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1   **Trophic impact of Atlantic bluefin tuna migrations in the North Sea**
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Abstract

Large highly migratory predators can have major impacts on local marine ecosystems by reducing prey populations and leading to trophic cascades that affect the entire fish community. These trophic interactions are typically non-linear and can alter both the migratory behavior of the predator and the stability of the fish community. The impact of a migrating top-predator is investigated here for Atlantic bluefin tuna in the North Sea. Bluefin tuna has been absent from the region for half-century, but recent years have seen recovery of migrations and a return of bluefin tuna in the area. We use a size spectrum model to analyse the trophic impact of the returning tuna on the entire fish community, under scenarios with varying levels of tuna consumption and fishing mortality on the prey. We show that with high level of prey fishing mortality in the North Sea, the effect of a tuna re-colonization results in only limited trophic cascades. However, high tuna consumption or changes in fishing mortality may result in a sudden recruitment failure of small-pelagic fish due to cascading effects on the fish community. In present-day conditions, the level of tuna consumption that triggers recruitment failure is lower at increasing fishing mortalities on their prey, providing indications for the future sustainable management of both small-pelagics and bluefin tuna in the area.

Keywords: *fish community, long distance migration, size spectrum model, trophic cascade*

Introduction

Trophic relationships form the backbone of the functioning and biodiversity of
ecosystems (Paine 1966, Worm and Duffy 2003). Several factors can affect the
magnitude and importance of trophic interactions driving non-linear processes and
complex dynamics in food webs (Levin 1998). For example, changes in the
abundance of individuals in one trophic level can elicit direct and indirect changes on
other trophic levels, a process known as a trophic cascade (Paine 1980, Pace et al.,
1999, Polis et al., 2000). Evidences of trophic cascades have been reported both in
terrestrial and in aquatic ecosystems (Pace et al., 1999, Shurin et al., 2002, Schmitz et
al., 2004, Casini et al., 2008, Frank et al., 2005) supporting the hypothesis of a
widespread process in ecosystem dynamics. Ecologists have often debated about how
ubiquitous trophic cascades are in ecosystems (Polis 1994, Polis et al., 2000) partly
because several compensatory mechanisms can dampen or eliminate the effects of
trophic cascades (Pace et al., 1999, Cury et al., 2003, Andersen and Pedersen, 2010,
Heath et al., 2014, Lindegren et al., 2016). It has been shown that in marine food
webs a high degree of connectivity, presence of omnivory, ontogenic diet shifts and
fishing can all prevent or dampen trophic cascades (Baum and Worm 2009, Andersen
and Pedersen, 2010). Nonetheless, high fishing pressure has been suggested to trigger
regime shifts in large marine ecosystems (Daskalov et al., 2007, Möllmann et al.,
2009) and are likely responsible for recent changes in the fish community structure in
coastal ecosystems (Jackson et al., 2001).

Generally, cascades are initiated by any external perturbation that can lower the
abundance of some part of the community. Thus apart from fishing, another example
of an external perturbation is the appearance of migrating larger predators that
consume substantial amounts of prey over a relative narrow time period (Polis, 1994,
Scheffer et al. 2005). Casini et al. (2012) showed that when high abundances of Baltic
cod *Gadus morhua* migrated into unoccupied habitats in the Baltic Sea, their
predatory impact induced four-level trophic cascades in the forage fish, zooplankton
and phytoplankton communities of the region.

Atlantic bluefin tuna (*Thunnus thynnus*) is one of the largest apex predators in some
north Atlantic marine ecosystems and have declined due mainly to overexploitation
(Fromentin and Powers, 2005). This species used to migrate into the North Sea region
for many years in the early-mid 1900s but ceased to do so in the mid-1960s and has
been rare or absent during most years ever since (Mather et al., 1995; MacKenzie and
Myers 2007; Fromentin and Restrepo 2008), but the last 2-3 years have provided
evidence of their reappearance (Waage 2016, Bursell 2016; Thuesen Bleeg 2016;
Christiansen and Gyldenkræne 2016). Bluefin tuna migrated mainly from the
Mediterranean Sea spawning ground and remained in the North Sea region for 2-4
months before migrating southward in the autumn (Tiews 1978). While present in the
North Sea, tuna consumption of prey (mainly mackerel and herring) has been
estimated to be large (~300 kton per year) with a likely large impact on the
distribution of the local fish community (Tiews 1978). This species has recently
reappeared in the northern North Sea and Norwegian Sea. Norway has recently been
allocated a commercial fishing quota from ICCAT increasing from about 36 Mt to 52
Mt in the period 2015 - 2017 (ICCAT 2014a), and its entire quota for 2016 was
captured in a single haul with 190 tunas (Waage 2016). The presence of tunas has
been also reported in the inner North Sea with observations of both vagrant
individuals and schools in the Skagerrak and Kattegat in 2015 and 2016 (Bursell

