Alteration of coastal productivity and artisanal fisheries interact to affect a marine food-web

M. Isidora Ávila-Thieme[1,2,3], Derek Corcoran[1,2], Alejandro Pérez-Matus[1,4], Evie A. Wieters[1,5], Sergio A. Navarrete[1,5,6], Pablo A. Marquet[1,2,7,8,9] & Fernanda S. Valdovinos[10*]

1. Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, CP 8331150, Santiago, Chile.

2. Instituto de Ecología y Biodiversidad (IEB), Las Palmera 345, Santiago, Chile

3. Universidad Católica de la Santísima Concepción, Concepción, Chile

4. Subtidal Ecology Laboratory, Estación Costera de Investigaciones Marinas, Departamento de Ecología, Facultad de Ciencias Biológicas Pontificia Universidad Católica de Chile, Santiago, Casilla 114-D, Santiago, Chile

5. Estación Costera de Investigaciones Marinas - Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, El Tabo 2690931, Chile

6. Centro de Ecología Aplicada y Sustentabilidad (CAPES), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, CP 8331150, Santiago, Chile.

7. Centro de Cambio Global UC (PUCGlobal), Alameda 340, CP 8331150, Santiago, Chile

8. The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe NM 87501, USA

9. Instituto de Sistemas Complejos de Valparaíso (ISCV), Artillería 470, Cerro Artillería, Valparaíso, Chile

10. Department of Environmental Science and Policy, University of California, Davis

* Corresponding author: fvaldovinos@ucdavis.edu

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ABSTRACT

Top-down and bottom-up forces determine ecosystem function and dynamics. Fisheries as a top-down force can shorten and destabilize food-webs, while climate-change driven effects can alter the bottom-up forces of primary productivity. We assessed the response of a highly-resolved intertidal food-web to these two global-change drivers, using network analysis and bioenergetic modelling. We quantified the relative importance of artisanal fisheries as another predator species, and evaluated the independent and combined effects of fisheries and plankton-productivity changes on food-web dynamics. The food-web was robust to the loss of all harvested species but sensible to plankton-productivity decline. Interestingly, fisheries dampened the negative impacts of decreasing plankton productivity on non-harvested species, while plankton-productivity decline increased the sensitivity of harvested species to fishing. Our results show that strategies for new scenarios caused by climate change are needed to protect marine ecosystems and the wellbeing of local communities dependent on their resources.

INTRODUCTION

Direct human impacts and the full suite of drivers of global change are the main cause of species extinctions in Anthropocene ecosystems[1,2], with detrimental consequences on ecosystem functioning and their services to human societies[3,4]. The world fisheries crisis is among those consequences, which cuts across fishing strategies, oceanic regions, species, and includes countries that have little regulation and those that have implemented rights-based co-management strategies to reduce overharvesting[5–8]. Chile has been one of the countries implementing Territorial Use Rights (TURFs[9]) over an unprecedented geographic scale to manage the diverse coastal benthic resources using a co-management strategy[10,11]. Over 60 coastal benthic species form part of these artisanal fisheries[10], with species that are extracted

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47   from intertidal and shallow subtidal habitats [12,13]. The Chilean TURFs system brought significant

48   improvements in sustainability of this complex socio-ecological system, helping to rebuild

49   benthic fish stocks[10,11], improving fishers' perception towards sustainability and increasing

50   compliance[9], as well as showing positive ancillary effects on conservation of biodiversity[14,15].

51   However, the situation of most artisanal fisheries is still far from sustainable, and many fish

52   stocks and coastal ecosystems show signs of over exploitation and ecosystem degradation, a

53   consequence of the low levels of cooperation and low enforcement of TURF regulations, which

54   leads to high levels of free-riding and illegal fishing[16–18]. Thus, it is imperative to improve our

55   understanding of the effects of these multi-species fisheries which simultaneously harvest

56   species at all trophic levels, from kelp primary producers to top carnivores[13,19].

57   To compound things, removal of biomass from the ocean occurs simultaneously with

58   multiple other stressors associated to climate change that compromise the individuals' capacity

59   to respond to perturbations[20–22]. Besides sea surface temperature (SST), climate change also

60   affects many other physical-chemical characteristics of marine coastal waters (stratification,

61   acidification, ventilation)[23,24], as well as the wind regimes that control surface water productivity

62   along the productive coastal upwelling ecosystems[25–29]. Changes in the productivity of the

63   oceans are reflected in changes of plankton biomass, which contributes approximately half of the

64   global primary production, supports the productivity of marine food-webs, and influences the

65   biogeochemical process in the ocean and strongly affects commercial fisheries[30–32]. Indeed, an

66   overall decrease in marine plankton productivity is expected over global scales[24,30,33]. Along

67   extensive regions of the Humboldt upwelling ecosystem off Chile, long-term increases and

68   decreases in plankton productivity have already occurred over the past two decades[34,35] and are

69   expected to propagate up the pelagic and benthic food webs. We therefore analyzed the bottom-

70   up impact of fluctuations in plankton productivity in combination with fisheries exploitation of

71   these food-webs using the concepts and methods of network ecology.

72   Network ecology has advanced our understanding of ecosystems by providing a powerful

73   framework to analyze biological communities[36,37]. Previous studies used this framework to

74   assess food-web robustness against species extinctions (i.e., the fraction of initial species that

75   remain present in the ecosystem after a primary extinction) [38–43], showing the importance for

76   food-web persistence of highly connected species[38,40,44,45], basal species[39] and highly connected

77   species that trophically support other highly connected species[42]. Most of these studies used a

78   static approach, which stems from network theory and analyzes the impacts of structural changes

79   on food-webs represented by nodes (species) and links (interactions) that connect nodes, but

80   ignores interaction strengths and population dynamics of interacting species[38]. Other studies used

81   a dynamic approach, which considers not only the structure and intensity of interactions in a

82   food-web, but also the changes in species biomasses through time and the indirect effects that

83   these changes have on other species[39–41,46,47]. Here we use both approaches to understand the

84   relative importance of harvested species in our food-web.

85   In this contribution, we analyze (1) the importance of harvested species for the structure

86   and persistence of the intertidal food-web by simulating a scenario of over-exploitation-driven

87   extinction of all harvested species. We then evaluate (2) the robustness of this food-web to the

88   extinction of species harvested by artisanal fisheries in comparison to three commonly used

89   extinctions sequences (see below), and (3) the effect of three fisheries scenarios on other species

90   abundance, persistence and food-web dynamics. We finally analyze the (4) independent and (5)

91   combined effects of fisheries and plankton productivity changes on the food-web dynamics

92   through altering plankton subsidy.

