Prey predator interactions in the face of management regulations: changes in Mediterranean small pelagics are not due to increased tuna predation

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Abstract :

Recently, the abundance of young Atlantic bluefin tuna (*Thunnus thynnus*) tripled in the North-western Mediterranean following effective management measures. We investigated whether its predation on sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) could explain their concurrent size and biomass decline, which caused a fishery crisis. Combining the observed diet composition of bluefin tuna, their modelled daily energy requirements, their population size and the abundance of prey species in the area, we calculated the proportion of the prey populations that were consumed by bluefin tuna annually over 2011-2013. To assess whether tuna could alter the size structure of the three small pelagic populations (anchovy, sardine and sprat), the size distributions of the consumed prey species were compared to those of the wild populations. We estimated that the annual consumption of small pelagic fish by bluefin tuna is less than 2% of the abundance of these populations. Furthermore, size selectivity patterns were not observed. We thus concluded that tuna predation is unlikely to be the main cause of major changes in the small pelagic fish populations from this area.

Introduction

33 Understanding predator-prey relationships is crucial for ecosystem-based management. One of the

34 key aspects of these relationships concerns estimates of predation strength, which can be affected

35 by conservation measures (Bailey et al. 2010). Assessing predation pressure is a data intensive issue

36 (Essington et al. 2001) and direct information at the population level is difficult to obtain for marine

37 systems due to the practical constraints and high costs of observing marine species (but see e.g.

38 Mann and Lazier 2005 for examples). Estimates are generally based on the predator population

39 abundance, energy requirements and prey composition, as well as the population abundance and

40 energetic value of the prey. Estimates of food requirements are particularly problematic due to the

41 limitations of the existing methods. Also, predation might influence aspects of the prey population

42 structure or dynamics, such as the size distribution.

43

44 Since 2007, significant changes have been observed in the small pelagic populations of the Gulf of

45 Lions in the north-western Mediterranean Sea. Size and condition of sardine (*Sardina pilchardus*) and

46 anchovy (*Engraulis encrasicolus*) have significantly decreased, resulting in important economic losses

47 for fisheries (Van Beveren et al. 2014, Brosset et al. 2015). Notably, sardine captures even slumped to

48 a 150 years low (Van Beveren et al. 2016a). Also, the biomass of both populations stayed at an

49 intermediate level for an extended period, which is rather remarkable for these usually highly

50 fluctuating populations (see supplementary files Fig. S1 for abundance and biomass time series).

51 Nonetheless, abundance was high due to high recruitment (especially for sardine), so that the ratio

52 biomass/abundance strongly decreased. In contrast, sprat (*Sprattus sprattus*), a species with no

53 commercial value in this area, has shown a remarkable upsurge (GFCM 2011). Several hypotheses

54 have been suggested as potential drivers for these changes, including changes in planktonic quantity

55 and/or quality (i.e. a bottom-up control), predation (i.e. a top-down-control) and an epizootic disease

56 (Van Beveren et al. 2014, 2016b, Brosset et al. 2015, 2016). These are not exclusive, but potentially

57 acting in synergy (Planque et al. 2010). For example, top-down controlling factors could result in a

58 truncation of the size distribution and impede populations from rebuilding.

59 In the present study, we investigated the potential impacts of top-down control, with the aim of

60 obtaining the most comprehensive insight in the pelagic ecosystem changes. As fishing is an unlikely

61 driver due to low exploitation rates of these populations (see Van Beveren et al. 2016), we consider

62 the potential impacts of natural predation due to the main predator of small pelagic fish in the area,

63 i.e. Atlantic bluefin tuna (Fromentin and Powers 2005).

64

65 Atlantic bluefin tuna (ABFT, *Thunnus thynnus*) predates on a variety of prey, among which small

66 pelagic fish, such as in the Northwest, central and east Mediterranean Sea, the Bay of Biscay and the

67 Northeast and Northwest Atlantic (see Fromentin and Powers 2005a for a review). Juveniles and

68 young adults may reside many months in the Gulf of Lions to feed on sardine, anchovy and sprat

69 (Fromentin and Lopuszanski 2014). Other top predators are also present (marine mammals,

70 predatory fish, sharks, seabirds and marine turtles) but their impact is estimated to be of lesser

71 importance, as they prey mostly on other species (e.g. dolphins, David and Di-Méglio 2013), consume

72 small pelagics only for a limited period of the year, are geographically restricted (such as some birds

73 to the surface and some marine mammals to deeper waters, Praca and Gannier 2008), and/or do

74 have significantly smaller populations than tuna (e.g. dolphins, Bauer et al. 2015b). Furthermore,

75 ABFT abundance in the Gulf of Lions has been much higher in recent years (Bauer et al. 2015). This is

76 probably due to the implementation of a recovery plan in 2007 (including fishing season restrictions,

77 quotas and a minimum landing weight of 30 kg), which has considerably decreased the fishing

78 pressure on juvenile ABFT in the NW Mediterranean (Fromentin et al. 2014). The increase in juvenile

79 ABFT abundance in this area thus occurred concomitantly with the small pelagic population changes.

80 This leads to the question: could the increase in ABFT abundance, and thus increased predation

81 pressure, have strongly impacted the small pelagic fish populations? Currently, most management

82   approaches focus on a single species, without considering subsequent impacts on other species in

83   the ecosystem. However, if these management measures have repercussions on other species,

84   management strategies should be adapted accordingly.

85   Thus, for the Gulf of Lions, which is an important nursery ground for ABFT (Druon et al. 2011), we

86   aimed at investigating the predation pressure exerted by ABFT on sardine, anchovy and sprat from

87   2011 to 2013 in terms of abundance and size distribution. We addressed three questions; (I) what is

88   the diet composition of ABFT in the area?, (II) what biomass does ABFT remove from this ecosystem

89   and how does this relate to the population size of each prey? and (III) are ABFT prey size selective

90   and could they affect their prey population's size distributions? The tuna diet composition, the

91   annual proportion of each small pelagic population consumed by ABFT and its size selectivity were

92   estimated, using: (a) ABFT population abundance estimates from an ABFT census, (b) a

93   comprehensive bioenergetics model to estimate consumption rates of ABFT, (c) stomach content

94   analyses to define the ABFT diet and (d) the population size and characteristics of each small pelagic

95   species estimated from a small pelagic fish census (Fig. 1). A large predation-associated mortality

96   could completely or partly explain the recently observed changes in the Gulf of Lions ecosystem.