88 2016; Thuesen Bleeg 2016; Christiansen and Gyldenkræne 2016). Additionally
89 Atlantic bluefin tuna has recently appeared in other northern areas of the north
90 Atlantic such as Denmark Strait and east Greenland (MacKenzie et al., 2014).
91
92 In this paper, our objective is to analyse the trophic effects induced by the
93 reappearance of Atlantic bluefin tuna (henceforth tuna) on the northern North Sea
94 food web. We investigate whether predation by tuna could have impacts on trophic
95 levels farther down the food web through trophic cascades and evaluate the effects of
96 interactions between tuna consumption and fishing mortality on the prey. We use a
97 size- and trait-based model for the fish community that is able to account for the
98 changes in trophic levels during ontogeny and resolve fishing mortality on larger sizes
99 (Andersen and Pedersen 2010). The model is used to reconstruct the North Sea fish
100 community size spectra under different scenarios of tuna migration and fishing
101 pressure and allows estimating trophic cascades induced by predation from this top
102 predator.
103
104
105 **Methods**
106 *Model formulation*
107 We use a previously published size-spectrum model to represent the baseline fish
108 community (Andersen and Pedersen, 2010; see appendix for concise description
109 including equations and parameters). The model is a trait-based size spectrum model
110 (Andersen et al., 2016) based on a description of the energy budget of individuals. All
111 rates and processes are parameterized using the size of individuals and the asymptotic
112 size of species (Hartvig et al., 2011). The result of the model is the distribution of
113 individual abundances $n(w, W_\infty, t)$ as function of size w, asymptotic size W_∞ and
114 variation over time, t. The central process in the model is predation of small
115 individuals by large individuals. The food obtained from predation fuels growth and
116 reproduction. Reproduction is limited by a Beverton-Holt stock-recruitment
117 relationship to ensure coexistence of a continuum of asymptotic sizes, by introducing
118 additional intra-specific density-dependence to population dynamics not represented
119 by other processes in the model. Fishing mortality is imposed as a function of
120 individual size and asymptotic size on all species (excluding tuna) and assuming a
121 logistic size selectivity function, calibrated to emulate the fishing pattern in the North
122 Sea (Pope et al., 2006). The total biomass of fish in the North Sea has been estimated
123 to be between 8,600 kton and 13,000 kton (Sparholt 1990), which is consistent with
124 estimates from multi-species fish stock assessment models providing 8,000 kton for
125 the entire North Sea (ICES 2016). To simulate the northern North Sea fish community
126 the total biomass of the ecosystem is set in the model as a fraction of what has been
127 estimated and we use a reference biomass of 5,000 kton.
128
129 The impact of predation by tuna on the resident fish community is represented in the
130 model as an extra predation mortality μ_T inflicted on the size within the tunas' prey
131 size preference $\phi_T(w_p)$ where w_p is the weight of prey. Bluefin tuna are opportunistic
132 predators and feed on a diverse diet, both in terms of species and sizes, and their diet
133 composition more likely reflects available prey distributions and abundances in the
134 surrounding environment than strong preferences for particular prey or sizes (Goñi,
135 and Arrizabalaga, 2010; Olafsdottir et al., 2016). We assume that the prey range of
136 tuna is constrained within a minimum value ($w_S = 100$ gr) and some large size
137 ($w_L = 2.5$ kg), i.e., $w_S \leq w_P \leq w_L$. This size range approximates the size range of

138 the dominant fish species known to be consumed by tuna in the North Sea during the
139 1950s-1960s (Tiews 1978) and by tunas in other northern shelf regions (e.g., Chase
140 2002, Overholtz 2005, Butler et al., 2010). However we also analyse the results at
141 different values of w_S to test the sensitivity of the model to this parameter.
142
143 The total consumption of tuna S_T can be calculated as (biomass per time):
144
145       $S_T = \mu_T \int w_p N(w_p) \, \phi_T(w_p) \, dw_p$ (1)
146
147 where $N(w)$ is the community spectrum which is the integral over all asymptotic
148 sizes: $N(w) = \int n(w, W_\infty) w \, dW_\infty$. Hence $w_P N(w_P)$ is equal to the total biomass in
149 the prey range on which tuna can impose a predation mortality μ_T with size
150 preference $\phi_T(w_p)$. The equation for S_T can be rewritten to isolate the mortality:
151       $\mu_T = S_T \dfrac{1}{\int w_p \, N(w_p) \phi_T(w_p) dw_p}.$ (2)
152 which is then used as an extra mortality term in the integration of the model
153 (Appendix 1).
154
155 We focus our analyses on four scenarios (Table 1): unperturbed ecosystems with no
156 fishing or tuna consumption, i.e., fishing mortality $F = 0$, consumption by tuna $S_T = 0$
157 (N_{00}); an unexploited ecosystem with no fishing but with tuna consumption, i.e., $F =$
158 0, $S_T = 150$ kton year^{-1} (N_{01}); an exploited ecosystem with high fishing but no tunas,
159 $F = 0.7$ year^{-1}, $S_T = 0$ (N_{10}); an exploited ecosystem with tunas, i.e., $F = 0.7$ year^{-1}, S_T
160 $= 150$ kton/year (N_{11}). In addition, we analyse the trophic impact of fishing and
161 migrations for a larger range of fishing mortalities ($F \in [0 - 1.5]$ year^{-1}) and tuna
162 consumptions ($S_T \in [0 - 800]$ kton/year).
163
164 Given a scenario with either fishing or tuna migration ($\{N_{10}, N_{01}, N_{11}\} \in \tilde{N}$), we can
165 calculate the direct impact of tuna predation as the difference between $\tilde{N}$ and the
166 unperturbed case: $\int w_p \tilde{N} - w_P N_{00} \, dw_P$. This difference in biomass estimates the
167 direct trophic impact on the tuna prey range relative to an unperturbed scenario.
168 Moreover, in order to estimate the trophic cascade initiated by tuna consumption we
169 develop an index that expresses the total magnitude (regardless of sign) of the change
170 in biomass relative to a reference size spectrum. The index (Δ) is defined as the
171 integral of the size-spectra relative to the case of no tuna predation:
172
173       $\Delta = - \int_{w_0}^{w_L} \left| \log \dfrac{N_{\alpha 1}(w)}{N_{\alpha 0}(w)} \right| \, d(\log w)$ (3)
174
175 where N_α indicates the specific fishing scenario considered (unexploited or exploited
176 at different levels). This index is always positive and measures the change in size
177 structure driven by tuna consumption for all sizes smaller than the maximum tuna's
178 prey size (w_L) but larger than the minimum size included in the model (i.e., fish egg
179 size, $w_0 = 0.5$ mg). We exclude from the computation effects on sizes larger than the
180 maximum prey size (w_L) as the abundance of those individuals is relatively low
181 compared to smaller size classes, hence although perturbation can propagate upwards
182 on the higher trophic levels and lead to a large change relative to the unexploited
183 biomass, they have negligible effects on the absolute biomasses.
184
185 *Consumption by tuna in the northern North Sea*

