

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

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28

29 **Abstract**

30

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

47

48 *Key words:* Australia; Fish diets; Herbivores; Marine protected areas; Marine
49 reserves; Trophic cascades

50

51 **1. Introduction**

52

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

66

67 The ecological role of aquatic species is highly flexible through their life history
68 (Cushing 1975, Edgar & Shaw 1995b, Jennings et al. 2002, Rudolf & Rasmussen
69 2013), with body size an important determinant of the location of individuals within
70 the food web (Dickie et al. 1987, Jennings & Warr 2003, Blanchard et al. 2011,
71 Zhang et al. 2014). In particular, similarly-sized taxa from vastly different
72 phylogenetic lineages may share greater similarity in diet than juveniles and adults of
73 the same species (Soler et al. 2016a). In a review of Ecopath with Ecosim,
74 Christensen & Walters (2004) highlight the value in creating separate trophic
75 categories at an intra-specific level, with complex trophic ontogeny. However, this is

76 computationally limited to few species in any community-level model, whereas an
77 ideal model would allow all species to change ecological roles as they grow, with
78 progression through prey types and sizes (Shin & Cury 2001, Brown & Gillooly 2003,
79 West & Brown 2005, Fulton et al. 2011). A recent advance in this area has been the
80 development of the statistical model *Consume*, which predicts the diet of individual
81 fishes with high accuracy on the basis of body size and taxonomic identity (Soler et
82 al. 2016a, Soler et al. 2016b). When predicted diets of individuals are aggregated at
83 the community level, ontogenetic changes for each species are included (Soler et al.
84 2016a, Soler et al. 2016b). Thus, a major benefit of this individual-based
85 agglomerative approach is that researchers do not have to decide how to delimit
86 groups by species or body size, as is necessary in dynamic models which involve
87 partitioning of the community.

88

89 Here we apply the *Consume* model using the extensive Reef Life Survey (RLS)
90 dataset for south-eastern Australia (Edgar & Stuart-Smith 2014). Species abundance
91 and size-distribution data were obtained through underwater visual surveys at 376
92 sites spanning 2500 km coastal distance and four marine ecoregions (sensu Spalding
93 et al. 2007). We estimate community-level consumption at each site, and use those
94 predictions to test hypotheses associated with key environmental and anthropogenic
95 drivers of fish community structure. Specifically, we address the questions:

96

97 (1) How do fishing and proximity to human population centres affect different
98 trophic levels of temperate reef ecosystems?

99

100 (2) How do ecological outcomes derived from predictions of community
101 consumption using *Consume* differ from those inferred using models with traditional
102 trophic group categories?

103

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

112

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

118

119 **2. Methodology**

120

121 *Consume model*

122

123 We used *Consume* (Soler et al. 2016a, Soler et al. 2016b) to predict prey
124 consumption for fish communities surveyed by visual census methods at shallow

125 rocky reef sites in the Australian states of Tasmania, Victoria and South Australia
126 (Fig. 1).

127

128 Data on fish community structure included species-level abundance and size
129 structure for all fishes sighted along 50 x 5 m belt transects by divers using RLS
130 methods, as described in detail by Edgar and Stuart-Smith (2014). At each site,
131 multiple transects (mean = 3.4) were undertaken along defined depth contours. Sites
132 were located in shallow reef habitats between 1 and 23 m depth, with mean depth of
133 7.5 m.