97   ## Material and methods

98   ### Estimating predator abundance and weight structure

99   Not the whole Atlantic bluefin tuna (ABFT) population was under study, but only the fraction that

100   inhabits permanently or not the Gulf of Lions and is known to be mostly composed of juveniles and

101   young adults (see Fromentin and Powers 2005a). Annual ABFT abundances (2011-2012) were

102   obtained from aerial surveys (Bauer et al. 2015). ABFT school abundances and densities were

103   estimated using strip and line transect approaches from the distance sampling theory (Thomas et al.

104   2012). Annual abundances (mean±sd) of ABFT in the NW Mediterranean were found to be of

105   $16,2\pm4,4.10^3$ in 2011 and $12,5\pm3,8.10^3$ in 2012 (Supplementary files Fig. S2 and Appendix 1).

106   Predation pressure also depends on the residence time of the tuna population in the area, which was

107   estimated based on tag data (Fromentin and Lopuszanski 2014). We considered that ABFT reside in

108   the Gulf of Lions for a total of six months (consistent with previous assumptions, see Bănaru et al.

109   2013), from approximately early-March to end-May and from end-July until end-October.

110   Finally, the mass distribution of the tuna population was assessed combining mass values of ABFT

111   sampled for stomach contents with additional measurements of commercially fished ABFT from

112   other periods but caught in the same area (sampling period: generally April-May and July-October of

113   2011-2014, with 3 individuals in November/December amongst N=310). The small scale fishery

114   catches are a good proxy for the ABFT demography (size and age composition) in this area. This is the

115   only fleet targeting ABFT, it operates all year round in this area and the size distribution of its catches

116   corresponds to this of the industrial purse seine fleet that operated in the Gulf of Lions until 2007

117   (Fromentin 2003). A gamma distribution (shape=15.21 and rate =0.57) was fitted on this empirical

118   histogram, which was also used to determine the ABFT weight range. This information is essential as

119   heavier tuna have a larger energetic requirement.

120   **Estimating ingestion rates of ABFT using a Dynamic Energy Budget model**

121   A Dynamic Energy Budget (DEB) model describes an individual's energy acquisition (food intake) and

122   use (for e.g. maintenance, growth, reproduction) throughout its life cycle, taking into account

123   external variables, such as temperature and food density (Nisbet et al. 2000, Kooijman 2010). DEB-

124   based modelling is a general and formal approach built on the guiding principle that the mechanisms

125   responsible for running a metabolism apply universally to organisms of all species (Sousa et al. 2008,

126   2010, Kooijman 2010). We ran a DEB model for ABFT (see Supplementary files Table S2, S3 and Fig.

127   S3) by reparameterising a calibrated and validated model for Pacific Bluefin tuna (Jusup et al. 2011,

128   2014). For our study, the most important usage of the DEB model is to relate tuna body size to the

129   ingestion rate function (Jusup et al. 2014):

130     $Ingestion rate = \frac{p_{Am}*M_1*L^2}{\kappa_x}$

131   where p_{Am} is the maximum surface-area-specific assimilation rate, M_1 is the shape correction

132   function (which accounts for morphological changes), L is the structural length and κ_x is the

133   assimilation efficiency. Food availability (f) and average temperature (T) were assumed to be 0.99

134   and 19.5°C, respectively (T is transformed with a temperature correction function to fit with the

135   optimal temperature range of ABFT, Kooijman 2010, Freitas et al. 2010). Energy intake estimates

136   were obtained using a conservative approach because we could hardly estimate the variance of the

137   ingestion rates, and the functional response type that needed to be selected is not precisely known

138   (i.e., it depends on multiple factors, see Valiela 1995). To do so, we assumed maximum intake that is

139   reached when prey abundance is very high and time lost for searching is zero. Note that in the

140   context of this study, a conservative approach means that an overestimation of the tuna ingestion

141   rate is preferred over an underestimation. The body mass distribution of ABFT was the most detailed

142   population information available (age or size structure data are lacking or more limited). Thus, we

143   focused on the relationship between ingestion rate (expressed in kJ per unit of time) and body mass.

144   Individual ingestion rate values were scaled up to the population level. To do this, ingestion rates

145   (kJ*day^{-1}) were estimated from the DEB for the full body mass gamma distribution of sampled tuna.

146   Total annual ingestion rates for each body mass class (±1 g) were then multiplied by their relative

147   frequency in the population (again based on the gamma distribution) and the annual tuna

148   abundance. The sum of those values was finally multiplied by the residence time of the population in

149   the Gulf of Lions.

150

151   **Tuna diet from stomach content analyses**

152   Stomach content analyses of tuna caught in the Gulf of Lions have been carried out annually from

153   2011 to 2013. Tuna were captured between late-July and early-December of 2011 (n=42), 2012

154   (n=39) and 2013 (n=37) by small-scale fisheries using longlines or handlines. Individuals were

155   measured (±1 cm, fork length) and weighed (±0.1 kg). Stomach contents were weighed and

156 completely and partially intact prey identified to the lowest possible taxonomic level. Prey items

157 were measured when possible (using total and/or standard length) and weighed to the nearest

158 millimetre and gram. All otoliths (fish) and beaks (cephalopods) were collected to determine the total

159 number of prey per species. For the three key prey species of this study (i.e. anchovy, sardine and

160 sprat), otolith lengths were converted to prey item length, using linear relationships based on

161 independent readings (see Supplementary files Table S1). Body mass of five key species was obtained

162 by converting indirectly from size (sardine, anchovy and sprat) or directly (mackerel, squid) from

163 otolith or beak length (using again independent readings, Supplementary files Table S1). Longline

164 baits of undigested sardines of sizes >17.5 cm were removed.

