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Moving beyond trophic groups: evaluating fishing-induced changes to temperate reef food webs

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ABSTRACT: Fish capture has far-reaching but inadequately assessed implications for marine food webs. At the community level, such effects are typically investigated using dynamic models that rely on partially subjective categorization of species into trophic groups and that mostly overlook the substantial contribution of ontogenetic dietary variation within fish species. Here, we estimate consumption by fish communities at 376 southern Australian sites by applying a recently developed statistical model that predicts diet for individual fish based on their body size and taxonomic identity, with predicted diets then summed to estimate total community consumption. Impacts of fishing and human population density as top-down pressures on shallow reef communities were thereby resolved at fine taxonomic scales. Fishes were estimated to consume 71% more prey biomass in southern Australian no-take marine protected areas (MPAs) relative to fished sites. Consumption of algae and sessile invertebrates was unexpectedly high in MPAs, an outcome not apparent with fish species allocated into pre-defined trophic groups. Extension of this individual size-structured modelling approach provides an opportunity to fill important knowledge gaps in understanding human impacts on marine food webs.

KEY WORDS: Australia · Fish diets · Herbivores · Marine protected areas · Marine reserves · Trophic cascades

INTRODUCTION

Environmental and human influences on marine food webs are typically assessed through dynamic trophic models that quantify, or in qualitative models link, connections between trophic groups. A limitation of these models is that they are computationally limited in the number of trophic compartments and typically require considerable subjectivity in decisions on how the multitudes of animals are grouped (Polovina 1984, Pauly et al. 2000). Species are assumed to act similarly within compartments, regardless that this assumption contradicts Hutchinson's well-known niche paradigm (Hutchinson 1978), in which each species inhabits a unique niche. The validity of dynamic trophic models clearly rests on the appropriateness of the theory that underlies modelled relationships, the realism of assumptions, and the purposes to which the model is put. However, the consequences of inappropriate trophic categorizations are generally unknown and unknowable, other than when field observations of manipulated communities can be undertaken to validate predictions.

The ecological role of aquatic species is highly flexible through their life history (Cushing 1975, Edgar & Shaw 1995b, Jennings et al. 2002, Rudolf & Rasmussen 2013), with body size an important determinant of the location of individuals within the food

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*Corresponding author: german.soler@utas.edu.au web (Dickie et al. 1987, Jennings & Warr 2003, Blanchard et al. 2011, Zhang et al. 2014). In particular, similarly sized taxa from vastly different phylogenetic lineages may share greater similarity in diet than juveniles and adults of the same species (Soler et al. 2016a). In a review of Ecopath with Ecosim, Christensen & Walters (2004) highlight the value in creating separate trophic categories at an intraspecific level, with complex trophic ontogeny. However, this is computationally limited to a few species in any community-level model, whereas an ideal model would allow all species to change ecological roles as they grow, with progression through prey types and sizes (Shin & Cury 2001, Brown & Gillooly 2003, West & Brown 2005, Fulton et al. 2011). A recent advance in this area has been the development of the statistical model Consume, which predicts the diet of individual fishes with high accuracy on the basis of body size and taxonomic identity (Soler et al. 2016a,b). When predicted diets of individuals are aggregated at the community level, ontogenetic changes for each species are included (Soler et al. 2016a,b). Thus, a major benefit of this individual-based agglomerative approach is that researchers do not have to decide how to delimit groups by species or body size, as is necessary in dynamic models which involve partitioning of the community.

Here, we apply the Consume model using the extensive Reef Life Survey (RLS) dataset for southeastern Australia (Edgar & Stuart-Smith 2014). Species abundance and size distribution data were obtained through underwater visual surveys at 376 sites spanning 2500 km coastal distance and 4 marine ecoregions (sensu Spalding et al. 2007). We estimate community-level consumption at each site and use those predictions to test hypotheses associated with key environmental and anthropogenic drivers of fish community structure. Specifically, we address the following questions: (1) How do fishing and proximity to human population centres affect different trophic levels of temperate reef ecosystems? (2) How do ecological outcomes derived from predictions of community consumption using Consume differ from those inferred using models with traditional trophic group categories?

For (1), we assess how fishing and proximity to human population centres influence mean prey size, prey type, and total consumption of rocky reef fish communities, after accounting for environmental influences. This analysis uses no-take marine protected areas (MPAs) as a broad-scale experimental framework for understanding the consequences of the removal of fishes by fishing pressure. For (2), we compare results from (1) with model output using the same reef fish community data but with fishes categorized into 4 commonly used trophic groups (higher carnivores, benthic carnivores, herbivores, and planktivores).

We hypothesize that reduced total fish biomass in locations that are fished or in close proximity to human population centres will result in not only reduced overall community consumption but also notable differences in the types and sizes of prey consumed, due to depressed abundance of large individuals and higher trophic level fishes (Edgar et al. 2014, Soler et al. 2015).

METHODS

Consume model

We used Consume (Soler et al. 2016a,b) to predict prey consumption for fish communities surveyed by visual census methods at shallow rocky reef sites in the Australian states of Tasmania, Victoria, and South Australia (Fig. 1).

