

1 **Running title:** Invasion impacts at different trophic levels

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5 **Ecological impacts of invading seaweeds: a meta-analysis of their**
6 **effects at different trophic levels**

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24 **ABSTRACT**

25 **Aim** Biological invasions are among the main threats to biodiversity. To promote a mechanistic
26 understanding of the ecological impacts of non-native seaweeds, we assessed how effects on
27 resident organisms vary according to their trophic level.

28 **Location** Global.

29 **Methods** We performed meta-analytical comparisons of the effects of non-native seaweeds on both
30 individual species and communities. We compared the results of analyses performed on the whole
31 dataset with those obtained from experimental data only and, when possible, between rocky and
32 soft-bottoms.

33 **Results** Meta-analyses of data from 100 papers revealed consistent negative effects of non-native
34 seaweeds across variables describing resident primary producer communities. In contrast, negative
35 effects of seaweeds on consumers emerged only on their biomass and, limited to rocky bottoms,
36 diversity. At the species level, negative effects were consistent across primary producers' response
37 variables, while only the survival of consumers other than herbivores or predators (e.g.
38 deposit/suspension feeders or detritivores) decreased due to invasion. Excluding mensurative data,
39 negative effects of seaweeds persisted only on resident macroalgal communities and consumer
40 species survival, while switched to positive on the diversity of rocky bottom consumers. However,
41 negative effects emerged for other consumers biomass and density in rocky habitats.

42 **Main conclusions** Our results support the hypothesis that seaweeds' effects on resident biodiversity
43 are generally more negative within the same trophic level than on higher trophic guilds. Finer
44 trophic grouping of resident organisms revealed more complex impacts than previously detected.
45 High heterogeneity in the responses of some consumer guilds suggests that impacts of non-native
46 seaweeds at higher trophic levels may be more invader- and species-specific than competitive
47 effects at the same trophic level. Features of invaded habitats may further increase variability in

48 seaweeds' impacts. More experimental data on consumers' response to invasion are needed to
49 disentangle the effects of non-native seaweeds from those of other environmental stressors.

50 **Keywords** biological invasions; effect size; impact analysis; mensurative and experimental data;
51 non-native seaweeds; trophic groups.

52

53 INTRODUCTION

54 Biological invasions are globally acknowledged among the major threats to biodiversity
55 (Parker et al. 1999, Simberloff et al. 2005). Concerns over their potential ecological, social and
56 economic consequences have resulted in a plethora of studies aiming to estimate the direction and
57 magnitude of the effects of non-native plants on resident species and communities (e.g. Britton-
58 Simmons 2004, Vilà et al. 2006, Liao et al. 2007, Bulleri et al. 2010). Despite such a large research
59 effort, a comprehensive framework for understanding the impacts of invaders is still lacking, likely
60 as a consequence of the difficulties in distilling generalities from disparate case studies (Vilà et al.
61 2011, Blackburn et al. 2014, Jeschke et al. 2014). In the last few years, some progress has been,
62 however, made through qualitative syntheses and quantitative meta-analyses of available
63 information (Schaffelke and Hewitt 2007, Williams and Smith 2007, Gaertner et al. 2009, Thomsen
64 et al. 2009, 2014, Powell et al. 2011, Vilà et al. 2011).

65 Some of these syntheses suggest a tendency for the effects of non-native plants on resident
66 plant communities to be consistently negative, while their effects on animal communities are more
67 variable (Gaertner et al. 2009, Thomsen et al. 2009, Powell et al. 2011, Vilà et al. 2011, Thomsen et
68 al. 2014). A recent meta-analysis by Thomsen et al. (2014) has shown that marine invaders
69 generally have negative effects on biodiversity at the same trophic level, but less negative, or indeed
70 positive effects on biodiversity at higher trophic levels. These patterns suggest that competition
71 would prevail in interactions between resident and non-native species within a trophic level, while
72 processes such as habitat-formation and food provision would ultimately result in neutral to positive
73 effects towards higher trophic levels (Thomsen et al. 2014).

74 In the meta-analysis by Thomsen et al. (2014), the first, to our knowledge, to assess how the
75 effects of invaders vary with trophic level, local communities were categorized as plant, animal or
76 mixed. Often, a finer trophic resolution of animal communities cannot be extracted from published
77 data because studies typically group species with disparate life-history traits and different trophic

78 levels together. In contrast, the trophic level of individual consumer species can be generally
79 established. Specific hypotheses formulated to explain differences in the effects of non-native plants
80 on species at different trophic levels can be, thus, formally tested, promoting a mechanistic
81 understanding of invaders impacts on resident biodiversity and ecosystem functioning.

82 To address this issue, we undertook a global meta-analytical comparison of the effects of non-
83 native seaweeds within and on higher trophic guilds. We focused on seaweeds since they play a key
84 role in providing habitat and represent a substantial component in the primary productivity of
85 marine environments (Mann 1973). Anthropogenic activities have greatly facilitated the global
86 spread of seaweeds, causing more than 400 cases of introduction to non-native locations worldwide
87 (Williams and Smith 2007). A relatively large proportion of these introduced seaweeds have been
88 successful in becoming invasive and establishing large populations in the invaded range. Over the
89 last two decades, non-native seaweeds have catalysed the attention of marine ecologists, producing
90 a large body of literature describing their impacts on extant communities.

91 Importantly, there are indications that non-native seaweeds have notable effects on resident
92 species throughout the food chain. For instance, generalist herbivores (including gastropods,
93 isopods, polychaetes, sea urchins, fishes) have been observed to consume non-native seaweeds in
94 the majority of feeding experiments (e.g. Britton-Simmons 2004, Dumay et al 2002), suffering, in
95 some cases, physiological damage (Trowbridge and Todd 2001, Box et al. 2009, Terlizzi et al.
96 2011, Tomas et al. 2011). Non-native seaweeds can, on the other hand, indirectly affect organisms
97 at higher trophic levels through the modification of the abiotic environment. For example, the
98 invasive epiphyte *Lophocladia lallemandii* can cause oxidative stress in a filter-feeding bryozoan
99 living within *Posidonia oceanica* meadows, by generating water anoxia (Deudero et al. 2010). In
100 contrast, the intricate web of stolons formed by the invasive *Caulerpa racemosa* provides small
101 crustaceans with a refuge from predators (Pacciardi et al. 2011). In other cases, non-native
102 seaweeds have been shown to decrease the density of dominant mesofauna (important to higher

103 level consumers), likely through a reduction in habitat complexity (Janiak and Whitlatch 2012).
104 Thus, the spread of non-native seaweeds represents an ideal model system to assess how the effects
105 of an invasion can propagate through different trophic levels of resident communities.