165 The importance of each prey species in the tuna diet was expressed as the percentage of prey

166 composition by number (%N), body mass (%M), and the frequency of occurrence of each item (%F).

167 For some rare species (referred to as "Other"), no body mass information was available so they were

168 excluded when calculating %M.

169 Feeding selectivity was calculated with the Chesson's index (α_i; Chesson 1978) for the 4 most

170 abundant species:

$$\alpha_i = \frac{\dfrac{r_i}{p_i}}{\sum_{j=1}^{k} \dfrac{r_j}{p_j}}$$

171 where r_i is the numerical proportion of prey species i (among k total prey species) and p_i is the

172 numerical proportion of this prey species in the environment. The index ranges between 0 and 1

173 (indicating complete avoidance and full selection, respectively), with $1/k$ indicating neutral selection

174 (here: 0.25).

175 Because our sampling size was limited (~40 stomachs per year), interannual differences in diet might

176 have been caused by small discrepancies in the annual sampling dates and tuna size. Therefore, we

177 tested whether prey length (anchovy, sardine and sprat) could be related to sampling date or tuna

178   size, using Spearman's rank correlation. We also tested whether the prey composition of the eight

179   most frequently occurring species (expressed as %N) could be related to the sampling date or tuna

180   size, using a Mantel test to correlate the two dissimilarity matrices. The prey item matrix was created

181   based on the Bray-Curtis method (as percentages are used, see Legendre and Legendre 1998) and

182   Euclidean distances were used for the tuna size and sampling date matrix.

183   To estimate the energetic importance of sardine, anchovy and sprat in the diet of ABFT, it is

184   necessary to also consider other relevant prey species (e.g., squid and mackerel). For example, a tuna

185   whose stomach comprises 50% fat sardine and 50% small squid will acquire more energy from

186   sardine than from squid. Thus, we must know the energetic density (J/g), body mass distribution and

187   %M of each major prey species consumed in order to estimate their energetic importance. Each body

188   mass class (0.5 g) of a given prey species was multiplied by the energetic density of that species (see

189   Appendix 1: Energetic density) and the relative frequency of that body mass class. These values were

190   summed per species to obtain the energetic value (J) of a standard individual, with which the number

191   of individuals per species consumed by all tuna was found.

192   **Estimating prey abundance: small pelagic fish census**

193   Annual standardised acoustic and pelagic trawl surveys (PELagiques MEDiterranée, PELMED) have

194   been carried out continuously since 1993 to estimate biomass and abundance of several small

195   pelagic fish and to collect basic biological parameters. Sampling is performed in July along nine

196   equidistant parallel transects perpendicular to the coastline, ranging between depths of 20 m and

197   200 m. Here, we used resultant abundance estimates for sardine, anchovy, sprat and mackerel for

198   2011-2013 and biological data to calculate size distributions and morphometric relationships (e.g. a

199   length-weight key to obtain prey item body mass) for these species (see Supplementary files Table

200   S1, Fig. S4, Van Beveren et al. 2014, Saraux et al. 2014).

201 **Predation pressure on small pelagic fish**

202 To obtain a percentage of "population consumption" (i.e. the percentage of each prey consumed by

203 ABFT at the population level), we divided the estimated total number of sardine, anchovy or sprat

204 consumed by ABFT by their corresponding abundance in the NW Mediterranean. To reflect

205 uncertainties in various estimates, all calculations were bootstrapped to estimate ABFT predation

206 (10,000 iterations). To reflect various sources of uncertainty in the estimation of ABFT abundance in

207 the Gulf of Lions (see Bauer et al. 2015), we used a uniform distribution spanning the ±95%

208 confidence intervals given by Bauer et al (2015). Because for 2013 no tuna abundance data was

209 available, we took the interval between the lowest and highest interval limit established for 2011 and

210 2012 (i.e. the largest range between the interval limits of the previous years, Appendix 1).

211 Additionally, a uniform distribution was also assigned to the prey energetic densities (between

212 minimal and maximal values, Supplementary files Table S1), given that data were derived from

213 literature that did not necessarily consider the same time and space domain. At last, other sources of

214 uncertainty (e.g. such as associated with the DEB) were taken into account by taking a conservative

215 attitude (see previously for the DEB).

216 ABFT selectivity for certain prey sizes was also investigated by comparing the size distributions of

217 sardine, anchovy and sprat in ABFT stomachs with the size distributions of those obtained from the

218 pelagic surveys. As the survey takes place in July and the tuna stomachs were collected from August

219 to November, the theoretical sizes of anchovy and sardine ingested by tuna were back-calculated for

220 comparative purposes, using age-length keys developed from PELMED otolith data (2008-2013,

221 Supplementary files Fig. S4), and accounting for seasonal variability (Somers 1988, García-Berthou et

222 al. 2012). This is important as small pelagic fish mainly grow in summer in this area. For sprat, an

223 annual linear model was used as only data for two age classes were available, and the back-

224 calculated difference in length was multiplied by 1.5, a factor estimated from the anchovy data

225 (Supplementary files Fig. S4). Also, ABFT consumed small-sized anchovy that could not be caught

226 during the survey because of the limiting mesh size (only 0.5% of all-time survey captures of anchovy

227   were smaller than 9 cm). Therefore, when comparing the diet and population census size classes,

228   ingested individuals smaller than 9 cm were not considered. As data were unbalanced, non-normally

229   distributed and obtained from different sources, only the percentage of overlap of the two size

230   distributions was calculated, as well as the differences between the frequencies of each size

231   distributions (so positive values correspond to positive selection).

232 **Results**

233 **Tuna diet and selectivity**

234 Length and mass of the tuna analysed for their stomach content ranged between 89 cm and 158 cm

235 and 12.5 kg and 51.2 kg, respectively. Of the 118 stomachs examined, only one was found empty (in

236 2011). No significant relationships were found between prey composition and the sampling date or

237 tuna length (p>0.05, Mantel test), nor between the prey length and the sampling date or tuna length

238 (p>0.05, Spearman's correlation), so that year-to-year differences in prey length and composition

239 could not be attributed to minor changes in these two factors.

