vary randomly with the predictor x

Response *Nereocystis* covariate	Model specification
Biomass spectrum	
Canopy score	$\log_2$(biomass) ~ M × rugosity × canopy score + M × depth stratum + (1 + M|site) + (1|year)
Stipe density	$\log_2$(biomass) ~ M × rugosity × canopy score + M × depth stratum + (1 + M|site) + (1|year)
Total biomass ($\Sigma(B)$)	
Canopy score	$\log_2(\Sigma(B))$ ~ rugosity × canopy score + depth stratum + (1|site) + (1|year)
Stipe density	$\log_2(\Sigma(B))$ ~ rugosity × stipe density + depth stratum + (1|site) + (1|year)
Mean individual body mass ($\overline{M}$)	
Canopy score	$\overline{M}$ ~ rugosity × canopy score + depth stratum + (1|site) + (1|year)
Stipe density	$\overline{M}$ ~ rugosity × stipe density + depth stratum + (1|site) + (1|year)

while both slope and intercept varied randomly with site nested within area for biomass spectrum models.

While it is not of specific interest in this study, we expected that the depth stratum of transects may be important, as shallow transects were generally inside or on the edge of the kelp canopy, while deep transects were generally outside the canopy. We included depth stratum as a fixed effect in all models to account for this.

Model and covariate comparisons

For each subset of models, we fitted a saturated model with all covariates using maximum likelihood (ML; see Table 1 for a list of saturated models). After fitting saturated models, we conducted all-combinations model selection based on Akaike's information criterion for small sample sizes (AIC_c) using the function dredge in the R package MuMIn (Burnham & Anderson 2002, Bartoń 2013). We retained models with delta $AIC_c < 2$, and generated model-averaged coefficient estimates and their associated confidence intervals using the natural average method (Burnham & Anderson 2002, Grueber et al. 2011). We chose the natural average method as it is not yet well established how best to calculate uncertainty around parameter estimates using the alternative zero method (Grueber et al. 2011). In doing so, we recognise that parameter estimates for poorly supported parameters are biased slightly away from zero (Grueber et al. 2011). For ease of interpretation, effect sizes are presented in standardised units, where a 1 unit change in a predictor coefficient implies that a change of 1 SD of that predictor would result in a change of 2 SD in the response (Gelman 2008, Schielzeth 2010).

This approach yields 3 lines of evidence that we use to evaluate the effect of habitat covariates on each measure of community size structure: (1) the magnitude and direction of averaged predictor coefficients; (2) the 95% confidence intervals around coefficient estimates, a measure of coefficient precision; and (3) the relative variable importance (RVI) of each predictor, which is the sum of the model weights of all the models in the model-averaged set that included the predictor.

To visualise the effects of substratum rugosity and canopy cover on community size structure, we used averaged models to calculate biomass spectra for different combinations of substratum rugosity and canopy cover, accounting for the other covariates and random effects.

RESULTS

We surveyed a total of 203 transects, encompassing 4537 reef fishes between 32 and 2048 g. This included 19 reef-associated species, predominantly from the families Sebastidae (rockfishes) and Hexagrammidae (greenlings; Table S1 in the Supplement) with a similar species assemblage throughout the study area (Fig. S2 in the Supplement). Across the reef fish community, total biomass tended to increase with increasing body-mass class (Fig. 2B). Consequently, the community biomass spectrum had a positive slope of 0.78 ± 0.08 (Fig. 2B).

Higher rugosity tended to be associated with relatively more small-bodied fishes and more fish biomass overall (Fig. 3A,B). The well-supported negative effects of rugosity on biomass spectra slopes and positive effect on intercepts (as indicated by RVIs shown in Fig. 4, and the inclusion of rugosity in the best-supported models listed in Table 1) indicate strong statistical support for these effects. These rugosity effects were also well supported in the models for mean and total biomass (as indicated by RVIs shown in Fig. 5, and inclusion of rugosity in top models listed in Table 3).

Higher kelp stipe density and canopy cover both tended to be associated with higher total biomass overall, evenly distributed across all size classes (Fig. 3C,E). The high RVI (density, 0.63; cover, 1) and positive effects of stipe density and canopy score on the biomass spectrum intercept (Fig. 4, Table 2) indicate statistical support for these effects, as does the support for the effect of the *Nereocystis* predictors in the models for total biomass (top panels of Fig. 5, Table 3).