134

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

150

151 For this study, *Consume* was trained using detailed dietary information from 137 fish
152 species collected across southern Australia (Edgar & Shaw 1995b, c), as well as
153 publicly-available information for an additional 2,230 species through Fishbase
154 (www.fishbase.org) and other published and unpublished sources (Table 1). Dietary
155 information was only utilized from published sources when the size of individual fish,
156 species identity, and percentage of different prey types were provided. Dietary
157 information was standardized to percentage volume whenever needed. A total of 134
158 of the 252 fish species present in the RLS data used for this study were matched with
159 the diet content data collected across southern Australia by Edgar and Shaw (1995c)
160 at the species-, genus- or family level. For the species not present in that dataset, the
161 component of *Consume* that predicts prey type (Soler et al. 2016a, Soler et al. 2016b)
162 used 107 species from Fishbase and other publicly-available data. Only 11 species
163 present in the RLS field survey data did not have a match to dietary information at
164 family-level or better (following the sequential process described in Soler et al.
165 (2016a)); prey type for these was estimated based only on wet weight of the consumer
166 fish. When diet information at the species-level was lacking, and genus- or family-
167 level dietary information was applied, the loss of accuracy was minimal, as assessed
168 and demonstrated in prior studies (Soler et al. 2016a, Soler et al. 2016b). The most
169 important predictor for prey type was the size of the individual consumer fish, while
170 the most important predictor for mean prey size was the consumer's taxonomic
171 identity (Soler et al. 2016a, Soler et al. 2016b).

172

173 Prey types were classed within 13 categories (algae (*a*), 'sponges' (*s*), epifaunal
174 polychaetes (*pe*), infaunal polychaetes (*pi*), infaunal molluscs (*mi*), epifaunal

175 molluscs (*me*), small fishes (*f*), planktonic fish larvae (*fp*), infaunal crustaceans (*ci*),
176 epifaunal crustaceans (*ce*), planktonic crustaceans (*cp*), other epifauna (*oe*), other
177 infauna (*oi*). The category ‘sponges’ included sponges, ascidians and hydroids, while
178 ‘algae’ included some seagrass, and ‘planktonic fish larvae’ also included fish eggs.
179 For details of how the prey items were grouped into prey types, see Table S4
180 (Supplementary material).

181

182 *Daily prey consumption estimates*

183

184 Daily prey consumption per fish was calculated by combining the model output
185 of the percentage of each prey type and daily consumption rates (in proportion to fish
186 weight). For daily consumption calculations we used the model developed by
187 Palomares and Pauly (1989), which considers the weight of the fish, ambient
188 temperature, aspect ratio of its tail, and food type (Equation 1; Palomares & Pauly,
189 1989).

190

191
$$\ln Q/B = -0.1775 - 0.2018\ln W + 0.6121\ln T + 0.5156\ln A + 1.26F$$

192 (Equation 1)

193

194 where Q/B is the daily food consumption of a fish population as a percentage of its
195 biomass, W the weight (g) of the fish in question, T is mean habitat temperature (°C),
196 A is an aspect ratio of the tail based on its height and surface, and F is food type (0 in
197 carnivores, 1 in herbivores) (Palomares & Pauly 1989). We used individual weights
198 for each fish for this equation. Temperature was based on mean annual sea surface
199 temperature (SST) for each location extracted from Bio-Oracle (Tyberghein et al.

200 2012). We did not have individual fish information for A (aspect ratio of the tail),
201 consequently we used the mean value 2.2 from 33 species examined in Palomares and
202 Pauly (1989) from temperate to tropical waters. For F we scored each species with 0
203 or 1 depending on their diet preferences. These calculations provided a predicted daily
204 consumption for each individual fish recorded on RLS surveys for each prey type. On
205 average the daily food consumption for all the fish in this study was 3.6% (minimum
206 0.6% and maximum 30%). The highest daily consumption values were for
207 herbivorous fishes from the genus *Parma* and the lowest for *Dasyatis*. Total
208 community consumption was calculated as the sum of values for all individuals at a
209 site, accounting for abundance and size structure of all the fishes observed on rocky
210 reef surveys.

211

212 *Mean prey size*

213

214 By binning the predicted mean prey size following the sieve size categorization
215 described in Edgar and Shaw (1995b), we estimated the prey consumed for each fish
216 community by prey type for each size bin. A total of 19 size bins were
217 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,
218 32, 45 and 64 mm. Because model accuracy was affected by long tails of the prey size
219 distribution, we also undertook an analysis that combined all size classes smaller than
220 0.5 mm (<0.5) and all size classes larger than 11.2 mm (>11.2). Outputs of this
221 analysis matched findings with the finer scale bins, and are presented as
222 supplementary material (Figs. S1, S2).

