
The key role of the Northern Mozambique Channel for Indian Ocean tropical tuna fisheries

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Abstract :

The Northern Mozambique Channel (NMC) is a tropical area of similar to 1 million km² where pelagic fisheries supply proteins to more than 9 million people living in Comoros, Mayotte, and along the coasts of Mozambique, Tanzania and Madagascar. Although uncertain, statistics suggest that about 20,000 mt of tropical tuna and other pelagic fish are annually caught by artisanal fisheries in the area. The NMC is also a major seasonal fishing ground for high-seas fleets that export an annual average catch of more than 20,000 mt to tuna can and sashimi markets of high-income countries for a value estimated to be more than 100 million USD. The fisheries productivity of the NMC appears to be highly variable in relation to strong annual and seasonal variability in oceanographic conditions. Our review shows that the NMC is a key feeding area for tropical tunas and a major spawning area for skipjack tuna thanks to warm waters and strong mesoscale activity that results in the enrichment of surface waters and efficient energy transfers enabled by short food chains. Projections of climate models under future warming scenarios predict some strong changes in the oceanographic conditions of the NMC which has already experienced substantial warming over the last decades. Changes in the pelagic ecosystem of the NMC could have dramatic consequences on the coastal populations that are expected to increase towards 100 million people by 2100. Improving monitoring systems and collecting information on the socio-economics of coastal fisheries is crucial to assess the dependence of NMC populations on tuna resources and empower the countries to more involvement in the management of tuna stocks.

Keywords : Bigeye, Fisheries management, Mozambique Channel, Skipjack, Yellowfin

34 **Acknowledgements** We are grateful to all the people involved in the collection and management of
35 the data used in the present study, in particular the staff of the IOTC Secretariat for their dedication
36 to their work. Special thanks to Fabio Fiorellato, James Geehan, Lucia Pierre, and Dan Fu. Catch
37 and effort data were extracted from the global tuna fisheries database initiated by Alain and Viceca
38 Fonteneau and further developed and consolidated through a collaboration between FAO and IRD.
39 Liam Campling provided information on international tuna prices (FFA Trade Bulletin). We are
40 grateful to the many persons involved in the Tuna Atlas project, in particular Paul Taconet, Julien
41 Barde, Emmanuel Blondel, Aymen Charef and Marc Taconet. The database and services of the Tuna
42 Atlas are currently hosted by the Institute of Information Science and Technologies (CNR-ISTI) and
43 the work received funding from the European Union's Horizon 2020 research and innovation
44 programme under the BlueBRIDGE project (Grant agreement No 675680). The tuna tagging data
45 analysed in this publication were collected by the Regional Tuna Tagging Project of the Indian
46 Ocean (RTTP-IO) funded under the 9th European Development Fund (9.ACP.RSA.005/006) of
47 the European Union. The RTTP-IO was implemented by the Indian Ocean Commission under
48 the technical supervision of the IOTC. We wish to acknowledge the contributions of the project
49 staff and all the technicians, recovery officers and fishers that have been involved in the RTTP-
50 IO. Reproduction and morphometric data were mostly collected through the project EMOTION

51 founded by the French National Research agency (ANR 11 JSV7 007 01), the EU Data
52 Collection Framework (Reg. 199/2008 and 665/2008), Fundación Centros Tecnológicos,
53 Department of Agriculture, Fisheries and Food of the Basque Government, and the PEVASA
54 fishing company. James Mbugua (CORDIO) provided assistance with NMC boundaries and
55 Umair Shahid useful comments on an earlier version of the manuscript. Many thanks to
56 Pierrick Penven for pointing out very useful references on the oceanographic features of the
57 Northern Mozambique Channel and Simon Hoyle for discussions and advice on statistical
58 models. Laurent Pinault provided information on fisheries agreements. We finally thank the
59 two anonymous reviewers for their constructive comments that helped improve the
60 manuscript. The present study was funded by a WWF grant as part of the Northern
61 Mozambique Channel Initiative.

62 **Introduction**

63 The Northern Mozambique Channel (NMC) is the part of the Mozambique Channel northwards of
64 the narrowest stretch between Madagascar and Mozambique. The NMC is bounded by northwest
65 Madagascar, northern Mozambique and southern Tanzania, with the Comoros archipelago at its
66 heart. The Aldabra group of islands lies just to the north at about 9°S. In its wider definition, the
67 northern limit of the NMC is operationally set to include Mafia Island in central Tanzania at about
68 7°S while its southern limit goes down to 19°S (Obura et al. 2015) (Fig. 1). The NMC is described
69 by a high diversity of marine habitats typical of shallow tropical seas, including coral reefs,
70 mangrove forests, seagrass beds, and a dynamic pelagic zone which constitutes a major habitat for
71 tropical tuna (Obura et al. 2015). Historical statistical data on artisanal fishing for subsistence are
72 sparse and uncertain for the countries bordering the NMC but available information suggests that
73 large pelagic species have long been a very small component of traditional fisheries since they were
74 restricted to the nearshore zone (Petit 1923; Fourmanoir 1954). Reviews available for coastal
75 fisheries of the NMC show that they are essentially supported by inshore fisheries (coral reef,
76 mangroves, etc.) as well as shrimp fisheries in the case of Madagascar (van der Elst et al. 2005; De
77 Young 2006). Tuna fisheries statistics for coastal and high seas fishing nations go back to the early
78 1950s with the expansion of the Japanese longline fleet across the Indian Ocean, including the
79 Mozambique Channel (Geehan et al. 2016). In the early 1970s, some exploratory cruises were
80 conducted by Japanese and French vessels along the coasts of Madagascar, Comoros, and
81 Seychelles to assess the potential for development of a commercial tuna fishery in the region
82 (Marcille and Veillon 1973). Following the implementation of the United Nations Convention on
83 the Law of the Sea (UNCLOS) in December 1982 concurrently with the arrival of a major purse
84 seine fleet from the Atlantic Ocean, a major seasonal surface fishery developed in the NMC from
85 1985 (Stéquert and Marsac 1989). Fishing agreements to access the national waters of the NMC
86 coastal countries by the European Union fishing fleets date back to 1986, 1987, and 1988 for

87 Madagascar, Mozambique, and Comoros, respectively. Since then, the NMC area has become a
88 major fishing ground for the tropical Indian Ocean tuna purse seine fishing fleets with catches
89 corresponding to more than 30000 mt per year over the last three decades, i.e. about 10% of their
90 annual production.