Bivariate relationships also suggest that there tended to be relatively more large-bodied fish associated with higher *Nereocystis* stipe density (Fig. 3D). The model for mean biomass showed support for this effect (bottom left panel of Fig. 5, Table 3), but there was no support for an effect of stipe density on the slope of size spectra (Fig. 4, Table 2), suggesting that this effect was outweighed by the stronger relationship with total biomass in size spectra models.

We found evidence that stipe density and rugosity effects on fish community size structure (but not total biomass) were compensatory, as indicated by the support for interaction between these predictors in both size spectrum (RVI = 0.29 in left panel of Fig. 4, Table 2) and mean body mass models (RVI = 0.67 in bottom left panel of Fig. 5, Table 3). This implies that the tendency for larger mean body size with increasing *Nereocystis* stipe density became weaker over
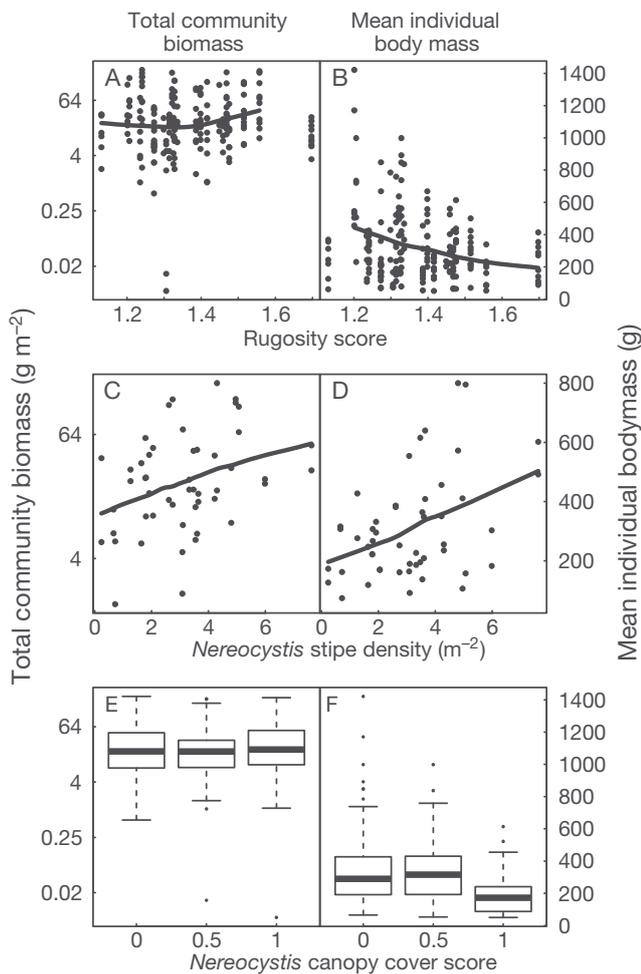
Fig. 3. Bivariate relationships between aspects of kelp forest reef fish community size structure (left panels: total community biomass; right panels: mean individual body mass) and habitat complexity covariates: (A,B) rugosity, (C,D) *Nereocystis* stipe density and (E,F) *Nereocystis* canopy cover. Lines are LOESS smoothers (span = 0.75). Midlines in boxplots are medians, boxes represent 25 and 75% quantiles, and whiskers extend to 95% quantiles

more rugose substratum. We did not find evidence of compensatory relationships between *Nereocystis* stipe density and rugosity on total fish community biomass, or between canopy cover and rugosity for either total fish biomass or mean individual body mass (as indicated by a relative lack of support for these interaction terms; Figs. 4 & 5, Tables 2 & 3).

Based on these models, the combined effects of *Nereocystis* canopy cover and substratum rugosity on fish community size structure can be summarised in predicted biomass spectra (Fig. 6, Fig. S3 in the Supplement). Greater kelp canopy cover was associated with more fish biomass overall, but no clear difference in size structure, while higher rugosity led to relatively more small-bodied fishes and more biomass overall. In terms of total biomass, the effect of kelp canopy translates to 75% more biomass overall for a closed versus open kelp canopy (with rugosity held constant). For rugosity, this translates to 60% less biomass of the largest fishes (1–2 kg) and 800% more biomass of the smallest fishes (32–64 g) at high-rugosity sites compared to the low-rugosity sites (with canopy cover held constant).