223

224 *Effects of environmental and anthropogenic factors on prey consumption*

225

226 The effects of fishing and general human impacts on predicted community
227 consumption were assessed using linear mixed models (LMMs), with effect of
228 protection from fishing (MPAs) introduced after the influences of other anthropogenic
229 and environmental variables (annual mean sea surface temperature (SST), SST range,
230 and photosynthetically-active radiation (PAR-mean) and a human population index
231 (Pop index)) were considered. This was done to remove the effect of these covariates
232 prior to assessing the effect of protection granted by MPAs. Environmental data
233 relating to SST, SST range, and PAR-mean, as provided by Bio-Oracle (Tyberghein
234 et al. 2012), were considered because they were identified as important correlates of
235 spatial patterns of fish composition and biomass at regional scales in prior analyses
236 (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015). The human population
237 index (Pop index) was calculated using a quadratic Kernel function (Silverman 1986)
238 to a smoothly tapered surface for each of the human settlements created with the
239 glp00g gridded world population density dataset, as described in Soler et al. (2015).
240 Analyses of MPA effects first accounted for these four factors, plus the random effect
241 of ecoregion (as defined by Spalding et al. (2007)). The level of MPA protection for a
242 given site was classed as fished or no-take. Fished sites lay outside MPAs or inside
243 MPAs when fishing was allowed or with no indication of enforcement (Edgar et al.
244 2014).

245

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

249

250
$$y_{pei} = \mu + \beta_1 \text{SSTmean}_i + \beta_2 \text{SSTrange}_i + \beta_3 \text{PARmean}_i + \beta_4 \text{POPindex}_i +$$

251
$$\beta_5 \text{Protection} + \gamma_e + \varepsilon_{ei}$$

252 (Equation 2)

253
254 where $y_{pei} = \ln_e$ (natural logarithm) prey consumed (in g) at the i th site, given the
255 effects of SST mean, SST range, PAR-mean, human population and protection; $\mu =$
256 overall mean; $\gamma_e =$ effect of the e th ecoregion (as random effect); $\varepsilon_{ei} =$ residual error.
257 Ln ratios of daily prey consumption in MPAs relative to fished zones were obtained
258 for each prey type from the coefficient for Protection, β_5 . Ratios were obtained for the
259 other β coefficients from Equation 2 and transformed into % increment in biomass,
260 by $100 * (\exp(\beta) - 1)$. Due to the absence of some prey consumed at some of the prey
261 sizes in some of the predictions, we added a constant (= 0.05) to all the predictions
262 [$\ln(y + 0.05)$]. Given the prey consumption predictions were scaled in grams, the
263 addition of 0.05 grams to the predictions was chosen as a reasonable ecological value
264 for the step between no prediction and minimum daily predicted prey consumed
265 (Ortiz et al. 2000). A 4th root transformation of the predictions for daily prey
266 consumption was also applied, generating the same conclusions as ln transformation
267 with 0.05 g constant added. Results from the ln transformation are presented here so
268 that the effect of the different covariates can be shown as percentage (%) difference in
269 predicted daily prey consumed.

270
271 Effectiveness of the no-take MPAs relative to fished sites was estimated within
272 LMMs by estimating the log ratios of biomass in MPA over biomass in fished sites. A
273 similar process was followed with Pop Index where the relative effect of population

274 centres was estimated within the LMMs by estimating the log ratio of biomass for a
275 given value of Pop Index over a zero value of Pop index (no human centres nearby).

276

277 *Comparison of community prey consumption with trophic group biomass*

278

279 Ecological inferences based on *Consume* predictions were compared with conclusions
280 arising from more classical trophic group analysis on the same dataset. Four trophic
281 groups that are commonly applied (e.g. Halpern (2003)) to predator reef fishes were
282 used: higher carnivores, benthic carnivores, planktivores and herbivores, based on
283 dietary information obtained from Fishbase (www.fishbase.org) and previous studies
284 with the same dataset (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015).