240 In total, 5,099 prey items belonging to 29 prey species or families were identified, resulting in a mean

241 prey abundance of 44 individuals per stomach. Anchovy and sardine were always the most important

242 species in terms of abundance, body mass and frequency of occurrence, although these indices

243 varied considerably between years (Fig. 2). Together they consistently accounted for more than 80%

244 of ABFT diet (both in mass and number) in the area and each was present in at least 79% of the

245 stomachs. In contrast, sprat was little present in 2011 and 2012 (4%N), but became relatively more

246 important in 2013 (14%N). Cephalopods and mackerel only constituted between 1% and 3% of the

247 diet (for both mass and number).

248 According to the Chesson's index, ABFT generally selected anchovy and mackerel, rather than sardine

249 and sprat (Fig. 2). Tuna always positively selected for anchovy, although this selection almost

250 doubled between years (i.e., 2011 and 2013). Mackerel were both positively and negatively selected,

251 depending on the year. Sardine and sprat were negatively selected (although sardine was preferred

252 to sprat). During the three years, anchovy was the only prey species for which the proportion in the

253 stomach fluctuated in parallel with its proportion in the ecosystem found by the pelagic survey.

254 Larger sardines were found more frequently in the tuna diet than during the pelagic survey (although

255 positive selectivity was also visible on small size classes in 2013, Fig. 3). No consistent or clear size

12

256 selectivity was present for anchovy, as both size distributions found had a high level of overlap (67-

257 77%). For sprat, there was a consistent difference between the two distributions over the three

258 years, with a greater proportion of small individuals in the tuna diet. No clear size selectivity of ABFT

259 (towards small or large preys) can thus be detected when considering the three dominant small

260 pelagic fish species together.

261 **Predation pressure on small pelagics**

262 For ABFT between 4 kg and 86 kg, the energetic requirement was ranging between 0.8 %Mb and 2.5

263 %Mb (% body mass*day-1), 758 Kj*day^{-1} and 5870 Kj*day^{-1} or 90 Kj*kg^{-1}*day^{-1} and 190 Kj*kg^{-1}*day^{-1}.

264 The body mass distribution of the part of the ABFT population under study (i.e., ABFT inhabiting the

265 Gulf of Lions) had a median of 24.55 kg (Fig. 4a). At this median mass, individual tuna ingestion rates

266 given by the DEB (Fig. 4b) were 2544 Kj*day^{-1}, 103 Kj*kg^{-1}*day^{-1} or dependent on the year (related to

267 the prey composition and resulting average prey energetic density) 1.3-1.4 %M_b. Thus, given ABFT

268 abundance and residence time in the study region, the total energetic requirement for ABFT was

269 estimated at $6.78 \times 10^{6} \pm 1.47 \times 10^{6}$ MJ on average over all three years.

270 Anchovy and sardine were the most important species in terms of caloric importance, given their

271 relatively high caloric density (Supplementary files Table S1) and %M (Fig. 2). The contribution of

272 sprat, mackerel and especially cephalopods was secondary. Given the abundance of those species in

273 the area (Table 1, based on pelagic survey data), the consumption by tuna represented a maximum

274 of 1.93%±0.55% of the anchovy, 0.61%±0.23% of the sardine and 0.07%±0.02% of the sprat

275 populations (Table 1). Thus, the predation pressure of ABFT in the Gulf of Lions on their main prey

276 species was low (< 2% of the prey populations).

277 **Discussion**

278

279 Effect on the abundance

280   Despite the fact that sardine and anchovy are the main prey of ABFT in the NW Mediterranean, the

281   influence of predation pressure on the abundance of these species appears to be negligible (<2%).

282   Moreover, these predation pressure estimates are based on calculations performed for the three

283   years (2011-2013) when tuna biomass was relatively high and sardine and anchovy biomass was

284   already relatively low (Van Beveren et al. 2014, Bauer et al. 2015). Hence, in previous years (when

285   ABFT abundance was smaller and the small pelagics ones often larger), tuna predation was likely to

286   have been even smaller. In addition, we used a conservative approach that considered the high

287   uncertainty around parameters, such as ABFT abundances (i.e., using a confidence interval of ±95%)

288   and energetic densities (i.e., using the range between minimal and maximal values). Although no

289   such uncertainty was included for the abundance of prey species in the area, values are thought to

290   be underestimated rather than overestimated (e.g., due to undetected biomass in unsampled

291   nearshore areas, Brehmer et al. 2006), thereby overestimating predation pressure. However, even if

292   an additive underestimation of predation resulted from the errors that were not included (e.g., on

293   the residence time), predation ratios would still remain too low to be considered as important. The

294   natural top-down control of ABFT on its prey populations in the studied area is further much lower

295   than this of the fisheries, even with sardine and anchovy not being overfished (GFCM 2011). Between

296   1995 and 2013, on average, 13% of the anchovy and 9% of the sardine population abundance was

297   fished annually, which is at least 6 to 10 times higher than the quantity consumed by ABFT. Thus,

298   taking into account reasonable levels of uncertainty, our results excluded predation pressure by ABFT

299   as the main cause for the recent changes in the sardine and anchovy populations of the Gulf of Lions.

300   **Effect on the size distribution**

301   If ABFT were to consume only the largest individuals, an effect on the size distribution of the prey

302   species might have occurred. However, tuna appear to be opportunistic and have little prey size

303   selectivity, as evidenced by a weak or inconsistent pattern of size selection between years and

304   among species (a result in agreement with past studies on ABFT feeding in the Mediterranean Sea,

305   see e.g. Karakulak et al. 2009). However, the size distributions of the small pelagic fish found in the

306   stomach contents and those caught in the survey are not exactly comparable, possibly due to the

307   temporal mismatch between the small pelagic survey and the one on ABFT, as well as the lower size

308   limit on the small pelagic fishing gear (although both were corrected for). For example, anchovy

309   spawns between May and June (in contrast to winter spawning sardine and sprat) and these young-

310   of-the-year fish were by July (when the PELMED survey operates) still too small to be captured by the

311   size-restrictive mesh size. ABFT were generally captured later, when anchovy had already slightly

312   grown. Also, small discrepancies in the size distributions might result from spatial heterogeneity in

313   size of the small pelagic fish populations and the tuna hunting area (e.g., tuna might hunt in a zone

314   were small pelagic fish are not averaged sized). Thus, we can conclude that observed differences

315   between the two distributions are most likely caused by factors other than a preferential

316   consumption of certain size classes by tuna and that the size distributions of the small pelagic fish are

317   not likely to have been affected by tuna predation.

