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Evaluating the Role of Large Jellyfish and Forage Fishes as Energy Pathways, and Their Interplay With Fisheries, in the Northern Humboldt Current Systems

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1 **Evaluating the role of large jellyfish and forage fishes as energy pathways, and their**
2 **interplay with fisheries, in the Northern Humboldt Current System**

3

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Abstract

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Large jellyfish are important consumers of plankton, fish eggs and fish larvae in heavily fished ecosystems worldwide; yet they are seldom included in fisheries production models. Here we developed a trophic network model with 41 functional groups using ECOPATH re-expressed in a donor-driven, end-to-end format to directly evaluate the efficiency of large jellyfish and forage fish at transferring energy to higher trophic levels, as well as the ecosystem-wide effects of varying jellyfish and forage fish consumption rates and fishing rates, in the Northern Humboldt Current system (NHCS) off of Peru. Large jellyfish were an energy-loss pathway for high trophic-level consumers, while forage fish channelized the production of lower trophic levels directly into production of top-level consumers. A simulated jellyfish bloom resulted in a decline in productivity of all functional groups, including forage fish (12%), with the exception of sea turtles. A modeled increase in forage fish consumption rate by 50% resulted in a decrease in large jellyfish productivity (29%). A simulated increase of 40% in forage fish harvest enhanced jellyfish productivity (24%), while closure of all fisheries caused a decline in large jellyfish productivity (26%) and productivity increases in upper level consumers. These outcomes not only suggest that jellyfish blooms and fisheries have important effects on the structure of the NHCS, but they also support the hypothesis that forage fishing provides a competitive release for large jellyfish. We recommend including jellyfish as a functional group in future ecosystem modeling efforts, including ecosystem-based approaches to fishery management of coastal ecosystems worldwide.

Keywords: ECOPATH, ECOTRAN, Peruvian anchoveta, sardine, *Chrysaora plocamia*, Humboldt Current, foodwebs

61

62 **1. Introduction**

63 Forage fishes, defined here as small pelagic planktivorous fishes, not only represent the
64 main food source of piscivorous fishes, seabirds, and marine mammals in marine ecosystems
65 worldwide, but also comprise ~30% of global marine fisheries catch (Pikitch et al., 2014).
66 Because of their importance as prey to broad diversity of predators, they are a crucial conduit for
67 energy transfer between lower and higher trophic levels within marine foodwebs. This is
68 particularly true in eastern boundary current ecosystems where fluctuations in forage fish
69 abundance can alter the dynamics, structure and function of ecosystems (Smith et al., 2011).
70 Forage fish production is highly susceptible to variations in environment and harvest rates
71 (Chavez et al., 2003), with subsequent changes cascading upwards and downwards through the
72 foodweb (Pauly et al., 1998; Daskalov et al., 2007). Such susceptibility has encouraged policy-
73 makers and managers to implement ecosystem-based fishery modeling efforts to conserve and
74 manage forage fish populations (Alder et al., 2008; Pikitch et al., 2012).

75 Ecosystem production models, however, focus only on parameters with a direct link to
76 fish, such as those associated with fish food and fish predators and prey (Walters et al., 2008;
77 Pauly et al., 2009). Less consideration is given to other ecologically important components with
78 indirect links to fish, such as large jellyfish. These gelatinous zooplanktivorous predators can not
79 only compete with forage fish for food and prey on their eggs and larvae (Hansson et al., 2005;
80 Zeman et al., 2016), but they also often form large, seasonal blooms that can dominate the
81 coastal pelagic biomass. The lack of adequate parameterization of jellyfish in ecosystem
82 production models may be due to the paucity of system-specific data (Condon et al., 2012), to an
83 under appreciation of their role in marine foodwebs (Pauly et al., 2009), or to the perception that

84 they are “trophic dead ends” (Robinson et al., 2014). However, recent studies have synthesized
85 biomass data for multiple gelatinous taxa (Lucas et al., 2014) and demonstrated that gelatinous
86 plankton are frequently consumed by fish (Mianzan et al., 1996; Cardona et al., 2012; Milisenda
87 et al., 2014), deep sea scavengers (Sweetman et al., 2014), and sea turtles (Heaslip et al., 2012;
88 Heithaus, 2013).

89 The absence of jellyfish in ecological foodweb models in heavily-fished ecosystems like
90 those in eastern boundary currents is concerning because evidence suggests that jellyfish
91 populations can go through extended periods of high abundance (Condon et al., 2013). Size and
92 frequency of jellyfish blooms are affected by climate (Lynam et al., 2011; Chiaverano et al.,
93 2013; Robinson and Graham, 2014), habitat modification (Lo et al., 2008), eutrophication (Oguz,
94 2005), hypoxia (Purcell et al., 2001; Graham, 2001), and overfishing (Roux et al., 2013).
95 Previous studies on ecosystem-wide effects of jellyfish blooms in intensively fished ecosystems
96 like the Northern California Current (Ruzicka et al., 2012), Gulf of Alaska (Ruzicka et al., 2013),
97 the Black Sea (Kideys et al., 2005), and the northern Gulf of Mexico (Robinson et al., 2015)
98 indicate an inverse relationship between jellyfish production and forage fish production. Because
99 jellyfish and forage fish overlap in space and time (Brodeur et al., 2008; Decker et al., 2018) and
100 diets (Brodeur et al., 2008), the removal of forage fish through harvest may indirectly enhance
101 jellyfish production by increasing prey availability (Robinson et al., 2014).

102 Eastern boundary currents, like the northern part of the Humboldt Current System
103 (NHCS) off the Peruvian coast, are among the most productive in the world (Pennington et al.,
104 2006; Bakun and Weeks, 2008). The NHCS experiences year-round upwelling (Carr 2001) and
105 supports large forage fish fisheries, including sardines *Sardinops sagax* (Chavez et al., 2008;
106 Cardenas-Quintana et al., 2015) and the world’s largest fishery by weight for anchovy *Engraulis*

107 *ringens* (Penington et al., 2006; Chavez et al., 2008). These forage fishes overlap spatially and
108 temporally in the NHCS with scyphomedusae of *Chrysaora plocamia* (Quiñones et al., 2015).
109 These large (~50 cm bell diameter) jellyfish at times dominate the pelagic biomass in this
110 system, comprising as much as 70% (wet weight) of the total pelagic catch during periods of
111 high abundance (Quiñones et al., 2013). Previous studies revealed that *C. plocamia* diets include
112 anchovy eggs (Riascos et al., 2014) and forage fish prey (see Espinoza and Bertrand, 2008;
113 Espinoza et al., 2009), thus, spatio-temporal overlap between forage fish and large jellyfish in the
114 NHCS may result in predatory and competitive interactions. These trophic interactions are
115 expected to affect forage fish harvests, which averages ~6.5 million tons year⁻¹ (1950 – 2001;
116 FAO, 2011). Although the NHCS has been modeled extensively using carbon and nitrogen
117 budget models (Walsh, 1981), mass balance models (Jarre and Pauly, 1993), carbon flow models
118 (Carr, 2002), and steady-state models (Tam et al., 2008), none of these models have included
119 large jellyfish and their interactions with forage fish.