Data on fish community structure included species-level abundance and size structure for all fishes

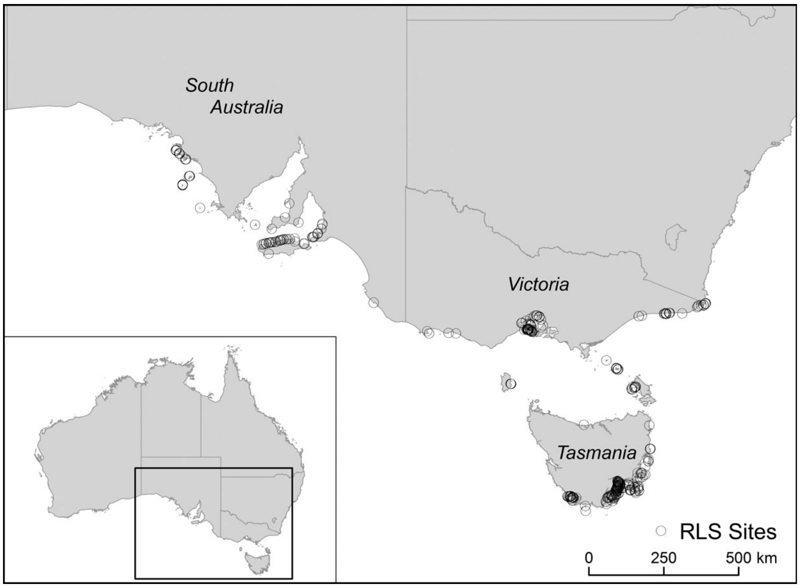

Fig. 1. Reef Life Survey (RLS) sites investigated in South Australia, Victoria, and Tasmania

sighted along 50 × 5 m belt transects by divers using RLS methods, as described in detail by Edgar & Stuart-Smith (2014). At each site, multiple transects (mean = 3.4) were undertaken along defined depth contours. Sites were located in shallow reef habitats between 1 and 23 m depth, with a mean depth of 7.5 m.

Consume possesses separate diet type and diet size components, both calculated using the taxonomic identity and size of the predator fish, the important predictors identified in prior studies (Soler et al. 2016a,b). The first component uses premises of *k*-nearest neighbours (Barber 2011, Conway & White 2012) to predict percentages of different prey categories for each individual fish observed in the RLS data. Diet predictions were achieved by assigning to each individual fish the diet in a literature-based archive for the closest match to taxonomic level (species, genus, or family) and size (wet weight). Decisions on taxonomy versus size were based on a probabilistic hierarchy. The second component applies linear models to predict the mean size of prey for each fish, considering the effect of taxonomy, wet weight of the predator fish, and prey type. Therefore, Consume used a step-by-step approach choosing the best match for a given fish from the available dataset. The results of the 2 models were then combined in an output matrix of percentages by prey type and mean prey size for each individual fish. Full details of the models and their predictive ability are provided in Soler et al. (2016a,b).

For this study, Consume was trained using detailed dietary information from 137 fish species collected across southern Australia (Edgar & Shaw 1995b,c) as well as publicly available information for an additional 2230 species through FishBase (www.fishbase.org) and other published and unpublished sources (Table 1). Dietary information was only utilized from published sources when the size of individual fish, species identity, and percentage of different prey types were provided. Dietary information was standardized to percentage volume whenever needed. A total of 134 of the 252 fish species present in the RLS data used for this study were matched with the diet content data collected across southern Australia by Edgar & Shaw (1995c) at the species, genus, or family level. For the species not present in that dataset, the component of Consume that predicts prey type (Soler et al. 2016a,b) used 107 species from FishBase and other publicly available data. Only 11 species present in the RLS field survey data did not have a match to dietary information at the family level or better (following the sequential process described in Soler et al. [2016a]); prey type for these was estimated based only on wet weight of the consumer fish. When diet information at the species level was lacking, and genus- or family-level dietary information was applied, the loss of accuracy was minimal, as assessed and demonstrated in prior studies (Soler et al. 2016a,b). The most important predictor for prey type was the size of the individual consumer fish, while the most important predictor for mean prey size was the consumer's taxonomic identity (Soler et al. 2016a,b).

Prey types were classed within 13 categories: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), infaunal molluscs (mi), epifaunal molluscs (me), small fishes (f), planktonic fish larvae (fp), infaunal crustaceans (ci), epifaunal crustaceans (ce), planktonic crustaceans (cp), other epifauna (oe), and other infauna (oi). The category sponges included sponges, ascidians, and hydroids, while algae included some seagrass, and planktonic fish larvae also included fish eggs. For details of how the prey items were grouped into prey types, see Table S4 in the Supplement at www.int-res.com/articles/suppl/m587p175_supp.pdf.

Table 1. Sources of diet information, number of fish and number of species included in the model as the prediction dataset. Level of information was based on the type of information available from each of the datasets. Prey type was expressed as percentage of diet

Region	No. of fish	No. of species	Level of information	Reference
Southern Australia	4336	137	Prey type; prey size	Edgar & Shaw (1995b,c)
Tasmania, Australia	11	4	Prey type; prey size	Soler & Edgar (unpubl.)
Easter Island	77	37	Prey type; some prey size information	DiSalvo et al. (2007)
Madagascar	110	110	Prey type; some prey size information	Harmelin-Vivien (1979)
West Indies	163	125	Prey type; some prey size information	Randall (1967)
Marshall Islands	75	70	Prey type	Hiatt & Strasburg (1960)
Hawaii	82	77	Prey type	Hobson (1974)
Global	3845	1586	Prey type	FishBase