106 Here, we provide the results of a systematic review and meta-analyses (Pullin and Stewart
107 2006, Lortie 2014) of the published literature on the effects of non-native seaweeds on resident
108 organisms. In addition to previous meta-analyses investigating the impacts of primary producers on
109 resident communities at different trophic levels (Thomsen et al. 2009, 2014, Vilà et al. 2011), we
110 explored variations in the effects of non-native seaweeds among consumer species characterized by
111 marked differences in life-traits. In particular, our aim was to assess how the effects of non-native
112 seaweeds on resident species and communities vary i) according to their trophic level (for species-
113 level responses: primary producers vs. herbivores vs. predators vs. other consumers; for community-
114 level responses: primary producers vs. consumers) and ii) among habitats. In addition, in order to
115 assess to which extent study selection criteria may account for contrasting results generated by
116 previous works (Thomsen et al. 2009, 2014), we compared the results of analyses performed on the
117 whole dataset (i.e. both mensurative and experimental data) with those of analyses on experimental
118 data only.

119 **METHODS**

120 **Literature search**

121 We searched the ‘ISI Web of Science’ database for relevant literature in June 2012, with no
122 restriction on publication year, using the following search term combinations: (alga* OR
123 macroalga* OR seaweed*) AND (alien* OR invasi* OR introduced OR allochthonous OR
124 nonindigenous OR non-indigenous OR “non native*” OR non-native* OR exotic*) AND (marine
125 OR brackish OR estuar*OR coastal OR shallow OR sea*OR aquatic OR maritime OR lagoon* OR
126 pelagic OR benth* OR demersal OR shore* OR intertidal OR subtidal OR ocean* OR bay OR

127 cove) AND (impact* OR effect* OR influence OR consequence* OR food-web* OR “food web*”
128 OR ecosystem* OR biomass OR biodiversity OR “biological diversity” OR communit* OR
129 richness OR diversity OR abundance OR evenness OR cover OR density OR “reproductive
130 capacity” OR mortality OR growth OR assemblage* OR producti* OR decomposition OR “nutrient
131 cycl*” OR oxygen OR carbon OR flux OR respiration OR “ecosystem metabolism” OR “sediment
132 stabilisation” OR epiphyte* OR “sediment mixing” OR resilience OR stability OR resistance OR
133 invasibility). Reference lists from all the retrieved articles were then screened for further relevant
134 publications.

135 Assessment of references obtained through the search was performed through a 3-step process:
136 1) scanning of article titles (mostly to exclude articles dealing with completely unrelated topics); 2)
137 reading of the abstract and 3) reading of full text. We required studies to quantitatively compare
138 relevant response variables between invaded and non-invaded units (with the term ‘unit’ meaning
139 organisms / individual / plots / treatments / areas / sites / locations / regions), invaded vs. invader
140 removal units or control (no invader) vs. invader-transplanted units. This resulted in an initial set of
141 144 papers that were evaluated against the following criteria for data inclusion:

142 1) Papers without replication or appropriate controls were excluded. We evaluated whether
143 controls and invaded units were sufficiently similar but spatially and temporally
144 independent.

145 2) Studies were excluded when manipulation (generally the removal) of the non-native
146 seaweed was not carried out independently from that of resident species. For example, the
147 manipulation of canopy stands including both non-native and resident seaweeds (Farrell &
148 Fletcher 2004).

149 3) Studies were excluded when non-invaded sites were characterized by the presence of other
150 non-native species. For example, sites invaded by *Caulerpa racemosa* compared to sites
151 heavily colonized by *Wormesleyella setacea* (Klein & Verlaque 2009).

- 152 4) Studies were excluded when variations in response variables could not be unambiguously
153 interpreted as positive or negative effects (e.g. relative proportion of individuals exhibiting a
154 certain colouring; Arigoni et al. 2002).
- 155 5) In the case of mensurative studies reporting time series, the first and last time of sampling
156 were used, in order to account for variation through time. In contrast, for experimental
157 studies, only the last time of sampling was extracted, assuming that the effects of
158 experimental manipulations (removal or addition of the invader) are more likely to manifest
159 on longer temporal scales.
- 160 6) When data could not be directly extracted from papers, the authors of the original study
161 were asked to provide either raw data or relevant information (e.g. means, standard
162 deviation/variance, sample size). Studies were not included when this procedure did not
163 allow us to obtain estimates of variation in the effect sizes, necessary for weighted analyses.

164 **Data extraction and effect sizes**

165 We extracted means, measures of variability (i.e. standard errors, standard deviations,
166 confidence intervals) and sample sizes for units where the non-native species was present or absent.
167 Data extraction from graphs was carried out by means of the image analysis software ImageJ
168 (Schneider et al. 2012). We retained variables accounting for the response to invasion of either
169 single species or communities. Our operative definition of community includes the presence of
170 more than one species or any taxonomic group higher than species, including morphological or
171 functional groups. We analysed data on variables related to density/cover, biomass, growth and
172 survival of individual species and density/cover, biomass, diversity (including both richness and
173 diversity indices) and evenness of communities (see Table 1 for the detailed list of variables
174 included within each category). Density and cover constitute somewhat different estimates of
175 abundance; however, data on percentage cover came almost exclusively from studies on plants, so
176 that no analyses could be run separately for this variable. Instead of losing a large amount of data on

177 plants, we, therefore, decided to merge density and cover data (Vilà et al. 2011). Studies reporting
178 data on species fitness variables different from growth or survival were not considered, and a total
179 of 100 studies were finally included in the analyses (see Appendix S1 and Table S1).