93 **RESULTS**

94 *1. Food-web description and the relative importance of harvested species to the food-web*

95 *structure*

96   The intertidal food-web contains 107 species, with the highly omnivorous fisheries node

97 (F node in Fig. 1A) contributing 22 links, from basal kelp species to top carnivores (Fig. 1A).

98 Among the species harvested by the artisanal fisheries, 10 belong to the 30 most connected

99 species of the food-web (Fig. 1A, and Supplementary Table S1). Moreover, these fisheries

100 exploit at least one species that is a resource or a consumer of about 70% of the species

101 (harvested and non-harvested species) in the intertidal food-web (Fig. 1B, C and D). With the

102 static approach we found that the removal of all 22 species (see Methods) negatively affected the

103 structural properties of the food-web, specially, reduces the overall number of trophic

104 interactions by 48%. This loss represents, on average, 100 more links lost than that expected

105 from randomly removing 22 species from the food-web (see supplementary Table S2 and

106 supplementary material for more detailed results).
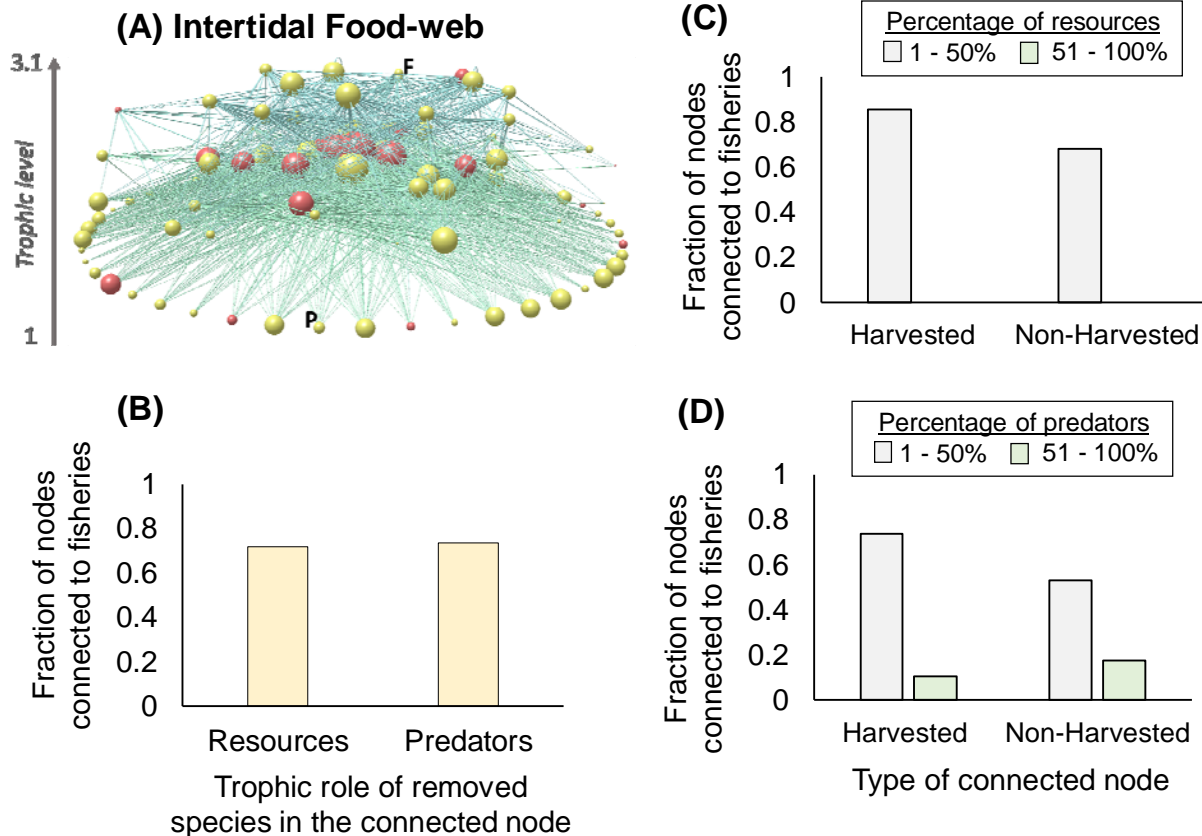
Figure 1. (A) Intertidal food-web. Node colors represent harvested (red) and non-harvested (yellow) species. Letter F and P represent the fisheries and plankton node, respectively. Node size represents the number of trophic interactions (degree) of each node. Nodes at the bottom represent basal species, while nodes at the top represent top predators. Y-axis represents trophic level (calculated as SWTL, see Methods). Drawn using Network3D software[48]. (B) Fraction of species in the food web that are trophically connected (at least once) with exploited species that are either a resource and/or a predator (x-axis). Each bar presented in (B) is further divided in: (C) the percentage of resources shared with fisheries by the harvested and non-harvested consumers of the food-web, and (D) the percentage of predators of harvested and non-harvested species extracted by fisheries. Grey and green bars, respectively, represent the categories of 1-50% and 51-100% of the resource species consumed by harvested and non-harvested species (C) and of the consumer species predating upon harvested and non-harvested species (D).

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2. Food-web robustness to species extinctions

123   Following previous work[38–41], we evaluated the robustness of the intertidal food-web to

124   species extinction by sequentially removing species and counting the subsequent secondary

125   extinctions, if any. We counted the secondary extinctions caused by the four deletion sequences

126   (harvesting, random, most-connected, supporting-basal) using both static and dynamic

127   approaches (see Methods). Our dynamic approach uses and extends the Allometric Trophic

128   Network[49,50] (ATN) model by including plankton subsidy. Both approaches found that the

129   intertidal food web is highly robust to the loss of all harvested species, as null secondary

130   extinctions were observed after removing all harvested species (Fig. 2). The robustness of the

131   intertidal food-web was further demonstrated by the sequential deletion of the most connected

132   species, which showed that over 30% of those species must be removed before any secondary

133   extinctions occur (Fig. 2). As expected from previous work, the loss of supporting-basal species

134   produced the most secondary extinctions (Fig. 2). Both approaches showed similar trends (Fig.