120 In this study, we adopted a steady-state trophic model for the NHCS previously
121 developed by Tam et al. (2008) and added data on large jellyfish (*C. plocamia*), marine turtles,
122 anchovy eggs, and fishery discards in order to quantify for the NHCS: 1) the efficiency of large
123 jellyfish and forage fish at transferring energy to upper trophic levels through the foodweb, and
124 2) the ecosystem-wide effects of changes in large jellyfish and forage fish consumption rates,
125 and fishery harvests.

126

127 **2. Data and models**

128 A steady-state foodweb model for the NHCS was constructed based on the models
129 previously developed by Tam et al. (2008). The model domain covers an area of 165,000 km²,

130 extending from 4°S to 16°S and out to 111 km (60 nm) from the shoreline (Fig. 1). The model
 131 was constructed using ECOPATH (Christensen and Pauly, 1992), which uses a mass-balance
 132 approach to estimate energy flows between pre-defined functional groups. Net production of a
 133 given group equals energy losses via predation, fishery catch rates, senescence, and net migration
 134 according the following equation (1).

$$135 \quad b_p \times \left(\frac{p}{b}\right)_p \times ee_p = y_p + \sum b_c \left(\frac{q}{b}\right)_p \times D_{pc} + ba_p + nm_p \text{ (Eq. 1)}$$

136 where b_p is the biomass of a producer or prey group (p), b_c is the biomass of a consumer group
 137 (c), $(p/b)_p$ is the production rate per unit of biomass, ee_p is the fraction of total group production
 138 utilized within the ecosystem (i.e., ecotrophic efficiency), y_p is the fisheries catch rate per unit
 139 area and time, $(q/b)_p$ is the food consumption rate per unit of biomass of consumer (c), D_{pc} is the
 140 contribution of producer (p) to the diet of consumer (c), ba_p is the biomass accumulation rate,
 141 and nm_p is the net migration rate of the producer. Using linear equations that represent each
 142 functional group (Eq. 1) and wet weight biomass, ECOPATH constructs a matrix Q_{pc} describing
 143 the energy demand for each consumer through each trophic linkage of the foodweb.

144 The fully resolved NHCS model developed for this study includes 41 groups, including
 145 36 living groups (-phytoplankton (2), zooplankton (3), jellyfish (2), macro invertebrates (3),
 146 bony fish (18), cartilaginous fish (2), fish eggs (1), seabirds (1), sea turtles (2), marine mammals
 147 (2)-), fisheries (2), and detritus pools (3) (Supplementary Table A). The 41 groups included in
 148 the fully resolved model were aggregated into 25 functional groups (Table 1) following the
 149 criteria described in Robinson et al. (2015).

150 Our base model was constructed using data on fisheries catch (y , t km⁻² y⁻¹), as well as
 151 biomass (b , t km⁻² y⁻¹), production/biomass ratio (p/b y⁻¹), consumption/biomass ratio (q/b), and
 152 diet composition for phytoplankton, zooplankton (including small gelatinous zooplankton), fish

153 (except sardine and anchovy), seabird, and marine mammals from Tam et al. (2008) and
154 averaged over the period 1995-1998. The ecotrophic efficiency (*ee*) data for other small and
155 large pelagic fish, hake, small and medium demersal fish, benthic elasmobranchs,
156 chondrichthyans, and seabirds were borrowed from Guénette et al. (2008). Large jellyfish (*C.*
157 *plocamia*) biomass data were obtained from Quiñones et al. (2015). Because the distribution of
158 *C. plocamia* medusae is not homogeneous within the model domain (see Quiñones et al., 2018),
159 annual (from 1975 to 2014) mean biomasses were estimated by using a delta-distribution
160 following the method described by Pennington (1996). Large jellyfish biomass was expressed in
161 kg wet weight (WW) 1000 m⁻³ and converted to tons (t) WW km⁻² y⁻¹ by integrating the top 7.5
162 m of the water column, which represents the layer in which *C. plocamia* medusae typically occur
163 (Quiñones, pers. obs.). Diet composition of *C. plocamia* was obtained from previous studies
164 (Ceh et al., 2015; Aller, 2017). Values of *p/b* and *q/b* for *C. plocamia* medusae were borrowed
165 from the Northern California Current models of Ruzicka et al. (2012). Diets of forage fishes
166 (anchovy and sardine) were updated from Tam et al. (2008) by adding data from Espinoza and
167 Bertrand (2008) and Espinoza et al. (2009). Abundances of green (*Chelonia mydas*) and
168 leatherback (*Dermochelys coriacea*) turtles in the NHCS were derived from fisheries by-catch
169 (Alfaro-Shigeto et al., 2011) and survey data (2010-2015, Quiñones, unpub. data). Sea turtle
170 biomass estimates were obtained from growth equations (Jones et al., 2011) using a mean curved
171 carapace length (CCL) of 58.7 cm and 139.6 cm for green and leatherback turtles, respectively
172 (Alfaro-Shigeto et al., 2011). Diets of sea turtles were compiled from IMPARPE (2001), Paredes
173 (2005) and Quiñones et al. (2010). Both *p/b* and *q/b* values for sea turtles were borrowed from
174 Robinson et al. (2015). Anchovy egg biomass was estimated using mean density of anchovy eggs
175 in the NHCS from Lett et al. (2007) and egg volume/mass (Castro et al. 2009). Production rates

176 of anchovy eggs were assumed to be 25% (Ruzicka et al. 2012; Robinson et al. 2015). Fishery
177 discards were obtained by reconstructing catches using gear-specific discard rates (%) described
178 in Kelleher (2005). A discard rate of 10% was assumed for all artisanal fisheries. In order to
179 achieve a balanced model, we only reduced sardine landings from $5.65 \text{ t km}^{-2} \text{ year}^{-1}$ (1995-1998
180 average; Tam et al., 2008) to $1.4 \text{ t km}^{-2} \text{ year}^{-1}$.

181 In order to estimate ecosystem-wide consequences of changes in forage fish and large
182 jellyfish abundances, or changes in fishery harvest rates (e.g., Robinson et al., 2015), the steady-
183 state ECOPATH solution for the foodweb as a “top-down” network of consumer demands (Q_{pc})
184 was re-expressed as a “bottom-up” map of production fate (A_{cp}) using the ECOTRAN technique
185 described in Steele and Ruzicka (2011).

$$186 \quad A_{cp} = \frac{D_{pc} Q_c}{\sum_c Q_c D_{pc}} \quad (\text{Eq. 2})$$

187 where A_{cp} is the production matrix, the fraction of the total production of each producer (p)
188 consumed by each consumer (c), and Q_c is the total consumption rate of consumer (c).
189 Senescence and egestion flows to detritus and bacterial metabolism of detritus into recycled
190 nutrient pools were added to the production matrix A_{cp} as separate functional groups. Thus, the
191 model is an end-to-end model in the strict sense of the term, tracking production flowing
192 upwards through the foodweb from nutrient inputs to the production of top consumers and
193 fisheries, and downwards via the recycling of detritus and nutrients. Metabolic rates were
194 estimated from the defined ECOPATH physiological parameters as described in Ruzicka et al.
195 (2012) and distributed between pelagic and benthic pools according to life histories and
196 behaviors of each functional group. The efficiency of large jellyfish and forage fish to transfer
197 energy to upper trophic levels in the foodweb was evaluated by using the “footprint” and “reach”
198 metrics (Ruzicka et al., 2012). The ecosystem level “footprint” of a particular group of interest is

199 the fraction of total production in the ecosystem required to support that group. The ecosystem
200 level “reach” is the fractional contribution of a particular group of interest to total consumer
201 production in the ecosystem via all direct and indirect trophic pathways.