91

92 The management of Indian Ocean tropical tunas is under the jurisdiction of the Indian Ocean Tuna
93 Commission (IOTC) since 1996 (Kambona and Marashi 1996). Its overarching objective is to
94 maintain the stocks of tuna and tuna-like species at levels which allow maximum sustainable yield.
95 The core work of the IOTC Secretariat is to collate and manage multiple fisheries data sets of catch,
96 effort, and size provided by each Commission member to support the assessment of the status of the
97 16 species under the IOTC mandate and develop and implement conservation and management
98 measures such as effort or catch limitation to ensure their sustainability. The IOTC is however faced
99 with major issues in both the quantity and the quality of the data provided by the contracting parties
100 and the conservation measures and stock assessments are developed with partial information
101 (Fiorellato et al. 2018; IOTC 2018). The three principal market tunas that represented more than
102 50% of the catch of all IOTC species over the last decade are skipjack (*Katsuwonus pelamis*;
103 ~26%), yellowfin (*Thunnus albacares*; ~22%), and bigeye (*Thunnus obesus*; ~7%) tuna,
104 characterized by small to medium size, rapid growth, early age-at-maturity, and long spawning
105 duration (Juan-Jordá et al. 2013; Murua et al. 2017). These highly migratory species can carry out
106 fast and extensive movements and migrations in search of a large variety of prey to address their
107 high energetic needs and fuel reproduction. Tropical tunas generally occur in mixed schools that can
108 be composed of tens of thousands of fish in the case of fishing sets exceeding 100 t and composed
109 of tuna of average weights 3-5 kg that are generally associated with floating objects (Chassot et al.
110 2015). This schooling behaviour combined with their associative behaviour with floating objects
111 (Fréon and Dagorn 2000; Castro et al. 2002) has a major influence on the spatio-temporal dynamics

112 of the purse seine fishery (Kaplan et al. 2014; Davies et al. 2014) and might affect their growth,
113 mortality and reproduction, although this needs to be further explored (Marsac et al. 2000; ISSF
114 2014). Schooling behaviour could also play a major role in stabilizing tuna populations (Maury
115 2017).

116

117 More than 9 million people currently live within the Comoros Archipelago and along the coasts of
118 Mozambique, Tanzania and Madagascar that border the NMC (Obura et al. 2018). This population
119 is expected to increase by close to an order of magnitude towards 100 million people by 2100,
120 which will result in exponential increases in demands and pressures on natural resources (Obura et
121 al. 2018). In parallel, projections of climate models under future warming scenarios suggest the
122 strengthening of the Somali coastal upwelling due to increased ocean-land thermal gradient in
123 conjunction with weakened nutrient mixing at regional scale because of enhanced ocean
124 stratification (Roxy et al. 2016; deCastro et al. 2016). Long-term analysis of oceanographic data
125 already showed that the western Indian Ocean has been warming for more than a century, at a rate
126 faster than any other region of the tropical ocean, which resulted in a major decrease in primary
127 productivity over the last decades due to weakened nutrient mixing and reduction of chlorophyll
128 concentrations over most of the Arabian Sea (Roxy et al. 2014, 2016). Changes in marine
129 ecosystems due to warming could deteriorate the habitat of tuna and modify their distribution and
130 abundance in the Indian Ocean (Dueri et al. 2014).

131

132 In this context, it is essential to assess the magnitude and economic importance of pelagic resources
133 exploited within the NMC for both the foreign markets of canned and sashimi tuna and the
134 livelihoods of coastal communities that are directly dependent on the region's natural marine and
135 coastal assets. The overarching objective of the present study is to review the available knowledge
136 on tuna biology, ecology and fisheries in the NMC to describe the specific features of this region

137 and its importance with regards to the whole Indian Ocean and evaluate the importance of tuna
138 resources on the domestic communities.

139

140 **Materials & Methods**

141 Public-domain data sets of total annual catch, monthly-spatially aggregated catch, effort, and size
142 collated from the IOTC Secretariat were available from the IOTC website (www.iotc.org) and used
143 to characterize the spatio-temporal patterns of tuna fisheries in the NMC area (Fig. 1). Here, we
144 follow the definitions of fisheries employed by the IOTC and use indifferently coastal and artisanal
145 for any fishing vessel less than 24 m that operates within its national Exclusive Economic Zone
146 (EEZ). No detailed information is available from the IOTC about the number of artisanal vessels as
147 the IOTC registry of fishing vessels only includes vessels that are larger than 24 m in length overall
148 and vessels less than 24 m that operate in waters outside the economic exclusive zone of the flag
149 state and that are authorized to fish for tuna and tuna-like species within the IOTC area of
150 competence. Data reported by the national fisheries of Comoros, Madagascar, Mayotte,
151 Mozambique, and Tanzania are not geo-referenced, with the exception of data from Mozambican
152 sport fisheries in 2016. Annual catch reported to the IOTC by these countries was assumed to
153 originate from their national waters since they essentially have coastal fleets operating within their
154 respective EEZ all year round (Geehan and Fiorellato 2017). The total tuna catch of coastal fisheries
155 within the NMC was computed by assuming that the catch of each country was evenly distributed
156 within their respective EEZ, i.e. the catch was weighted by the proportion of each EEZ within the
157 NMC boundaries (Fig. 1). Mayotte and Comoros are fully included in the NMC and the proportions
158 of EEZ within the NMC area are 20%, 32%, and 44% for Madagascar, Mozambique, and Tanzania,
159 respectively (Table 1). Overall, the national waters of Madagascar represent 33% of the NMC,
160 followed by Mozambique (24%) and Comoros (21%) while Tanzania and Mayotte only represent
161 14% and 8% of the area, respectively (Table 1). Quantitative information on recreational sport

162 fisheries is very scarce within the NMC area while these fisheries target oceanic pelagic species
163 such as tunas and billfishes (Pepperell et al. 2017). Also, no information is currently available from
164 non-commercial small-scale fishing that is mainly conducted for subsistence within this region.