We included depth stratum in models to avoid confounding its effects with rugosity and *Nereocystis* canopy characteristics, and consistently found support for a trend for less biomass in the shallow depth stratum. The negative effect of depth on size spectrum intercepts can be seen in Fig. 4 and Table 2, and on total community biomass in the top panels of Fig. 5, and Table 3 (note that the deep stratum was the reference level, hence the negative effect implies lower biomass in the shallow stratum). There was also support for a weak tendency for fish to be smaller in the shallow depth stratum (bottom panels of Fig. 5). Although an effect of depth on biomass spectra slopes was included in
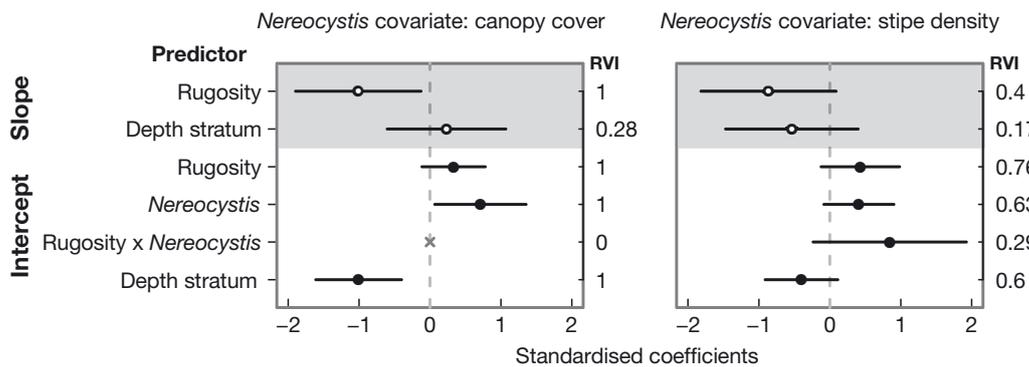

Fig. 4. Standardised predictor coefficients and 95% confidence intervals for the relationships of habitat covariates with the slopes (open circles, gray background) and intercepts (closed circles, white background) of reef fish community biomass spectra from averaged models with a $\Delta AIC_c < 2$. The left panel is for models including canopy cover score as the covariate for *Nereocystis*; the right panel is for models with stipe density as the *Nereocystis* covariate. A relative variable importance (RVI) score of zero indicates that the variable was not in any of the best-supported models
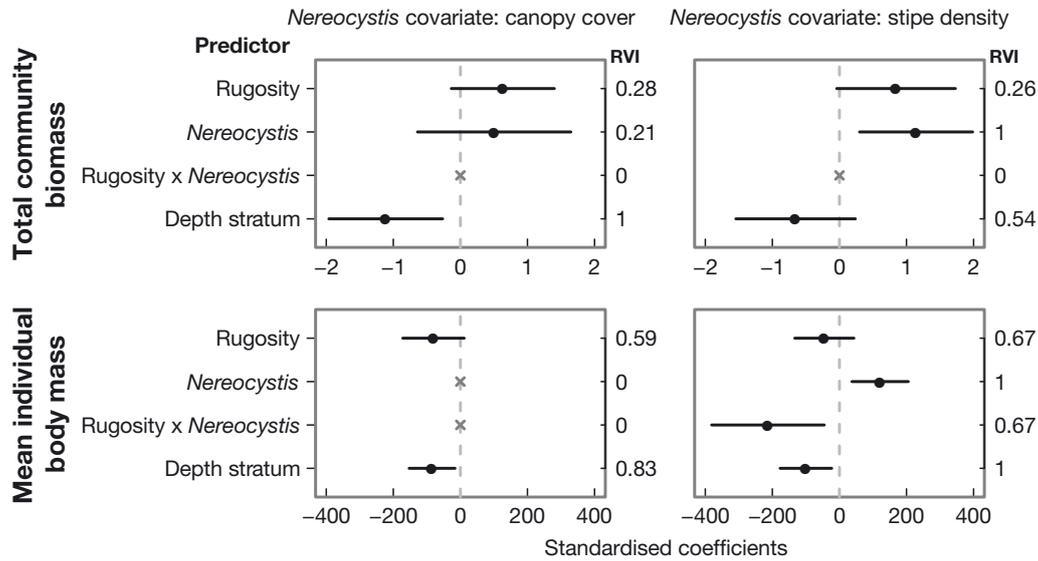
Fig. 5. Standardised predictor coefficients and 95% confidence intervals for the relationships of habitat covariates with total fish community biomass (top) and mean individual body mass (bottom) from averaged models with a $\Delta AIC_c < 2$. Left-hand panels are for models including canopy cover score as the covariate for *Nereocystis*; right-hand panels are for models with stipe density as the *Nereocystis* covariate. A relative variable importance (RVI) score of zero indicates that the variable was not in any of the best-supported models