285 A more detailed list of prey types consumed by each trophic group is described in
286 (Soler et al. 2015) based on the Fishbase classification. Trophic groups were further
287 categorised into three size classes: small (<7.5 cm), medium (7.5 – 30 cm) and large

288 (>30 cm), based on the total length of fishes observed during the surveys. Fish

289 biomass was subsequently estimated using the abundance and sizes of fishes on

290 transects and species-specific length-weight relationships provided in Fishbase. When

291 length weight relationships were unknown for a species, values were obtained from a

292 related species with similar shape. LMMs were then applied to the 376 sites to assess

293 the effects of protection (MPAs vs fished sites) and other environmental and

294 anthropogenic variables on the biomass of fishes in the twelve categories of trophic

295 group by size-class. The same environmental and anthropogenic variables were

296 investigated as with *Consume* output, and calculated as % difference in relative

297 biomass of the predator fish for the same set of sites.

298

299 Community consumption differences in MPAs compared with fished sites were
300 assumed to be proportional to relative biomass differences, partitioned between the
301 twelve trophic groups by size class categories. Even though the ratios for prey types
302 and trophic groups come from different calculations and their magnitudes differed,
303 they show similar relationships. For planktivores and herbivores, total % biomass
304 differences of the three size classes were estimated as the geometric mean of the
305 ratios and transformed to percentage difference of the increase in consumption of
306 plankton and algae, respectively. Consumption of small fishes (*f*) as prey was
307 predicted as the geometric mean of the ratios of medium and large higher carnivores,
308 as small individuals were likely to feed on fishes. The geometric mean estimates were
309 transformed into percentage increase of medium and large higher carnivores.
310 Consumption of benthic invertebrates was predicted from the geometric mean of the
311 ratios of small higher carnivores and all sizes of benthic carnivores; this geometric
312 mean estimate was then transformed to a percentage difference. A similar process was
313 applied when assessing the influence of human population, including an assumption
314 that consumption differences were proportional to biomass differences for the twelve
315 categories of trophic group by size.

316

317 **3. Results**

318

319 *Effects of environmental and anthropogenic factors on prey consumption*

320

321 Prey type, mean prey size and daily prey consumption were estimated for 44,024
322 fishes observed in 376 sites across Tasmania, South Australia and Victoria. Dietary
323 information was not available for many species; estimates of mean prey size based on

324 species-level matches (plus wet weight) were possible in 14,089 cases (32%), genus-
325 level matches in 6,662 cases (15%), family-level matches in 14,946 cases (34%),
326 while wet weight only was used to generate diet predictions in 8,327 cases (19%).
327 Based on initial testing of *Consume*, the accuracy of predictions of prey size decreases
328 slightly when not all the taxonomic information of the predator fish is available, and
329 decreases further when predictions are based only on wet weight of the predator fish,
330 albeit still with reasonable accuracy (Soler et al. 2016a, Soler et al. 2016b). These
331 numbers imply poorer predictions of prey size than prey type (Table 1), with prey
332 type predictions from family-level or better matches in 42,270 cases (96%), and
333 predictions based only on wet weight of the consumer fish in 1,754 cases (4%).

334

335 The prey types of 30,831 (70%) of a total of 44,024 fishes were estimated using
336 comparative temperate Australian data from Edgar & Shaw (1995a, b) and Soler and
337 Edgar (*unpublished*) (Table 1). The prey types of the remaining 13,193 (30%) fishes
338 were estimated using other datasets (Table 1).

339

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

349

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

360

361 Most prey size classes greater than 1.4 mm were consumed in greater quantities
362 by fish communities protected in MPAs relative to fished areas (Fig. 3A; Table S2).
363 Larger prey consumed inside MPAs reflected recovery of populations of larger fish
364 species, and larger average sizes of fishes at protected sites. Prey size predictions
365 were not significantly different between locations of high and low human population
366 density; except for the 1.4 and 2 mm size classes (Fig. 3B).