165

166 Data reported by high seas fishing fleets have a spatial resolution of 1° and 5° grids for purse
167 seiners and longliners, respectively. Time-area catches were first raised to the total catch to account
168 for some gaps in reporting and then allocated to the NMC proportionally to the area of each grid
169 cell within the NMC area¹. Uncertainty on catch was estimated through lower and higher bounds
170 where the lower bound excludes all the catch reported within a cell grid that includes a part of area
171 outside the NMC while the higher bound includes it. Official catch statistics available from the
172 IOTC were considered to constitute the best available information for both coastal and high seas
173 fisheries occurring in the NMC. It should be noted, however, that generally these values do not
174 include figures for tuna discarded at sea (Martin et al. 2016). Moreover, under- and misreporting
175 issues have been identified, particularly in artisanal fisheries in which the species composition is not
176 corrected through port sampling despite some systematic bias due to anatomical similarity between
177 juveniles of yellowfin and bigeye tunas (Fiorellato et al. 2018).

178

179 Time series of economic data for tuna fisheries are scattered, difficult to access, and generally not
180 available across fisheries (Galland et al. 2016). A preliminary estimate of the total annual value of
181 the tuna catch from foreign fleets operating within the NMC was obtained based on the monthly
182 average prices of purse-seine frozen tuna imported in Thailand (<http://www.customs.go.th>) and
183 longline frozen tuna imported in Japan (L Campling, *pers. comm.*). This value overestimates the
184 value paid to the fishermen as it includes additional costs of international freight and tax fees (i.e.
185 Cost-Insurance-Freight) as compared to Free On Board prices which were not available for the
186 present study. Also, an increasing, but still minor, part of the purse seine catch is now destined to

8 ¹ The processing steps and resulting data set are fully described here: <https://doi.org/10.5281/zenodo.1164128>.

187 higher-value tuna products such as loins and steaks with the development of deep-freezing storage
188 onboard several purse seiners in recent years. The part of the catch as well as price information for
189 these products remain confidential for competitive reasons. For these reasons and due to the
190 uncertainties associated with estimates of catch from IOTC spatially-aggregated data, in particular
191 for longline, estimates of catch value should be considered with great caution. They are mainly used
192 here to provide general figures of the importance of the NMC for high seas fisheries.

193

194 Information on stock delineation, movements, growth, reproduction, and trophic ecology of Indian
195 Ocean tropical tunas was retrieved from the literature, including peer-review articles and reports of
196 IOTC working groups and Scientific Committees. Growth, maturity and natural mortality at age
197 used in stock assessment models for skipjack, bigeye, and yellowfin were available from the IOTC
198 Secretariat (Langley 2015, 2016a, b; Fu and Fiorellato 2017). Movements between large areas are
199 estimated as part of the assessments of the status of yellowfin and bigeye while the current
200 configuration of the skipjack stock assessment model does not include any spatial stratification (Fu
201 and Fiorellato 2017). In addition, the apparent horizontal movements and daily growth rates of the
202 three species tagged within the NMC were analysed from the mark-recapture data set collected
203 throughout the Indian Ocean Tuna Tagging Programme (IOTTP) (Supplementary Online Materials).

204

205 **Setting the oceanographic scene**

206 The Mozambique Channel plays a major role in the circulation of the Indian Ocean through the
207 meridional flow of water from the tropical to the sub-tropical regions in the southern Indian Ocean
208 (Ganachaud et al. 2000; Schott et al. 2009). The north of Madagascar is a peculiar oceanographic
209 area where the Indian Ocean cross-equatorial flow supplies the coastal upwelling regimes off
210 Somalia and Arabia at 5-20°N during June-September and open ocean upwelling at 3-12°S through
211 subsurface northward water flow (i.e. East African Coastal Current), while the Northeast

212 Madagascar Current originating from the South Equatorial Current supplies water for the
213 Mozambique Channel flow (Schott et al. 2009). The NMC has been shown to be characterized by a
214 large anticyclonic gyre within the Comoros basin and a variable current flowing south-eastward in
215 the central part of the Mozambique Channel (Donguy and Piton 1991; Schouten et al. 2005).

216

217 In the mid-1990s, the advent of satellite altimetry revealed that the ocean circulation in the NMC is
218 predominated by Rossby wave forcing which results in the annual occurrence of several large
219 eddies of diameter 300-350 km that propagate southward through the Channel (de Ruijter et al.
220 2002; Schouten et al. 2003). Recent analysis of the mesoscale activity within the Comoros Basin
221 combining satellite altimetry data with a high-resolution ocean circulation model confirmed that the
222 anticyclonic eddies are mainly generated west of the northern tip of Madagascar due to barotropic
223 instabilities (Collins et al. 2014). Most of these anticyclonic eddies propagate west across the
224 basin in about 1 month and move south into the Mozambique Channel about 3 months later (Fig. 2).
225 Some cyclonic eddies likely generated from baroclinic instability are also generated within the
226 Comoros Basin, mainly along the Northwest coast of Madagascar (Collins et al. 2014). Mesoscale
227 and sub-mesoscale oceanographic features have been shown to result in enrichment processes
228 through localized upwelling of deeper nutrient-rich waters as well as entrainment of high Chl-a
229 concentration coastal waters by the eddies in their southward progression (Tew-Kai and Marsac
230 2009; Roberts et al. 2014). In addition, eddies rotation as well as eddy-eddy interactions were found
231 to affect both the occurrence and pattern of aggregation of micronekton (Sabarros et al. 2009;
232 Béhagle et al. 2014). Such mechanisms of exchange between the shelf and open water have been
233 suggested to support the production of micronekton organisms, i.e. small fish, cephalopods, and
234 crustaceans which are the main prey of tuna (Roger 1994; Ménard et al. 2014) and other top
235 predators such as seabirds (Weimerskirch et al. 2004), whale sharks (Sequeira et al. 2012), and
236 cetaceans (Laran et al. 2017). The seasonal NMC productivity appears strongly dependent on

237 mesoscale activity which has been shown to intensify during the 1990s-2000s and to be affected by
238 large-scale Indian Ocean variability (Palastanga et al. 2006; Backeberg et al. 2012).