135   2A and B), but our dynamic approach presented relatively lower food-web robustness

136   (Supplementary Fig. S1).

137   Although the plankton node ("species") was directly connected only to filter-feeders, it

138   proved to be the most important in the supporting-basal deletion sequence for both static and

139   dynamic approaches, as its removal caused 15 and 29 secondary extinctions, respectively. The

140   species that went extinct included not only sessile filter-feeders, but also four harvested species

141   important for the fisheries: the Chilean muricid whelk *Concholepas concholepas*, the giant

142   barnacle *Austromegabalanus pssitacus*, the sea squirt *Pyura chilensis* and the whelk *Acanthina*

143   *monodon*. These results suggest that while the intertidal food-web is robust to harvest-driven

144   extinctions, it can be sensitive to a drastic decrease in plankton productivity.
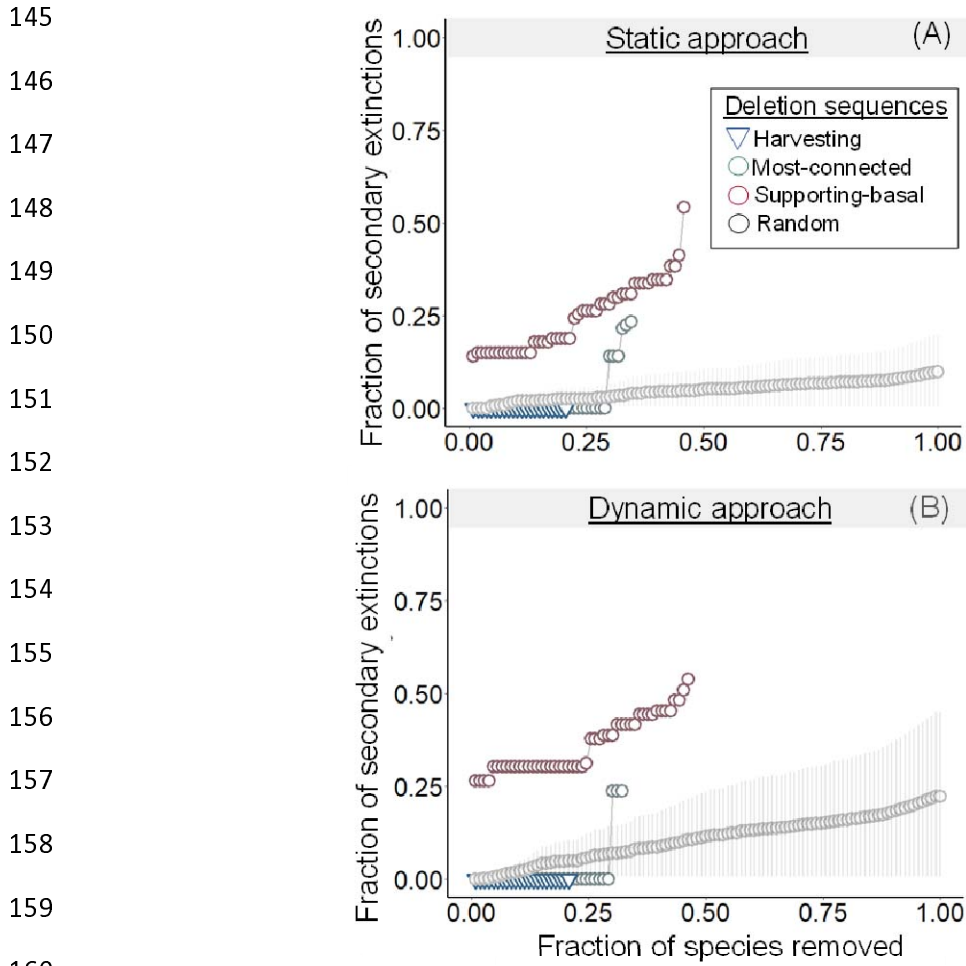
Figure 2. Fraction of secondary extinctions (y-axis) produced by the sequential removal of species (x-axis) with static (A) and dynamic (B) approaches. Gray and red circles represent most-connected and supporting-basal deletion sequences, while blue tringle represents harvesting deletion sequence. In the random deletion sequence, circles represent the average and the error bars represent the 95% confidence interval over 1000 simulations.

3. Effects of artisanal fisheries on food-web dynamics

We assessed the effects of fisheries on the biomass of every species in the food-web using our extension of the ATN model (see Methods). Fig. 3A and 3B illustrates with a simplified diagram our results shown in Supplementary Fig. S2. We simulated three fishing scenarios, where we applied exploitation rates needed to decrease the biomass of all 22 harvested species in 50%, 80%, and 100% (see F_{max} in Supplementary Table S3). These three fishing

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172　scenarios allowed us to simulate an approximately well managed fisheries (which removes

173　between 40% and 60% of biomass stock[5]), an overexploitation scenario (which removes 80%)

174　and nearly extinction scenario, respectively. We found that basal species required much lower

175　exploitation rate to decrease their biomass than filter-feeders, herbivores, and other consumers

176　(Supplementary Table S3). Harvested basals went extinct with an extraction above 0.3% of their

177　available biomass, while harvested consumers went extinct with an extraction above 90% of their

178　available biomass.

179　　The decrease in biomass of harvested species led to an increase in the biomass of most

180　non-harvested species at all trophic levels, especially in basal and herbivorous species (compare

181　Figs. 3A and 3B). On average, 82-86% of non-harvested species increased their biomass by 5-

182　25% after 50-100% fishing impacts on biomass stocks (Supplementary Fig. S2). This biomass

183　increase is explained by two mechanisms: i) decreasing the biomass of harvested species that are

184　consumers reduces the predation intensity on their resources (note that fisheries harvest more

185　species in higher than lower trophic levels, compare Figs. 1D and 1C), and (ii) decreasing the

186　biomass of harvested basal species reduces their competitive effects on the non-harvested basal

187　species, allowing them to grow (Supplementary Fig. S3).

188　　The positive effect of artisanal fisheries on the biomass of non-harvested species was

189　qualitatively similar across the different fishing scenarios, becoming larger with an increase in

190　fishing intensity (Supplementary Fig. S2). The exceptions were top predators, which had

191　opposite responses between the weakest and strongest fishing scenarios. A 50% reduction in

192　harvested species biomass caused a slight decrease in non-harvested top predators' biomass,

193　while 80% and 100% reductions caused an increase in their biomass. This suggests that artisanal

194　fisheries negatively impact top predators by extracting their prey species but, when the

195   exploitation rates are stronger, the indirect positive effects of fisheries on the biomass of the non-

196   harvested species become strong enough to dampen those effects.