186   Estimating the total prey consumption by tuna requires knowledge of their abundance,
187   their body size, and their daily ration. No abundance estimates are available for this
188   time period. However, by combining commercial catch data (ICCAT 2012) and
189   estimates of instantaneous fishing mortality rates (Fromentin and Restrepo 2008) for
190   the most important fishery in the region (i.e., the Norwegian fishery), it is possible to
191   derive approximate estimates of biomass. Most of the Norwegian catches were made
192   in ICES Subdivision IVa (Tiews 1978). We therefore assume that most of the
193   foraging by this tuna biomass occurred in this region. Our tuna biomass and
194   consumption estimates will therefore underestimate the total consumption because
195   they exclude the catches by other countries; however non-Norwegian landings were
196   relatively small (ca. 27% of all tuna landings in ICES Areas II-VII; Huse et al.,
197   2015). We therefore provide sensitivity analyses of the model results to changes in S_T.
198
199   We expressed the instantaneous fishing mortality rates on an annual basis, which
200   allows estimation of the percentage of stock biomass removed annually. This removal
201   rate can be considered as an annual exploitation rate, U (Dick and MacCall 2011).
202   Consequently, given the reported catches (C) and the estimated U, biomass in the
203   region can be calculated (Worm et al., 2009; Rosenberg et al., 2014) as $B = C/U$,
204   where B is the total biomass. Note that U is the fraction of the biomass removed by
205   the fishery on an annual basis (i.e., obtained by converting the instantaneous fishing
206   mortality rate to annual removal rates). The instantaneous fishing mortality rates were
207   estimated to be $F = 0.3$, $F = 0.2$ and $F = 0.1$ per year, for the years 1950s, 1960s and
208   1970s respectively (Fromentin and Restrepo 2008). These fishing mortality rates
209   correspond approximately to annual removal rates of 26%, 18% and 10% respectively
210   for the three time periods. As most of the individuals captured in this fishery were
211   adults (Tiews 1978, Fromentin and Restrepo 2008), the biomass would correspond
212   only to a spawning stock biomass (i.e., excluding juveniles) in this region. Indeed the
213   reported weights in the catches (Tiews 1978) were mainly in the range 150 – 400 kg.
214   We used two reference tuna weights, $w_1 = 200$ kg and $w_2 = 300$ kg, to derive the
215   total number of fish in the area ($n_1 = B/w_1$; $n_2 = B/w_2$) and the average daily
216   consumptions of the population (S_T) using the allometric relationship (Innes et al.,
217   1987, Overholtz 2005):
218
219                    $$S_T = 0.5\, k\, (w_1^{0.8}\, n_1 + w_2^{0.8}\, n_2) \qquad (4)$$
220
221   where $k = 0.123$ and S_T has units of kg per day. Based on the relationship above we
222   obtain an average daily individual consumption rate of 4% body weight. The daily
223   ration of tuna in the North Sea and during the 1950s-60s has been previously assumed
224   to be 3-6% day^{-1} (Tiews 1978) and 1-4.7% day^{-1} for tuna in the Gulf of Maine-
225   Georges Bank during 1970-2002 (Overholtz 2005), which are then consistent with the
226   estimates obtained above.
227
228   **Results**
229   *Consumption by tuna in the northern North Sea*
230   Norwegian landings of tuna in the region varied between 15 kton in 1952 to 0 kton
231   after 1987. This corresponds to an estimated maximum biomass of about $B = 60$ kton
232   ($B = 14$ kton, as average 1950 – 1987). We can then estimate the total annual
233   consumption by tuna assuming a residence period of 100 days (Figure 1). This
234   consumption is estimated to be between 100 - 200 kton/year with a maximum value
235   of 232 kton/year in 1952. Moreover, as the catches declined, the tuna consumption