367

368 *Comparison of community prey consumption vs trophic group biomass*

369

370 Large and medium size classes of the four trophic groups had significantly
371 greater biomass inside MPAs relative to fished sites (Fig. 4A; Table S3). Trophic
372 group analysis indicated average consumption of fishes and large invertebrates was
373 116% higher, and algae 62% higher, in MPAs (Table 2). The small size class of

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

384

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

395

396 **4. Discussion**

397

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

405

406 Sponges were partly included amongst items consumed by ‘benthic carnivores’,
407 but are functionally very different to crabs or urchins, which are also included within
408 this dietary group. In the trophic group analysis, the category ‘benthic carnivores’
409 includes most predators of sponges based on diet information from Fishbase
410 (www.fishbase.org), but some sponge predators could also be classed as herbivores or
411 in other trophic categories, depending on the dietary mix and ontogenetic stage. Diet
412 predictions of daily consumption at the species level indicate that sponges were
413 consumed by different fish species of different sizes for the four trophic groups. Thus,
414 a weakness of the trophic group analysis is that model outputs are based on
415 compartmentalization into four predetermined trophic groups, whereas the predictive
416 diet model provides finer taxonomic and size-related resolution.

417

418 The *Consume* model provided new insights into fishing-induced changes to food
419 webs. Of particular interest was much higher consumption of sessile biota such as
420 algae and sponges in MPAs when the whole fish community is considered, which
421 differs from expectations that fishing primarily removes top predators. Our conclusion
422 is, however, based solely on south-eastern Australian MPAs, and for generalization

423 needs confirmation over a greater geographical span. Reduction of sessile biota
424 represents a key mechanism through which fishes can directly shape their habitat,
425 with changes to habitat-formers expected to affect other species and ramify further
426 through food webs. Macroalgal stands represent a fundamental habitat for
427 invertebrates and fishes on temperate rocky reefs through increased habitat
428 complexity. Moreover, interactions between sponges and other taxa, including
429 macroalgae and coral, are also widespread (Wulff 2006). Larger benthic invertebrate
430 and fish populations are also generally associated with vegetated habitats (Ling 2008).
431 Thus, a larger biomass of fishes in MPAs has the potential to alter the habitat
432 complexity of macrophyte- and sponge-dominated systems. Such effects are likely to
433 persist through the long term due to regulatory balances between primary producers,
434 grazers and predators (Christie et al. 2009).

435

436 Increased total consumption by the fish community as a result of recovering
437 biomass in MPAs, as predicted through both modelling approaches, has important
438 implications for energy flow through the system. Community consumption was
439 greater, and mean prey size larger, in MPAs relative to fished sites, presumably a
440 direct consequence of increased abundance of large fishes in MPAs (Babcock et al.
441 2010, Edgar et al. 2014). Depression of the fish community through exploitation has
442 clearly altered energy pathways involving invertebrates. Lower prey consumption at
443 fished sites may mean that a substantial proportion of the benthic invertebrate
444 productivity does not get eaten by the fish community, but rather is consumed by
445 invertebrates or suffers other sources of mortality. If this were the case, then higher
446 abundances of benthic invertebrates should be present at fished sites compared to
447 MPA sites (Langlois et al. 2005, 2006). MPAs either have higher invertebrate

448 production to support the overall higher fish consumption rates, a disproportionately
449 greater influence of fishes on lower trophic levels, or food is not limiting.
450 Discriminating between these alternatives requires direct assessment of whether
451 production of infaunal and epifaunal communities is higher, lower or similar inside
452 MPAs relative to outside.

453

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

462

463 Greater fish biomass inside MPAs in south-eastern Australia was observed in
464 most trophic groups, but the opposite pattern was evident for small herbivores. This
465 result contrasts with results of a study based on the full global RLS dataset, where no
466 reduction in small herbivores was evident in MPAs (Soler et al. 2015). Top-down
467 control by larger carnivores preying on small herbivores inside MPAs may be
468 responsible, as inferred to occur elsewhere (Graham et al. 2003, Willis & Anderson
469 2003, Micheli et al. 2004). We suggest that differences between our regional and
470 global studies arise because of a lack of extreme fishing pressure on small as well as
471 large fishes in Australia. Subsistence fishing does not occur in south-eastern
472 Australia, so small fishes are not directly reduced in numbers at fished sites, and thus

473 have little potential to recover when protected in MPAs. Rather, numbers decline as
474 populations of their predators increase. Interestingly, all size classes of herbivores
475 showed a significant increase in biomass near human population centres, a likely
476 response to organic enrichment and increased macroalgal production in temperate
477 Australian seas where recreational anglers do not generally target herbivores.