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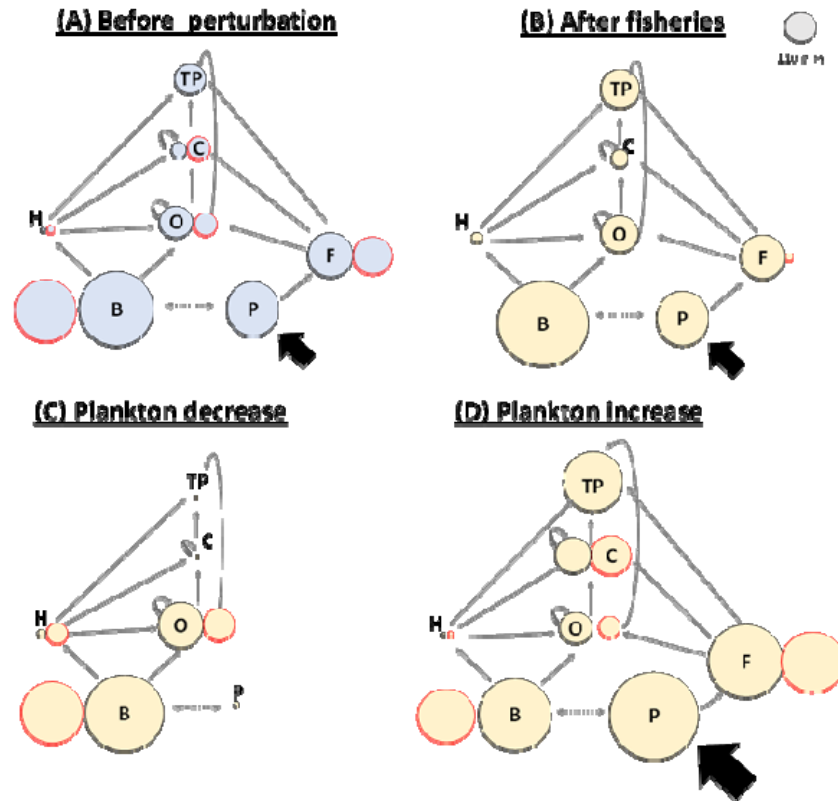
Figure 3. Diagram illustrating the effect of fisheries (B) and the effect of perturbing plankton subsidy (C and D) on food-web dynamics. Nodes represent the total biomass of each trophic level before (A) and after reducing in 100% the biomass of all harvested species (B) and after decreasing (C) or increasing (D) plankton subsidy in 100%. Each trophic level is indicated by TP: top predators, C: carnivores, O: omnivores, H: herbivores, F: filters-feeders, B: basal species, and P: plankton. Red and black outlined nodes represent the biomass of harvested and non-harvested species, respectively. Solid black, solid grey, and dashed grey arrows represent the plankton subsidy (7355 g/m^2), the trophic interactions, and competitive interactions, respectively. Note that the ATN model explicitly models competition only between basal species, while competition between consumers emerges from the depletion of shared resources.

208

4. Effects of plankton-subsidy alteration on food-web dynamics

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210   We considered a subsidy term to plankton as an external-controlled subsidy of plankton

211 productivity. We both decreased (Fig. 3C) and increased (Fig. 3D) the plankton subsidy in 50%,

212 80%, and 100% to simulate the alteration of plankton productivity expected as a response of

213 climate change (see Methods). All biomass changes can be found in Supplementary Fig. S4.

214 Both decreasing (Fig. 3C) and increasing (Fig. 3D) plankton subsidy can deeply alter food web

215 dynamics. The magnitude of plankton subsidy increases or decreases (i.e., 50%, 80%, 100%)

216 only quantitatively affected the food-web patterns shown in Figs. 3C and 3D, becoming more

217 intense with an increasing alteration of the plankton subsidy. Decreasing plankton subsidy had

218 larger impacts on the species biomasses than increasing plankton subsidy in the same magnitude,

219 even causing species extinctions (i.e., -1 in Supplementary Fig. S4E) when the subsidy was

220 removed (i.e., decreased in 100%). The number of total extinctions that occurred after

221 completely removing the plankton subsidy was 29 species, highlighting the bottom-up

222 propagation of effects through the web (Supplementary Fig. S4E).

223   A drastic decrease in plankton subsidy (100%) resulted in the extinction of all filter-

224 feeder species (specialist consumers of plankton) and decreased the biomass of carnivores and

225 top predators by 99% (compare Figs. 3A and 3C). The biomass reduction in carnivores and top

226 predators, in turn, released predation pressure on omnivores and herbivores, which consequently

227 increased their biomass by 30% and 110%, respectively. The increased biomass of herbivores

228 and omnivores, in turn, increased consumption pressure on basal species, but we found that the

229 biomass of basal species slightly increased by 4% (Fig. 3C). This suggests that the reduction in

230 plankton subsidy positively affects basal species by releasing pressure on the community level

231 carrying capacity (see Methods). Conversely, a 100% increase in plankton subsidy increased the

232   total biomass of filters, carnivores, and top predators by 76%, 107%, and 105%, respectively

233   (compare Figs. 3A and 3D). As a consequence, the increased predation pressure from higher

234   trophic levels decreased the total biomass of omnivores, herbivores, and basal species by 2%,

235   20%, and 3%, respectively. Carnivore species were the most vulnerable to the reduction of

236   plankton productivity, going extinct with a reduction of 80% in plankton subsidy

237   (Supplementary Fig. S4C), followed by filter-feeders and top predators, which went extinct with

238   a 100% of subsidy reduction (Supplementary Fig. S4E). Regarding harvested species, 18% of

239   them strongly decreased their biomass when plankton subsidy decreased, while 81% of them

240   slightly decreased their biomass when plankton subsidy increased (compare Supplementary Figs.