236   decreases to around 30 kton/year after 1963 and then to 0 in most recent periods.
237   Those values compare well with previous estimates of tuna consumption in the area
238   (Tiews 1978) (Figure 1).
239
240   *Community response to tuna migration and fishing*
241   At equilibrium and under unperturbed conditions (N_{00}; $F = 0$, $S_T = 0$) the simulated
242   ecological community in the northern North Sea distributes according to a size spectra
243   (slope of -1.47), which provides the assumed total biomass of about 5,000 kton
244   (Figure 2).
245
246   Assuming migration of tuna in this unperturbed system (Figure 3a), we find that the
247   tuna consumption can substantially reduce the abundance of the larger prey in the
248   feeding range ($w > 1$ kg) and have positive indirect impacts on the smaller prey size
249   classes (0.1 kg $< w <$ 0.3 kg). This is mainly because smaller sizes outside the tuna
250   prey range experience a reduction of both predation pressure and competition from
251   the larger sizes, thus contributing to more fish growing into the smallest tuna prey
252   range. The perturbation generated by tuna consumption in the preferred prey range
253   cascades down to smaller size ranges with gradually weaker effects (oscillations). The
254   perturbation is indeed damped while moving from larger to smaller individuals and it
255   becomes very small in the region dominated by zooplankton biomass ($w < 0.5$ g).
256
257   The structure of this type of ecosystem is qualitatively different from the fish
258   community simulated when fishing pressure is introduced (N_{10}). In case of a fishing
259   mortality $F = 0.7$ year^{-1} and no tuna consumption ($S_T = 0$) the model results in a 20%
260   increase in fish biomass within the range 0.1 kg $< w <$ 1 kg. As above the increase in
261   biomass in a certain range of sizes has cascading effects in the community size
262   spectra. Hence, while negligible effects are predicted on the smaller size classes in the
263   model, $w < 10^{-2}$ g, biomass increase and decreases are alternated throughout the fish
264   community. Small perturbations to this general trophic cascade are introduced when
265   tuna consumption is considered in this exploited scenario (N_{11}, Figure 3a). The main
266   effect is the slight shifts of the peaks of the perturbation towards smaller sizes as a
267   larger reduction of biomass occur in the larger tuna prey range. At equilibrium the
268   highest biomass in the range 0.1 kg $< w <$ 2.5 kg is obtained in the exploited case with
269   no tuna (N_{10}) while the opposite conditions (no fishing, but tuna present, N_{01})
270   provides the lowest (Table 1). Trophic impact is then largest when tuna is introduced
271   in an exploited scenario, while it becomes much smaller when the ecosystem is
272   exposed to fishery (index Δ in Table 1).
273
274   The sensitivity of the fish community to tuna consumption in exploited or unexploited
275   ecosystems is smaller when a larger prey size range is considered in the model
276   (Figure 3b). Assuming tuna able to feed on prey as small as $w_s = 1$ g the relative
277   change for both ecosystems is always very close to 1 with a trophic impact Δ ≈ 0.1 in
278   both cases (Figure 3c). In general an increase in the prey size range has damping
279   effects on trophic cascades. Reducing the prey size range, by increasing w_s, larger
280   effects of tuna consumption are simulated in the community structure and those are
281   generally much stronger for unexploited ecosystems (Δ ≈ 0.4, Figure 3c). Indeed the
282   similarities between exploited and unexploited ecosystems rapidly disappear as the
283   smallest prey item is increased to values larger than 20 g.
284
285   *Model sensitivity*