239

240 **The fisheries**

241 National coastal fisheries

242 Statistical data available at IOTC indicate that the artisanal fisheries of Comoros, Mayotte,
243 Madagascar, Mozambique, and Tanzania annually caught about 20000 mt of tuna and tuna-like
244 species within the NMC during 2012-2016. These fisheries are confined to nearshore coastal areas
245 and comprised of thousands of small motorized and non-motorized boats (<15 m) that use a large
246 diversity of fishing gears, including trolling, hand lines, longlines, small purse seine, and manually
247 handled small-scale drift gillnets (De Young 2006; Mutombene et al. 2017; Tohir 2017). Projects of
248 deployments of anchored Fish Aggregating Devices (FADs) have been conducted throughout the
249 1980s in the five countries bordering the NMC to support the development of artisanal fisheries
250 (Venkatasami 1990). Within Comorian and Mayotte waters, a few dozen of FADs have been
251 moored and maintained since the late 1980s at a distance of 2-5 nm from the shore where they
252 attract tuna and other pelagic fishes that are generally fished with hooks and lines by motorized
253 boats (Doherty et al. 2015; Soilihi 2017). The maintenance of anchored FADs experimentally
254 deployed in Madagascar, Mozambique and Tanzania have been less successful due to their quick
255 loss and absence of maintenance, and their overall contribution to the artisanal catch might be
256 negligible in these countries (Richmond and Mohamed 2006; Cofrepêche 2013).

257

258 Overall, data reported to the IOTC for the NMC artisanal fisheries are considered to be incomplete
259 and highly uncertain in absence of proper monitoring systems (Fiorellato et al. 2018). In the case of
260 Madagascar for instance, artisanal catches are not provided to the Secretariat and assumed constant

261 from one year to the next. Total catch estimates for these fisheries suggest an increasing trend from
262 the 1970s to the mid-1990s followed by a decline until the late 2000s (Fig. 3). Total tuna catch
263 might have sharply increased in recent years due to a major increase in the skipjack catch by
264 Comorian domestic fisheries although the reasons for this remain unclear and might be due to the
265 recent change in the data management system (Toihir 2017). Over the last decade, Comoros
266 accounted for 46% of the total artisanal catch reported within the NMC, followed by Tanzania
267 (~28%) and Madagascar (17%) while Mayotte and Mozambique would have represented together
268 less than 10% of the total catch. The small contribution of Mozambique to the tuna and tuna-like
269 catch in the NMC seems mainly explained by the low targeting of tuna by most Mozambican
270 coastal fisheries (Moreno 2013; Mutombene et al. 2017).

271

272 Tropical tunas account for about 50% of the annual reported artisanal catch within the NMC, i.e.
273 10000 mt during 2012-2016, with skipack and yellowfin being equally represented and bigeye
274 almost absent from the catch. The remaining of the artisanal catch during 2012-2016 was composed
275 of sharks reported as an aggregate category (21%), Spanish mackerels (13%), neritic tunas (8%),
276 and billfishes (8%) (Fig. 3). In addition to the major uncertainties on the magnitude and
277 composition of the catch, there is a general lack of knowledge on the ex-vessel fish price required
278 for estimating the value of artisanal fisheries. Tuna catches from both commercial and recreational
279 coastal fisheries are sold fresh, essentially consumed locally and contribute substantially to the
280 protein supply to national populations as well as to their economy through a network of suppliers,
281 processors and traders (Moreno 2013; Soilihi 2017).

282

283 Overall, the poor monitoring of the national fisheries within the NMC may result in some
284 substantial under-reporting of the tuna catch of both total amounts and species and size
285 composition. More generally, this under reporting may understate the importance of these resources

286 for the livelihood, welfare, and food security of the NMC coastal populations (Teh et al. 2011; Le
287 Manach et al. 2012; Barnes-Mauthe et al. 2013).

288

289 Foreign high seas fisheries

290 Foreign high seas fishing vessels have operated within the Mozambique Channel since the
291 expansion of the Japanese longline fishery across the Indian ocean in the mid-1950s (Geehan et al.
292 2016). Following the adoption of UNCLOS, the coastal States of the NMC established a 200-nm
293 EEZ and licensing systems were developed to grant access to foreign vessels to the national waters
294 of Comoros, Mozambique, Mayotte (France), Tanzania, and Madagascar (Tahindro 2004). Over the
295 last six decades, longline fisheries within the NMC showed a high interannual variability (Fig. 4a)
296 which may be related to several factors such as fishing access and effort allocation, as well as
297 variation in environmental conditions and tuna availability. A maximum of about 14000 mt of
298 tropical tuna was annually caught in the late 1960s while no catch was observed in some years
299 during 1955-2016 (Fig. 4a). It is noteworthy that tropical tuna represented on average 60% of the
300 total longline catch, which also included albacore tuna (*Thunnus alalunga*), billfishes, and sharks.
301 Yellowfin represented the bulk of the longline catch but showed a decreasing trend over time,
302 representing more than 80% of the tropical tuna catch in the 1950s and less than 50% in recent
303 years. Concurrently, the relative importance of bigeye in the tropical tuna catch increased over time,
304 from less than 20% prior to the 1970s to about 50% in recent years. The increased contribution of
305 bigeye in longline catch over time is mainly explained by the increased targeting of this species in
306 relation with the development and global expansion of deep longline from the early 1970s (Miyake
307 et al. 2010). Conducting longline operations at a range of 250-300 m and deeper was made possible
308 by increasing the number of branchlines between floats (Ward and Hindmarsh 2007).

309

310 During 2012-2016, longliners from Chinese Taipei, China, Korea, Japan, and Seychelles annually
311 caught about 2500 mt of large yellowfin and bigeye tuna within the NMC, mainly during
312 November-March (Fig. 5). This catch might be under-reported because of illegal fishing by some
313 longliners as the national systems of monitoring, control, and surveillance are poorly operational
314 (Le Manach et al. 2012). Overall, the NMC is a seasonally important fishing ground for the Indian
315 Ocean longline fishery, accounting for about 8% of the tropical tuna longline catch over the last
316 decade, and more than 20% in 2015. Tuna caught and retained by high seas longliners is frozen
317 onboard the vessels at about -40°C or lower and exported to the Japanese high-value sashimi market
318 (Miyake et al. 2010). Estimates of total annual value of bigeye and yellowfin based on Japanese
319 import prices and average catch over the last decade varied between a minimum of about 5 million
320 USD in 2011 and a maximum of >80 million USD in 2007, with an annual average value >54
321 million USD. It is noteworthy that the uncertainty on longline catch is high due to the coarse level
322 of the public-domain data available at IOTC, resulting in large uncertainties associated with the
323 catch and associated value (Fig. 3a).