Table 2. Summary of relative strength of support for models in the averaged set for the effects of biophysical predictors on the slope and intercept of site-scale biomass spectra. Models are compared via differences in Akaike's information criterion (corrected for small sample size, AIC_c, with Δ_i being the difference between the AIC_c score of model i and the AIC_c score for the best candidate model, and only models with $\Delta_i < 2$ included in the averaged set), likelihood of the model given the data ($\log(L)$), and normalized Akaike's weight (W_i), indicating the weight of evidence in favour of model i. Predictors listed under slope and intercept are included with 2-way interactions with body mass, and predictors listed under intercept only are included without interactions. Nereo: *Nereocystis* covariate (i.e. canopy score or stipe density) –: not applicable

Nereocystis covariate	df	$\log(L)$	AIC_c	Δ_i	W_i	Intercept only	Slope and intercept
Canopy score	11	−635.10	1293.04	0.00	0.72	Depth stratum, Nereo	Rugosity
	12	−634.95	1294.91	1.87	0.28	Nereo	Rugosity, depth stratum
Stipe density	12	−447.73	920.92	0.00	0.08	Nereo, depth stratum, Nereo × Rugosity	Rugosity
	7	−453.30	921.11	0.19	0.07	Body mass only, no covariates	
	8	−452.27	921.20	0.28	0.07	Nereo	–
	11	−449.00	921.22	0.30	0.07	Nereo, Nereo × Rugosity	Rugosity
	10	−450.12	921.24	0.33	0.06	Depth stratum	Rugosity
	11	−449.02	921.26	0.34	0.06	Nereo, depth stratum	Rugosity
	10	−450.24	921.50	0.58	0.06	Rugosity, Nereo, depth stratum	–
	9	−451.45	921.72	0.80	0.05	–	Rugosity
	9	−451.49	921.80	0.88	0.05	Rugosity, depth stratum	–
	11	−449.35	921.92	1.00	0.05	Rugosity, Nereo, depth stratum, Nereo × Rugosity	–
	10	−450.46	921.94	1.02	0.05	Nereo	Rugosity
	11	−449.53	922.29	1.37	0.04	Rugosity, Nereo	Depth stratum
	8	−452.84	922.35	1.43	0.04	Depth stratum	–
	9	−451.81	922.44	1.52	0.04	Nereo, depth stratum	–
	12	−448.51	922.47	1.55	0.04	Rugosity, Nereo, nereo × Rugosity	Depth stratum
	9	−451.82	922.47	1.55	0.04	Rugosity, Nereo	–
	10	−450.75	922.52	1.60	0.03	Rugosity	Depth stratum
	10	−450.76	922.54	1.62	0.03	Rugosity, Nereo, Nereo × Rugosity	–
	8	−452.94	922.54	1.63	0.03	Rugosity	–
	13	−447.54	922.78	1.87	0.03	Nereo, Nereo × Rugosity	Rugosity, depth stratum
	9	−452.01	922.85	1.93	0.03	–	Depth stratum