202 Structural scenarios were performed to evaluate the ecosystem-wide effects of changes in
203 biomass and consumption rates of large jellyfish and forage fish, as well as changes in fishery
204 catch rates (see Ruzicka et al., 2012; Robinson et al 2015). A structural scenario is generated by
205 changing the consumption demands or production rates of one or more groups and re-calculating
206 the energy flow rates through a steady state representation of the foodweb (matrix A_{cp} , Eq. 2).
207 Structural scenarios represent linear, asymptotic solutions of time-dynamic simulations (Collie et
208 al., 2009; Steele et al., 2009). Four scenarios were run: I) jellyfish boom (jellyfish consumption
209 increased by 50%), II) forage fish dominance (forage fish consumption increased by 50%), III)
210 increased fishing pressure (40% increase in forage fish harvest by fisheries, considering a mean
211 harvest rate of $29 \text{ t km}^{-2} \text{ y}^{-1}$, corresponding to forage fish landings and discards; see Table 1), and
212 IV) fishery moratorium (the closing of all fisheries). Total predation pressure on each prey type
213 was left unchanged. Changes in predation pressure upon a prey group by a modified consumer
214 were balanced by proportional changes to the predation pressure exerted by all other consumers
215 of the shared prey (Robinson et al., 2015). Scenario results are reported as the fractional change
216 in production of each functional group caused by the scenario modifications (fractional change =
217 $(P_{\text{scenario model}} - P_{\text{base model}}) / P_{\text{base model}}$). Indices of confidence for all model-derived metrics and
218 scenarios were estimated via Monte Carlo analysis. One thousand alternate models were
219 randomly generated by drawing from a normal distribution about each trophic connection
220 defined within production matrix A_{cp} . The level of uncertainty about each element of the
221 production matrix was calculated from the defined levels of uncertainty for each model

222 parameter (biomass, P/B, P/Q, AE, diet, landings, and discards; see Supplementary Table I).
223 Scenarios were repeated using each randomly generated model. Scenarios I and II were also run
224 under alternate levels of uncertainty about biomass, growth efficiency (P/Q), and diet (see
225 Supplementary Material).

226

227 **3. Results**

228 The input data for the aggregated base model of the NHCS is summarized in Table 1. Additional
229 details on the fully resolved and aggregated model parameters can be found in the
230 Supplementary Material section.

231

232 *3.1. Foodwebs*

233 Forage fish and large jellyfish exhibited similar system footprint values (7.3×10^{-2} and 4
234 $\times 10^{-2}$, respectively). However, the system reach of forage fish (7×10^{-3}) was four orders of
235 magnitude larger than that of large jellyfish (*C. plocamia*) (2×10^{-7}), suggesting that in the
236 NHCS forage fish are considerably more important as an energy transfer nexus to top consumers
237 than jellyfish (Fig. 2). Foodweb network diagrams of flow patterns to (footprint) and from
238 (reach) forage fish and large jellyfish illustrate how forage fish are a more efficient, direct energy
239 pathway from phytoplankton to top-level consumers than are large jellyfish which act as an
240 energy-loss pathway by diverting energy away from higher trophic-level consumers (Figure 3).
241 The greater energy transfer efficiency of forage fish is highlighted by the large fraction of energy
242 (i.e., thicker lines) flowing from phytoplankton and zooplankton groups to forage fish, and from
243 there to upper trophic levels, including apex pelagic fish predators, piscivorous demersal fish,
244 seabirds, marine mammals, and fisheries (Fig. 3A). In contrast, large jellyfish diverted

245 zooplankton and phytoplankton production away from top consumers, which is highlighted by
246 the smaller fraction of energy (i.e., thinner lines) transferred upwards to higher trophic levels
247 (Fig. 3B). Instead, large jellyfish in this system directly supported production of only small
248 planktivorous fishes and marine turtles (Fig. 3B).

249

250 3.2. *Structural scenarios*

251 In our jellyfish bloom scenario (Scenario I), we found that the modeled NCHS could only
252 support only a 39% increase in large jellyfish consumption, limited by the production of jellyfish
253 prey. A 39% increase in jellyfish biomass and consumption demands resulted in declines in
254 productivity among most mid-trophic level and upper-trophic level groups (Fig. 4A, Table 2). By
255 contrast, sea turtles were the only group that exhibited an increase in production (Fig. 4A, Table
256 2). Interestingly, a 39% increase in large jellyfish consumption yielded a 13% decline in
257 productivity of fisheries (Fig. 4A, Table 2).

258 The impacts of increasing forage fish consumption by 50% (Scenario II) had a
259 considerable negative impact upon the production of large jellyfish, mesopelagic fish
260 cephalopods, pelagic planktivorous fish, and sea turtles (Fig. 4B, Table 2). Production of
261 seabirds, anchovy eggs and fisheries however, increased under this scenario (Fig. 4B, Table 2).
262 Relatively small negative effects on the production of zooplankton, all piscivorous fish, and top
263 predatory fish were observed under this scenario (Fig. 4B, Table 2).

264 The increased fishing pressure scenario (Scenario III, 40% increase in removal of forage
265 fish by fisheries) resulted in large productivity increases of mid-trophic groups (demersal and
266 pelagic planktivorous fish and large jellyfish) and upper level consumers (mesopelagic fish,

267 cephalopods, and sea turtles (Fig. 4C, Table 2). Seabird and anchovy egg production exhibited
268 the largest decline in productivity (-30% and -44%, respectively) (Fig. 4C, Table 2).

269 The closure of all fisheries (Scenario IV) resulted in large productivity increases of
270 forage fish and demersal benthivorous fish, as well as in most upper-level consumers, including
271 demersal piscivorous and apex predatory fish, seabirds, and marine mammals (Fig. 4D, Table 2).
272 By contrast, relatively large productivity declines were observed in most mid-trophic level
273 groups, including large jellyfish, mesopelagic fish, and pelagic and demersal planktonic fish
274 (Fig. 4D, Table 2). Productivity of upper-level consumers, such as cephalopods and sea turtles
275 also declined (Figure 4D and Table 2).