180 We calculated Hedges' g^* , which measures the unbiased, standardized mean difference
181 between invaded and non-invaded means (Borenstein et al. 2009). Negative and positive Hedges'
182 g^* values indicate, respectively, negative and positive effects of non-native species on resident
183 communities or species. Hedges' g^* was calculated as:

184 $g^* = gJ$ where

$$185 \quad g = \frac{x_{Invaded} - x_{Not\,invaded}}{SD_{pooled}} \text{ with } SD_{pooled} = \sqrt{\frac{(n_{Invaded}-1)SD_{Invaded}^2 + (n_{Not\,invaded}-1)SD_{Not\,invaded}^2}{n_{Invaded} + n_{Not\,invaded} - 2}}$$

$$186 \quad \text{and } J = 1 - \frac{3}{4(n_{Invaded} + n_{Not\,invaded} - 2) - 1}$$

187 Effect sizes for primary producers and consumers were estimated from the dataset and its
188 subsets (experimental data only, rocky bottom or soft bottom data only) by means of mixed-effects
189 models (Borenstein et al. 2009). In mixed-effects models, a fixed-effect was used to model among
190 groups variability (trophic level in this case), while a random-effect was used to model within
191 groups variability. The effect sizes of individual comparisons were weighted by the inverse of
192 within-study variance plus between-study variance, the latter being calculated within levels of the
193 moderator (i.e., trophic levels). Effect sizes were first calculated using all the data available in the
194 dataset or in the subsets, including multiple estimates from each study, when available. However,
195 this procedure does not take into account potential autocorrelation among observations within
196 studies, thus violating the assumption of independence in the data (Borenstein et al. 2009). In
197 addition, when computing summary effects across studies, it assigns more weight to studies with
198 multiple outcomes. One approach to solve this issue is to average within studies across sources of
199 independence (e.g. multiple sites, different times of sampling, comparison of the same invasive

200 species with several native species) in order to generate one single effect size per response variable
201 per study. However, unless the degree of autocorrelation among observations being averaged is
202 known and explicitly incorporated into calculations, the estimates of variances associated to the
203 means are based on the assumption of a zero correlation (Borenstein et al. 2009). This is likely to
204 lead to over- or under-estimation of variance and underestimation of the precision of the difference
205 (Borenstein et al. 2009). For the reasons explained above and following Gibson et al. (2011) and He
206 et al. (2013), median effect sizes and 95% confidence intervals were calculated by resampling one
207 observation per publication, using 10000 bootstrap samples, generated with replacement. Median
208 effect sizes were considered significantly different from zero when their 95%-confidence intervals
209 do not overlap zero.

210 For analyses focusing on variables at the species level, resident consumers were categorized
211 as “predators” (parasites were excluded), “herbivores” or “other consumers” (such as suspension
212 feeders, deposit feeders and/or detritivores) based on information obtained from MarLIN (The
213 Marine Life Information Network; <http://www.marlin.ac.uk/>) and FishBase
214 (<http://www.fishbase.org/>) databases and expert opinion when information on feeding habit was not
215 available. Predators and herbivores included also species that, in addition to either herbivory or
216 predation, may exhibit other lower order feeding habits.

217 The null hypothesis (no difference in the effect size between primary producers and
218 consumers) was tested through the Q statistic, a weighted sum of squares following a χ^2 distribution
219 describing variation in the effect size between groups (Borenstein et al. 2009; Viechtbauer 2010).
220 To test for the significance of differences between trophic levels (primary producers vs. consumers
221 for community level variables; primary producers vs. predators vs. herbivores vs. other consumers
222 for species level variables) we used the between-group heterogeneity of the mixed-effect models (a
223 weighted sum of squares describing variation in effect size between groups; Borenstein et al. 2009;
224 Viechtbauer 2010). The effects of the moderator (i.e. the trophic level) were deemed as significant

225 when the median Q_M , generated by data permutations, exceeded the critical value (corresponding to
226 $\alpha = 0.05$) obtained from the null distribution generated by permutations with re-shuffling of labels
227 (trophic levels). The exact significance level (P_{Between}) was estimated as the proportion of times out
228 of 10000 permutations in which the median Q_M was smaller than the critical Q value from the null
229 distribution (i.e., $(Q_{M\text{Null}} \geq \text{median}Q_M)/10000$).

230 **Tests for publication bias**

231 To assess publication bias we visually examined funnel plots of effect size standard errors
232 against residuals (based on mixed-model effect size calculations) and tested their asymmetry
233 through a rank correlation test (Viechtbauer 2010). Asymmetry in funnel plots emerged for
234 community density/cover ($\tau=-0.21$, $P<0.0001$) and diversity ($\tau=-0.34$, $P<0.01$), but not for the other
235 variables (Table S2, Figure S1). Asymmetry emerged as a consequence of some data with large
236 residual values and high variances. Following He et al. (2013), these data were removed to adjust
237 for potential publication bias (Figure S1). Adjusting for publication bias did not change the
238 outcomes of the analyses on resident community density/cover (Tables S3), suggesting that
239 publication bias did not have a severe effect on our results. In contrast, adjusting for potential bias
240 in the diversity data caused the difference in effect sizes between the two trophic levels to be not
241 significant (see “Mensurative and experimental studies” in Table S3). We conducted analyses using
242 the *metafor* package (Viechtbauer 2010), in R v2.15 (R Development Core Team 2013).

243

244 **RESULTS**

245 Among the 100 papers we retained, experimental data (both from field or laboratory studies)
246 were extracted from a total of 48 papers, and mensurative data were extracted from 65 papers. Data
247 related to the effects of 12 seaweeds, which were generally described as invasive in the study
248 regions (Parker et al. 1999, Ricciardi and Cohen 2007): *Caulerpa racemosa*, *Caulerpa taxifolia*,

249 *Codium fragile* spp., *Fucus evanescens*, *Fucus serratus*, *Grateloupia turuturu*, *Gracilaria*
250 *vermiculophylla*, *Lophocladia lallemandii*, *Neosiphonia harvey*, *Sargassum muticum*, *Undaria*
251 *pinnatifida* and *Wormesleyella setacea*. Experimental data were available for only 8 non-native
252 seaweeds (*C. racemosa*, *C. taxifolia*, *C. fragile* spp., *F. evanescens*, *G. vermiculophylla*, *N. harvey*,
253 *S. muticum* and *U. pinnatifida*). Studies had been performed in the Mediterranean Sea (34), along
254 the coasts of Atlantic Europe (27), Australia (16), Atlantic (16) and Pacific (4) North America, and
255 Argentina (3).