Daily prey consumption estimates

Daily prey consumption per fish was calculated by combining the model output of the percentage of each prey type and daily consumption rates (in proportion to fish weight). For daily consumption calculations, we used the model developed by Palomares & Pauly (1989), which considers the weight of the fish, ambient temperature, aspect ratio of its tail, and food type (Eq. 1; Palomares & Pauly 1989),

$$\begin{aligned}\ln Q/B = -0.1775 - 0.2018\ln W \\ + 0.6121\ln T + 0.5156\ln A + 1.26F\end{aligned} \tag{1}$$

where Q/B is the daily food consumption of a fish population as a percentage of its biomass, W the weight (g) of the fish in question, T is mean habitat temperature (°C), A is an aspect ratio of the tail based on its height and surface, and F is food type (0 in carnivores, 1 in herbivores) (Palomares & Pauly 1989). We used individual weights for each fish for this equation. Temperature was based on mean annual sea surface temperature (SST) for each location extracted from Bio-Oracle (Tyberghein et al. 2012). We did not have individual fish information for A (aspect ratio of the tail); consequently we used the mean value 2.2 from 33 species examined in Palomares & Pauly (1989) from temperate to tropical waters. For F, we scored each species with 0 or 1 depending on their diet preferences. These calculations provided a predicted daily consumption for each individual fish recorded on RLS surveys for each prey type. On average, the daily food consumption for all the fish in this study was 3.6% (minimum 0.6% and maximum 30%). The highest daily consumption values were for herbivorous fishes from the genus *Parma*, and the lowest were for *Dasyatis*. Total community consumption was calculated as the sum of values for all individuals at a site, accounting for abundance and size structure of all the fishes observed on rocky reef surveys.

Mean prey size

By binning the predicted mean prey size following the sieve size categorization described in Edgar & Shaw (1995b), we estimated the prey consumed for each fish community by prey type for each size bin. A total of 19 size bins were considered: 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6, 8, 11.2, 16, 22.5, 32, 45, and 64 mm (these are the lower values for each size bin). Because model accuracy was affected by long tails of the prey size distribution, we also undertook an analysis that combined all size classes smaller than 0.5 mm (<0.5) and all size classes larger than 11.2 mm (>11.2). Outputs of this analysis matched findings with the finer-scale bins and are presented in Figs. S1 & S2 in the Supplement.

Effects of environmental and anthropogenic factors on prey consumption

The effects of fishing and general human impacts on predicted community consumption were assessed using linear mixed models (LMMs), with the effect of protection from fishing (MPAs) introduced after the influences of other anthropogenic and environmental variables (annual mean SST, SST range, photosynthetically active radiation [PAR] mean, and a human population index [Pop index]) were considered. This was done to remove the effect of these covariates prior to assessing the effect of protection granted by MPAs. Environmental data relating to SST, SST range, and PAR mean, as provided by Bio-Oracle (Tyberghein et al. 2012), were considered because they were identified as important correlates of spatial patterns of fish composition and biomass at regional scales in prior analyses (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015). The human population index (Pop index) was calculated using a quadratic Kernel function (Silverman 1986) to a smoothly tapered surface for each of the human settlements created with the glp00g gridded world population density dataset, as described in Soler et al. (2015). Analyses of MPA effects first accounted for these 4 factors, plus the random effect of ecoregion (as defined by Spalding et al. [2007]). The level of MPA protection for a given site was classed as fished or no take. Fished sites lay outside MPAs or inside MPAs when fishing was allowed or with no indication of enforcement (Edgar et al. 2014).

LMMs allowed the influence of protection to be examined while considering other factors (environmental and anthropogenic) plus the random effect of ecoregion (Spalding et al. 2007), using the following equation:

$$\begin{aligned}y_{\mathrm{pe}i} = \mu + \beta_1\,\mathrm{SSTmean}_i + \beta_2\,\mathrm{SSTrange}_i + \beta_3\,\mathrm{PARmean}_i \\ + \beta_4\,\mathrm{POPindex}_i + \beta_5\,\mathrm{Protection} + \gamma_e + \varepsilon_{ei}\end{aligned} \tag{2}$$

where $y_{\mathrm{pe}i} = \ln_e$ (natural logarithm) prey consumed (in g) at the ith site, given the effects of SST mean, SST range, PAR mean, human population, and protection; μ = overall mean; γ_e = effect of the eth ecoregion (as random effect); and ε_{ei} = residual error. Ln ratios of daily prey consumption in MPAs relative to fished zones were obtained for each prey type from the coefficient for Protection, $\beta 5$. Ratios were obtained for the other β coefficients from Eq. (2) and transformed into percent increment in biomass, by $100 \times [\exp(\beta) - 1]$. Due to the absence of some prey consumed at some of the prey sizes in some of the predictions, we added a constant (= 0.05) to all the predictions, $\ln(y + 0.05)$. Given the prey consumption predictions were scaled in grams, the addition of 0.05 g to the predictions was chosen as a reasonable ecological value for the step between no prediction and minimum daily predicted prey consumed (Ortiz et al. 2000). A 4th root transformation of the predictions for daily prey consumption was also applied, generating the same conclusions as the ln transformation with 0.05 g constant added. Results from the ln transformation are presented here so that the effect of the different covariates can be shown as percentage (%) difference in predicted daily prey consumed.

Effectiveness of the no-take MPAs relative to fished sites was estimated within LMMs by estimating the log ratios of biomass in MPAs over biomass in fished sites. A similar process was followed with Pop index, where the relative effect of population centres was estimated within the LMMs by estimating the log ratio of biomass for a given value of Pop index over a zero value of Pop index (no human centres nearby).

Comparison of community prey consumption with trophic group biomass

Ecological inferences based on Consume predictions were compared with conclusions arising from more classical trophic group analysis on the same dataset. Four trophic groups that are commonly applied (e.g. Halpern 2003) to predator reef fishes were used: higher carnivores, benthic carnivores, planktivores, and herbivores; these groups are based on dietary information obtained from FishBase (www.fishbase.org) and previous studies with the same dataset (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015). A more detailed list of prey types consumed by each trophic group is described in Soler et al. (2015) based on the FishBase classification. Using the total length of fishes observed during the surveys, trophic groups were further categorized into 3 size classes: small (<7.5 cm), medium (7.5 to 30 cm), and large (>30 cm). Fish biomass was subsequently estimated using the abundance and sizes of fishes on transects and species-specific length–weight relationships provided in FishBase. When length–weight relationships were unknown for a species, values were obtained from a related species with similar shape. LMMs were then applied to the 376 sites to assess the effects of protection (MPAs vs. fished sites) and other environmental and anthropogenic variables on the biomass of fishes in the 12 categories of trophic group by size class. The same environmental and anthropogenic variables were investigated as with the Consume output and calculated as percent difference in relative biomass of the predator fish for the same set of sites.