324

325 The NMC is also a major seasonal fishing ground for purse seine fishing since the mid-1980s and
326 the EU bilateral Fisheries Partnership Agreements (FPA) were developed to access the national
327 waters of Madagascar, Comoros, and Mozambique. It is noteworthy that the protocols for
328 Mozambique, Comoros, and Madagascar expired in January 2015, December 2016, and December
329 2018, respectively, and have not been renewed in 2019. For Tanzania, private agreements have been
330 made with purse seine fishing companies although this information is not publicly available. The
331 FPA protocols set out the period, number of vessels by gear type that can access the national waters
332 of each country, the fishing opportunities, and the financial contribution provided by the EU.
333 During the most recent period of bilateral agreements, the annual contribution of the EU tuna
334 agreements was 980000 Euros for Mozambique during 2012-2015, 600000 Euros for Comoros

335 during 2014-2016 and about 1.5 million Euros for Madagascar during 2015-2018 (Table 3). About
336 half of the total amount was devoted to the support of the national fisheries sectors, e.g.
337 development of capacity for the monitoring, control, and surveillance of fishing activities. Over the
338 last decade, annual purse seine catch varied around 27000 mt, with a minimum of about 2000 mt in
339 2014 and more than 40000 mt in 2009 (Fig. 4b). This illustrates the massive variations in tuna
340 availability in the region which may stem from a combination of variability in environmental
341 conditions, fishing access and catchability. The seasonality of high seas fisheries within the NMC
342 described by the average monthly catch of tropical tuna during the period 2007-2016 showed that
343 the purse seine fleet essentially operates within the NMC during the inter-monsoon period of
344 March-April (Fig. 5).

345

346 Tuna catch associated with drifting floating objects represented more than 80% of the purse seine
347 catch over the decade 2007-2016. Tuna caught with purse seine within the NMC are generally
348 small. The median size of skipjack, yellowfin, and bigeye caught in association with floating
349 objects was 47 cm (2.3 kg), 56 cm (3.8 kg) and 54 cm (3.7 kg), respectively. Interestingly, the
350 Mozambique Channel is a peculiar area where many logs discharged from the rivers of the coastal
351 countries drift in the surface waters and aggregate tunas. During 2010-2013, these natural objects
352 represented about 1/3 of the floating objects used by the purse seine fishery while the remaining
353 objects were artificial bamboo rafts deployed at sea (Maufroy et al. 2017). Over the last decade,
354 skipjack represented about 2/3 of the catch and yellowfin less than 30%, with bigeye composing the
355 rest. Compared to other fishing grounds of the western Indian Ocean, the NMC is described by a
356 higher proportion of skipjack and smaller proportion of yellowfin in the purse seine catch on
357 floating objects. During 2007-2016, the yellowfin proportion increased but less than in the other
358 areas. Within the NMC, the mean annual proportion of yellowfin in purse seine catch on floating

359 objects increased to about 34% during 2012-2015 while it was more than 40% in the rest of the
360 western Indian Ocean during the same period.

361

362 Using Bangkok import prices as a proxy, the total annual value of the purse seine catch within the
363 NMC during the last decade was estimated to vary around 40 million USD, between a minimum of
364 less than 3 million USD in 2014 and a maximum of about 60 million USD in 2012-2013.

365

366 Synthesis

367 Despite their uncertainty, official fisheries statistics indicate that >30000 mt of tropical tuna were
368 annually caught within the NMC in recent years, with about one third of this catch being taken by
369 national coastal fisheries for local consumption, while the rest was harvested by foreign high seas
370 fleets to mainly supply the low value, high volume, cannery-grade markets of the EU (~200000 mt
371 y⁻¹ caught with purse seine) and the high value, low volume, sashimi-grade market of Japan (~2,500
372 mt y⁻¹ caught with longline). Based on available tuna prices, the total tuna catch from the high seas
373 fisheries would reach an annual value of about 100 million USD over the last decade, although
374 large uncertainties surround this estimate due to the aggregated dimension of IOTC public-domain
375 data. The magnitude of annual catch appears to be highly variable due to tuna availability affected
376 by both environmental variability and accessibility, supporting the interest of multi-annual
377 agreements with minimum reference catch volumes to ensure stable incomes to the countries, as
378 well as additional interest in good years. With the exception of Mayotte, the coastal countries
379 bordering the NMC, namely Comoros, Madagascar, Mozambique, and Tanzania, currently lack
380 proper monitoring and compliance systems for both their coastal fisheries and the high seas foreign
381 fleets accessing their national waters. This strongly affects the data provided to IOTC for tuna
382 fisheries management (Fiorellato et al. 2018) but also the ability of the countries to negotiate fishing
383 agreements in the area (Gagern and van den Bergh 2013).

385 Biology and ecology of Indian Ocean tropical tunas

386 Population structure

387 The IOTC currently considers that skipjack, yellowfin, and bigeye consist of single panmictic
388 spawning populations at the scale of the Indian Ocean. Some studies using classical genetic markers
389 (i.e. mitochondrial DNA and DNA microsatellites) suggested that the three species might display a
390 high degree of differentiation at small geographic scales (Dammannagoda et al. 2008, 2011;
391 Menezes et al. 2012; Kunal et al. 2013; Suman et al. 2013). These results however appear to be
392 inconsistent with the lower degree of differentiation observed at much broader scales (Ely et al.
393 2005; Pecoraro et al. 2018) and the long-distance movements observed from mark-recapture data
394 collected throughout the IOTTP (section Movements & Migrations). The identification of apparent
395 fine-scale isolated populations of tuna might be explained by the small number of molecular
396 markers used and their limited resolution to deal with the high migration rates and large population
397 sizes that characterize tuna populations. Alternative approaches based on more powerful genomic
398 approaches that rely on the advent of Next Generation Sequencing (Davey et al. 2011) technology
399 have been recently advocated as a promising tool to separate neutral evolutionary processes (i.e.,
400 genetic drift) from those influenced by selection (i.e., involved in adaptive divergence) in high
401 gene-flow species such as tunas (Kolody et al. 2013; Grewe et al. 2015; Pecoraro et al. 2016).
402 Based on about 1000 co-dominant single nucleotide polymorphism markers identified with a Next
403 Generation Sequencing method, Pecoraro et al. (2018) did not detect any population structure in
404 yellowfin sampled in different locations of the western Indian Ocean. Overall, information currently
405 available from genetic studies supports the assumption that tropical tunas occurring within the
406 NMC belong to single species-specific stocks that are well mixed across the western Indian Ocean.