256 **Effects on communities**

257 Non-native seaweeds had significant negative effects on the density/cover (median effect size:
258 -1.18, CI: -1.76/-0.62), biomass (median: -0.4, CI: -0.63/-0.18), diversity (median: -1.7, CI: -2.28/-
259 1.24) and evenness (median: -1.26, CI: -2.18/-0.63) of native primary producer communities and on
260 the biomass of consumer communities (median: -0.64, CI: -1.47/-0.02) (Fig. 1). Effects on
261 consumer communities were statistically different from those on primary producer communities for
262 density/cover ($P_B=0.014$) and diversity ($P_B=0.023$) (Table S3).

263 Following the exclusion of mensurative studies from the dataset, significant negative effects
264 on density/cover and diversity of resident primary producers persisted (density/cover: median: -
265 1.04, CI: -1.61/-0.42; diversity: median: -1.45, CI: -1.71/-1.2). Lack of a sufficient number of
266 studies prevented analyses on community biomass and evenness. Exclusion of mensurative studies
267 also reduced differences between trophic levels, which did not differ significantly for any of the
268 response variables investigated (Fig. 1, Table S3).

269 In rocky bottom habitats, non-native seaweeds had significant negative effects on the diversity
270 of both resident primary producers (all data: median: -1.90, CI: -2.55/-1.40; experimental data only:
271 median: -1.40, CI: -1.69/-1.12) and consumers (all data: median: -0.57, CI: -1.07/-0.11). Negative
272 effects on the diversity of consumers switched to positive when analyses were performed on

273 experimental data only (median: 0.63, CI: 0.20/1.22). The effects on the diversity of consumer
274 communities did not, however, statistically differ from those on primary producers (Fig. 2, Table
275 S4).

276 Lack of a sufficient number of studies prevented us to repeat the analyses on other community
277 variables or on soft-bottom habitats data (i.e. intertidal and subtidal soft bottoms, soft vegetated
278 habitat and seagrass).

279 **Effects on species**

280 Non-native seaweeds had significant negative effects on the density/cover of resident primary
281 producer species (median: -0.7, CI: -1.24/-0.14). These effects were evident in soft- (median: -1.40,
282 CI: -2.46/-0.33), but not in rocky-bottom habitats. In contrast, effects on density/cover of higher
283 trophic groups were always neutral (Fig. 3) (Table S5-S6).

284 Following the exclusion of mensurative data, negative effects on density/cover of resident
285 primary producer species disappeared when all data or soft bottom habitats only were analysed. In
286 contrast, they changed to significantly negative in rocky bottom habitats (median: -0.58, CI: -0.98/-
287 0.15) (Fig. 3) (Table S5-S6).

288 A significant negative effect on density/cover of other consumers was detected when all
289 experimental data (median: -0.63, CI: -1.43/-0.06) or only those from rocky bottom habitats
290 (median: -0.42, CI: -0.79/-0.08) were included. Effects on herbivores and predators remained
291 neutral in all cases (Fig. 3) (Table S5-S6).

292 Differences in the effects of non-native seaweeds on density/cover between primary producers
293 and higher trophic levels were not significant for any dataset examined (Fig. 3) (Tables S5-S6).

294 Non-native seaweeds had significant negative effects on the biomass (median: -0.39, CI: -
295 0.95/-0.09), growth (median: -0.6, CI: -0.82/-0.41) and survival (median: -1.04, CI: -1.75/-0.76) of

296 resident primary producer species. In contrast, significant negative effects on consumers emerged
297 only for the survival of suspension feeder/deposit feeder/detritivore species (other consumers;
298 median: -1.11, CI: -1.68/-0.52) (Fig. 4) (Table S5).

299 Following the exclusion of mensurative data, the analyses did not detect any significant effect
300 on primary producer species or herbivores. In contrast, negative effects remained significant on the
301 survival of other consumer species (median: -1.12, CI: -1.68/-0.52) and emerged for their biomass
302 (median: -0.85, CI: -2.61/-0.09) (Fig. 4) (Table S5).

303 Differences in the effects of non-native seaweeds between primary producers and higher
304 trophic levels were not significant for any of the response variables examined (Fig. 4) (Table S5).
305 Lack of a sufficient number of studies prevented us from running additional analyses on data of
306 biomass, growth or survival from experimental data only. Likewise, it was not possible to assess
307 variations in these variables at the level of predators or to focus on specific habitats.

308

309 **DISCUSSION**

310 Negative effects of non-native seaweeds on resident plant communities were consistent across
311 the response variables we examined (i.e., density/cover, biomass, diversity and evenness),
312 supporting previous findings of strong negative impacts of plant invaders on resident primary
313 producer assemblages (Gaertner et al. 2009, Thomsen et al. 2009, 2014, Powell et al. 2011, Vilà et
314 al. 2011). A significant negative effect of non-native seaweeds on resident consumer communities
315 was, in contrast, detected only on their biomass. Despite the fact that effects on native producers
316 were significantly different from those on consumers only for density/cover and diversity of
317 communities, our results generally support the relative trophic position hypothesis of Thomsen et al.
318 (2014), which proposed that invaders' effects on resident biodiversity might be more negative
319 within the same than on higher trophic levels.

320 Thomsen et al. (2014) found significant positive effects of invading seaweeds on resident
321 consumer biodiversity. Apparent discrepancies between the present study and that of Thomsen et al.
322 (2014) likely arise from the use of different study inclusion criteria (both mensurative and
323 experimental in this study *versus* experimental data only in that of Thomsen et al.), as well as the
324 inclusion of more recent studies in our meta-analyses (for a total of 100 papers *versus*. 29 papers
325 included by Thomsen et al. 2014). Interestingly, on rocky bottoms, the exclusion of mensurative
326 studies caused the effects of non-native seaweeds on the diversity of consumers to switch from
327 negative to positive. These results suggest that, in the marine environment, effects of invading
328 plants on resident consumer communities might be the outcome of different mechanisms in
329 different habitats.