Community consumption differences in MPAs compared with fished sites were assumed to be proportional to relative biomass differences, partitioned between the 12 trophic groups by size class categories. Even though the ratios for prey types and trophic groups come from different calculations and their magnitudes differed, they show similar relationships. For planktivores and herbivores, total percent biomass differences of the 3 size classes were estimated as the geometric mean of the ratios and transformed to percentage difference of the increase in consumption of plankton and algae, respectively. Consumption of small fishes (f) as prey was predicted as the geometric mean of the ratios of medium and large higher carnivores, as small individuals were not likely to feed on fishes. The geometric mean estimates were transformed into percentage increase of medium and large higher carnivores. Consumption of benthic invertebrates was predicted from the geometric mean of the ratios of small higher carnivores and all sizes of benthic carnivores; this geometric mean estimate was then transformed to a percentage difference. A similar process was applied when assessing the influence of human population, including an assumption that consumption differences were proportional to biomass differences for the 12 categories of trophic group by size.

RESULTS

Effects of environmental and anthropogenic factors on prey consumption

Prey type, mean prey size, and daily prey consumption were estimated for 44024 fishes observed in 376 sites across Tasmania, South Australia, and Victoria. Dietary information was not available for many species; estimates of mean prey size based on species-level matches (plus wet weight) were possible in 14089 cases (32%), genus-level matches in

6662 cases (15%), and family-level matches in 14946 cases (34%), while wet weight only was used to generate diet predictions in 8327 cases (19%). Based on initial testing of Consume, the accuracy of predictions of prey size decreases slightly when not all the taxonomic information of the predator fish is available and decreases further when predictions are based only on wet weight of the predator fish, albeit still with reasonable accuracy (Soler et al. 2016a,b). These numbers imply poorer predictions of prey size than prey type (Table 1), with prey type predictions from family-level or better matches in 42270 cases (96%) and predictions based only on wet weight of the consumer fish in 1754 cases (4%).

The prey types of 30831 (70%) of a total of 44024 fishes were estimated using comparative temperate Australian data from Edgar & Shaw (1995a,b) and Soler & Edgar (unpubl.) (Table 1). The prey types of the remaining 13193 (30%) fishes were estimated using other datasets (Table 1).

Community-level predictions of type and size of prey consumed were influenced by several anthropogenic and environmental factors (Figs. S3 & S4 in the Supplement). For each 1°C rise in annual mean SST, daily consumption by the fish community of most prey types increased, especially crustacean infauna (ci), fish as prey (f), and sponges (s). Temperature fluctuation through the year (temperature range) had a negative effect on community consumption of most prey types, with algae (a), mollusc epifauna (me), other epifauna (oe), and sponges (s) most affected (Fig. S3). PAR mean, a metric of light available for primary production, had a positive influence on consumption of crustacean infauna (ci) but not of algae (a).

After accounting for these environmental drivers of fish community structure, and therefore total consumption, greater biomass of fishes in all trophic groups within MPAs resulted in significantly higher predicted community daily consumption of most prey types compared with fished sites outside of MPAs (Fig. 2A; Table S1 in the Supplement). Consumption of algae (a), small fishes (f), and sponges (s) differed most between fish communities inside MPAs relative to fished sites (281, 262, and 273% positive difference, respectively). Human population density had little effect on daily consumption of most prey types; nevertheless, algae (a), mollusc infauna (mi), and polychaete infauna (pi) were positively affected by increasing human population density, and crustacean infauna (ci) was negatively affected (Fig. 2B; Table 2).

Most prey size classes greater than 1.4 mm were consumed in greater quantities by fish communities