318   **Tuna energy requirement**

319   Assessing predation pressure is particularly challenging for pelagic fish, as their abundance and the

320   daily energy requirement of their predator are not easily estimated. Here, predation estimates were

321   possible due to the availability of a calibrated model and a large amount of diverse multi-annual data

322   sources, including stomach content samples of ABFT, size distribution data of both preys and

323   predator and abundance estimates from extensive acoustic and aerial surveys.

324   The DEB model provided us with energy intake estimates by weight of Mediterranean bluefin tuna,

325   which were unavailable so far. For tuna, information on energetics lags far behind on other smaller

326   species because of its size and difficulty of handling. Several of the studies estimating tuna energy

327   requirement (see next paragraph) used caging experiments. Obviously, such analyses are expensive,

328   time consuming and impossible on many locations. Only Essington et al. (2002) did not use caging

329   experiments, but a bio-energetic model to Yellowfin tuna (*Thunnys albacares*). Although the

330   approach appears more simplistic (and thus perhaps more attractive) from a statistical point of view,

331   they still used a heavy dataset and relied on several previously published values and equations.

332   Additionally, other methods exist to estimate energy intake that have not yet been applied to tuna,

333   including stomach content analysis (e.g. Elliott & Persson 1978), contaminant mass balance analyses

334   (e.g. Trudel et al. 2011), regression models (e.g. Palomares & Pauly 1998) or a combination of

335   different approaches (Ferriss & Essington 2014). Each of these methods has its proper limitations. In

336   our case, the DEB model was the preferred approach, given that a lot of extra data collection or

337   caging experiments would have been needed elsewise, that it is more general than the previously

338   used bio-energetic models (e.g. Essington 2002) and that results so far have been shown to be

339   promising.

340   We found that ABFT between 4 kg and 86 kg (i.e. between 1.5 and 9.2 years) consume about 0.8%M_b

341   to 2.5%M_b, i.e. about 181 kcal to 1403 kcal (or 758 kJ to 5870 kJ) daily. The estimates of %M_b are in

342   the lower range of results from previous studies on other tuna species (Glencross et al. 2002,

343   Essington et al. 2002, Wexler et al. 2003, Takii et al. 2005, Fitzgibbon et al. 2007). For example,

344   Essington et al. (2002) reported daily consumption rates of 3.5-6%M_b for 0.5-6 year old yellowfin

345   tuna, while Wexler et al. (2003) described rates of 1-10%M_b for yellowfin of 1-6 kg. For a more

346   closely related species, the southern bluefin tuna (*Thunnus maccoyii*), Fitzgibbon et al. (2007)

347   estimated a daily consumption of 2-9%M_b for fish of around 10 kg. ABFT individuals in this study

348   were generally larger (about 26 kg on average) and were exposed to different ambient temperatures,

349   two factors that greatly alter the energetic requirements of tuna. Smaller fish consume fewer

350   calories but have a higher energetic need relative to their mass and the endothermic system of tuna

351   includes a specific relationship between ambient temperature and metabolic rate (Blank et al. 2007).

352   Additionally, %M_b depends on the energetic density of the food ingested and captive individuals

353   might have an increased metabolic rate because of stress. But even considering the maximum

354   reported ingestion rate found in literature (0.43 MJ*kg^{-1}*day^{-1}, Wexler et al. 2003), reported for

355   small yellowfin and thus theoretically overestimating ingestion values for larger ABFT, the estimated

356   predation pressure of ABFT on small pelagic fish would still be relatively low (<10%).

357 **Atlantic bluefin tuna diet**

358 In contrast to studies on tuna energy requirements, studies on the diet composition of ABFT are

359 ample (e.g., Karakulak et al. 2009, Varela et al. 2013). As the diet of tuna varies significantly between

360 years, seasons, regions and life stages, our results deviated from other studies. For example, other

361 studies from the Mediterranean found more empty stomachs (Varela et al. 2013) supporting the

362 hypothesis that the Gulf of Lions act as an important feeding area for juvenile tuna (Druon et al.

363 2011, Fromentin and Lopuszanski 2014). Our results are consistent with other studies that found that

364 ABFT prey composition is diverse but dominated by few species, that differ among ABFT feeding

365 grounds (Fromentin and Powers 2005). However, we found a predominance of sardine and anchovy

366 in the diet (e.g., up to 76%N of anchovy), as opposed to more elevated feeding on cephalopods

367 and/or crustaceans highlighted in other Mediterranean areas (Sinopoli et al. 2004, Sarà and Sarà

368 2007, Goñi et al. 2011, de la Serna et al. 2012). Cephalopods were of limited importance (<4%N) and

369 crustaceans were rarely encountered (<1%N). This may be partly because tuna sampling for stomach

370 analyses of this study was limited to the shelf of the Gulf of Lions and could thus not fully reflect the

371 prey composition of ABFT in the NW Mediterranean. Note, however, that our results are in

372 agreement with past studies, which also found a dominance of anchovy in ABFT stomachs from the

373 Gulf of Lions and other nursery areas, such as the Bay of Biscay (Fromentin and Powers 2005).

374 Although tuna are generally considered to be opportunistic predators (Crane 1936), the individuals in

375 this study appeared to negatively select sardine and sprat and positively select anchovy (a similar

376 finding was suggested for albacore, *Thunnus alalunga*, in the bay of Biscay; Goñi et al. 2011). This is

377 surprising as sprat has a higher fat content than anchovy (Brosset et al. 2014). Therefore, this

378 apparent selection may actually be due to a difference in the geographic distribution and/or

379 behaviour of the prey species, or an error in the relative abundance estimates of the prey in the

380 environment (see before) or the stomachs. For example, sardine and sprat in the Gulf of Lions are

381 more coastal than anchovy and depths of 150 m to 200 m are unfavourable to them (Saraux et al.