286   In case of no fishing the introduction of tuna in the ecosystem generates a lower
287   equilibrium biomass in the prey range (Figure 4a). The higher the tuna consumption,
288   the larger the reduction in prey biomass. A sharp transition towards low values of
289   biomass (around 500 kton) is shown by the model at $S_T \approx 400$ kton/year and no
290   fishing (F = 0). At this level of consumption, the prey biomass reaches a critical
291   minimum spawning stock size that cannot support recruitment. With a low
292   recruitment of the larger species in the prey range, the smaller prey can increase their
293   biomass because of reduced predation. Hence, at this critical level, the temporal
294   dynamic of the size spectrum model shows an oscillatory behaviour of the abundance
295   of tunas' prey. The coefficient of variation (CV, i.e., standard deviation relative to the
296   mean) in the abundance of prey fish within the tuna size range calculated over the last
297   realizations of the model (i.e., last year) is generally small (CV < 0.05), while it
298   suddenly increases when the model approaches the critical transition (CV ≈ 0.6).
299   However, those oscillations start occurring when the fish biomass is low, hence
300   further increases in tuna consumption do not affect the outcome.
301
302   Introducing fishing will generally have positive effects on biomass in the range of the
303   tuna prey. This occurs because the reduction of large fish (such as cod) reduces the
304   predation pressure on small fish, which then increase in abundance. Indeed, at a
305   moderate level of fishing ($0.5 \leq F \leq 1$ year^{-1}) and no tuna migration, there is a
306   maximum increase of 500 kton of tuna prey biomass produced (Figure 4a). Further
307   increases in fishing mortality can however reduce smaller fish including the tuna prey
308   size. The same conclusions can be drawn when both tuna migration and fishing are
309   present in the model, resulting in a general non-linear relation between the two
310   processes (Figure 4). Interestingly, at relatively low levels of fishing mortality ($F =$
311   0.5 year^{-1}) up to 500 kton/year of tuna consumption can be present in the model
312   without largely altering the prey biomass compared to an unperturbed scenario.
313
314   The direct impact of tuna on the entire fish community size structure can be evaluated
315   at different values of consumption using the perturbation index Δ (Figure 4b). Since Δ
316   is a measure relative to the absence of tuna migration (Eq. 3), the index start from
317   Δ= 0 at all levels of fishing mortality and can be generally described as the area
318   below a perturbation curve (Figure 3). Tuna can significantly affect the size structure
319   of the community, Δ> 0.5, at high level of consumption or at low level of fishing
320   mortality (Figure 4b). If F is high the effect of tuna consumption on the size-structure
321   is negligible. While at lower levels of fishing ($F \leq 0.6$) the larger the tuna
322   consumption, the greater is the effect on the food web. This pattern is evident up to
323   the critical transition described above, where the collapse of the tuna prey range will
324   largely impact the size-structure and any further increase in S_T will not have any
325   effects.
326
327   **Discussion**
328   Although it is recognized that predation in marine ecosystems is an important factor
329   explaining food webs dynamics and community structure (Verity and Smetacek 1996,
330   Heithaus et al., 2008, Baum and Worm 2009, Mariani et al., 2013), effects of top
331   predators on the marine food web are more complex because of their cascading
332   impact on the entire community (Cury et al., 2003, Ferretti et al., 2012, Blenckner et
333   al., 2015). Our results show how effects of fishing and consumption of top predators
334   can produce large changes in the small pelagic fish communities with cascading
335   effects that are stronger at lower fishing mortalities. In the northern North Sea, with

high level of fishing mortality, the biomass of small pelagic fish is only marginally
controlled by predation of large top predators (e.g., cod, tunas, etc.). On the other
hand at lower fishing mortality, consumption by top predators can significantly
reduce the biomass of the small pelagic having cascading effects on other components
of the food web.

Thus, with an intermediate exploitation rate ($F \approx 0.3$ year^{-1}), fishing may have
beneficial effects for increasing small pelagic fish biomass, which can then potentially
sustain consumption by migratory species such as tunas. Above these intermediate
values ($F > 0.5$ year^{-1}), small pelagic fish biomass will also be reduced. Moreover,
the model shows a critical threshold for tuna consumption above which both trophic
impact on the fish community and small pelagic biomass are independent from
predation (Figure 4). This can be explained by a strong decline of fish biomass in the
preferred prey size range of tuna and the consequent failure in their recruitment.
Assuming that the feeding ground in the northern North Sea has a total fish biomass
of 5,000 kton and that tuna consumption could be in the range 100 - 200 kton/year,
then $2 - 4\%$ of the entire fish community could be consumed by tunas in about 100
days. However, the consumption is concentrated in the preferred size range
($w_S \leq w_P \leq w_L$) and at certain levels can become critical for the recruitment of
species in this range. Presently this critical level is at high values of tuna consumption
for the prey size range $0.1 \leq w_P \leq 1.5$ kg. Indeed, when consumption by migrating
predators is at 650 kton (13% of the entire fish community) and $F = 0.7$ per year, the
recruitment of some prey species (Eq. M10 in the Appendix) oscillates around values
of $R_0 \approx 1$, hence the biomass of fish within the tuna preferred size range remains at a
minimum level with large impact on the trophic cascade.

Overall tuna biomass in the northeast Atlantic and Mediterranean Sea has been
increasing during the past 5-10 years (ICCAT 2014b) which should also stimulate
tuna to explore new (or former) foraging areas. There is ample evidence that
migratory species can explore the environment and discover new areas for feeding
(Dingle and Drake 2007, Alerstam et al., 2003, Aidley 1981, Hays et al., 2014).
Recently, migrations of mackerel and bluefin tuna have been observed in waters east
of Greenland (Denmark Strait), an area that was not previously occupied by either
species (MacKenzie et al., 2014; Jansen et al., 2016). Those changes are likely driven
by improved conditions of the habitats in northern areas (e.g., increase in temperature
and food) and can now have cascading effects on the local fish community. Indeed, a
re-appearance of tuna in the northern North Sea would presently have negligible
effects on both size-structure and pelagic biomass, since the fishing pressure in the
area is much greater than the potential impact of tuna feeding. Despite the presently
negligible food web effects of tuna consumption in the northern North Sea a future
increase in tuna biomass could lead to pronounced changes in both size-structure and
pelagic biomass acting across larger spatial scales. Although a higher tuna biomass
would inevitably lead to calls for tuna fishing quotas by several Countries
surrounding the North Sea, the historical lesson learned from the past stock collapse
and disappearance of tuna would arguably motivate exploitation levels to be kept at a
low and sustainable level. Whether these levels would promote a tuna biomass at a
level at which consumption critically affects the prey population and the ecosystem as
a whole remains to be seen. However any fishing-related removal of tunas would
reduce the trophic impacts by reducing the tuna consumption within a range
consistent with that considered in the present study.