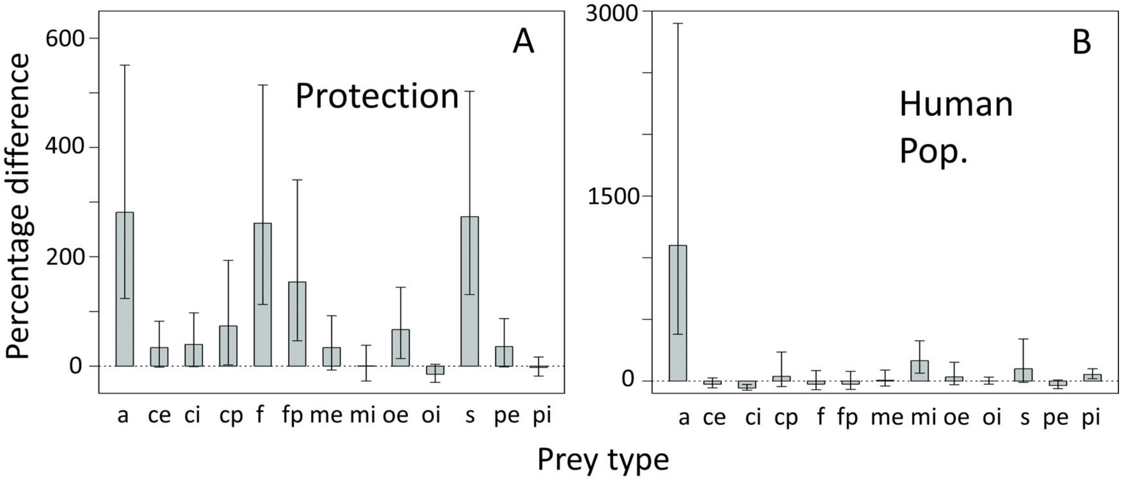

Fig. 2. (A) Percentage difference in prey types consumed (±95% CI) by the fish community at sites in protected areas relative to fished zones. Ln ratios of daily prey consumption in marine protected areas relative to fished zones were obtained for each prey type from the coefficient for Protection, β_5. (B) Percentage difference for a single-unit increase in the index of local human population density obtained for each prey type from the coefficient for the human population index (Pop index), β_4. Ratios were obtained from the coefficients for Pop index, β_4, and Protection, β_5, and transformed into percentage difference in biomass using the relation $100 \times [\exp(\beta_4) - 1]$ and $100 \times [\exp(\beta_5) - 1]$, respectively, from Eq. (2). Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the CI bars did not overlap zero. Prey types: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), infaunal molluscs (mi), epifaunal molluscs (me), fishes (f), planktonic fish larvae (fp), infaunal crustaceans (ci), epifaunal crustaceans (ce), planktonic crustaceans (cp), other epifauna (oe), other infauna (oi)

Table 2. Comparison of community consumption estimates from the Consume model with those derived from the trophic group model, with results expressed as percent ratio increase for marine protected areas (MPAs) / fished areas and for 1 unit increase in the human population index (Pop index). Means of the biomass change of trophic groups and total means were calculated as the geometric mean of the ratios and converted to percentage change. ^{NS}: no significant difference; S: small; M: medium; L: large

Trophic group	Prey category	Trophic group predictions for MPAs	Consume predictions for MPAs	Trophic group predictions per unit increase in Pop index	Consume predictions per unit increase in Pop index
Herbivores	Algae	62	281	132	1100
Higher carnivores L + M	Fishes	116	262	−41	-24^{NS}
Benthic carnivores S + M + L and higher carnivores S	Sponges	28	273	−27	99^{NS}
	Epifaunal crustaceans		34		-26^{NS}
	Epifaunal molluscs		34		6^{NS}
	Epifaunal polychaetes		36		-36^{NS}
	Other epifauna		67		34^{NS}
	Infaunal crustaceans		40		−57
	Infaunal molluscs		1^{NS}		165
	Infaunal polychaetes		-3^{NS}		54
	Other infauna		-15^{NS}		-1^{NS}
Planktivores S + M + L	Planktonic fish larvae	27	154	34	-24^{NS}
	Planktonic crustaceans		73		37^{NS}
Total mean		48	71	9	27

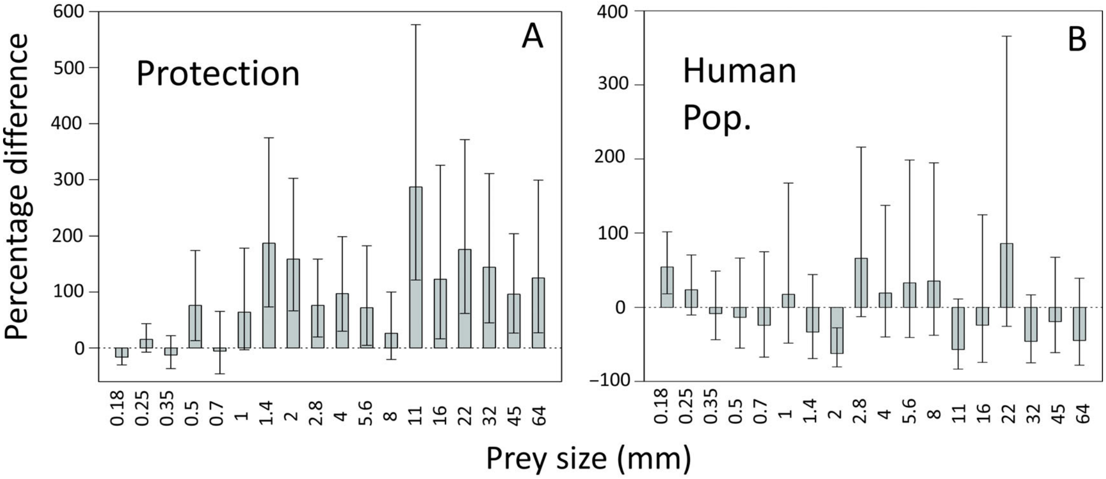

Fig. 3. (A) Percentage difference in daily consumption of different size classes for all prey types consumed by the fish community in protected areas relative to fished zones (±95% CI). (B) Percentage difference for a single-unit increase in the index of local human population density obtained for each prey size bin from the coefficient for the human population index (Pop index), β_4. Ratios were obtained as described in Fig. 2. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the CI bars did not overlap zero

protected in MPAs relative to fished areas (Fig. 3A; Table S2). Larger prey consumed inside MPAs reflected recovery of populations of larger fish species and larger average sizes of fishes at protected sites. Prey size predictions were not significantly different between locations of high and low human population density, except for the 0.18 and 2 mm size classes (Fig. 3B).