330 In particular, the provision of a complex habitat by non-native seaweeds (such as *S. muticum*,
331 *C. fragile* and *U. pinnatifida*), offering shelter and/or food (Britton-Simmons 2004, Schmidt and
332 Scheibling 2007, Irigoyen et al. 2011), is of major importance in rocky bottom habitats, where
333 consumers dwell above ground. In contrast, consumer communities in soft sediments may be
334 affected negatively by non-native seaweeds also through the modification of below ground
335 conditions, for example through the release of secondary metabolites into the detritus (Taylor et al.
336 2010). This may, to some extent, explain the lack of effects on diversity of consumers when all
337 habitats were included. Thus, mensurative studies, being not able to correctly disentangle the effects
338 of non-native seaweeds from other stressors, may overestimate negative effects on consumers
339 diversity (Lotze et al. 2006).

340 As emerged at the community-level, there was a trend for the effects of non-native seaweeds
341 on resident primary producer species to be negative. Analyses including both mensurative and
342 experimental data showed that non-native seaweeds depressed the density/cover, biomass, growth
343 and survival of local plant species. The magnitude of these effects was, however, reduced by the
344 exclusion of mensurative data from the analyses. In addition, analyses on density/cover data ran

345 separately for soft bottom or rocky bottom habitats yielded contrasting results, likely due to
346 differences between target species in the two habitats (i.e. seagrasses vs. macroalgae, respectively).

347 Seagrass meadows, characterized by low taxonomic diversity and unique physiological
348 characteristics, are globally threatened by alterations to abiotic conditions (Orth et al. 2006). Again,
349 mensurative studies might have overestimated invaders' impact on seagrass density (Lotze et al.
350 2006, Orth et al. 2006). In fact, analyses of experimental data only, although characterized by lower
351 statistical power (i.e., they were based on a small number of studies), did not show significant
352 effects of invading seaweeds on seagrass density, suggesting a trade-off between negative (e.g.
353 competition for light availability, Drouin et al. 2012) and positive (e.g. enhanced reproductive shoot
354 density; Ceccherelli and Campo 2002) effects of invaders.

355 In contrast, there is high variability in physiological and ecological traits among macroalgae;
356 for example, several macroalgal species are weak competitors that can opportunistically take
357 advantage of degraded environmental conditions (e.g. filamentous species forming turfs; Benedetti-
358 Cecchi et al. 2001). In this case, mensurative studies might have underestimated the competitive
359 effects of invaders on density/cover of resident macroalgae in degraded environments.

360 Competition for resources with non-native seaweeds is likely to underpin the changes
361 observed in resident plant communities (Thomsen et al. 2014). The heterogeneity of invaders' traits
362 (e.g., including siphonous species, such as *C. racemosa*, *C. taxifolia* and *C. fragile* spp., filamentous
363 species, such as *W. setacea*, and canopy-formers, such as *C. fragile* spp., *Fucus* spp., *U. pinnatifida*,
364 *S. muticum* and *G. turuturu*) may translate into a wide range of mechanisms through which these
365 seaweeds compete with resident primary producers, and macroalgae in particular. For example,
366 *Caulerpa* species produce three-dimensional networks of stolons that generate adverse
367 physical/chemical conditions for native plants, by enhancing sediment retention and reducing water
368 flow (Piazzi et al. 2007). The same species can release allelochemicals against macroalgal
369 competitors (Raniello et al. 2007). In contrast, mechanisms underpinning negative effects of

370 canopy-forming non-native species, such as *U. pinnatifida* or *S. muticum*, are linked to pre-emption
371 of resources (light, nutrient, space availability; Britton-Simmons 2004, Casas et al. 2004).

372 The lack of significant effects of non-native seaweeds on herbivore species suggests that
373 alterations caused to resident primary producer communities did not imply detrimental changes to
374 their value as food or habitat (i.e., they serve as an alternative food or habitat source in the invaded
375 system). The response of individual herbivore species was, however, highly variable, indicating that
376 some species were influenced negatively and others positively. Some studies clearly indicate that
377 some siphonous green invading seaweeds, if ingested, can induce physiological damage to
378 herbivorous fish through production of chemical defences (Box et al. 2009, Terlizzi et al. 2011), or
379 reduce growth and reproductive rates of resident sea urchins as a consequence of their low
380 nutritional value (Lyons and Scheibling 2007, Tomas et al. 2011). In other cases, non-native
381 seaweeds are preferred over the resident macroalgal species, either as habitat or food (Trowbridge
382 and Todd 2001, Siddon and Witman 2004).

383 The lack of effects of non-native seaweeds on predator species density/cover and biomass (the
384 only two variables that could be analysed) may partly reflect the absence of effects on their prey
385 (herbivores or other consumers). However, predator species might be also indirectly affected by
386 habitat modifications caused by non-native seaweeds (Vàsquez-Luis et al. 2009, Janiak and
387 Whitlatch 2012). Non-native macroalgae may largely influence resident predators through this
388 mechanism, but effects can be either negative or positive. For example, small predators may be
389 disadvantaged by the loss of habitat complexity, as it is the case of *G. turuturu* replacing *Chondrus*
390 *crispus* (Janiak and Whitlatch 2012), or favoured by an increase in refuges created by the invading
391 alga (e.g. Vàsquez-Luis et al. 2009). A similar positive effect has been shown for recruits/juveniles
392 of larger predators(e.g., *G. vermiculophylla*, *C. fragile* spp. *tomentosoides* on crabs, seastars, fish)
393 (Schmidt and Scheibling 2007, Thomsen 2010). It is worth stressing that the small number of
394 studies available for this group could have limited the statistical power of our analyses.

395 Non-native seaweeds decreased the survival of other consumers. This group was mainly
396 composed of suspension and deposit feeders, for which anoxic and sulphide-rich sediments usually
397 found in presence of some habitat-forming non-native seaweeds (e.g. *C. taxifolia*; Crisholm and
398 Moulin 2003) can be toxic (Shumway et al. 1985, Laudien et al. 2002). Non-native seaweeds may
399 also increase post-settlement mortality of epiphytic species, possibly through the release of
400 chemicals (e.g. effects of *Fucus evanescens* on *Balanus improvisus*, Wikstrom and Pavia 2004).

401 The removal of mensurative data caused effect sizes of density/cover and biomass of other
402 consumers to be more (and significantly) negative. When density/cover data were analysed
403 separately between habitats, significant negative effects from experimental studies emerged only in
404 rocky bottom habitats (e.g., Wikstrom and Pavia 2004). Lack of effects in soft bottoms might
405 suggest the existence of positive below-ground effects of non-native seaweeds on this group of
406 consumers, likely able to counterbalance negative ones. For example, Olabarria et al. (2010) have
407 suggested that decomposition of wrack of *S. muticum* might act as a source of organic matter, thus
408 facilitating the opportunistic worm *Capitella capitata*. However, results from these analyses must
409 be interpreted with caution, due to the relatively small number of studies.