386   In addition, it may be suggested that not only tuna but also other large fish predators
387   with similar size and partially overlapping diet preferences could invade or recolonize
388   the North Sea under future climate change. One such competing species could be the
389   warm-water predator swordfish (*Xiphias gladius*) (Stillwell and Kohler 1985), which at
390   least during the Stone Age used to inhabit these waters and could potentially recolonize
391   given future increases in temperature (Enghoff et al. 2007). Recent occurrences in
392   Norwegian waters suggest that such a scenario is indeed very likely (Sundby et al.,
393   2013) . Given that our model approach is not species-specific but generalizable to all fish
394   across a great range of sizes, a potential increase in such ecologically similar predators
395   would simply serve to increase the consumption of prey fish within the size range of
396   tuna and support our findings on potential future changes in the North Sea food with
397   respect to its fish prey biomass and size structure.
398
399   Evidences of rapid trophic cascades driven by seasonal migration of top predators
400   have been suggested in the Baltic Sea where periodic migrations of cod and its
401   consumption on herring led to cascading effects across multiple trophic levels in the
402   Gulf of Riga (Casini et al., 2012). We note that fishing mortality on herring in the area
403   is about $F = 0.4$ yr^{-1} (ICES 2014) which in our model would allow a significant
404   trophic impact also at low values of predator consumption (Fig 4b). Moreover, the
405   patterns in trophic cascades observed in the Gulf of Riga are consistent with our tuna
406   results because they show larger impact on the prey (herring) and weaker impact on
407   the other components of the ecosystem (plankton) (Fig 3).
408
409   Recent estimates of the total amount of fish in the entire North Sea are ca. 8,000 kton,
410   (ICES 2016) thus our assumption of 5,000 kton could be reasonable for the northern
411   North Sea. However, changes in prey size range or total fish biomass can affect our
412   results. A change in the total fish biomass in the model is equivalent to a change in
413   the consumption levels of tunas, hence similar effects are produced both in terms of
414   biomass available to tuna feeding or in terms of trophic impact (Figure 4). Indeed, if
415   the fish community is assumed to have a lower total biomass, the critical transition
416   point is shifted towards smaller consumption levels. Beyond this threshold the
417   decrease in prey biomass becomes insensitive to further increases in tuna
418   consumption or, similarly, to reduction in total fish biomass. A wider prey size range
419   for tuna can significantly reduce the trophic impact of consumption. This is because
420   the amount of biomass available to tuna is larger and the feeding impact evenly
421   distributed over a wider size-spectra. On the contrary, a narrower prey size range can
422   induce stronger trophic-cascades illustrated by larger values of the perturbation index
423   Δ.
424
425   Our findings illustrate interactions between migration behaviour and trophic impacts
426   of a migratory predator on a food web. As such, they provide an additional ecosystem
427   context for the management of both forage species in the North Sea and for tuna
428   itself. This knowledge could be useful for understanding the conditions that could
429   allow tuna to re-establish a migration path that was lost in the 1960s, as well as the
430   food web consequences of such a feeding migration. The sudden interruption of fish
431   migration towards certain feeding areas has been explained by a loss of group
432   collective memory driven by the breaking of the social transmission of the
433   information (Petitgas et al., 2010; De Luca et al., 2014). Removing those individuals
434   that had some information and preference for specific feeding areas has likely
435   produced a rapid change in the migratory behaviour of the rest of the group that has
436   likely moved towards other areas (De Luca et al., 2014). Hence, given that food

437 resources are now available for tuna, the recent re-appearance in the region might
438 represent the beginnings of a re-establishment of the migratory path towards the
439 northern North Sea. This re-establishment will proceed if some of the individuals that
440 were able to rediscover this historical feeding area will survive to restore this
441 information in the tuna population.
442
443
444
445 **Acknowledgements**
448

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450 **References**

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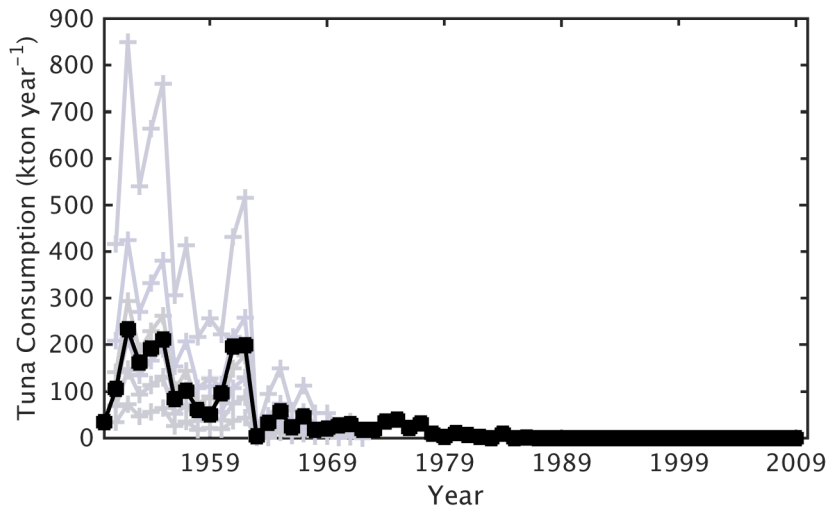730
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734 Tables and Figures
735 Table 1. Description of case studies with indication of fishing mortality (F) and tuna consumption (S_T).
736 Fishing mortality does not include tuna population. Also shown calculated values of fish biomass in the
737 tuna's preferred size range and the trophic impact index (Δ).
738

| Case	F year^{-1}	S_T kton year^{-1}	Prey biomass kton year^{-1}	Δ
N_{00}	0	0	775	-
N_{01}	0	150	633	0.33
N_{10}	0.7	0	1286	-
N_{11}	0.7	150	1181	0.14