Comparison of community prey consumption vs. trophic group biomass

Large and medium size classes of the 4 trophic groups had significantly greater biomass inside MPAs relative to fished sites (Fig. 4A; Table S3 in the Supplement). Trophic group analysis indicated average consumption of fishes and large inverte-

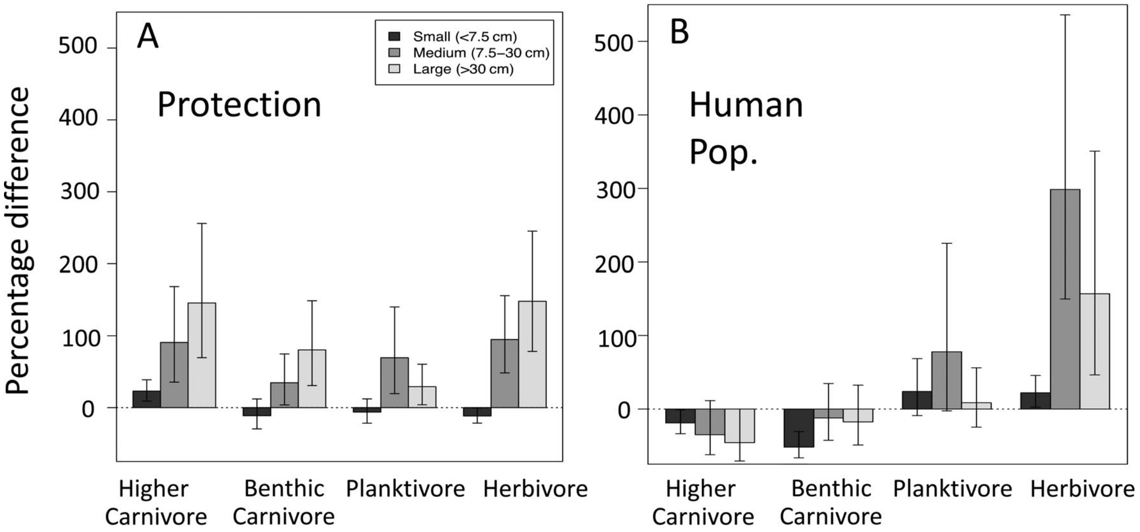

Fig. 4. (A) Percentage difference in biomass for different trophic groups and size categories due to the level of protection at sites surveyed in Tasmania, Victoria, and South Australia (±95% CI). (B) Percentage difference for single-unit increase in the human population density index (±95% CI) for different trophic groups and size categories in the surveyed sits. Ratios were obtained as described in Fig. 2. The model adjusted for sea surface temperature (SST) mean, SST range, photosynthetically active radiation mean and human population. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the CI bars extended above or below zero

brates was 116% higher, and of algae was 62% higher, in MPAs (Table 2). The small size class of higher carnivores, medium and large classes of benthic carnivores, and medium and large classes of planktivores also had greater biomass in MPAs, with corresponding implications for consumption of mobile invertebrates, small fishes, and plankton. An increase in small invertebrate consumption was identified for the small higher carnivores and benthic carnivores combined. These results contrast those from the predictions from Consume, particularly the proportional magnitude of increased consumption of sponges and other sessile invertebrates in MPAs (Consume predictions are substantially greater; Table 2). The correlation of the geometric means of the ratios between prey types and trophic groups due to the effect of protection was high and significant ($r^2 = 0.83$).

The human population index (Pop index) had a varied effect on the biomass of different trophic groups (Fig. 4B) based on the results of the LMMs. In general, the mean biomasses of higher carnivores and benthic carnivores were both negatively influenced by higher population densities, whereas herbivore biomass tended to be greater; however, not many differences were statistically significant. The small differences in prey consumption estimates were generally similar to those predicted by Consume but notably overlooked the increased consumption of molluscan infauna and polychaete infauna (Table 2). The correlation of the geometric means of the ratios between prey types and trophic groups due to the effect of the population index was high and significant ($r^2 = 0.84$).

DISCUSSION

Differences between Consume and trophic group analyses

Comparison of outputs of the trophic group analysis with those from the Consume model indicated that simplification of trophic structure using the former did not provide misleading conclusions when assessing ecological implications for fish communities; however, some important trends were not detected. In particular, these included a failure to detect increased consumption of sponges in protected communities and increased consumption of infaunal soft-sediment prey types by reef-dwelling fishes near human population centres.

Sponges were partly included among items consumed by benthic carnivores but are functionally very different to crabs or urchins, which are also included within this dietary group. In the trophic group analysis, the category benthic carnivores includes most predators of sponges based on diet information from

FishBase (www.fishbase.org), but some sponge predators could also be classed as herbivores or in other trophic categories, depending on the dietary mix and ontogenetic stage. Diet predictions of daily consumption at the species level indicate that sponges were consumed by different fish species of different sizes for the 4 trophic groups. Thus, a weakness of the trophic group analysis is that model outputs are based on compartmentalization into 4 predetermined trophic groups, whereas the predictive diet model provides finer taxonomic and size-related resolution.

Human influences on reef food webs

The Consume model provided new insights into fishing-induced changes to food webs. Of particular interest was much higher consumption of sessile biota such as algae and sponges in MPAs when the whole fish community is considered, which differs from expectations that fishing primarily removes top predators. Our conclusion is, however, based solely on southeastern Australian MPAs and for generalization needs confirmation over a greater geographical span. Reduction of sessile biota represents a key mechanism through which fishes can directly shape their habitat, with changes to habitat formers expected to affect other species and ramify further through food webs. Macroalgal stands represent a fundamental habitat for invertebrates and fishes on temperate rocky reefs through increased habitat complexity. Moreover, interactions between sponges and other taxa, including macroalgae and coral, are also widespread (Wulff 2006). Larger benthic invertebrate and fish populations are also generally associated with vegetated habitats (Ling 2008). Thus, a larger biomass of fishes in MPAs has the potential to alter the habitat complexity of macrophyte- and sponge-dominated systems. Such effects are likely to persist through the long term due to regulatory balances between primary producers, grazers, and predators (Christie et al. 2009).