410 Overall, despite large variability in the effects of non-native seaweeds among different groups
411 of consumers, a negative effect emerged on whole consumer community biomass when both
412 mensurative and experimental data were analysed. More data from experimental studies are,
413 however, needed in order to provide unambiguous estimates of the effects of non-native seaweeds
414 on consumer communities.

415 Context-dependency has prevented the identification of simple empirical rules for predicting
416 invasion impacts (Parker et al. 2009). Matching the attributes of invading and resident species has
417 resulted in broad conceptual frameworks, such as the distinctiveness hypothesis, predicting larger
418 impacts if non-native and resident species are functionally and/or taxonomically different from each
419 other (Diamond and Chase 1986, Ricciardi 2003). Building on this concept, Thomsen et al. (2014)

420 have recently evaluated the effects of invading species belonging to different trophic groups (i.e.
421 marine plants, mobile consumers or sessile filter feeders) on the biodiversity of both resident plants
422 and animals. Their results highlight that matching the trophic position between invading and
423 resident species can contribute to explain some of the variability in effect sizes usually observed.
424 However, as a novel finding of our study, taking into account key features of resident species, such
425 as the trophic level and habitat-specific life-traits, can reveal greater complexity in the outcome of
426 invasion (e.g. Vilà et al. 2011, Thomsen et al. 2014).

427 In summary, our results support the view of a generalized competitive effect of non-native
428 plants within the same trophic level (Thomsen et al. 2014). Large heterogeneity in invader effects
429 on herbivores and predators suggests, on the contrary, that impacts on resident species belonging to
430 higher trophic levels could be more invader- and species-specific, due to the diversity and
431 complexity of paths through which bottom-up effects can take place. Features of invaded habitats
432 may further increase the variability in the effects on consumer species.

433 As clearly emerged from this study, the inclusion of data from mensurative studies can greatly
434 influence estimates of the direction and intensity on the effects of invaders on resident species or
435 communities. Gaining more data through experimental studies able to correctly disentangle the
436 effects of non-native species from those of other stressors (Gurevitch and Padilla 2004, Didham et
437 al. 2005, Bulleri et al. 2010), should be thus considered a priority if we are to develop a robust
438 theoretical framework for predicting the ecological impacts of plant invaders across trophic levels.

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621 Table 1. Summary of the ecological impacts due to exotic seaweeds classified by ecological levels,
 622 impact types and response variables analyzed.
 623

| Level | Impact type | Variables |
|---|---------------|--|
| Primary producer species (e.g. macroalgae or phanerogams) | Density/cover | density or cover of adults/ recruits |
| | Biomass | above/below ground biomass of leaves/roots/rhizomes; biomass primary productivity/production |
| | Growth | size/change in size of whole organisms or parts |
| | Survival | % survival, mortality, longevity |
| Primary producer community | Density/cover | density or cover of adults/ recruits |
| | Biomass | biomass of plants, biomass production |
| | Diversity | number of species/taxa, Shannon diversity index |
| | Evenness | Pielou's evenness |
| Consumer species | Density/cover | density or cover of adults/recruits/juveniles/colonies |
| | Biomass | biomass of whole organisms or parts |
| | Growth | size/change in size of whole organisms or parts |
| | Survival | % survival, mortality rates, predation rates |
| Consumer community | Density/cover | density or cover of individuals/colonies |
| | Biomass | biomass |
| | Diversity | number of species/taxa, diversity indices (Shannon, Margalef) |
| | Evenness | Pielou's evenness |

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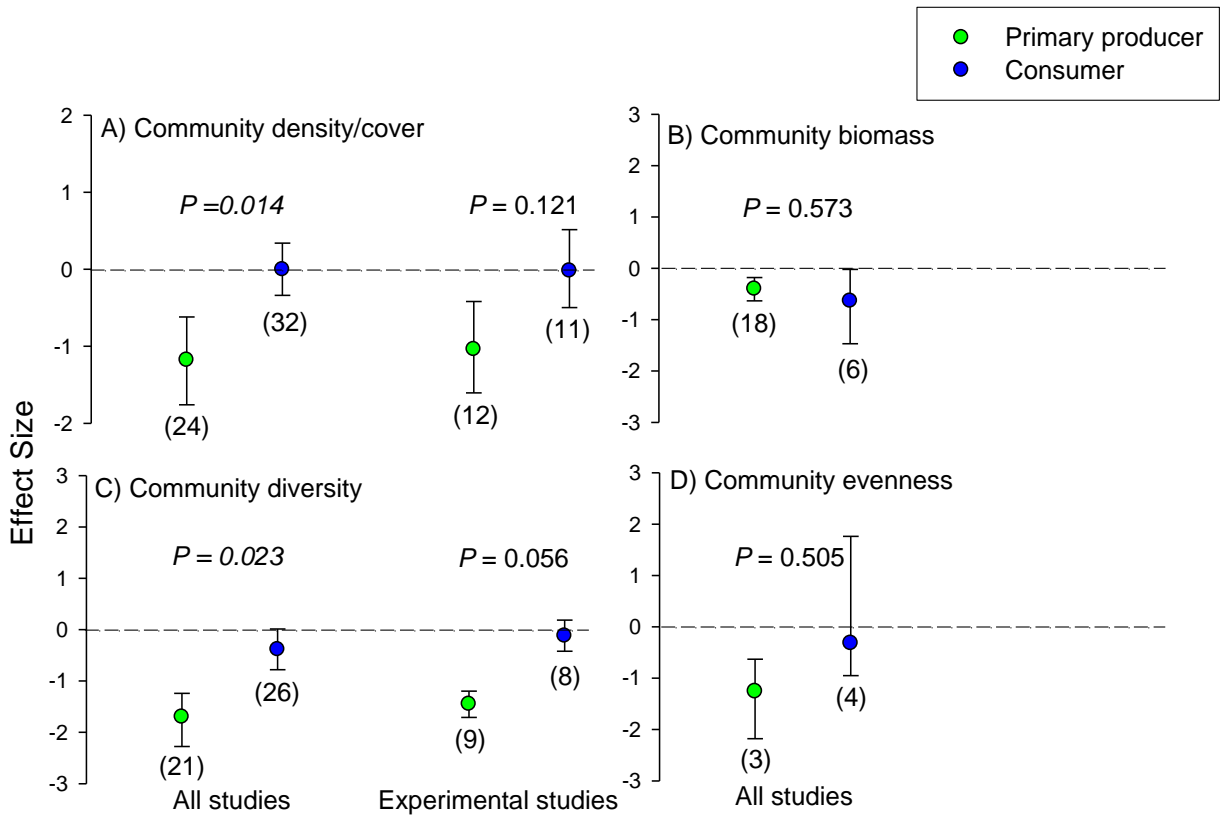
626 **Legend to figures**