276

277 **4. Discussion**

278 *4.1. Foodwebs*

279 Footprint and reach metrics calculated from the NHCS foodweb model indicate that
280 increases in large jellyfish (*C. plocamia*) could make the foodweb considerably less efficient at
281 transferring energy to upper trophic levels than when forage fish are abundant. Forage fish in this
282 system had a larger footprint (0.07) than jellyfish (0.04), indicating that forage fish are using
283 more of the total system production relative to jellyfish. Large jellyfish however, had a reach (2
284 $\times 10^{-7}$) four orders of magnitude smaller than forage fish (7.3×10^{-3}), resulting in a much smaller
285 contribution by jellyfish to the production of upper-level consumers. Large jellyfish in the NHCS
286 directly contributed to the production of only planktivorous fish (mostly butterfishes) and sea
287 turtles (mainly leatherbacks). However, considering all direct and indirect pathways of energy
288 flow in the NHCS, large jellyfish indirectly supported several higher-order consumers in the
289 system (Fig. 3). Therefore, large jellyfish cannot be considered as trophic dead-ends in the

290 NHCS. This is in line with previous studies showing that large jellyfish can support the
291 production of several taxa, such as parasitic cnidarians (Chiaverano et al., 2015), crustaceans
292 (Fleming et al., 2014), fish (Purcell and Arai, 2001), and sea turtles (Cardona et al., 2012).

293 Forage fish in the NHCS represented one of the most important mid-trophic level groups
294 for transferring energy upwards within the foodweb, channeling plankton production directly
295 into production of upper-level consumers (Fig. 3). Therefore, when large jellyfish become
296 highly abundant in this system (i.e., during blooms), the fraction of total ecosystem production,
297 and the efficiency at which it is transferred upwards in the foodweb, can be substantially reduced
298 compared to situations when forage fish dominate (i.e., non-bloom periods). These findings are
299 in agreement with previous studies of the northern Gulf of Mexico (Robinson et al., 2015), the
300 Northern California Current (Ruzicka et al., 2012), and the Eastern Bering Sea (Robinson et al.,
301 2014) ecosystems, adding support to the proposed role of forage fish and large jellyfish as energy
302 conduits and production-loss pathways, respectively, in pelagic marine ecosystems worldwide
303 (Robinson et al., 2014).

304

305 *4.2. Structural scenarios*

306 Ecosystem-wide responses to a simulated jellyfish bloom (39% increase in jellyfish
307 consumption, Scenario I) resulted in a decline in the productivity of almost all NHCS mid-
308 trophic and upper level consumers (Fig. 4A). This finding is similar to the ecosystem responses
309 observed in other marine pelagic ecosystems, including the Northern California Current (Ruzicka
310 et al., 2012) and the Gulf of Mexico (Robinson et al., 2015). Previous studies indicate that forage
311 fish and large jellyfish can overlap in their diets (Brodeur et al., 2008). Therefore, an increase in
312 consumption by jellyfish could lead to decline in forage fish productivity by reducing prey

313 availability. Forage fish and *C. plocamia* medusae appear to share prey items in the NHCS (see
314 Ceh et al., 2016; Espinoza and Bertrand 2008; Espinoza et al., 2009; Supplementary Table B).
315 Thus, during a jellyfish bloom there is likely a reduced prey availability to forage fish and other
316 pelagic planktivorous taxa can consume in this system, which could result in productivity
317 declines of planktivorous fish (Fig. 4A). Since scenario analyses account for trophic energy
318 flows to functional groups via all direct and indirect pathways, the productivity declines of
319 piscivorous and benthivorous fish, apex predatory fish, seabirds, and marine mammals (mainly
320 pinnipeds) obtained in our modeled jellyfish bloom scenario are likely due to the declines in the
321 production of their forage fish prey (Table 2). Considering how important forage fish are at
322 transferring energy through the NHCS foodwebs (Fig. 3A), any factors affecting forage fish
323 production are expected to have strong subsequent effects throughout the entire ecosystem.
324 Under the jellyfish bloom scenario, sea turtles represented the only functional group that
325 responded positively to an increase in jellyfish consumption. This outcome can be explained by
326 the fact that *C. plocamia* medusae appear to be an essential prey item in the diet of leatherback
327 and green sea turtles (Paredes, 2015; Quiñones et al., 2015) in the NHCS.

328 Increasing forage fish consumption by 50% (Scenario II) negatively impacted production
329 of large jellyfish (29% decrease), while increasing forage fishing pressure by 40% (Scenario III)
330 resulted in the opposite effect (24% increase in large jellyfish production). These model
331 outcomes may be also explained by the aforementioned dietary overlap between *C. plocamia*
332 medusae and forage fish in the NHCS. Increased forage fish consumption would therefore re-
333 direct zooplankton production away from large jellyfish, which would negatively affect medusa
334 growth and production (Parsons and Lalli, 2002). By contrast, the opposite effect is likely to
335 happen when forage fish are removed by fisheries (Robinson et al., 2014). In addition, this is

336 likely the mechanism driving the observed changes in productivity of cephalopods (excluding
337 jumbo squid), mesopelagic fish, and planktivorous fish obtained under scenarios II and III
338 because these groups are primarily zooplanktivorous in this system (see Supplementary Table
339 B).

340 Despite the importance of forage fish in the NHCS as energy pathways to upper trophic
341 levels, the changes in productivity of piscivorous fish obtained under these two scenarios were
342 unexpectedly low (Table 2). Similar results were obtained under the same modeled scenarios for
343 the northern Gulf of Mexico (Robinson et al., 2015). Plausible explanations for these outcomes
344 are that most piscivorous fishes may not be food limited in this highly productive system (Carr,
345 2002), and that a 50% increase in forage fish consumption or a 40% increase of forage fish
346 removal by fisheries is perhaps not sufficient to cause large changes in piscivorous fish
347 productivity. In addition, most piscivorous fish included in our model have diverse diets and do
348 not feed exclusively on forage fish (Supplementary Table B). Therefore, they may be able to
349 compensate for reduced forage fish availability by consuming other prey items, such other small
350 mesopelagic fish and macrozooplankton (Table 2). Nevertheless, our increased fishing pressure
351 scenario resulting in changes in productivity of high-level consumers, including *C. plocamia*,
352 supports findings from previous studies on other heavily fished systems in which forage fish
353 harvesting altered the structure and dynamics of marine ecosystems (Jackson et al., 2001; Pikitch
354 et al., 2014), and resulted in increased jellyfish populations (Lynam et al., 2011; Roux et al.,
355 2013). Although *C. plocamia* abundance in the NHCS has not increased during periods of high
356 fishing pressure on forage fish (Quiñones et al., 2015), overfishing could contribute to larger
357 jellyfish blooms if it took place during periods of favorable environmental conditions for polyp
358 asexual propagation and medusa growth. Previous work has shown that *C. plocamia* blooms

359 occur mostly during the warm phase of ENSO events throughout the sardine-dominated El Viejo
360 regime (Quiñones et al., 2015). Hence, during these periods, stock managers should design
361 appropriate adaptation methods to determine fishing quotas in the NHCS.