Table 3. Summary of relative strength of support for models in the averaged set for the effects of biophysical predictors on total biomass (sum(B)) and mean individual body mass ($\overline{M}$). Models are compared via differences in Akaike's information criterion (corrected for small sample size, AIC_c, with Δ_i being the difference between the AIC_c score of model i and the AIC_c score for the best candidate model, and only models with $\Delta_i < 2$ included in the averaged set), likelihood of the model given the data (log(L)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favour of model i

| Response Nereocystis predictor	Predictors	df	log(L)	AIC_c	Δ_i	W_i
$\Sigma(B)$						
Canopy score	Depth stratum	5	−136.29	283.46	0.00	0.51
	Depth stratum, rugosity	6	−135.72	284.70	1.24	0.28
	Depth stratum, canopy score	6	−135.99	285.24	1.77	0.21
Stipe density	Stipe density	5	−89.47	190.31	0.00	0.46
	Depth stratum, stipe density	6	−88.69	191.33	1.02	0.28
	Depth stratum, stipe density, rugosity	7	−87.40	191.46	1.15	0.26
$\overline{M}$						
Canopy score	Depth stratum, rugosity	6	−471.73	956.72	0.00	0.42
	Depth stratum	5	−472.94	956.77	0.05	0.41
	Rugosity	5	−473.84	958.57	1.84	0.17
Stipe density	Depth stratum, stipe density, rugosity, stipe density × rugosity	8	−315.12	649.75	0.00	0.67
	Depth stratum, stipe density	6	−318.61	651.17	1.42	0.33
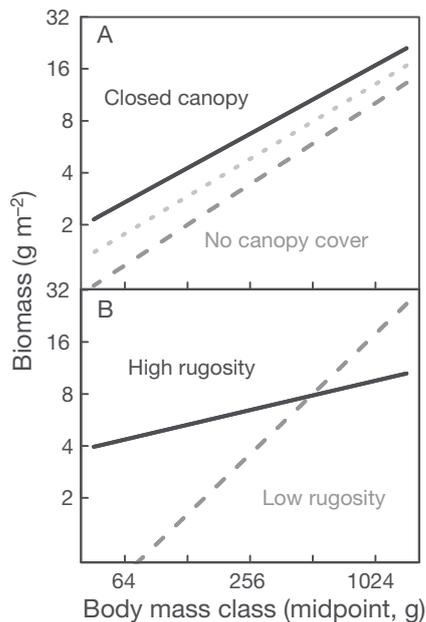
Fig. 6. Predicted kelp forest reef fish biomass spectra for (A) high (closed canopy with cover score = 1, solid line), medium (fragmented canopy with cover score = 0.5, dotted line) and low (cover score = 0, dashed line) kelp canopy cover at intermediate rugosity (rugosity = 1.35), and (B) for high (rugosity = 1.7, solid line) and low (rugosity = 1.0, dashed line) rugosity while holding kelp canopy cover constant (at 0.5)

the best-supported models (Fig. 5, Table 3), the effect was imprecise and did not have a clear direction, as reflected by the confidence intervals about the parameter estimate extensively overlapping zero (Fig. 4).

DISCUSSION

Here we provide evidence that kelp canopy cover, stipe density and substratum rugosity have important and interdependent effects on fish community size structure and total fish community biomass in a temperate rocky reef ecosystem. Higher kelp canopy cover and higher stipe density were both associated with greater total fish biomass. Presence of a closed kelp canopy was associated with increased overall fish biomass, on average by 75%, compared to open-canopy reefs. Higher substratum rugosity was associated with both higher overall fish biomass and relatively more small-bodied fishes. On the highest-rugosity reefs the biomass of small fishes (32–64 g) was 800% higher than on the lowest-rugosity reefs, while large fish (1–2 kg) biomass was 60% lower.

Both kelp canopy characteristics and substratum rugosity have previously been recognised as important determinants of fish abundance (Ebeling et al. 1980, Larson & DeMartini 1984, Willis & Anderson 2003), but our findings are novel in several important respects. By examining the effects of canopy and substratum characteristics simultaneously, we demonstrate that the main effect of kelp is to increase total fish biomass (evenly across all size classes), while the main effect of reef rugosity is to boost the biomass of smaller fish, resulting in a more even (flatter) distribution of biomass across body sizes and more biomass overall. The size spectra approach

also shows that the effects of rugosity and kelp are interdependent. Although higher kelp stipe densities tended to be associated with larger fishes, this effect was outweighed by the trend for more small-bodied fishes at high rugosity. We also demonstrate how size-based analyses can shed new light on the ecology of kelp forest communities.