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742
743 Figure 1. Total prey biomass consumed per year by tuna migrating into the northern North Sea between
744 1950 and 2009. Our values (black line) are compared with a series of estimates from Tiews (1978) (cfr.
745 Table 150, grey lines). Catch data of the Norwegian fleet have been transformed to total biomass and
746 then into daily consumption. The total consumed biomass is calculated assuming 100 days of feeding
747 in the area and is used to define the parameter S_T.
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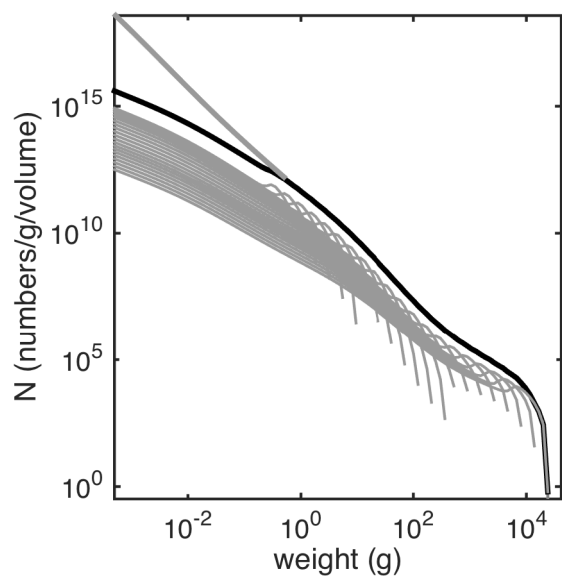
751
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753 Figure 2. Abundance size spectra of 25 asymptotic size classes in an unperturbed ecosystem (thin grey
754 lines) and community spectrum (black line) and the zooplankton resource spectrum (thick grey line).
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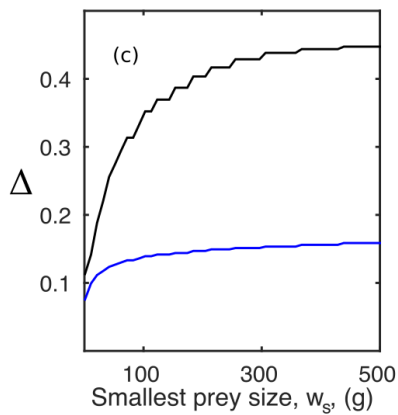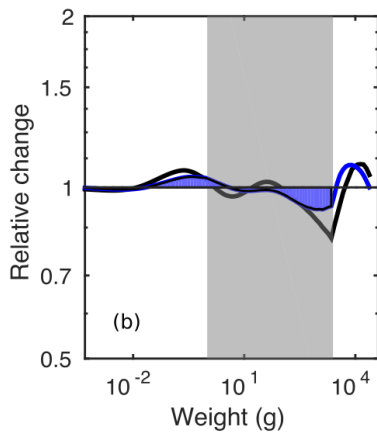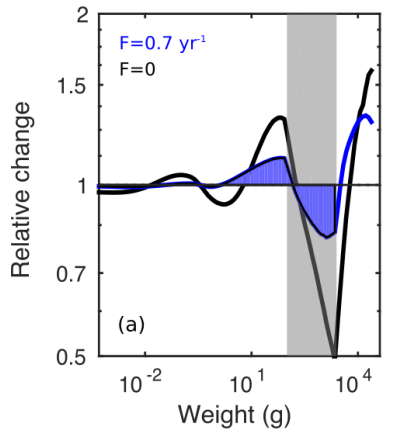
757
758   Figure 3. Impact of tuna in the northern North Sea using the ratio N_{01}/N_{00} (black) and N_{11}/N_{10} (blue)
759   to evaluate the effects of tuna consumption on an unexploited and exploited ($F = 0.7$ year^{-1}) ecosystem
760   respectively. Tuna consumption ($S_T = 150$ kton year^{-1}) is applied in the prey size range $w_S \leq w_P \leq w_L$
761   (grey areas) with w_L=2.5 Kg and (**a**) $w_S = 100$ g (**b**) $w_S = 1$ g. The index Δ Eq. 3 is graphically shown
762   as the area under the relative change curve (blue shaded area). In (**c**) the value of Δ is shown at
763   different values of w_S for unexploited (black) and exploited (blue) ecosystem.
764