Increased total consumption by the fish community as a result of recovering biomass in MPAs, as predicted through both modelling approaches, has important implications for energy flow through the system. Community consumption was greater, and mean prey size larger, in MPAs relative to fished sites, presumably a direct consequence of the increased abundance of large fishes in MPAs (Babcock et al. 2010, Edgar et al. 2014). Depression of the fish community through exploitation has clearly altered energy pathways involving invertebrates. Lower prey consumption at fished sites may mean that a substantial proportion of the benthic invertebrate productivity does not get eaten by the fish community but rather is consumed by invertebrates or suffers other sources of mortality. If this were the case, then higher abundances of benthic invertebrates should be present at fished sites compared to MPA sites (Langlois et al. 2005, 2006). MPAs either have higher invertebrate production to support the overall higher fish consumption rates, a disproportionately greater influence of fishes on lower trophic levels, or unlimited food that. Discriminating between these alternatives requires direct assessment of whether production of infaunal and epifaunal communities is higher, lower, or similar inside MPAs relative to outside.

Infaunal polychaetes have long been associated with locations that are heavily urbanized. For example, as human population density increases in nearby catchments, macrobenthic assemblages in Tasmanian estuaries undergo a pronounced shift from crustaceans to infaunal molluscs and polychaetes, a consequence of silt runoff transforming sedimentary habitats from sand to mud (Edgar & Barrett 2000). Notably, our model detected relatively high foraging rates on infaunal molluscs (mi) and polychaetes (pi) by the fish community at sites with high human population densities, regardless that the model is not informed by prey availability.

Greater fish biomass inside MPAs in southeastern Australia was observed in most trophic groups, but the opposite pattern was evident for small herbivores. This result contrasts with results of a study based on the full global RLS dataset, where no reduction in small herbivores was evident in MPAs (Soler et al. 2015). Top-down control by larger carnivores preying on small herbivores inside MPAs may be responsible, as inferred to occur elsewhere (Graham et al. 2003, Willis & Anderson 2003, Micheli et al. 2004). We suggest that differences between our regional and global studies arise because of a lack of extreme fishing pressure on small as well as large fishes in Australia. Subsistence fishing does not occur in southeastern Australia, so small fishes are not directly reduced in numbers at fished sites and thus have little potential to recover when protected in MPAs. Rather, numbers decline as populations of their predators increase. Interestingly, all size classes of herbivores showed a significant increase in biomass near human population centres, a likely response to organic enrichment and increased macroalgal production in temperate Australian seas where recreational anglers do not generally target herbivores.

Potential sources of error in predictions

Accuracy of the predictive diet model was potentially affected by several sources of error and bias. Error introduced by non-species level matches was considered negligible for estimates of prey type, given that the lack of any taxonomic information in a prior southern Australian study only decreased accuracy from 67 to 66% (Soler et al. 2016a), where accuracy was defined as the mean percentage of overlap between predicted prey types and those recorded independently in stomach contents. However, mean prey size accuracy, defined as the correlation (r^2) between predicted and observed mean prey size, declined from 0.56 to 0.39 when no taxonomic information was available, indicating the introduction of statistical noise into our estimates of prey size. Regardless, the very high correlation observed between the wet weight of the fish and the predicted mean prey size ($r^2 = 0.94$) for the southern Australian study (Soler et al. 2016a) indicates that estimates of prey size based solely on the size of the fish should be accurate.

Summation of prey predicted to be consumed by individuals across the community added additional error. Even though the predictions of daily food consumption were made for individual fish using the method of Palomares & Pauly (1989), and regardless of the high correlation (R = 0.87) between observed and predicted values in their study, we did not have specific values for the aspect ratio of the tail (A), which possibly added statistical noise to our calculations. However, Eq. (1) accommodates increased per capita consumption of small fishes, including relatively higher rates of consumption for immature individuals of a species compared with mature animals (Trites 2003) and for species of small body size (Rudolf & Rasmussen 2013).

An associated potential source of error relates to a general decline in metabolic rates, and hence consumption rates, per unit biomass as individual animals progress from juveniles to adults. Total community consumption inside MPAs could potentially be lower than predicted if a relatively high number of older fishes are present, given that daily consumption rates per unit body mass are lower for older individuals. Nevertheless, we consider that this has been reasonably accounted for by using size (biomass) as a proxy for age of the fish in the individual daily food consumption calculations based on Palomares & Pauly (1989) and because ontogenetic decline in metabolic rates with age is low compared to the influences of absolute body size and temperature. For example, Edgar & Shaw (1995a) found that these 2 factors explained 91% of the variation in log daily production among 62 species, and thus only 9% of variation was attributable to all other factors influencing net metabolic rates, including life history stage as well as stochastic sampling errors. Moreover, biases associated with individual animals should approximately balance overall in communities with a mixture of old and young individuals.

A further source of error arises from the predator–prey database used for mapping diets. The diet of 70% of fishes assessed was linked to temperate Australian gut contents studies (Edgar & Shaw 1995a, Soler & Edgar unpubl.), which included information on prey types and prey sizes for individual fishes. The remaining fish component (30% of total) was estimated using other datasets including FishBase (Table 1), which were not as detailed. Nevertheless, data analyzed here comprised means for thousands of individuals; consequently, error associated with calculations should partly average out and be consistent in relative comparisons and so should not greatly affect the general trends identified.

CONCLUSIONS

Estimates of prey consumption generated by Consume provide more nuanced descriptions of material and energy fluxes through the food web than have been generated to date by dynamic models reliant on trophic groups. The application of Consume has identified an additional trophic pathway affected by fishing in southeastern Australia. Selective fish capture has resulted in food webs with reduced consumption of habitat-forming algae and sessile invertebrates outside no-take MPAs, potentially indicating altered habitat complexity of rocky reef systems. Consume outputs describing prey consumption by fish communities should be linked to mechanistic models as part of an integrated modelling process for complex ecosystems (Weijerman et al. 2015), with the ultimate aim to improve decision making by management agencies dealing with conservation and fisheries issues (Lehuta et al. 2016).