382 2014). Furthermore, sardine and anchovy might be different in terms of behaviour and movement,

383 so that anchovy are when hunted more easily caught. For instance, diurnal differences in densities of

384 both populations have been previously reported (Barange and Hampton 1997, Saraux et al. 2014),

385 possibly resulting in a dissimilar predation risk. Additionally, a larger tuna stomach sampling effort

386 would have better covered variables such as time and space. Although our sampling size is fully

387 comparable (and sometimes higher) to those of previous studies on tuna stomach analyses, more

388 samples would have resulted in less uncertainty., We also found that when the relative proportion

389 of sardine in the ecosystem increases this does not relate to a concurrent increase in their relative

390 consumption by tuna. This might be because sardine are coastal and when their relative proportion

391 in the ecosystem is higher, they may increase school densities rather than expand their spatial

392 distribution to areas where tuna hunts more intensely (Saraux et al. 2014).

393 In conclusion, we provided an integrative framework based on previously developed techniques for

394 conducting predator-prey analyses. Such a state-of-the-art framework has not yet been used to

395 estimate predation pressure in the marine environment, and could further be applied to other prey-

396 predator studies, with some input estimates perhaps being obtained through an equivalent approach

397 (e.g. to estimate prey or predator abundance, or by the use of a simpler less data-consuming

398 energetic model such as empirical regression models). In this case, the effect of tuna predation on

399 the small pelagic fish populations was found to be extremely small, so this specific ecosystem

400 considerations would not affect the fishery management.

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555 **Tables**

556 Table 1. The annual percentage of population consumption, ecosystem abundance and total number

557 consumed by tuna (*Thunnus thynnus*) of anchovy (*Engraulis encrasicolus*), sardine (*Sardina*

558 *pilchardus*) and sprat (*Sprattus sprattus*).

Total abundance consumed by tuna (millions)		
	2011	2012	2013
Anchovy	69.6±19.8	27.1±9.6	25.0±9.4
Sardine	33.7±9.6	39.8±14.1	48.6±18.3
Sprat	4.0±1.2	1.6±0.6	6.1±2.3
Ecosystem abundance (millions)		
	2011	2012	2013
Anchovy	3601	5142	2685
Sardine	5655	9370	7927
Sprat	5577	4649	9969
Population consumption		
	2011	2012	2013
Anchovy	1.93±0.55%	0.53±0.19%	0.93±0.35%
Sardine	0.60±0.17%	0.42±0.15%	0.61±0.23%
Sprat	0.07±0.02%	0.01±0.00%	0.06±0.02%

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561 **Figures**
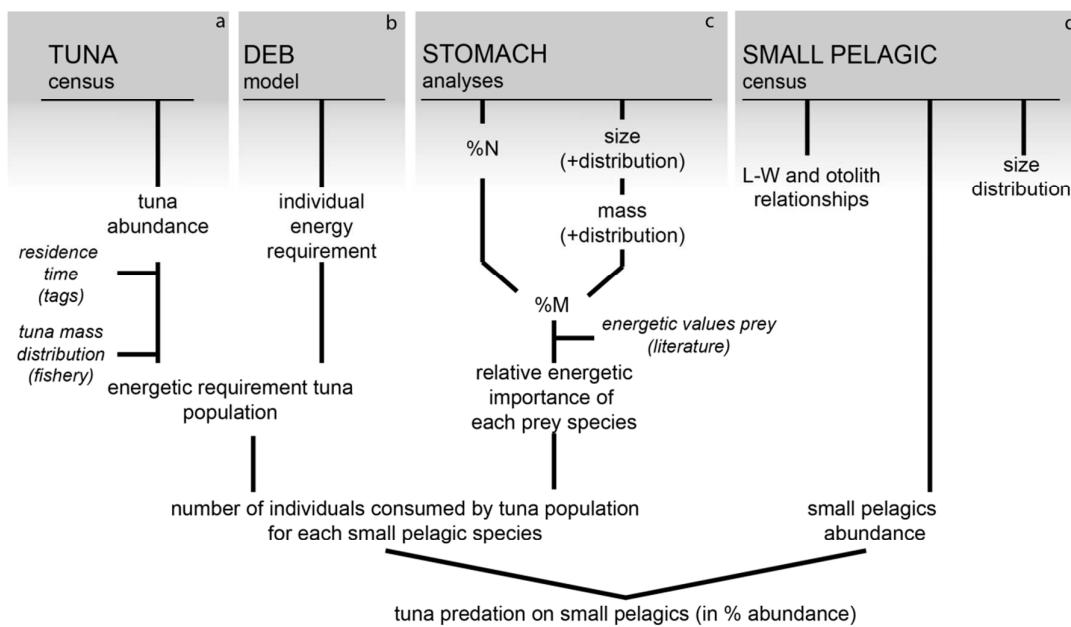
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563 Fig 1.   Schematic representation of the data/estimates and the analyses to calculate the percentage

564   of abundance of each small pelagic population consumed by tuna (*Thunnus thynnus*). Each of the

565   four blocks (a, b, c and d) represents a major data source, from which the ensuing information

566   was obtained. Smaller data sources are indicated in italics.