478

479 *Potential sources of error in predictions*

480

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

494

495 Summation of prey predicted to be consumed by individuals across the community
496 added additional error. Even though the predictions of daily food consumption were
497 made for individual fish using the method of Palomares and Pauly (1989), and

498 regardless of the high correlation ($R = 0.87$) between observed and predicted values in
499 their study, we did not have specific values for the aspect ratio of the tail (A), which
500 possibly added statistical noise in our calculations. However, Equation 1
501 accommodates increased per capita consumption of small fishes, including relatively
502 higher rates of consumption for immature individuals of a species compared with
503 mature animal (Trites 2003), and for species of small body size (Rudolf & Rasmussen
504 2013).

505

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

521

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

531

532 *Conclusion*

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

545

546

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548

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554 *Consume* model. Additionally, we thank Dr. Stuart Kininmonth for providing
555 estimates of human population across the study area. Input and comments by Dr.
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- 690

691 **Tables**

692 **Table 1** Sources of diet information and number of fish included in the model as
693 prediction data set. Level of information was based on the type of information
694 available. Prey type was expressed as percentage of diet.

695

Region	Reference	# of fish	# of species	Level of information
Southern Australia	(Edgar & Shaw 1995b, c)	4336	137	Prey type; prey size
Tasmania, Australia	Soler and Edgar (<i>unpublished</i>)	11	4	Prey type; prey size
Easter Island	DiSalvo et al. (2007)	77	37	Prey type; some prey size information
Madagascar	Harmelin-Vivien (1979)	110	110	Prey type; some prey size information
West Indies	Randall (1967)	163	125	Prey type; some prey size information
Marshall Islands	Hiatt and Strasburg (1960)	75	70	Prey type
Hawaii	Hobson (1974)	82	77	Prey type
Global	Fishbase	3845	1586	Prey type

696

697

698

699 **Table 2.** Comparison of community consumption estimates from *Consume* with those
 700 derived from the trophic group model, with results expressed as percent ratio increase
 701 for MPAs/fished areas and for one unit increase in the population index. Means of the
 702 biomass change of trophic groups and total means were calculated as the geometric
 703 mean of the ratios and converted to percentage change. *N.S.* = no significant
 704 difference. S = Small; M=Medium; L=Large.

Trophic group	Prey category	Trophic group predictions for MPAs	<i>Consume</i> predictions for MPAs	Trophic group predictions per unit increase in Pop index	<i>Consume</i> predictions per unit increase in Pop index
Herbivores	algae	62	281	132	1100
Higher carnivores L + M	fish	116	262	-41	-24 (<i>N.S.</i>)
Benthic carnivores S+M+L & Higher carnivores S	sponges	28	273	-27	99 (<i>N.S.</i>)
	epifaunal crustaceans		34		-26 (<i>N.S.</i>)
	epifaunal molluscs		34		6 (<i>N.S.</i>)
	epifaunal polychaetes		36		-36 (<i>N.S.</i>)
	other epifauna		67		34 (<i>N.S.</i>)
	infaunal crustaceans		40		-57
	infaunal molluscs		1 (<i>N.S.</i>)		165
	infaunal polychaetes		-3 (<i>N.S.</i>)		54
	other infauna		-15 (<i>N.S.</i>)		-1 (<i>N.S.</i>)
Planktivores S+M+L	planktonic fish larvae	27	154	34	-24 (<i>N.S.</i>)
	planktonic crustaceans		73		37 (<i>N.S.</i>)
Total mean		48	71	9	27