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LITERATURE CITED

Babcock RC, Shears NT, Alcala A, Barrett NS and others (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proc Natl Acad Sci USA 107:18256–18261

Barber D (2011) Bayesian reasoning and machine learning. Cambridge University Press, Cambridge

Blanchard JL, Law R, Castle MD, Jennings S (2011) Coupled energy pathways and the resilience of size-structured food webs. Theor Ecol 4:289–300

Brown JH, Gillooly JF (2003) Ecological food webs: high-quality data facilitate theoretical unification. Proc Natl Acad Sci USA 100:1467–1468

Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Modell 172: 109–139

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396: 221–233

Conway D, White J (2012) Machine learning for hackers. O'Reilly Media, Sebastopol, CA

Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, Cambridge

Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem structure. Ecol Monogr 57:233–250

DiSalvo LH, Randall JE, Cea A (2007) Stomach contents and feeding observations of some Easter Island fishes. Atoll Res Bull 548:1–22

Edgar GJ, Barrett NS (2000) Effects of catchment activities on macrofaunal assemblages in Tasmanian estuaries. Estuar Coast Shelf Sci 50:639–654

Edgar GJ, Shaw C (1995a) The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. J Exp Mar Biol Ecol 194:53–81

Edgar GJ, Shaw C (1995b) The production and trophic ecology of shallow-water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. J Exp Mar Biol Ecol 194:83–106

Edgar GJ, Shaw C (1995c) The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. J Exp Mar Biol Ecol 194:107–131

Edgar GJ, Stuart-Smith RD (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. Sci Data 1:140007

Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S and others (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature 506: 216–220

Fulton EA, Link JS, Kaplan IC, Savina-Rolland M and others (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish Fish 12:171–188

Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environ Conserv 30: 200–208

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13(Suppl):117–137

Harmelin-Vivien M (1979) Ichtyofaune des recifs coralliens de Tulear (Madagascar): ecologie et relations trophiques. PhD dissertation, Universite Aix-Marseille II

Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol Monogr 30:65–127

Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish Bull 72:915–1031

Hutchinson GE (1978) An introduction to population ecology. Yale University Press, New Haven, CT

Jennings S, Warr KJ (2003) Smaller predator–prey body size ratios in longer food chains. Proc R Soc B 270:1413–1417

Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator–prey body mass ratios in food webs. Mar Ecol Prog Ser 240:11–20

Langlois TJ, Anderson MJ, Babcock RC (2005) Reef-associated predators influence adjacent soft-sediment communities. Ecology 86:1508–1519

Langlois TJ, Anderson MJ, Babcock RC (2006) Inconsistent effects of reefs on different size classes of macrofauna in adjacent sand habitats. J Exp Mar Biol Ecol 334:269–282

Lehuta S, Girardin R, Mahévas S, Travers-Trolet M, Vermard Y (2016) Reconciling complex system models and fisheries advice: practical examples and leads. Aquat Living Resour 29:208

Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia 156:883–894

Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. Ecol Appl 14:1709–1723

Ortiz M, Legault C, Ehrhardt N (2000) An alternative method for estimating bycatch from the US shrimp trawl fishery in the Gulf of Mexico, 1972–1995. Fish Bull 98: 583–599

Palomares M, Pauly D (1989) A multiple regression model for predicting the food consumption of marine fish populations. Mar Freshw Res 40:259–273

Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57:697–706

Polovina JJ (1984) Model of a coral reef ecosystem. Coral Reefs 3:1–11

Randall JE (1967) Food habits of reef fishes of the West Indies. Institute of Marine Sciences, University of Miami, FL

Rudolf VH, Rasmussen NL (2013) Ontogenetic functional diversity: size structure of a keystone predator drives functioning of a complex ecosystem. Ecology 94:1046–1056

Shin YJ, Cury P (2001) Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquat Living Resour 14: 65–80

Silverman B (1986) Density estimation for statistics and data analysis. Chapman and Hall, New York, NY

Soler GA, Edgar GJ, Thomson RJ, Kininmonth S and others (2015) Reef fishes at all trophic levels respond positively to effective marine protected areas. PLOS ONE 10: e0140270

Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (2016a) Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size. J Exp Mar Biol Ecol 480:1–7

Soler GA, Thomson RJ, Stuart-Smith RD, Smith ADM, Edgar GJ (2016b) Contributions of body size, habitat and taxonomy to predictions of temperate Australian fish diets. Mar Ecol Prog Ser 545:239–249

Spalding MD, Fox HE, Allen GR, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573–583

Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE and others (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501: 539–542

Trites AW (2003) Food webs in the ocean: Who eats whom and how much. In: Sinclair M, Valdimarsson G (eds) Responsible fisheries in the marine ecosystem. FAO, Rome, p 125–141

Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob Ecol Biogeogr 21:272–281

Weijerman M, Fulton EA, Janssen AB, Kuiper JJ and others (2015) How models can support ecosystem-based management of coral reefs. Prog Oceanogr 138:559–570

West GB, Brown JH (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. J Exp Biol 208:1575–1592

Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. Mar Ecol Prog Ser 257:209–221

Wulff JL (2006) Ecological interactions of marine sponges. Can J Zool 84:146–166

Zhang L, Hartvig M, Knudsen K, Andersen KH (2014) Size-based predictions of food web patterns. Theor Ecol 7: 23–33

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