362 Our modeled fishery moratorium (Scenario IV) resulted in an increase in productivity of
363 forage fish and in a decline in productivity of large jellyfish and other planktivorous groups
364 (mesopelagic fish and small cephalopods), most likely as a result of food competition.
365 Competition for resources can also explain the declined productivity of pelagic piscivorous
366 fishes, since this group is mainly represented (93%) by horse and chub mackerel, which also feed
367 on zooplankton in this system (see Supplementary Table B). Under this scenario, productivity of
368 most piscivorous fish, apex predatory fish, seabirds, and marine mammals increased, most likely
369 due to the increased availability of forage fish as prey. Similar results have been obtained from
370 “no fishing” scenarios modeled for the northern Gulf of Mexico, the Northern California
371 Current, and the Bering Sea ecosystems, suggesting that forage fish, as well as piscivorous, apex
372 predatory fish, and seabird production, are likely most susceptible to complete fishery closures
373 (Robinson et al., 2014; 2015). Although a “no fishing” scenario is perhaps extreme and
374 unrealistic, it represents a valuable exercise to examine the potential ecosystem-wide effects of
375 fisheries, not only in the NHCS, but in heavily fished marine ecosystems worldwide.

376 An important result from our jellyfish bloom scenario (Scenario I) was a 13% decline in
377 fisheries productivity overall (Table 2). In Peru, forage fish (anchovies and sardines) make up
378 >95% of the country’s annual fishery (commercial and artisanal) landings, with the Peruvian
379 anchoveta (*Engraulis ringens*) accounting for 99% of total forage fish landings (FAO, 2011).
380 Thus, this model outcome suggests that when large jellyfish are abundant in this system, fisheries
381 production can decrease mainly due to a negative effect of jellyfish increased consumption on

382 forage fish production (Table 2), presumably through resource competition (see above).
383 Although a 13% decrease in fisheries production may seem relatively low, consider that the
384 Peruvian anchoveta fishery is one of the largest fisheries in the world, with an average annual
385 landing of 6.5 million metric (FAO, 2011). Thus, a 13% decrease in productivity of this fishery
386 would translate to a potential decline of ~845,000 tons of fish. In addition, our modeled jellyfish
387 bloom represents a very conservative scenario (39% increase) in which the system is supporting
388 ~12 t WW km⁻² of jellyfish biomass. During exceptionally large bloom events in the NHCS,
389 such as those occurred during 1976, 1982-83, 1986-87, and 2014 (Quiñones et al., 2015, 2018),
390 *C. plocamia* biomass can reach up to 62, 37, 81 and 43 t WW km⁻², respectively, a biomass
391 increase 2.9 – 6.4 times greater than our scenario. Hence, such events are expected to have a
392 much higher negative impact on forage fish production, and consequently, on forage fish
393 fisheries. During years of exceptionally large jellyfish blooms, harvest rates for forage fish and
394 other upper-level fish may require to be adjusted so the system can support production of higher-
395 trophic level consumers, including piscivorous fish, seabirds, and marine mammals (Cury et al.,
396 2011; Pikitch et al., 2012). Our model scenarios did suggest that the ecosystem could support a
397 maximum level increase in jellyfish consumption of about 39%. The structural scenarios run here
398 estimated sustained production levels in perpetuity and were designed specifically to prevent the
399 complete extinction of any model group. In reality, jellyfish blooms in the NHCS can greatly
400 exceed this level for short time periods in localized regions (Quinones et al., 2018). Future
401 research including a seasonal, regional model will help to evaluate the potential effects of very
402 large jellyfish blooms on forage fish and fisheries production in this upwelling region.

403

404 *4.3. Limitations and caveats*

405 As with all modeling approaches, there are certain aspects of our model that could be
406 improved. First, additional quantitative estimates on the contribution of large jellyfish (and
407 gelatinous zooplankton in general) to the diets of other consumers in this system are needed.
408 Future studies should aim at evaluating the role of jellyfish as primary and alternative food
409 sources of apex predatory fish and sea birds, as shown by recent studies in other marine systems
410 (Cardona et al., 2012; Thiebot et al., 2017). In addition, our model may also be improved by
411 including biomass of small jellyfish estimated from surveys using sampling gears that
412 specifically target this group. Moreover, large jellyfish carcasses have been shown to play a
413 critical role as energy pathways to benthic communities (Sweetman et al., 2014). In the NHCS,
414 large aggregations of dead *C. plocamia* medusae have been observed during May-June on the
415 seafloor of Bahía Independencia, Peru (14 ° 14'S; 76 ° 08'W), with various species of crabs, such
416 as *Hepatus chilensis*, *Platymera gaudichaudii* and *Cancer plebejus* preying upon them
417 (Quiñones, pers. obs.). Future studies on pelagic-benthic trophic links in the NHCS will also help
418 to improve our model and to better understand the roles of large jellyfish in this ecosystem.

419

420 **5. Conclusions**

421 The present study represents the first evaluation of the role of forage fish and jellyfish as
422 energy pathways, as well as the combined effect of fisheries, in energy pathways of the Northern
423 Humboldt Current System. In the present study we have showed that forage fish are highly
424 efficient at transferring energy from producers to top-level consumers, while large jellyfish are
425 considerably less efficient as energy conduits by diverting energy from plankton producers into
426 several low and mid-trophic level consumers. The results from all structural scenarios indicate
427 that forage fish, large jellyfish, and forage fish fisheries are likely interrelated in the NHCS.

428 Increases in jellyfish consumption led to reduced forage fish productivity, while increased forage
429 fish consumption lead to a decline in jellyfish productivity. In addition the removal of forage fish
430 by fisheries increased jellyfish production, while a fisheries moratorium resulted in a decrease in
431 jellyfish production, presumably through competition for resources. Our findings therefore
432 suggest a negative effect on forage fish productivity not only through fisheries harvest, but also
433 through blooms of large jellyfish. These suggestions are in line with results from model
434 simulations for other marine ecosystems, where removal of forage fish through fisheries yielded
435 an increase in forage fish competitors, including large jellyfish (Robinson et al., 2014; 2015).
436 Our findings, together with previous studies (Ruzicka et al., 2012; Robinson et al., 2014; 2015),
437 suggest that interactions among large jellyfish, forage fish, and fisheries can have ecosystem-
438 wide implications, particularly on upper trophic levels, since a decrease in forage fish production
439 can result in reduced productivity of seabirds (Cury et al., 2011) and economically important
440 pelagic fish (Smith et al., 2011; Pikitch et al., 2014). Therefore, we recommend jellyfish to be
441 included as a functional group in future ecosystem modeling, as well as be considered as an
442 indicator of ecosystem perturbations, in ecosystem-based approaches to fishery management of
443 coastal ecosystems worldwide (Brodeur et al., 2016).