Previously, kelp canopy cover has mainly been observed to benefit small fishes (recruits and young-of-the-year; Carr & Syms 2006, Springer et al. 2006, Siddon et al. 2008), while higher substratum rugosity (or relief) has been observed to be associated with increased total abundance and biomass (Ebeling et al. 1980, Anderson et al. 1989, Cloutier 2011). Contrastingly, we observed a positive effect of substratum rugosity on smaller fish, while higher kelp canopy cover and density tended to be associated with increased biomass across body sizes. These differences may be partly due to the fact that the range of body sizes we considered did not include young-of-the-year or recruits, which depend strongly on kelp habitat (Carr & Syms 2006, Springer et al. 2006, Siddon et al. 2008) but contribute little to total biomass. While our findings for rugosity contrast with previous work in kelp forests, they are congruent with observations on coral reefs, where less complex substrata have been shown to lead to relatively fewer small-bodied fishes and more positive/less negative size spectrum slopes (Graham et al. 2005, Wilson et al. 2010, Alvarez-Filip et al. 2011, Rogers et al. 2014).

Kelp forests contribute a vertical dimension to habitat complexity that is less extensive or absent on coral reefs (Choat & Ayling 1987, Ebeling & Hixon 1993). An underlying mechanism by which increased substratum rugosity leads to increased biomass at small sizes is thought to be the provision of refuges from predation (Friedlander & Parrish 1998, Rogers et al. 2014). Our findings suggest that the mechanism by which canopy-forming kelps affect community structure may be quite different. Because mass-specific production is a direct outcome of mass-dependent metabolism and therefore scales predictably with individual body mass (Brown et al. 2004), increases in total biomass and size spectrum intercepts are generally accepted to reflect increased total production (Kerr & Dickie 2001, Jennings 2005). Hence, our results lead to the hypothesis that canopy-forming kelps may affect fish community structure by directly or indirectly enhancing the resource base, possibly through the capture of pelagic subsidies, rather than solely by providing refuge from predation for small fishes. Elucidating the mechanism for this enhancement will be an im-

portant goal for future research, as will be exploring whether these responses are consistent for kelp forest communities with different species compositions.

Several issues that we were not able to address in this study represent key avenues for future research:

(1) The substratum structural complexity measurement we used (rugosity) is representative of one scale of habitat complexity, but multiple different scales of complexity are likely to be important in shaping fish communities (Nash et al. 2013). The 3 m chain measurement we used is likely to be more effective for capturing habitat features at the scale of tens of centimetres (i.e. uneven substrate, small boulders and crevices) but may not be representative of larger-scale features such as boulders and outcroppings or smaller-scale features such as narrow cracks and fissures in bedrock. The scale of habitat features is an important determinant of the size range of fish that can use them as shelter (Hixon & Beets 1993) and the availability of specific types of shelter habitat can be an important determinant of community structure (Syms 1995). Previous work suggests that rugosity may be fractal, i.e. self-similar across different spatial scales (Nash et al. 2013), and that different methods of assessing rugosity that capture different scale features tend to be well correlated (Wilson et al. 2007). Nevertheless, explicitly measuring how different scales of substratum complexity affect community structure on temperate reefs deserves further attention.

(2) Previous work has demonstrated that the amount of kelp edge may be more important to fishes than the absolute amount of kelp habitat (Leaman 1980). The fact that the kelp effects we observed were consistent for both canopy cover and stipe density supports total habitat being more important than edge size in this system, but this could be directly addressed in future studies via kelp removal experiments.

(3) It is interesting to note that previous studies have documented higher fish abundance and biomass in *Macrocystis* forests than in *Nereocystis* forests where they co-occur elsewhere in the NE Pacific (Leaman 1980, Bodkin 1986). While the data we have presented here are limited to *Nereocystis* forests, there are also *Macrocystis* patches in the area we surveyed, and these patches have relatively few fishes (R. Trebilco & A. K. Salomon pers. obs.). It would be interesting to ascertain whether this difference is driven by substratum characteristics or other characteristics.