241   S4A, S4C, S4E with S4B, S4D, S4F).

242   *5. Interacting effects of fisheries and plankton-subsidy alteration on food-web dynamics*

243   We evaluated the combined effects of the biomass extraction by fisheries and the

244   alteration of plankton subsidy on the food-web dynamics using a full factorial design that

245   maintains the same fishing and subsidy levels used in each of the last two sections. We found

246   that regardless of the fishing scenario, all non-harvested trophic levels persisted when the

247   plankton subsidy increased or decreased (Fig. 4A and B) by 50%. Conversely, when the plankton

248   subsidy decreased in 80%, carnivores went extinct under all fishing scenarios (compare

249   Supplementary Figs. S5C and D with S5A, B, E and F) as well as the top-predators and filter-

250   feeders when the plankton subsidy decreased in 100% (Fig. 4C and D).

251   The level of plankton subsidy affected the impact of fishing on the biomass of harvested

252   species. Decreasing plankton subsidy decreased the biomass of harvested carnivores and filter-

253   feeders, intensifying the negative effect of fishing on their biomasses (see black arrows pointing

254   down to such result for "Harvested Carnivores" in panels A and C of Fig. 4). The reverse

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255   occurred when increasing plankton subsidy, which dampened the effect of fishing on the biomass

256   of harvested carnivores and filter-feeders. Interestingly, decreasing plankton subsidy also

257   increased the biomass of harvested and non-harvested omnivores and herbivores (see results of

258   subsection 2.3), which therefore dampened slightly the negative effect of fisheries on harvested

259   omnivores and herbivores (Fig. 4 A and C).
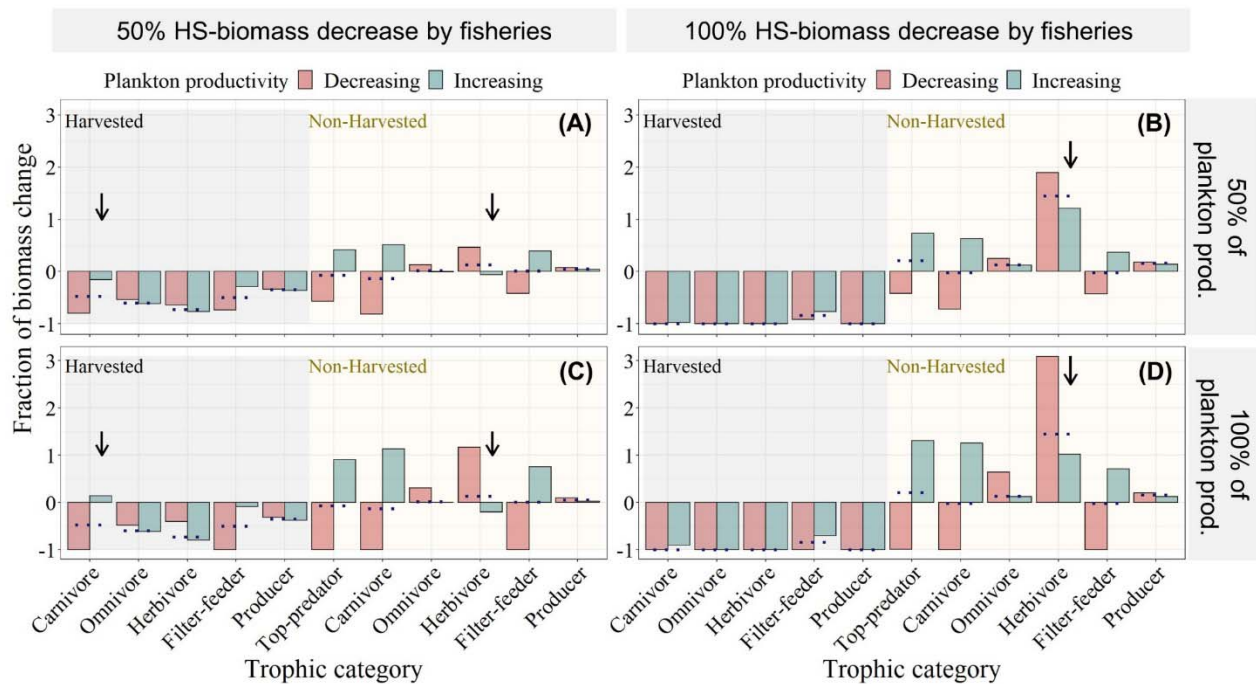
260   **Figure 4.** Combined effects of artisanal fisheries and plankton-productivity alterations on food-

261   web dynamics. Fraction of total biomass change (y-axis) of each trophic category (x-axis) after

262   decreasing (red bars) and increasing (blue bars) the plankton productivity (plankton prod.) in

263   50% (A and B) and 100% (C and D), and after decreasing the biomass of all harvested species

264   (HS) in a 50% (A and C) and in a 100% (B and D). The grey and yellow shading represent the

265   biomass change of harvested and non-harvested species, respectively. The arrows highlight the

266   most remarkable changes between the two levels of plankton subsidy perturbation and the two

267   levels of fishing. The dotted lines represent the independent effect fishing (i.e., without plankton

268   subsidy perturbation) on the biomass of each trophic category as a reference point.

269

270   Fisheries also affected the impacts of perturbing plankton subsidy on species biomasses.

271   Increasing fishing increased the biomass of non-harvested species (see results of subsection 2.2)

272   and, therefore, dampened the negative effects of altering plankton subsidy on the biomass of

273   these species while intensifying the positive effects of altering plankton subsidy in those species

274   (compare panels A and C with B and D of Fig. 4). Specifically, fisheries reversed the negative

275   effect of increasing plankton subsidy on the biomass of non-harvested herbivores (see 4 black

276   arrows pointing down to such result in panels A-C).

277   **DISCUSSION**

278   An overall decrease in marine plankton productivity is expected over global scales[24,30,33]

279   as a result of climate change. Our results show that a decline in plankton productivity of the

280   proportions expected with climate change can strongly impact an intertidal food-web in the

281   Southern Pacific Coast. A decrease in plankton subsidy caused several species extinctions and

282   shorten the food-web, with strong impacts on fisheries because of the biomass reduction of

283   harvested species. Conversely, the simulated extinction of all harvested species caused null

284   secondary extinctions, result that we also found in the subtidal food-web of the same Pacific

285   Coast (see Supplementary Discussion and Supplementary Fig. S6). This despite artisanal

286   fisheries harvesting on more than 20% of the food-web species (also highly connected species),

287   which suggests that harvested species are embedded in redundant[51] trophic interactions,

288   conferring the food-web alternative routes of energy and stability[47,52]. These results, however, do

289   not imply that local fisher communities will be similarly tolerant to the extinction of harvested

290   species. The socio-economic system in which fishers are embedded will be directly impacted[53] if

291   resource management by local TURFs fails and drive the harvested species extinct (see

292   Supplementary Discussion).

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293   Our results also highlight the vulnerability of basal species to fishing. We found that

294   basal species went extinct with an extraction above 0.3% of their available biomass. Harvested

295   basal species are consumed by 2.5 more species than harvested consumers, and their intrinsic

296   growth rate is 3 times lower than that of non-harvested basal species because they are the

297   macroalgae that have the largest body size. Among the harvested basal species is kelp, which

298   plays an important ecological and economical role. Kelp provides habitat structure and shelter to

299   many species[12] and via this non-trophic interaction, it promotes the biodiversity of coastal

300   ecosystems[54]. Its commercial value is also high, with Chile being one of the main exploiters of

301   kelp natural populations[55]. Kelp extraction in Chile is managed but hardly supervised[55].