705

706

707

708 **Figures**



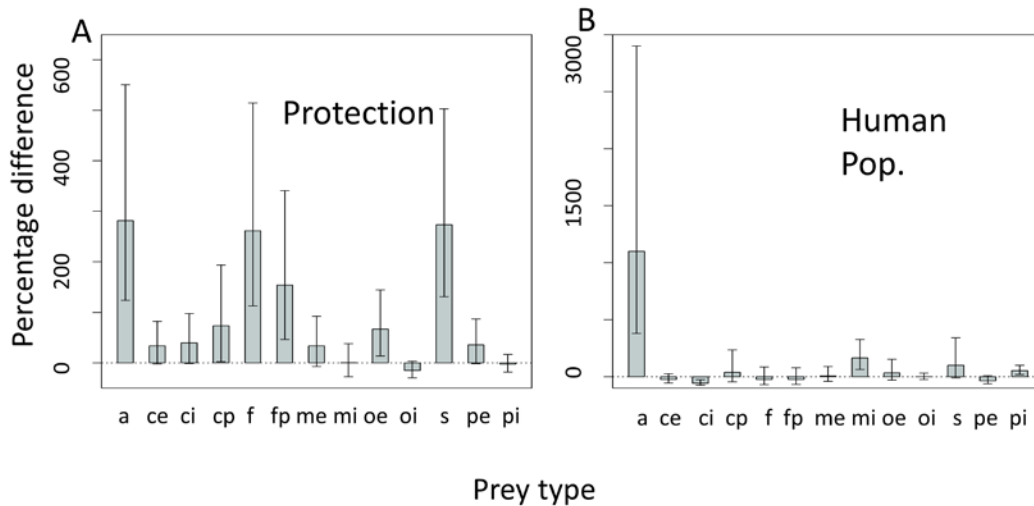
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711 **Figure 1** Reef Life Survey (RLS) sites investigated in South Australia, Victoria and

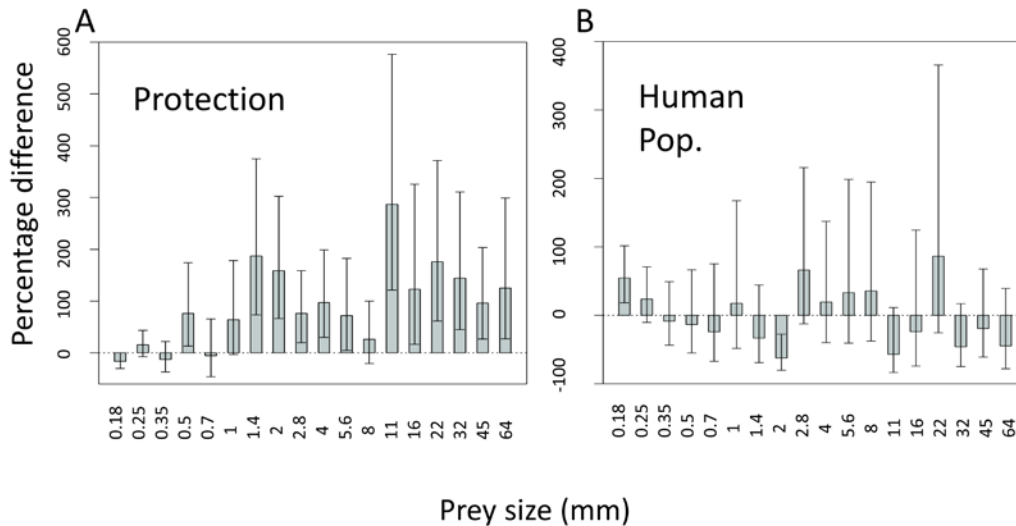
712 Tasmania.