444

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451 **References**

- 452 Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., Pauly, D. 2008. Forage fish: from
 453 ecosystems to markets. *Annual Review of Environment and Resources* 33, 153–166.
- 454 Alfaro-Shigueto, J., Mangel, J. C., Bernedo, F., Dutton, P. H., Seminoff, J. A., Godley, B. J.
 455 2011. Small-scale fisheries of Peru: a major sink for marine turtles in the Pacific. *Journal*
 456 *of Applied Ecology* 48, 1432-1440.
- 457 Aller, O. 2017. Descripción de la dieta de la medusa *Chrysaora plocamia* (Lesson, 1830) en la
 458 bahía Independencia, Perú durante el evento El Niño costero 2017. Universidad
 459 Científica del Sur, Lima, Perú. 50 pp.
- 460 Bakun, A., Weeks, S. J. 2008. The marine ecosystem off Peru: What are the secrets of its fishery
 461 productivity and what might its future hold? *Progress in Oceanography* 79, 290-299.
- 462 Brodeur, R.D., Link, J.S., Smith, B.E., Ford, M.D., Kobayashi, D.R. and Jones, T.T. 2016.
 463 Ecological and economic consequences of ignoring jellyfish: A plea for increased
 464 monitoring of ecosystems. *Fisheries* 41, 630-637.
- 465 Brodeur, R. D., Suchman, C. L., Reese, D. C., Miller, T.W., Daly, E. A. 2008. Spatial overlap
 466 and trophic interactions between pelagic fish and large jellyfish in the northern California
 467 Current. *Marine Biology* 154, 649–659.
- 468 Cardenas-Quintana, G., Franco-Melendez, M., Salcedo-Rodriguez, J., Ulloa-Espejo, D., Pellon-
 469 Farfan, J. 2015. The Peruvian sardine, *Sardinops sagax*: Historical analysis of the fishery
 470 (1978-2005). *Ciencias Marinas* 41, 203-216.
- 471 Cardona, L., Alvarez de Quevedo, I., Borrell, A., Aguilar, A. 2012. Massive consumption of
 472 gelatinous plankton by Mediterranean apex predators. *PLoS ONE* 7, e31329.
- 473 Carr, M. E. 2001. Estimation of potential productivity in Eastern Boundary Currents using
 474 remote sensing. *Deep Sea Research Part II: Topical Studies in Oceanography* 49, 59-80.
- 475 Castro, L. R., Claramunt, G., Krautz, M. C., Llanos-Rivera, A., Moreno, P. 2009. Egg trait
 476 variation in anchoveta *Engraulis ringens*: a maternal response to changing environmental
 477 conditions in contrasting spawning habitats. *Marine Ecology Progress Series* 381, 237-
 478 248.
- 479 Ceh, J., Gonzalez, J., Pacheco, A. S., Riascos, J. M. 2015. The elusive life cycle of scyphozoan
 480 jellyfish–metagenesis revisited. *Scientific Reports*, 5, 12037.
- 481 Chavez, F. P., Bertrand, A., Guevara-Carrasco, R., Soler, P., Csirke, J. 2008. The northern
 482 Humboldt Current system: brief history, present status and a view towards the future.
 483 *Progress in Oceanography* 79, 95–105.
- 484 Chavez, F. P., Ryan, J., Lluch-Cota, S., Miguel Niquen, C. 2003. From anchovies to sardines and
 485 back: multidecadal change in the Pacific Ocean. *Science* 299, 217–221.
- 486 Chiaverano, L. M., Graham, W. M., Costello, J. H. 2015. Parasites alter behavior, reproductive
 487 output, and growth patterns of *Aurelia* medusae in a marine lake. *Marine Ecology*
 488 *Progress Series* 540, 87-98.
- 489 Chiaverano L. M., Holland, B. S., Crow, G. L., Blair, L., Yanagihara, A. A. 2013. Long-term
 490 fluctuations in circalunar beach aggregations of the box jellyfish *Alatina moseri* in
 491 Hawaii, with links to environmental variability. *PLoS ONE* 8(10), e77039.
- 492 Christensen, V., Pauly, D. 1992. ECOPATH II—software for balancing steady-state ecosystem
 493 models and calculating network characteristics. *Ecological Modelling* 61, 169–185.
- 494 Christensen, V., Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations.
 495 *Ecological Modelling* 172, 109–139.

- 496 Collie, J. S., Gifford D. J., Steele J. H. 2009. End-to-end foodweb control of fish production on
497 Georges Bank. ICES Journal of Marine Science 66, 2223-2232.
- 498 Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R.,
499 Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B., Uye, S. I. 2013. Recurrent
500 jellyfish blooms are a consequence of global oscillations. Proceedings of the National
501 Academy of Sciences 110, 1000-1005.
- 502 Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H.D.,
503 Sutherland, K. R., et al. 2012. Questioning the rise of gelatinous zooplankton in the
504 World's Oceans. BioScience 62, 160–169.
- 505 Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W.,
506 Mills, J. A., Murphy, E. J., Österblom, H., Paleczny, M., Piatt, J. F. 2011. Global seabird
507 response to forage fish depletion—one-third for the birds. Science 334, 1703-1706.
- 508 Daskalov, G. M., Grishin, A. N., Rodionov, S., Mihneva, V. 2007. Trophic cascades triggered by
509 overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the
510 National Academy of Sciences 104, 10518–10523.
- 511 Decker, M. B., Robinson, K. L., Dorji, S., Ciciel, K., Barcelo, C., Ruzicka, J. J., Brodeur, R. D.
512 2017. Jellyfish and forage fish spatial overlap on the eastern Bering Sea shelf during
513 periods of high and low jellyfish biomass. Marine Ecology Progress Series 591, 57-69.
- 514 Espinoza, P., Bertrand, A. 2008. Revisiting Peruvian anchovy (*Engraulis ringens*)
515 trophodynamics provides a new vision of the Humboldt Current system. Progress in
516 Oceanography 79, 215-227.
- 517 Espinoza, P., Bertrand, A., van der Lingen, C. D., Garrido, S., de Mendiola, B. R. 2009. Diet of
518 sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with
519 the diets of clupeoids in this and other eastern boundary upwelling systems. Progress in
520 Oceanography 83, 242-250.
- 521 FAO, 2011. Fisheries and aquaculture software. FishStatJ - software for fishery statistical time
522 series. In: FAO Fisheries and Aquaculture Department. Rome.
523 www.fao.org/fishery/statistics/software/fishstatj/en
- 524 Fleming, N. E., Harrod, C., Griffin, D. C., Newton, J., Houghton, J. D. 2014. Scyphozoan
525 jellyfish provide short-term reproductive habitat for hyperiid amphipods in a temperate
526 near-shore environment. Marine Ecology Progress Series 510, 229-240.
- 527 Graham, W. M. 2001. Numerical increases and distributional shifts of *Chyrsarora quinquecirrha*
528 (Desor) and *Aurelia aurita* (Linne) (Cnidaria: Scyphozoa) in the northern Gulf of
529 Mexico. Hydrobiologia 451, 97–111.
- 530 Guénette, S., Christensen, V., Pauly, D. 2008. Trophic modelling of the Peruvian upwelling
531 ecosystem: towards reconciliation of multiple datasets. Progress in Oceanography 79,
532 326-335.
- 533 Hansson, L. J., Moeslund, O., Kiorboe, T., Riisgard, H. U. 2005. Clearance rates of jellyfish and
534 their potential predation impact of zooplankton and fish larvae in a neritic ecosystem
535 (Limfjorden, Denmark). Marine Ecology Progress Series 304, 117–131.
- 536 Heaslip, S. G., Iverson, S. J., Bowen, W. D., and James, M.C. 2012. Jellyfish support high
537 energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from
538 animal-borne cameras. PLoS ONE, 7(3): e33259.
- 539 Heithaus, M. R. 2013. Predators, prey, and the ecological roles of sea turtles. The Biology of Sea
540 Turtles, Volume III, 249-284. Ed by J. Wyneken, K. J. Lohmann, and J. A. Musick. CRC
541 Press, Boca Raton, FL USA. 446 pp.