408 Movement & migration

409 Skipjack, yellowfin, and bigeye tunas are highly mobile species that occupy vast pelagic habitats
410 extending across entire ocean basins and make extensive migrations (Block et al. 2011; Schaefer et
411 al. 2015). These species swim quickly and continuously, day and night, and are characterized by
412 high swimming performance supported by several physiological and morphological adaptations,
413 including extended pectoral fins providing hydrodynamic lift, high metabolic capacity, and presence
414 of a gas bladder in yellowfin and bigeye (Magnuson 1978; Dewar and Graham 1994). Results from
415 experiments in the wild and in captivity have shown that tropical tunas can swim at sustained
416 speeds of 4-6 knots and burst speeds up to 13-14 knots (Yuen 1966; Magnuson 1973). A model of
417 swimming speeds for maintaining hydrostatic equilibrium for tropical tunas of 50 cm length
418 accounting for lifting area gives speeds of about 70, 50 and 35 cm s⁻¹ for skipjack, yellowfin and
419 bigeye, respectively (Magnuson 1973). The model also shows that yellowfin and bigeye at larger
420 sizes can swim at slower speeds than their smaller counterparts to counter their weight in water as
421 their lifting areas increase more quickly than their weight (Magnuson 1973).

422

423 At large scales, information collected from mark-recapture studies in the Pacific, Atlantic, and
424 Indian oceans over the last decades indicates average monthly distances travelled of 600-950 nm
425 with major differences between species and oceanic regions (Fonteneau and Hallier 2015). In the
426 Indian Ocean, more than 160000 tropical tunas were tagged throughout the IOTTP operations
427 conducted during 2005-2007, among which 34000 were tagged within the NMC (Murua et al.
428 2015). Although most tags were recovered with purse seine in the Somali basin due to the spatio-
429 temporal dynamics of the fishery (Kaplan et al. 2014; Davies et al. 2014), observations of all
430 recovery positions show large-scale movements across the Indian Ocean (Fig. 6). The main tagging
431 area along the coast of Tanzania was described as a 'tuna-hub' following the quick movements of
432 the tunas outside the area and the general extent of the dispersal (Hallier and Fonteneau 2015).

433 Tropical tunas were found to travel distances within one month that exceeded the radius of the
434 NMC area of about 350 nm. About 2100 yellowfin, 1600 skipjack, and 900 bigeye tagged within
435 the NMC were recovered with different gears in both artisanal (hand line, gillnet, troll line) and
436 industrial (purse seine, longline) fisheries during 2005-2013. The apparent distance travelled
437 between tagging and recovery positions for these fish suggests a quick dispersal from the tagging
438 area after release, with median distances travelled >1000 nm after 5 months at sea (Fig. 7).
439 Modelling the distance travelled as a function of species, average length between tagging and
440 recovery (L_F), time at liberty, and month of tagging confirmed that the distance quickly increased
441 with days at sea and was >430 nm after 1 month for the three tuna species (Supplementary Online
442 Materials; Fig. S1). Results also showed that the distance travelled varies with species and size. The
443 best model included a linear effect for length and an interaction between species and length,
444 explaining 38.3% of the total variance (Supplementary Online Materials; Table S2). Bigeye was
445 found to travel significantly less than skipjack and yellowfin. Model predictions for a tuna tagged in
446 May and of size 56.9 cm L_F (i.e. average fork length observed in the data set of mark-recapture)
447 indicate that a bigeye would have travelled 608 ± 43 nm, a skipjack 791 ± 34 nm, and a yellowfin
448 828 ± 28 nm after 60 days at sea (Supplementary Online Materials; Fig. S1).

449
450 Recent results from pop-up satellite tags deployed on adult tunas on the east coast of Madagascar
451 and in the vicinity of Saya-de-Malha Bank and Reunion Island also showed more extensive
452 displacements in yellowfin than bigeye, with daily distances travelled observed for some
453 individuals larger than 30 nm (Sabarros et al. 2017). Surprisingly, larger bigeye and yellowfin were
454 found to travel less than their smaller counterparts in the IOTTP data set while the distance travelled
455 increased with size in skipjack (Supplementary Online Materials; Fig. S2). This may be explained
456 by the hydrostatic equilibrium requirement of continuous swimming whereby larger yellowfin and
457 bigeye (>50 cm) can have slower swimming speeds thanks to the extensive development of their

458 lifting area and gas bladder while the swimming speed required to maintain hydrostatic equilibrium
459 in skipjack continuously increases with size (Magnuson 1973).

460

461 A full mixing of the tagged fish with the untagged population is necessary to ensure that tagged
462 individuals are equally vulnerable to recapture and might result in bias in tag-based abundance
463 estimates if the assumption is not met (Hoenig et al. 1998). Despite observations of large active
464 displacements, analyses of tuna tag dynamics conducted at the scale of the ocean basin also
465 revealed some evidence for incomplete mixing of the tags within each population following release
466 (Langley and Million 2012; Kolody and Hoyle 2013). Consequently, tags with a duration at sea of
467 less than 9, 12, and 6-12 months for yellowfin, bigeye, and skipjack respectively, were removed
468 from the most recent stock assessment models to allow for a sufficiently good mixing of the tags
469 within the large areas used in the models (Langley 2015, 2016a; Fu and Fiorellato 2017). Within the
470 NMC, a few tunas tagged ($n = 16$) were found to remain within the area after 1 month, indicating
471 some potential but limited residency. The reasons for some tuna restricted displacements within the
472 NMC are unknown and could be addressed in the future by collecting information on both the
473 environment and the physiology of fish with archival tags equipped with sensors measuring internal
474 features such as temperature, pH, and fat contents (Whitlock et al. 2015).