627 Figure 1. Effects of exotic seaweeds on A) density/cover, B) biomass, C) diversity (including both
628 species/taxa richness and diversity indices) and D) Pielou's evenness of communities of primary
629 producers and consumers, calculated using the entire dataset or experimental studies only. Symbols
630 report median effect size calculated using 10000 bootstrap samples and 95% confidence intervals.
631 Probabilities refer to the comparison of effect sizes between primary producers and consumers for
632 all studies and experimental studies only, separately. Number of studies in parentheses.

633 Figure 2. Effects of exotic seaweeds on diversity of communities of primary producers and
634 consumers living on rocky bottoms (intertidal and subtidal), calculated using the entire dataset or
635 experimental studies only. Symbols report median effect size calculated using 10000 bootstrap
636 samples and 95% confidence intervals. Probabilities refer to the comparison of effect sizes between
637 primary producers and consumers for all studies and experimental studies only, separately. Number
638 of studies in parentheses.

639 Figure 3. Effects of exotic seaweeds on species-level density/ cover of primary producers,
640 herbivores, predators and other consumers in all (A), rocky bottom (B) or soft bottom (C) habitats,
641 calculated using the entire dataset or experimental studies only. Symbols report median effect size
642 calculated using 10000 bootstrap samples and 95% confidence intervals. Comparisons of effects
643 sizes between primary producers and consumers were never significant. Number of studies in
644 parentheses.

645 Figure 4. Effects of exotic seaweeds on species-level A) biomass, B) growth and C) survival of
646 primary producers, herbivores, predators and other consumers, calculated using the entire dataset or
647 experimental studies only. Symbols report median effect size calculated using 10000 bootstrap
648 samples and 95% confidence intervals. Comparisons of effects sizes between primary producers
649 and consumers were never significant. Number of studies in parentheses.

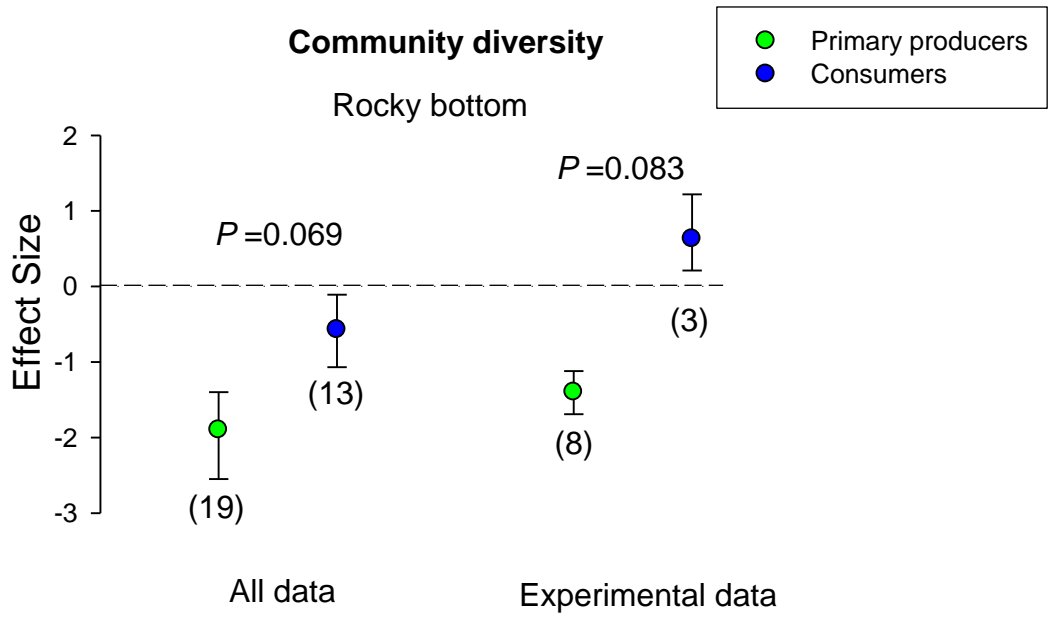


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Fig. 1 Maggi et al.



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Fig. 2 Maggi et al.