(4) While we focus on size-based analyses here, integrating size-based analyses with taxonomic

information will be an important goal for future work (Petchey & Belgrano 2010). For example, it will be interesting to investigate how numerically dominant species (such as yellowtail and black rockfish in this system) drive observed patterns.

(5) Finally, linear size spectra are an 'equilibrium' expectation, and are well-supported empirically by analyses (such as ours) that temporally and spatially 'average' across samples, but there is no expectation for 'snapshots' views (i.e. for individual site–time combinations) to be linear. Indeed, model-derived evidence shows that seasonally pulsed production and fishing can both result in 'waves' that propagate through size spectra and result in non-linearities (Pope et al. 1994, Benoît & Rochet 2004). There is emerging evidence that explicitly exploring departures from linearity can be highly informative (Rogers et al. 2014), and exploring whether and how habitat complexity is associated with non-linearities in size spectra for temperate reef fishes is an important direction for future study.

Our findings have conservation and management implications for temperate rocky reefs, particularly those at high latitudes dominated by *Nereocystis*. Along the northwest coast of North America, marine protected areas have been established with the specific goal of protecting and restoring depleted rock-fish populations (Parker et al. 2000, Yamanaka & Logan 2010, Haggarty 2014). Our finding that increased kelp cover is associated with greater fish biomass adds to the body of evidence that suggests that protection and/or enhancement of kelp habitat will be important in ensuring the success of existing protected areas (Dayton et al. 1998, Graham 2004, Airoldi et al. 2008). Kelp cover should also factor into decisions on where to site new protected areas if the stated objective is to protect and sustain reef-associated fishes. Importantly, in this context of site selection for new protected areas, our findings show that substratum characteristics should also be considered. Several studies have reported that higher substratum rugosity is associated with higher abundance of rockfish and other bottom-associated fishes (Richards 1987, Love et al. 1991, Cloutier 2011), but the size-based nature of this association has not, to our knowledge, been previously recognised. Within the size range we consider, our results suggest that observed trends of increased fish abundance with increased substratum rugosity may be largely driven by small-bodied fishes. Hence, if the goal of management is to protect a diverse size structure (i.e. including large fishes), then it will likely be beneficial if reserves encompass not only high-rugosity areas, but

also a diverse range of rugosities. It is also worth noting that almost all fish observed in this study were members of species that, at their maximum size, would fall in the largest mass bin included in our analysis. This implies that the pattern for increased biomass of small fish with higher rugosity is driven by small individuals of species that attain large maximum size.

Size spectra and other forms of body-size distributions are increasingly well recognised as key indicators of community state and structure. Several recent studies on coral reefs have demonstrated their utility for quantifying the relative effects of both habitat degradation and overfishing on fish communities (Dulvy et al. 2004, Wilson et al. 2010, Alvarez-Filip et al. 2011). Our study demonstrates that size spectra can also provide new insights into the factors that shape fish communities in temperate kelp forests. Size-based analyses have been particularly useful for quantifying and tracking community-scale changes in other marine ecosystems; similarly, we expect that forecasting and tracking important changes in kelp forest communities in the coming decades will be an application for which size-based analyses, such as those we have presented here, will be particularly useful. For example, sea otter range expansion, well known to affect kelp abundance on high-latitude reefs (Estes & Palmisano 1974, Watson & Estes 2011), is continuing along the northwest coast of North America (Nichol & Abernathy 2009). While some evidence for indirect effects of otter expansions on kelp-associated fish species has been revealed (Reisewitz et al. 2006), we have very little understanding of the magnitude of community-level effects on commercially and recreationally important reef-associated fish. Furthermore, changes in the spatial extent and composition of kelp forest are expected with changes in ocean temperature, sea level and pH associated with increasing human-induced atmospheric carbon dioxide (Harley et al. 2012). Yet, the implications for reef fish communities remain unclear. Lastly, quantifying the community-scale effects of fishing is an increasingly common application of size-based approaches (an application that is closely inter-related with assessing marine protected area effects). Given that fishing appears to be the greatest manageable threat to kelp forest ecosystems over the 2025 time horizon (Steneck et al. 2002), we suggest that the field of kelp forest ecology and fisheries management may benefit from more widespread applications of these approaches.

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