475

476 Information available from the few pop-up tags deployed in the western Indian Ocean illustrates
477 some site fidelity, with some tunas showing very limited movements for periods >50 days (Sabarros
478 et al. 2017). Based on the IOTTP data set, current assessment models for bigeye and yellowfin
479 estimate seasonal, constant, stage-dependent movements between areas assumed to characterize
480 different oceanographic features and the spatio-temporal patterns of the fisheries. Estimates of
481 population parameters derived through the assessments of the status of yellowfin and bigeye
482 indicate large-scale movements between areas with quarterly displacements inside and outside the

483 area comprising the Mozambique Channel, although there is some large uncertainty associated with
484 these results (Langley 2015, 2016a). Although some movements across the western Indian Ocean
485 are expected for skipjack (see above), the non-availability of spatial abundance indices due to the
486 difficulties of analysing and interpreting catch rates of purse seiners and pole and liners currently
487 prevents considering spatial stratification in the assessment (Fu and Fiorellato 2017). Recent
488 progress in the standardisation of purse seine catch rates and future work focusing on the
489 development of spatial mark-recapture models might provide a better way of including the spatial
490 dimension of tuna demography into scientific advice.

491

492 In addition and despite evidence of massive swimming speeds and active movements, preliminary
493 modelling predictions of bigeye recaptures on a small spatial grid ($2^{\circ} \times 2^{\circ}$ squares) using ocean
494 current flows appeared to yield promising results that could explain the observed retention of tags in
495 the western equatorial area of the Indian Ocean (Langley 2013). This approach makes the strong
496 assumption that the movements of juveniles of bigeye are essentially driven by currents, likely
497 because they are closely associated with floating objects that drift passively in near-surface currents.
498 Preliminary results suggest the major role of ocean circulation in tuna movements along the east
499 African coasts and some passive movements of skipjack and juveniles of yellowfin and bigeye that
500 might occur in association with the floating objects drifting within the fast East African Coastal and
501 Somali Currents towards the north, and Mozambique Channel eddies towards the south. Tuna
502 movements are however a combination of both active and passive components and ecosystem
503 models have recently been developed to better capture the complex dynamics of these movements
504 by linking them to some indices of habitat suitability that depend on water temperature, food
505 availability, oxygen, and light (Dueri and Maury 2010; Dueri et al. 2014).

506

507 Floating objects have been suspected for some time to play a role in the detection of biologically-
508 rich waters in the pelagic realm and could therefore influence tuna movements (Hall 1992). Our
509 understanding of the processes driving schooling and associative behaviours in oceanic fishes
510 remains however limited (Fréon and Dagorn 2000; Castro et al. 2002). Experiments at sea with
511 acoustic tags show that the fusion and fission processes driving the grouping of tropical tunas are
512 highly dynamic in space, depth, and time, resulting in unpredictable times of residency with drifting
513 FADs (Govinden et al. 2010; Schaefer and Fuller 2013; Matsumoto et al. 2014; Lopez et al. 2017).
514 Such fast dynamics of school formation were also observed during the IOTTP tagging operations
515 characterized by a high turn-over rate of tunas joining and leaving the school associated with the
516 pole and liners (Hallier and Fonteneau 2015). At large scales, the massive deployment of dFADs in
517 purse seine fisheries has been suggested to modify the movements of tropical tunas (Hallier and
518 Gaertner 2008; Wang et al. 2014). Although further studies are required to improve our
519 understanding of the relationships between abundance, schooling, and movements in gregarious
520 fish, recent reviews of the mechanisms driving the dynamics of aggregations point out how
521 individual interactions could play a key role in stabilizing tuna populations (Rieucan et al. 2015;
522 Maury 2017).

523

524 Growth

525 Growth is an essential parameter for assessing tuna populations as their reproduction, mortality, and
526 movements are age-dependent (Hampton 2000). Observations of maximum size of the three tropical
527 tunas in the wild illustrate the major differences in life history traits between small-sized skipjack
528 described by a maximum fork length of about 100 cm and maximum round weight of about 30 kg,
529 and larger-sized yellowfin and bigeye that can reach 200 cm (i.e. ~165 kg) and 206 cm (i.e. ~207
530 kg), respectively (Table 2). In the absence of fishing, skipjack could live up to 7 years and the
531 longevity of yellowfin and bigeye would be 9 and 15 years, respectively (Table 2). Tuna growth has

532 been the focus of a large number of studies since the early 1950s (Murua et al. 2017). Overall, the
533 growth of tropical tunas raises several issues that are linked to: (i) the difficulty of sampling large
534 populations distributed in extensive habitats and caught with selective fishing gears, (ii) the high
535 individual variability in growth exacerbated by high genetic variability and habitat extent, (iii) the
536 limited detection of clear annual signals in calcified structures such as otoliths, and (iv) the tracking
537 of population cohorts through modal progression analysis when tropical tunas spawn all year round.
538 Three principal data sources are available for studying the growth of Indian Ocean bigeye, skipjack,
539 and yellowfin tunas. First, a large data set of increased individual fish lengths over known times-at-
540 liberty has been collected as part of the IOTTP (Murua et al. 2015). Second, direct ageing from
541 daily increments deposited in sagittal otoliths was conducted for about 500 tropical tunas collected
542 during the IOTTP (Sardenne et al. 2015). Micro-increments appeared however difficult to read in
543 skipjack and adult bigeye (>100 cm) resulting in uncertainties in the interpretation of otolith micro-
544 structural features (Williams et al. 2013; Sardenne et al. 2015). Third, modal progression in length-
545 frequency distributions obtained from the purse seine fishery catches was used to track the
546 population cohorts over months and provide both mean age and length estimates of yellowfin and
547 bigeye populations during their juvenile phase (Dortel et al. 2012). Gear selectivity might however
548 affect estimates obtained from modal progression through individual size-specific selection (Kolody
549 et al. 2016).