542 IMARPE. 2011. Informe nacional sobre la conservación de las tortugas marinas en el Perú.
543 IMARPE Internal Report, 72 pp.

544 Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J.,
545 Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P. 2001. Historical
546 overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629-637.

547 Jarre, A., Pauly, D. 1993. Seasonal changes in the Peruvian upwelling ecosystem. *Trophic*
548 *Models of Aquatic Ecosystems*, Vol 26, 307–331. Ed. by V, Christensen and D. Pauly,
549 ICLARM Conference Proceedings, 390 pp.

550 Jones, T. T., Hastings, M. D., Bostrom, B. L., Pauly, D., Jones, D. R. 2011. Growth of captive
551 leatherback turtles, *Dermochelys coriacea*, with inferences on growth in the wild:
552 Implications for population decline and recovery. *Journal of Experimental Marine*
553 *Biology and Ecology* 399, 84-92.

554 Kelleher, K. 2005. Discards in the world’s marine fisheries: an update. Rome: Food and
555 Agriculture Organization of the United Nations, FAO. 131pp.

556 Kideys, A. E., Roohi, A., Bagheri, S., Finenko, G., Kamburska, L. 2005. Impacts of invasive
557 ctenophores on the fisheries of the Black Sea and Caspian Sea. *Oceanography* 18, 76–85.

558 Lett, C., Penven, P., Ayón, P., Fréon, P. 2007. Enrichment, concentration and retention
559 processes in relation to anchovy (*Engraulis ringens*) eggs and larvae distributions in the
560 northern Humboldt upwelling ecosystem. *Journal of Marine Systems* 64, 189-200.

561 Lo, W-T., Purcell, J., Hung, J -J., Hsu, P -K. 2008. Enhancement of jellyfish (*Aurelia aurita*)
562 populations by extensive aquaculture rafts in a coastal lagoon in Taiwan. *ICES Journal of*
563 *Marine Science* 65, 453–461.

564 Lucas, C. H., Jones, D. O., Hollyhead, C. J., Condon, R. H., Duarte, C. M., Graham, W. M.,
565 Robinson, K. L., Pitt, K. A., Schildhauer, M., Regetz, J. 2014. Gelatinous zooplankton
566 biomass in the global oceans: geographic variation and environmental drivers. *Global*
567 *Ecology and Biogeography* 23, 701-714.

568 Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., Hays, G. C. 2011. Have
569 jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change*
570 *Biology* 17, 767–782.

571 Mianzan, H. W., Mari, N., Prenschi, B., Sanchez, F. 1996. Fish predation on neritic ctenophores
572 from the Argentine continental shelf: A neglected food resource? *Fisheries Research* 27,
573 69–79.

574 Milisenda G., Rosa S., Fuentes V. L., Boero F., Guglielmo L., Purcell J. E., et al. (2014) Jellyfish
575 as prey: frequency of predation and selective foraging of *Boops boops* (Vertebrata,
576 Actinopterygii) on the mauve stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). *PLoS*
577 *ONE* 9, e94600. <https://doi.org/10.1371/journal.pone.0094600>

578 Oguz, T. 2005. Long-term impacts of anthropogenic forcing on the Black Sea ecosystem.
579 *Oceanography* 18, 112–121.

580 Paredes, E. 2015. Hábitos alimentarios de la tortuga verde del Pacífico Este *Chelonia mydas*
581 *agassizii* (Boucart, 1868) en la bahía de Paracas, Ica, Perú, durante el año 2010.
582 Universidad nacional Mayor de San Marcos, Lima, Perú. 69 pp.

583 Parsons, T.R., Lalli, C.M. 2002. Jellyfish population explosions: revisiting a hypothesis of
584 possible causes. *La Mer* 40, 111-121.

585 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F. 1998. Fishing down marine food
586 webs. *Science* 279, 860-863.

587 Pauly, D., Graham, W. M., Libralato, S., Morissette, L., Palomares, M. L. D. 2009. Jellyfish in
588 ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616, 67–85.

589 Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., Chavez, F. P.
590 2006. Primary production in the eastern tropical Pacific: A review. *Progress in*
591 *Oceanography* 69, 285-317.

592 Pennington, M. 1996. Estimating the mean and variance from highly skewed marine data.
593 *Fishery Bulletin* 94, 498-505.

594 Pikitch, E. K., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., Heppell, S.
595 S., et al. 2012. Little Fish, Big Impact: managing a crucial link in ocean food webs.
596 Lenfest Ocean Program, Washington, DC. 108 pp.

597 Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U.
598 R., et al. 2014. The global contribution of forage fish to marine fisheries and ecosystems.
599 *Fish and Fisheries* 15, 43–64.

600 Purcell, J. E., and Arai, M. N. 2001. Interactions of pelagic cnidarians and ctenophores with fish:
601 a review. *Hydrobiologia* 451: 27-44.

602 Purcell, J. E., Breitbart, D. L., Decker, M. B., Graham, W. M., Youngbluth, M. J., Raskoff, K.
603 A. 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a
604 review. In *Coastal hypoxia: consequences for living resources and ecosystems*. Ed. by N.
605 N. Rabalais, and R. E. Turner. American Geophysical Union, Washington, D.C., *Coastal*
606 *and Estuarine Studies* 58: 77–100.

607 Purcell, J. E., Sturdevant, M. V. 2001. Prey selection and dietary overlap among
608 zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine*
609 *Ecology Progress Series* 210, 67–83.

610 Quiñones, J., Carman, V. G., Zeballos, J., Purca, S., Mianzan, H. 2010. Effects of El Niño-driven
611 environmental variability on black turtle migration to Peruvian foraging grounds.
612 *Hydrobiologia* 645, 69-79.

613 Quiñones, J., Chiaverano, L.M., Ayón, P., Adams, G.S., Mianzan, H.W., Acha, E.M. 2018.
614 Spatial patterns of large jellyfish *Chrysaora plocamia* blooms in the Northern Humboldt
615 Upwelling System in relation to biological drivers and climate. *ICES Journal of Marine*
616 *Science* (in press), doi:10.1093/icesjms/fsy004.