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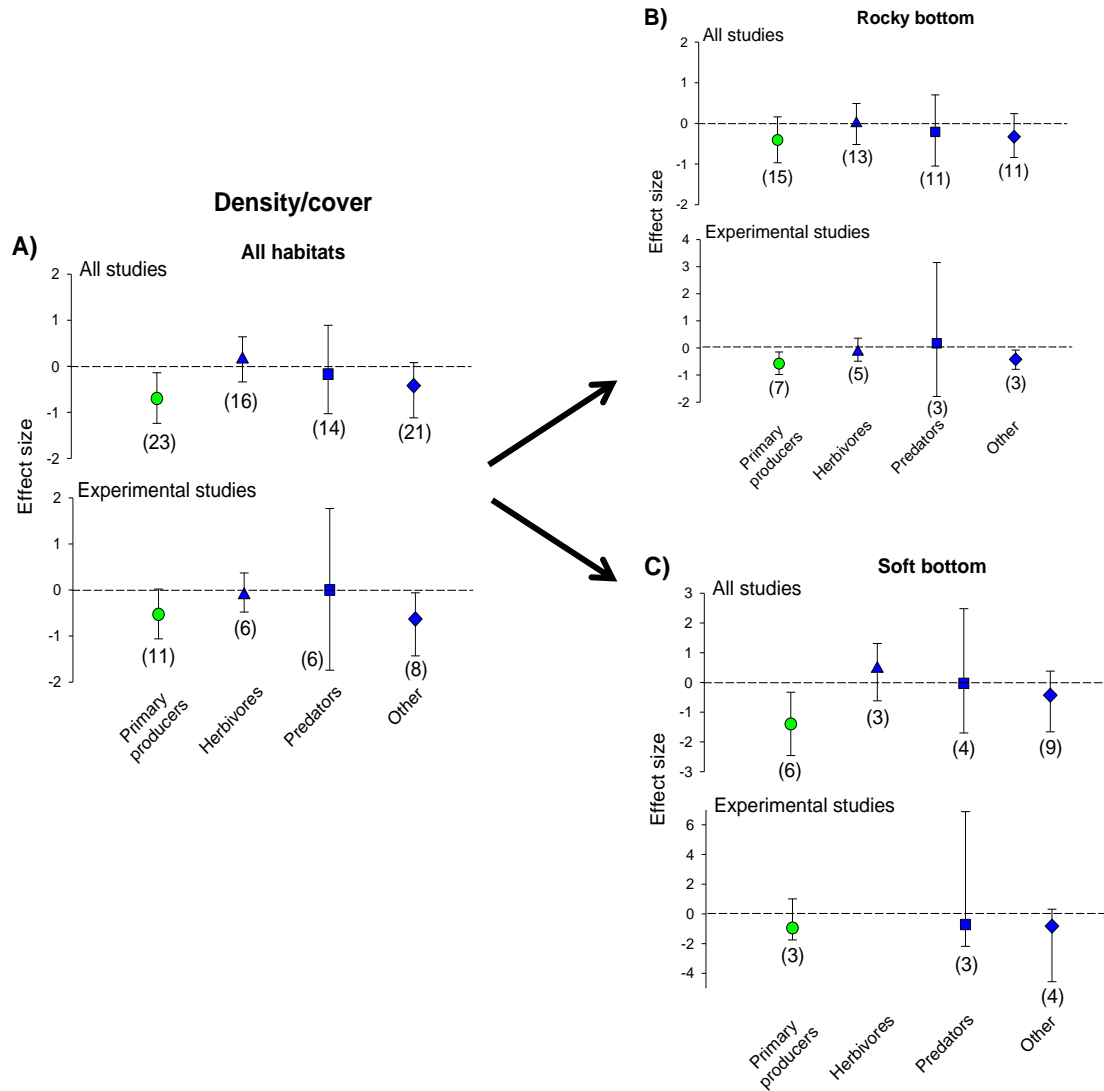
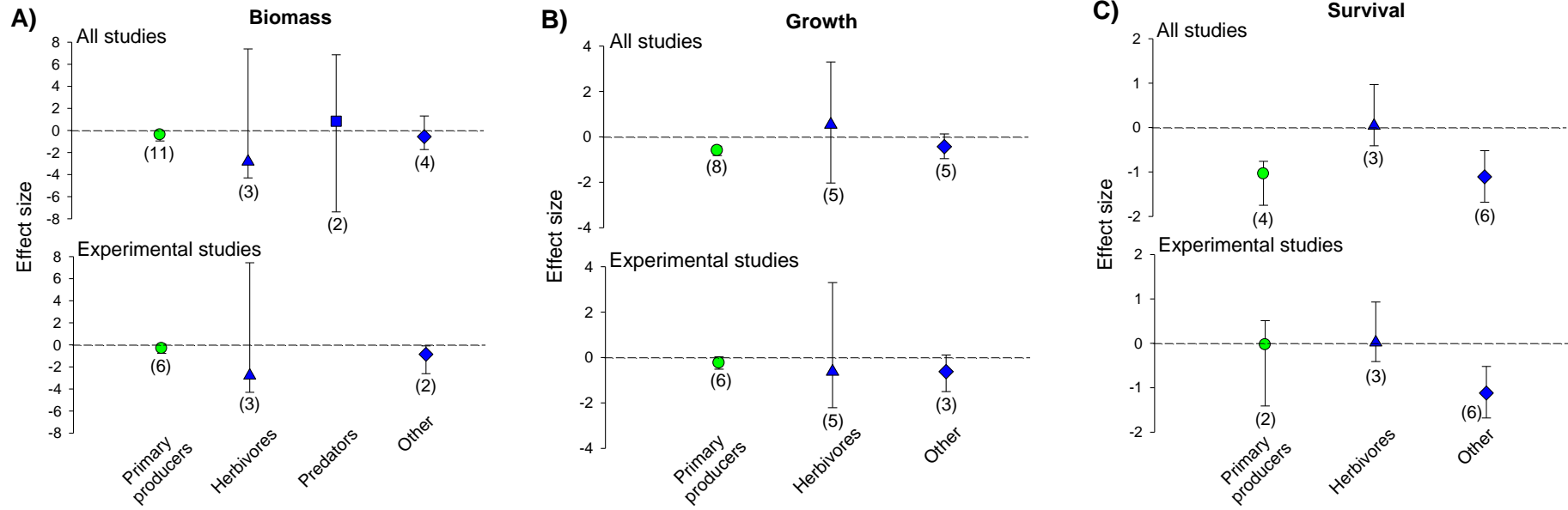


Fig. 3 Maggi et al.

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Fig. 4 Maggi et al.

679 **Supporting Information**

680 Additional Supporting Information may be found in the online version of this article:

681

682 **Appendix S1** {list of retained papers}

683 **Appendix S2** {Datasets}

684 **Figure S1-S2** {Funnel plots for community and species level variables}

685 **Table S1** {Excluded papers and reasons for exclusions}

686 **Table S2** {Rank correlation tests}

687 **Table S3** {Summary of mixed-effect models_communities}

688 **Table S4** {Summary of mixed-effect models_community diversity_rocky bottom}

689 **Table S5** {Summary of mixed-effect models_species}

690 **Table S6** {Summary of mixed-effect models_species density/cover_rocky and soft bottom}

691 **Biosketch**

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693 VECTORS (Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors).

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696 EM, EC,TC, JK, DL and GR within project meetings; EM, FB, CR, GG, and JK collected the data;

697 AC greatly contributed to information on feeding habits of consumers; EM, FB and LR analyzed

698 the data; EM and FB led the writing. All authors commented on drafts of the manuscript.