302   Therefore, kelp's high demand, high value, and low control, leave these algae prone to illegal

303   fishing. In this context, we highlight the urgency of increasing supervision of kelp fisheries and

304   enforcing their compliance with management plans.

305   We found that the effects on the food-web dynamics of coastal-productivity changes and

306   artisanal fisheries interact, which reinforces the call made by previous studies[56–58] that more

307   research is needed to understand the interaction of several environmental stressors on

308   ecosystems. Fisheries dampened the negative impacts of decreasing plankton productivity on

309   non-harvested species, while plankton-productivity decline increased the sensitivity of harvested

310   species to fishing. Previous work[59] shows that human-gatherers enhance the species persistence

311   of coastal marine ecosystems in the North Pacific. This suggests that, at least in the intertidal

312   food-web studied here, small-scale artisanal fisheries play a similar role as human-gatherers in

313   the North Pacific, that is, as keystone species to non-harvested species into the food-web.

314   Our study shows that the effects of climate change threaten the biodiversity of marine

315   intertidal rocky-shore ecosystems as well as the services they provide, and emphasize the

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316   relevance of understanding and predicting the population dynamics of plankton and their impacts

317   on entire food-webs (see Supplementary Discussion). New strategies for these new scenarios

318   caused by climate change are needed to also protect the economy and wellbeing of the local

319   communities dependent on these coastal ecosystems.

320   **METHODS**

321   ***Food-web description and the relative importance of harvested species to the food-web***

322   ***structure***

323   We studied a well-resolved food-web of the intertidal rocky shore communities of the

324   central coast of Chile[12], which is harvested exclusively by small scale artisanal fisheries[11]. The

325   web represents all species that are found to co-occur on wave exposed rocky platforms of central

326   Chile, from the very low to the highest intertidal and is composed of 107 species (including a

327   fisheries node), with 44% of its species corresponding to primary producers, 53% to

328   invertebrates, and 3% to endotherm vertebrates. In the food-web, we consider as basal level all

329   species of benthic primary producers plus plankton (phytoplankton + zooplankton, single node).

330   Therefore, we represented filter-feeders (sessile filter-feeders + porcenallidae crabs) as specialist

331   consumers of plankton and not as basal species (see detailed description of the food-web in

332   Supplementary Material).

333   Species harvested by artisanal fisheries were identified using information from the

334   Chilean national fishing service (www.sernapesca.cl) and previous work[13]. A high diversity of

335   species distributed across all trophic levels are harvested by artisanal fisheries (red nodes in Fig.

336   1), including numerous species of macroalgae (n= 7), filter-feeders (n= 2), herbivores and

337   omnivorous (n= 11), and carnivores (n= 2), totaling 22 species. Using the static approach

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338   (without population dynamics, see nest subsection), we compared the structure of the food-web

339   with and without the harvested species to the distribution of 1000 food-web structures produced

340   by randomly removing the same amount of harvested species (see more details about this method

341   in supplementary materials).

342   ***Static and dynamic approaches for evaluating food-web robustness***

343   The static approach stems from network theory and analyzes the impacts of structural

344   changes on food-webs represented by nodes (species) and links (interactions) that connect nodes,

345   but ignores interaction strengths and population dynamics of interacting species[38]. In this

346   approach, a non-basal species is considered extinct after a perturbation (defined here as a

347   secondary extinction) if all its resource species (food) go extinct. Basal species are assumed to be

348   autotrophs or otherwise obtain resources from outside the modeled web, e.g. through subsidies

349   from other ecosystems and, therefore, do not experience extinctions unless directly removed

350   (defined here as a primary extinctions). Thus, the static approach only considers extinctions

351   produced by direct bottom-up effects. A dynamic approach considers not only the structure and

352   intensity of interactions in a food-web, but also the changes in species abundances through time

353   and the indirect and dynamic effects that these changes have on the abundances of other

354   species[39–41,46,47]. A species is then considered to be secondarily extinct when its abundance drops

355   below a threshold as a consequence of its population losses being higher than its population

356   gains. Therefore, a dynamic approach can take into account both bottom-up and top-down effects

357   of perturbations on the system, and both forces can contribute to produce secondary

358   extinctions[39]. We use both the static network-based approach and a dynamic approach based on

359   energy-transfer (see dynamic model below) to evaluate the impacts of artisanal fisheries and

360   changes in primary productivity on the intertidal food-web.

361   *The dynamic model*

362   The Allometric Trophic Network (ATN) model[49,50] consists of two basic sets of

363   equations, one set describing the biomass changes of primary producers (eq. 1) and the other

364   describing that of consumers (eq. 2), where $\boldsymbol{B}$ is the biomass vector with the biomasses of every

365   species population in the food-web and B_i is the biomass of the population of species i, as

366   follows:

367
$$\frac{dB_i}{dt'} = \overbrace{r_i B_i G_i(\boldsymbol{B})}^{\substack{Autotrophic \\ growth\ gain}} - \sum_j \overbrace{\frac{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}{e_{ji}}}^{\substack{Herbivory \\ loss}} - \overbrace{F_{\max i} B_i}^{\substack{Fisheries \\ loss}} \qquad \text{(eq. 1)}$$

368
$$\frac{dB_i}{dt'} = \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})}^{\substack{Resources \\ consumption\ gain}} - \overbrace{f_m x_i B_i}^{\substack{Maintenance \\ loss}} - \sum_j \overbrace{\frac{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}{e_{ji}}}^{\substack{Predation \\ loss}} - \overbrace{F_{\max i} B_i}^{\substack{Fisheries \\ loss}} \qquad \text{(eq. 2)}$$