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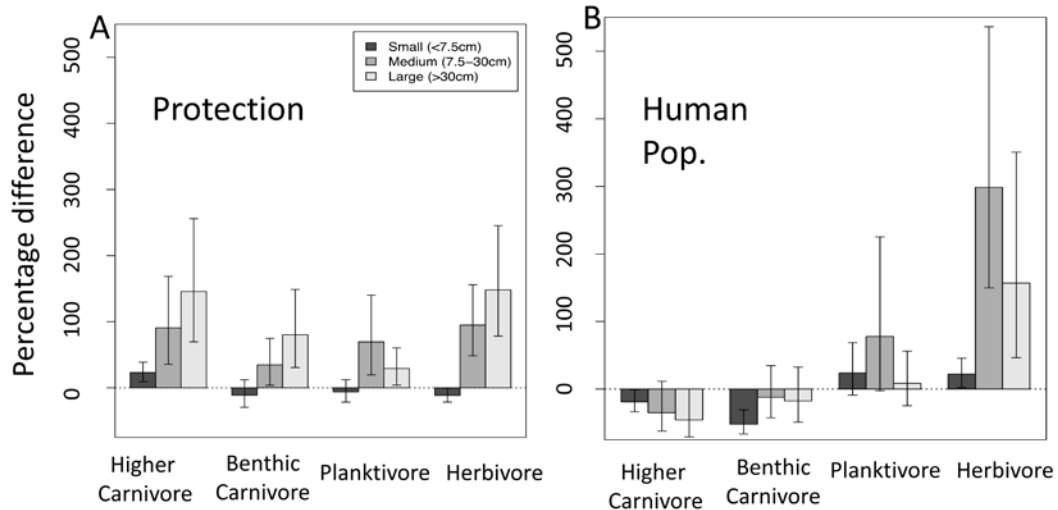
714

715 **Figure 2** (A) Percentage difference in prey types consumed (\pm 95% confidence
716 intervals) by the fish community at sites in protected areas relative to fished zones. Ln
717 ratios of daily prey consumption in MPAs relative to fished zones were obtained for
718 each prey type from the coefficient for Protection, β_5 . (B) Percentage difference for a
719 single unit increase in the index of local human population density obtained for each
720 prey type from the coefficient for Pop index, β_4 . Ratios were obtained from the
721 coefficients for Pop index, β_4 and Protection, β_5 , and transformed into percentage
722 difference in biomass using the relation $100 * (\exp(\beta_4) - 1)$ and $100 * (\exp(\beta_5) - 1)$ from
723 Equation 2 on this manuscript. Significant differences ($p < 0.05$) were evident when
724 the maximum and minimum values of the confidence interval bars did not overlap
725 zero. Prey types: algae (*a*), sponges (*s*), epifaunal polychaetes (*pe*), infaunal
726 polychaetes (*pi*), infaunal molluscs (*mi*), epifaunal molluscs (*me*), fishes (*f*),
727 planktonic fish larvae (*fp*), infaunal crustaceans (*ci*), epifaunal crustaceans (*ce*),
728 planktonic crustaceans (*cp*), other epifauna (*oe*), other infauna (*oi*).



729

730 **Figure 3** (A) Percentage difference in daily consumption of different size classes for
731 all prey types consumed by the fish community in protected areas relative to fished
732 zones (\pm 95% confidence intervals). (B) Percentage difference for a single unit
733 increase in the index of local human population density obtained for each prey size
734 bin from the coefficient for Pop index, β_4 . Ratios were obtained from the coefficients
735 for Pop index, β_4 and Protection, β_5 , and transformed into percentage difference in
736 biomass using the relation $100*(\exp(\beta_4)-1)$ and $100*(\exp(\beta_5)-1)$ from Equation 2 on
737 this manuscript. Significant differences ($p < 0.05$) were evident when the maximum
738 and minimum values of the confidence interval bars did not overlap zero.



739

740 **Figure 4** (A) Percentage difference in biomass for different trophic groups and size
741 categories due to the level of protection at sites surveyed in Tasmania, Victoria and
742 South Australia (\pm 95% confidence intervals). (B) Percentage difference for single
743 unit increase in the population density index (\pm 95% confidence intervals) for each of
744 four major trophic groups and size classes in the surveyed sites. Ratios were obtained
745 from the coefficients for Pop index, β_4 and Protection, β_5 , and transformed into
746 percentage difference in biomass using the relation $100*(\exp(\beta_4)-1)$ and
747 $100*(\exp(\beta_5)-1)$ in Equation 2 of (Soler et al. 2015). The model adjusted for SST
748 mean, SST range, PAR-mean and human population. Significant differences ($p <$
749 0.05) were evident when the maximum and minimum values of the confidence
750 interval bars extended above or below zero.