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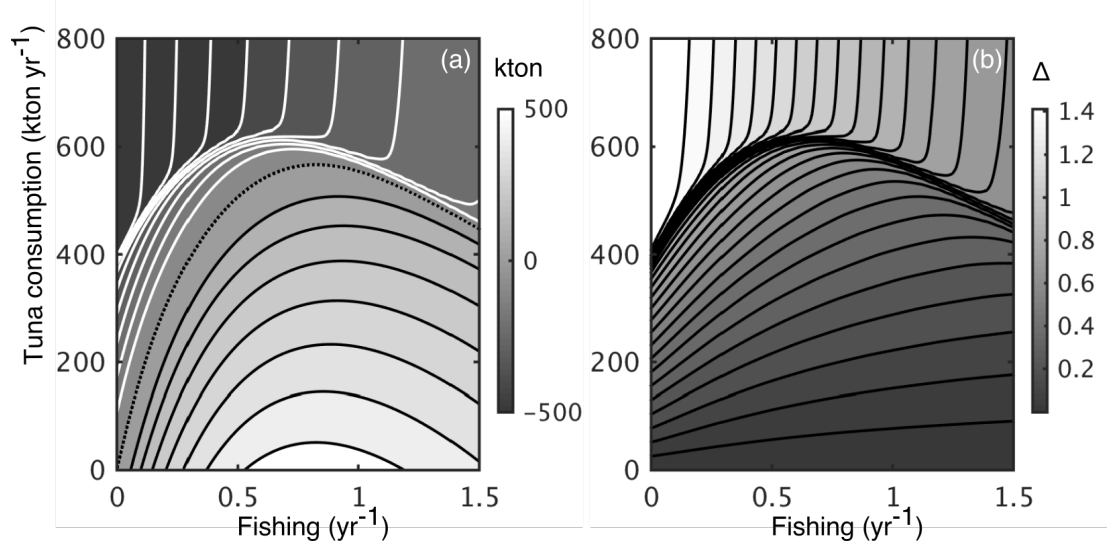
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767
768 Figure 4. Direct impact of fishing (F) and consumption by tuna (S_T) on (a) prey biomass (a) and (b)
769 size-structure index Δ (Eq. 3). The tuna prey biomass is calculated as the difference between the
770 equilibrium prey biomass, in a specific fishing and consumption scenario, and the unperturbed case,
771 when F = 0 and S_T = 0. White contour lines are for negative values, black solid lines for negative
772 biomass values and the zero contour line is shown with a dashed line. The prey interval is $w_S \leq w_P \leq$
773 w_L, with $w_S = 100$ gr and $w_L = 2.5$ kg. The index Δ is defined in Eq. 3 as the changes in size
774 structure for $w \leq w_L$.
775
776

777 Appendix

Encounter and consumption		
Prey size selection	$\phi\left(\dfrac{w_{prey}}{w}\right) = \exp\left[-\left(\ln\left(\dfrac{\beta w_{prey}}{w}\right)\right)^2 / (2\sigma^2)\right]$	M1
Volumetric search rate	$V(w) = \gamma w^q;\ \gamma = \dfrac{f_0 h \beta^{n-q}}{(1-f_0)\sqrt{2\pi}\kappa_r \sigma}$	M2
Encountered food	$E(w) = V(w) \sum_j \int_0^{\infty} \phi\left(\dfrac{w_{prey}}{w}\right) N_j(w_{prey})\, w_{prey}\, \mathrm{d}w_{prey}$	M3
Maximum consumption rate	$I_{max} = h w^n$	M4
Feeding level	$f_i(w) = \dfrac{E_i(w)}{E_i(w) + I_{max.i}}.$	M5
Growth and reproduction		
Maturation function	$\psi(w) = \left[1 + \left(\dfrac{w}{w_{mat.i}}\right)^{-10}\right]^{-1}\left(\dfrac{w}{W_i}\right)^{1-n}$	M6
Somatic growth	$g_i(w) = (\alpha f_i(w) I_{max.i} - k_i w^p)(1 - \psi(w))$	M7
Egg production	$g_r(w) = (\alpha f_i(w) I_{max.i} - k_i w^p)\psi(w)$	M8
Recruitment		
Population egg production	$R_{p.i} = \epsilon/(2 w_0 N_i(w_0) g(w_0)) \int_{w_0}^{W_i} \psi(w) N_i(w) g_r(w)\, dw$	M9
Recruitment	$R_i = R_{max.i} \dfrac{R_{p.i}}{R_{max.i} + R_{p.i}} \xi(t)$	M10
Mortality		
Background mortality	$\mu_0 = Z_0 W_i^z$	M11
Predation mortality	$\mu_{p.i}(w_{prey}) = \sum_j \int_{w_0}^{\infty} \phi\left(\dfrac{w_{prey}}{w}\right)\left(1 - f_j(w)\right) V_j(w) \theta_{ij} N_j(w)\mathrm{d}$	M12
Fishing selectivity	$S_i(w) = 1/(1 + e^{(S1 - S2\, w)})$	M13
Fishing mortality	$\bar{F}_i(w) = S_i(w) F_i$	M14
Resource spectrum		
Growth rate	$\dfrac{\partial N_r(w)}{\partial t} = r_0 w^{n-1}(\kappa(w) - N_r(w)) - \mu_{p.r}(w) N_r(w)$	M15
Carrying capacity	$\kappa(w) = \kappa_r w^{-\lambda}$	M16

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