617 Quiñones, J., Mianzan, H., Purca, S., Robinson, K. L., Adams, G. D., Acha, E. M. 2015.
618 Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru.
619 *Marine Biology* 162, 2339–2350.

620 Quiñones, J., Monroy, A., Acha, E. M., Mianzan, H. 2013. Jellyfish bycatch diminishes profit in
621 an anchovy fishery off Peru. *Fisheries Research* 139, 47-50.

622 Riascos, J. M., Villegas, V., and Pacheco, A. S. 2014. Diet composition of the large scyphozoan
623 jellyfish *Chrysaora plocamia* in a highly productive upwelling centre off northern Chile.
624 *Marine Biology Research* 10, 791-798.

625 Robinson, K. L., Ruzicka, J. J., Decker, M. B., Brodeur, R.D., Hernandez, F. J., Quiñones, J.,
626 Acha, M.E., et al. 2014. Jellyfish, forage fish and the world’s major fisheries.
627 *Oceanography* 27, 104–115.

628 Robinson, K. L., Ruzicka, J. J., Hernandez, F. J., Graham, W. M., Decker, M. B., Brodeur, R. D.,
629 Sutor, M. 2015. Evaluating energy flows through jellyfish and gulf menhaden
630 (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico
631 ecosystem. *ICES Journal of Marine Science* 72, 2301-2312.

- 632 Roux, J. P., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D.
633 M., Cury, P. M. 2013. Jellyfication of marine ecosystems as a likely consequence of
634 overfishing small pelagic fishes: lessons from the Benguela. *Bulletin of Marine Science*
635 89, 249–284.
- 636 Ruzicka, J. J., Brodeur, R. D., Emmett, R. L., Steele, J. H., Zamon, J. E., Morgan, C. A.,
637 Thomas, A. C., et al. 2012. Interannual variability in the Northern California Current
638 food web structure: Changes in energy flow pathways and the role of forage fish,
639 euphausiids, and jellyfish. *Progress in Oceanography* 102, 19–41.
- 640 Ruzicka, J. J., Steele, J. H., Gaichas, S. K., Ballerini, D. J., Brodeur, R. D., Hofmann, E. E. 2013.
641 Analysis of energy flow in US-GLOBEC ecosystems using End-to-End models.
642 *Oceanography* 26, 24–39.
- 643 Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-
644 Montes, H., et al. 2011. Impacts of fishing low trophic level species on marine
645 ecosystems. *Science* 333, 1147–1150.
- 646 Steele, J. H., Collie, J. S., Bisagni, J. J., Gifford, D. J., Fogarty, M. J., Link, J. S., Sullivan, B. K.,
647 Sieracki, M. E., Beet, A. R., Mountain, D. G. and Durbin, E. G. 2007. Balancing end-to-
648 end budgets of the Georges Bank ecosystem. *Progress in Oceanography* 74, 423-448.
- 649 Steele, J. H., Ruzicka, J. J. 2011. Constructing end-to-end models using ECOPATH data.
650 *Journal of Marine Systems* 87, 227-238.
- 651 Sweetman, A. K., Smith, C. R., Dale, T., Jones, D. O. 2014. Rapid scavenging of jellyfish
652 carcasses reveals the importance of gelatinous material to deep-sea food webs.
653 *Proceedings of the Royal Society of London B: Biological Sciences* 281, 2014-2210.
- 654 Tam, J., Taylor, M. H., Blaskovic, V., Espinoza, P., Ballón, R. M., Díaz, E., Wosnitza-Mendo,
655 C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L. 2008. Trophic modeling of the
656 Northern Humboldt Current Ecosystem, part I: comparing trophic linkages under La Niña
657 and El Niño conditions. *Progress in Oceanography* 79, 352-365.
- 658 Thiebot, J.B., Arnould, J.P., Gómez-Laich, A., Ito, K., Kato, A., Mattern, T., Mitamura, H.,
659 Noda, T., Poupart, T., Quintana, F., Raclot, T. 2017. Jellyfish and other gelata as food for
660 four penguin species—insights from predator-borne videos. *Frontiers in Ecology and the*
661 *Environment* 15, 437-41.
- 662 Walsh, J. J., 1981. A carbon budget for overfishing off Peru. *Nature* 290, 300–304.
- 663 Walters, C., Martell, S. J. D., Christensen, V., Mahmoudi, B. 2008. An Ecosim model for
664 exploring Gulf of Mexico ecosystem management options: implications of including
665 multistanza life-history models for policy predictions. *Bulletin of Marine Science* 83,
666 251–271.
- 667 Zeman, S. M., Brodeur R. D., Daly E. A., Sutherland K. R. 2016. Prey selection patterns of
668 *Chrysaora fuscescens* in the northern California Current. *Journal of Plankton Research*
669 38, 1433-1443.

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674 Figure and table captions:

675 Fig. 1. Map of the study area (shaded area) covering from 4°S to 16°S, and up to 111 km (60 nm)
676 from the coastline, in the Northern Humboldt Current Ecosystem.

677
678 Fig. 2. System-wide reach (dark grey) and footprint (light grey) metrics for forage fish and large
679 jellyfish in the northern Humboldt Current System. Reach is the percent of total system
680 production produced by, or passing through, each target group, while footprint is the total system
681 production consumed by the target group. The reach of large jellyfish does not show up in the
682 graph because of a comparatively much lower value than that of forage fish (see Results).

683
684 Fig. 3. Comparative food web diagrams highlighting energy flow patterns to (footprint, green)
685 and from (reach, red) forage fish (A) and large jellyfish (B) in the Northern Humboldt Current
686 system. Box size is proportional to functional group biomass. Color intensity and width of lines
687 are scaled to the amount of energy flow between forage fish and large jellyfish and the rest of the
688 functional groups.

689
690 Fig. 4. System responses to a modeled A) jellyfish bloom (Scenario I), B) forage fish dominance
691 (scenario II), C: overfishing of forage fish (scenario II), and D: fisheries moratorium (Scenario
692 IV). MES: mesozooplankton, MAC: macrozooplankton, JEL: large jellyfish, FOF: forage fish,
693 DPI: demersal piscivorous fish, DPL: demersal planktivorous fish, DBE: demersal benthivorous
694 fish, CEP: cephalopods, PPL: pelagic planktivorous fish, PPI: pelagic piscivorous fish, APE:
695 apex predatory fish, SEB: seabirds, TUR: sea turtles, MAM: marine mammals, FIS: fisheries.
696 Box: 25-75% quartile, whiskers: min-max. Notice different scale in Y-axis.

697

698 Table 1. Aggregated ECOPATH model parameterization for the Northern Humboldt Current
699 System (NHCS).

700

701 Table 2. Mean (standard deviation) fractional changes (%) in the production of aggregated

702 functional groups in response modeled scenarios. Scenario I: jellyfish bloom. Scenario II: forage

703 fish dominance. Scenario III: increased fishing pressure. Scenario IV: fisheries moratorium.

704 Fractional change = (scenario model - base model)/ base model) x 100. Values lower than 0.01%

705 are indicated by dash symbols.