369   The biomass of producer i changes according to the balance of autotrophic growth gain

370   and losses due to predation. The net autotrophic growth is determined by the logistic growth

371   function $G_i(B) = 1 - \left(\sum_{j=productores} c_{ij} B_j\right)/K$, where r_i is the intrinsic growth rate of producer

372   i, c_{ij} is the inter-specific competition coefficient between producer i and j, and K is the total

373   carrying capacity of primary producers in the system. The biomass loss of producer i by

374   herbivory (caused by herbivores or omnivores) increases with the mass-specific metabolic (x_j)

375   and attack (y_j) rates of consumer i, and decreases with the assimilation efficiency of consumer i

376   for resource j (e_{ij}). The consumers' population dynamics (eq. 2) depend on their mass-specific

377   metabolic rates (x_j) and on the balance between biomass gains by resource consumption, biomass

378   loss by metabolic maintenance, and biomass loss to predation. From the total amount of

379   resources ingested by the consumer population i, $\sum_j y_{ij} F_{ij}(\boldsymbol{B})$, only a fraction f_a is assimilated

19

380   into consumer available energy for maintenance and biomass growth. The functional response

381      $F_{ij}(\boldsymbol{B})$ determines the consumption rate of each consumer i for each resource j, defined by:

382
$$F_{ij}(\boldsymbol{B}) = \frac{\omega_{ij} B_j^q}{B0_{ij}^q + d_i B_i B0_{ij} + \sum_{l=resources} \omega_{il} B_l^q} \qquad \text{(eq. 3)}$$

383   where ω_{ij} is the relative preference of consumer i for resource j, q controls the shape of eq. 3

384   which becomes an intermediate functional response between type II and type III when $q=1.2$ [60].

385      $B0_{ij}$ is the biomass of resource j at which the consumer i achieves half of its maximum

386   consumption rate on resource j, and d_i is the intra-specific interference of consumer i when it

387   forages resource j. In Eq. 2, f_m defines the fraction of the consumer biomass that is respired for

388   maintenance of basal metabolism. F_{max} defines the fraction of biomass i that is removed by

389   small-scale artisanal fisheries. In the case of non-harvested species $F_{max} = 0$.

390   The biological rates of production, R, metabolism, X, and maximum consumption, Y,

391   follow a negative power law with the species body size, with an exponent -1.4[61]:

392
$$R_P = a_r M_P^{-0.25} \quad \text{(eq. 4)}$$

393
$$X_C = a_x M_C^{-0.25} \quad \text{(eq. 5)}$$

394
$$Y_c = a_y M_C^{-0.25} \quad \text{(eq. 6)}$$

395   Where a_r, a_x, and a_y are allometric constants and the subscripts P and C denote producers

396   and consumers, respectively. The timescale to examine the dynamics of the system is defined

397   based on the primary producer with the highest mass-specific growth rate (reference species).

398   The mass-specific growth rate and the metabolic rate of each species were normalized by the

399   growth rate of the reference species, and the maximum consumption rate was normalized by

400   each species' metabolic rate[61]. These normalizations translate to the following expressions of

401   intrinsic growth rate (r_i), metabolic rate (x_i), and maximum consumption rate (y_i) of each species

402   i:

403
$$\mathrm{r_i} = \frac{R_P}{R_{Pref}} = 1 \left(\frac{M_P}{M_{Pref}}\right)^{-0.25} \qquad \text{(eq. 7)}$$

404
$$\mathrm{x_i} = \frac{X_C}{R_{Pref}} = \frac{a_x}{a_r} \left(\frac{M_C}{M_{Pref}}\right)^{-0.25} \qquad \text{(eq. 8)}$$

405
$$\mathrm{y_i} = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \qquad\qquad \text{(eq. 9)}$$

406   Since most benthic marine communities are characterized by the presence of sessile

407   filter-feeders at the bottom, these communities are heavily 'subsidized' by the pelagic

408   phytoplankton, which is captured by filter-feeders and transferred up the benthic food web[62]. In

409   general, phytoplankton dynamics is thought to vary primarily due to 'external processes' (e.g.

410   water advection, nutrient loadings, etc.,), including climate fluctuations[34]. To account for this

411   phenomenon, our implementation of the ATN model assumed that the intertidal community is

412   permanently subsidized by plankton biomass. Therefore, we modeled plankton dynamic as a

413   primary producer (eq. 1) and following [75, 76] we incorporated a constant subsidy s into the

414   plankton dynamics as:

415
$$\frac{dBi}{dt'} = d_{local} + s, \qquad\qquad \text{(eq. 10)}$$

416   where d_{local} represents plankton local dynamics (i.e., right hand of eq. 1).

417

418   To our knowledge, the ATN model we develop here is the largest empirical dynamic

419   food-web model ever parameterized (our intertidal food-web contains 107 species, see model

420   parametrization in supplementary materials and parameters values in Supplementary Table S4),

421   which by itself represents an advancement in food web modeling. Moreover, the added realism

422   of plankton subsidy allows us to simulate the effect of climate-change driven effects described

423   above as the alteration of such subsidy.

Food-web robustness to species extinctions

425   Using the static and dynamic approaches (see the model above), we evaluated the food-

426   web robustness to species extinctions using four deletion sequences. First, we evaluated the

427   food-web robustness to the extinction of harvested species by removing them in descending

428   order of total catch amount (hereafter "harvesting" deletion sequence), according to the Chilean

429   national fishing service (www.sernapesca.cl). Second, we performed three additional deletion

430   sequences: (1) randomly (hereafter "random" deletion sequence), (2) from the most to the least

431   connected species (hereafter "most-connected" deletion sequence[38,41]), and (3) from the most

432   connected species that trophically support highly connected species to the least connected

433   species supporting low connected species[42]. This last sequence causes the fastest route of

434   collapse[42] by first deleting the basal species that support most of the species in the food-web

435   (hereafter "supporting-basal" deletion sequence). These last three deletion sequences allow us to

436   compare the food-web sensitivity to the extinction of harvested species with that to the extinction

437   of other species, and to identify the most important species for food-web persistence. For the

438   harvesting deletion sequence, species were removed until all the harvested species were deleted,

439   while for all other sequences the procedure was repeated until all species were removed

440   (including the harvested species). In the case of species with an equal number of interactions, the

441   removed species was chosen at random[40].