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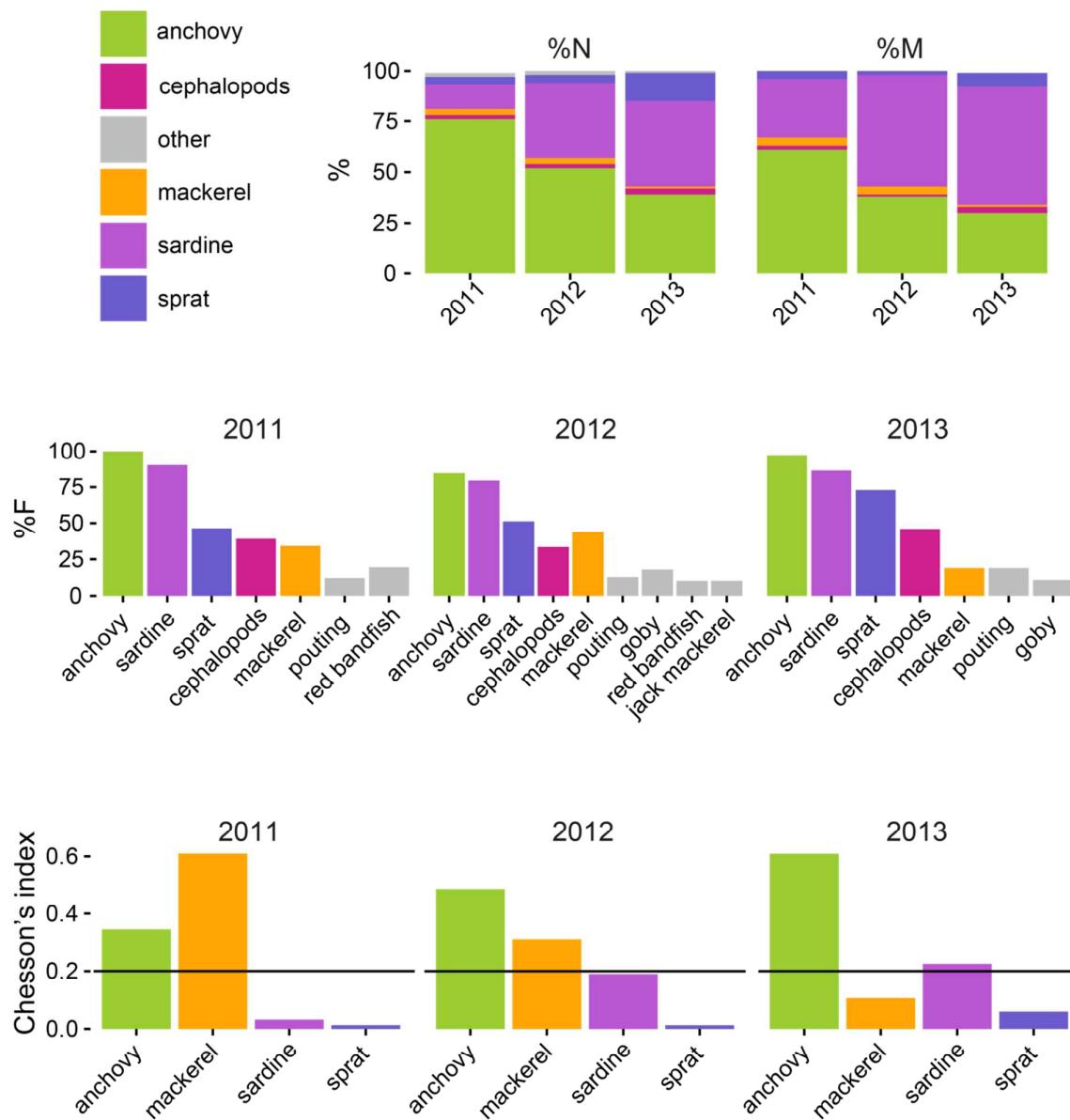
569   Fig 2.   Annual results of the stomach analyses (2011-2013): the prey's relative abundance (%N),

570   mass (%M), occurrence (%F) and Chesson's selectivity index, with the horizontal line indicating

571   neutral selectivity (α_i = 0.25). The "other" class groups all species less abundant than 1%N. The

572   relative mass of this group is unknown and thus not included when calculating %M. Chesson's

573   index is given only for species whose proportion in the ecosystem is known (based on the prey

574   population census) and the percentage of occurrence is given only for the most prevalent species

575   (%F>10), i.e. sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*), sprat (*Sprattus*

576   *sprattus*), pouting (*Trisopterus luscus*), goby (Family Gobiidae), hake (*Merluccius merluccius),* jack

577   mackerel (*Trachurus* spp.), red bandfish (*Cepola macrophthalma*), mackerel (*Scomber colias* and

578   *S. scombrus*) and cephalopods (mostly *Illex* spp.).