442   To compare the food-web robustness across the different patterns of species deletion,

443   except the "harvesting" deletion sequence, we use the R_{50} index[38]. For the harvesting deletion

444   sequence, only the number of secondary extinctions was registered. The R_{50} index represents the

445   proportion of species that have to be removed to cause the extinction of 50% of the species in the

446   network (including primary and secondary extinctions). The highest and lowest possible values

447   of R50 are 0.5 and 1/S, respectively (S is the number of species in the network), which are

448   reached when no secondary extinctions are caused by species deletions and when only one

449   primary species deletion is needed to cause the extinction of 50% of species, respectively. Thus,

450   larger values of R_{50} mean higher robustness. The static approach was simulated using the R

451   package *NetworkExtinction*[63], while the dynamical model was simulated using ODE45 in

452   MATLAB.

453   For the dynamic approach, we first ran the dynamic model for 3650 time-steps which

454   corresponds to 10 years, and ensures that the food-web reached a dynamic equilibrium. Then, we

455   started the removal simulations. In each removal step, the number of extinct species was

456   recorded after 10 years, when the system had reached, again, a steady state. A species was

457   considered extinct if its biomass diminished to less than 10^{-6} [64]. Note that in all deletion

458   sequences we removed the nodes from the food-web, so in the harvesting deletion sequence the

459   F_{max} parameter in the ATN model is zero to all harvested species.

Effects of artisanal fisheries on food-web dynamics

461   We assessed the effects of artisanal fisheries on food-web dynamics by simulating

462   simultaneous fishing on all harvested species and assessing the subsequent effects on the

463   biomass of all species in the food-web. We simulated three fishing scenarios, where we applied

464   exploitation rates needed to decrease the biomass of all harvested species in 50%, 80%, and

23

465   100% (see F_{max} in Supplementary Table S3). Note that basal species required much lower

466   exploitation rate to decrease their biomass (see discussion) than filter-feeders, herbivores, and

467   other consumers, which means that harvested basal species were the most sensitive species to

468   fishing. Note also that a biomass decrease of 100% does not necessarily mean that the harvested

469   species go extinct, because the biomass available to be removed by fishing is the biomass that

470   was produced a time step earlier (i.e., fishing exploitation is simulated as part of the population

471   dynamics of harvested species, see eqs. 1 and 2). These three fishing scenarios allowed us to

472   simulate an approximately well managed fisheries (which removes between 40 and 60% of

473   biomass stock[5]), an overexploitation scenario (which removes 80%) and nearly extinction

474   scenario, which allowed us to assess overall stability if all harvested species go extinct. For each

475   fishing scenario, we first ran the model for 10 years (3650 time-steps) to ensure that the system

476   reached a dynamic equilibrium. Then, we applied the biomass removal ($F_{maxi}B_i$ in eqs. 1 and 2) at

477   each time step in the model to all harvested species simultaneously and we ran the food-web

478   dynamics for another 3650 time-steps to reach post perturbation equilibrium, when final

479   biomasses were considered "after perturbation" state.

480   In each treatment and for each species i, we evaluated the effect of the simulated scenario

481   as:

482    $$Biomass\ change_i = \left[\left(\frac{after\ perturbation_i}{before\ perturbation_i}\right) - 1\right] * 100 \qquad \text{(eq. 11)}$$

483

484   ***Effects of plankton subsidy alteration on food-web dynamics***

485   We assume that the food-web is subsidized by an external source, by including a subsidy

486   in the plankton node, which is considered to be controlled by advective processes, unaffected by

24

487   local benthic consumption. This represents well the situation of most marine benthic

488   ecosystems[62]. To compare the top-down effects of fisheries against bottom-up variation in

489   productivity, we perturbed the plankton subsidy to simulate climate-induced changes in plankton

490   productivity. We simulated both a decrease and an increase in plankton subsidy, as both long-

491   term increased and decreased productivity has been documented to occur in the Humboldt

492   Ecosystem[34]. We used three different perturbation intensities, decreasing or increasing basal

493   subsidy in 50%, 80% and 100%. Note that, a 100% in the basal plankton subsidy decreasing does

494   not translate into plankton extinction (Fig. 3C). A variation of 50% of the basal subsidy is in the

495   order of natural seasonal variability of net primary productivity in central Chile[31]. We assumed

496   that a variation above 50% simulates the effects of extreme changes of plankton subsidy due to

497   climate change, and also, such magnitudes allow comparable perturbation intensities to those

498   used to assess the impacts of fisheries on the food-web dynamics (see previous section). In each

499   scenario, we first ran the model for 3650 time-steps to ensure that the system reached a dynamic

500   equilibrium, and the final species biomasses obtained were considered "*before perturbation*"

501   state. Then, we reduced/increased plankton subsidy at each time step and ran the model for

502   another 3650 time-steps to reach post perturbation equilibrium. The final biomasses were

503   considered "*after perturbation*" state. Changes in biomass were expressed as shown in Eq.11.

504   ***Interacting effects of fisheries and plankton-subsidy alteration on food-web dynamics***

505   To evaluate combined effects of fisheries and climate-induced changes in plankton

506   subsidy, we simulated both fishing on all harvested species and simultaneously altered plankton

507   subsidy. We used the three fisheries scenarios (i.e., 50%, 80% and 100% biomass removed) and

508   crossed these scenarios with each of the six productivity scenarios (i.e., increasing or decreasing

509   plankton subsidy in 50%, 80% and 100%). In each treatment, we first ran the model for 3650

25

510   time-steps and the final species biomasses obtained were considered "*before perturbation*" state.

511   Then, we applied a given plankton subsidy scenario, and at the same time, we started the fishing

512   simulations. Changes in biomass were expressed as shown in Eq.11.

513   **DATA AVAILABILITY:** Simulation code and the Chilean intertidal data will be available

514   upon acceptance at the repository https://github.com/fsvaldovinos/Chilean_Fisheries. The

515   Chilean intertidal food-web and species body sizes can also be found in[12]

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<u>Author Contributions:</u>

M.I.A., S.A.N., P.A.M., and F.S.V. conceived the study. M.I.A. and F.S.V. formulated the

dynamic model, designed and implemented simulations, analyzed results, and wrote the first

draft of the manuscript. S.A.N. E.A.W and A.P. created the trophic interaction database and led

food web compilation. M.I.A. and D.C. created the code to perform the static extinction analysis.

All authors contributed to the final version of the paper.

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