579
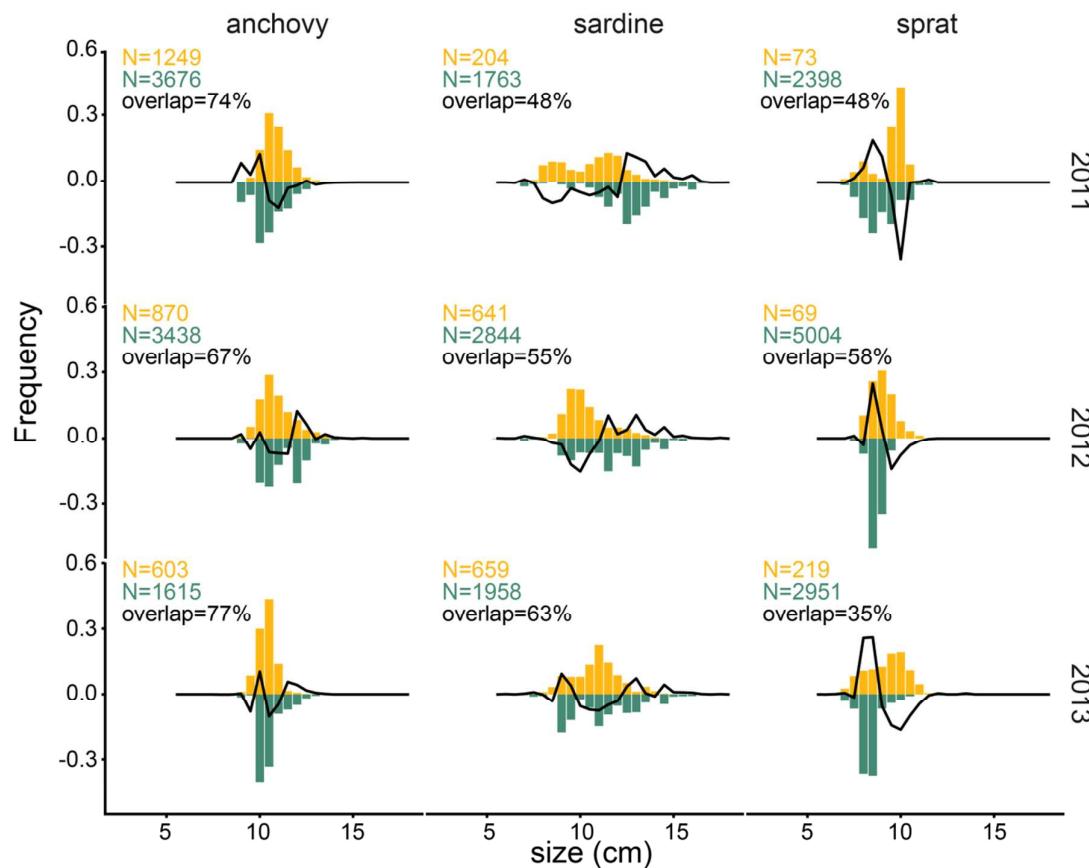
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Fig 3. Size distributions per year and per species, i.e. sardine (*Sardina pilchardus)*, anchovy (*Engraulis encrasicolus)* and sprat (*Sprattus sprattus*), found in the stomachs of Atlantic bluefin tuna (*Thunnus thynnus*) (green and made negative) and by the small pelagic survey (orange). Small anchovy (<9cm) were removed (see material and methods). The black line is the difference between the frequencies of each size class (positive values correspond to positive size selectivity by tuna). The numbers of individuals sampled is indicated (N), as well as the percentage of overlap of the two distributions.
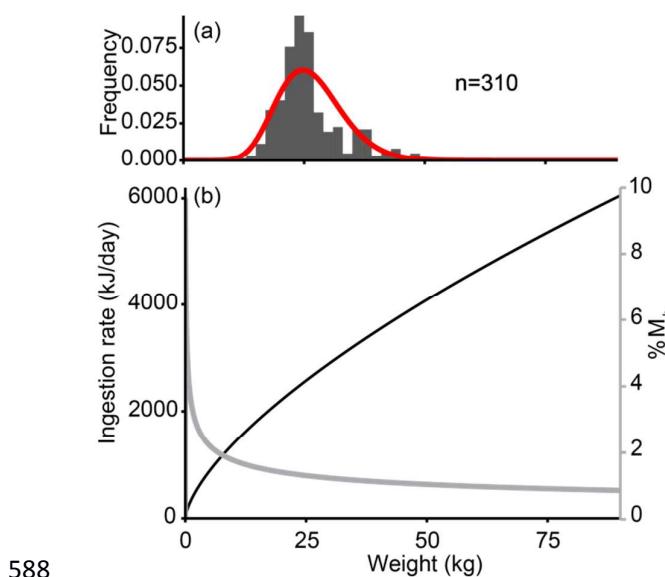
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589 Fig 4.   (a) The mass distribution of Atlantic bluefin tuna (*Thunnus thynnus*) juveniles and (b) tuna

590   mass as a function of their ingestion rate (black line) and percentage of body mass consumed

591   (%M_b, grey line). The bottom figure is the final output of the Dynamic Energy Budget model, for

592   the range of tuna mass observed in the Gulf of Lions.

593

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Appendices

Prey predator interactions in the face of management regulations: changes in Mediterranean small pelagics are not due to increased tuna predation

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Appendix 1

Material and methods

Tuna abundance

Annual aerial surveys have been performed between June and October from 2000 to 2003 and from 2009 until present in the Gulf of Lions to construct a unique fishery-independent index of tuna density (Fromentin *et al.* 2003; Bonhommeau *et al.* 2010; Fromentin, Bonhommeau & Brisset 2013; Bauer *et al.* 2015). Using the annual estimates of bluefin tuna densities given by Bauer *et al.* (2015), we calculated the abundance of tuna in the studied area by simply multiplying those annual densities with the surface area of the aerial survey transects. We did not account for the differences in spatial coverage of the small pelagic fish surveys (<200 m) and the tuna surveys (including waters >200 m) as small pelagic fish are primarily concentrated over the continental shelf (Saraux *et al.* 2014), and an increased survey area would not significantly affect the estimates of abundance or biomass of these species.

Energetic density

To consider the energetic importance of the prey species of interest in the tuna diet, information on the energetic density and body mass distribution of the other main prey species needs to be known as well. Therefore, all prey species that constituted more than 1%N of the tuna diet over a three year period were also examined, accounting for 98.3%N of the prey consumption. Multiple species of mackerel (97.5%N *Scomber japonicus* and 2.5%N *S. scombrus*) and cephalopods (mostly *Illex coindetii* and some other *Illex* spp., as well as some *Todaropsis eblanae*) were grouped because individuals were not often identified to the species level and species-specific otolith length *versus* body length relationships and energetic densities were not available.

Energetic densities (kJ/g of wet weight) were obtained from the literature for sardine (Rosa *et al.* 2010; Harmelin *et al.* 2012; Spitz & Jouma'a 2013), anchovy (Tirelli *et al.* 2006; Dubreuil & Petitgas 2009; Harmelin *et al.* 2012; Spitz & Jouma'a 2013), sprat (Hislop, Harris & Smith 1991; Arrhenius 1998; Spitz & Jouma'a 2013), mackerel (Montevecchi *et al.* 1984; Spitz & Jouma'a 2013) and cephalopods (Lawson, Magalhes & Miller 1998; Eder & Lewis 2005; Ciancio, Pascual & Beauchamp 2007). As energetic densities may change considerably between seasons, places and individuals (e.g., because of differences in length or condition), maximal and minimal values were noted (Table S1) and a uniform distribution between these two values was used, rather than the average, to represent the energetic values of the prey species, thereby accounting for some uncertainty.

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