550

551 Integrated parametric growth models developed and fitted to the different growth data sources and
552 accounting for individual variability support a complex growth curve characterized by two stanzas
553 for all three tuna species (Dortel et al. 2015; Eveson et al. 2015). The three tropical tunas have
554 different growth patterns over their lifespan in the Indian Ocean (Fig. 8). Skipjack appear to
555 experience fast growth until 45-50 cm (i.e. 8-13 months old) followed by slower growth in larger
556 fish. This pattern might be linked to a change in energy allocation and trade-off with reproduction

557 investment since the length at which 50% of the females are mature is 40 cm (section Reproduction
558 section for more details). By contrast, the growth curve for yellowfin suggests they experience
559 slower growth as juveniles, followed by rapid growth from around 70 cm (Fig. 8). A similar but less
560 marked pattern is observed for bigeye (Eveson et al. 2015). Ontogenetic changes in physiological
561 and anatomical features combined with habitat expansion that would reduce intra- and inter-specific
562 competition within schools has been put forward to explain the two-stanza growth in yellowfin
563 (Dortel et al. 2015; Maury 2017). Values of the growth parameter estimated in the first phase show
564 the differences in life history traits with skipjack described by faster growth ($K_1 = 1.41 \text{ y}^{-1}$) than
565 yellowfin ($K_1 = 0.21 \text{ y}^{-1}$) and bigeye ($K_1 = 0.06 \text{ y}^{-1}$) tuna (Table 2). In addition, information
566 collected on the sex of tagged yellowfin and bigeye at recovery showed a strong sexual dimorphism
567 in growth for these two species, with old yellowfin males growing about 10 cm larger than females
568 (Eveson et al. 2015).

569

570 For a given size in the range 44-60 cm, skipjack grow much slower than yellowfin and bigeye.
571 Observations of raw individual growth rates derived from tunas tagged within the NMC for similar
572 sizes show median values of $0.66 \pm 0.14 \text{ cm mo}^{-1}$ for skipjack while bigeye and yellowfin
573 display significantly higher median growth rates of $1.55 \pm 0.26 \text{ cm mo}^{-1}$ and $1.29 \pm 0.15 \text{ cm mo}^{-1}$,
574 respectively (Fig. 9). Modelling the mean growth rates with generalized additive models that
575 account for both month of tagging and duration at liberty supports the assumption that juveniles of
576 yellowfin and bigeye grow faster than skipjack of similar sizes in the NMC. The best model
577 explained more than 45% of the variance and showed species-specific differences in growth
578 patterns as indicated by the significant interaction effect between length and species
579 (Supplementary Online Materials; Table S2). Model predictions for tunas tagged within the NMC
580 during the month of May show an increasing trend in growth rate for bigeye over the size range
581 observed between tagging and recovery, i.e. 37-78 cm. Growth rates of juveniles of bigeye increase

582 from about 1 cm mo⁻¹ at 45 cm to >2 cm mo⁻¹ at 60 cm L_F (Supplementary Online Materials; Fig.
583 S3). By contrast, juveniles of yellowfin show a decreasing trend with mean growth rates varying
584 from about 1.4 cm mo⁻¹ at about 45 cm to about 1.1 cm mo⁻¹ at 60 cm L_F (Supplementary Online
585 Materials; Fig. S3). The lower growth rates of skipjack compared to yellowfin and bigeye are also
586 shown, and decrease from about 0.86 cm mo⁻¹ at 45 cm to a minimum of 0.55 cm mo⁻¹ at about 52
587 cm L_F , followed by an increase to about 0.9 cm mo⁻¹ at 60 cm L_F (Supplementary Online Materials;
588 Fig. S3). Overall, information derived from mark-recapture data shows distinct growth patterns
589 between tropical tunas when they occur within the NMC, with bigeye and yellowfin being
590 described by concave up and concave down curves during their juvenile phase, respectively. Also,
591 although growth is assumed to be very fast in their early-juvenile phase (<30 cm), there is currently
592 a lack of information on the growth of tropical tunas in the wild before their recruitment to the
593 fisheries. Information collected on micro-increments deposited in calcified structures such as
594 otoliths would be useful to better understand the dynamics of growth in larvae and early juveniles of
595 tropical tunas which determine the timing of arrival in the purse seine fishery (Campana and
596 Neilson 1985). Finally, the development of full-life cycle models built on physiological and
597 metabolic theoretical grounds appears necessary to establish the mechanistic links between
598 physiology, biology (e.g. growth, reproduction) and environmental conditions (i.e. prey availability
599 and oceanographic parameters) in order to assess the spatio-temporal variability in tuna growth and
600 eventually quantify the role of each biogeographic province such as the NMC in supporting Indian
601 Ocean tuna populations (Dueri and Maury 2010).

602

603 Reproduction

604 Tropical tunas are iteroparous species characterized by indeterminate fecundity, asynchronous
605 oocyte development, protracted spawning periods, and multiple batch spawning (Schaefer 2001;
606 Juan-Jordá et al. 2013). Estimating the reproductive potential of multiple batch spawners requires

607 knowledge of the sex ratio, spawning frequency, i.e. the mean spawning interval between sequential
608 spawning events, and batch fecundity, i.e. the number of eggs produced per spawning (McBride et
609 al. 2015). Obtaining a representative sample of the spawning female population is difficult in the
610 wild as tunas spawn in surface waters principally at night and fish collection can be biased by the
611 selectivity of sampling gears, i.e. timing of fishing, size selection, and water column depth (Itano
612 2000; Schaefer 2001). Spawning frequency can be derived from females containing hydrated
613 oocytes or from females containing postovulatory follicles of known age through ovarian histology
614 (Hunter and Macewicz 1985). Sampling tuna females containing hydrated oocytes is however
615 generally difficult due to the short duration of the hydration process and general lack of operations
616 at night of surface fishing gears (Schaefer 2001). Degenerating postovulatory follicles can be used
617 for estimating spawning frequency as they have been shown to remain up to 24 hours in the ovary
618 after ovulation in tropical tunas (Hunter et al. 1986; McPherson 1991; Schaefer et al. 2005).

619

620 In the Indian Ocean, a large set of information has been collected on spawning period, sex ratio,
621 maturity, and batch fecundity for yellowfin and skipjack tunas since the mid-1970s (Stéquent 1976;
622 Hassani and Stéquent 1991; Stéquent and Ramcharrun 1995, 1996; Stéquent et al. 2001; Zudaire et
623 al. 2013; Grande et al. 2014). By contrast, little information is currently available for bigeye tuna
624 (Zudaire et al. 2016). Knowledge acquired on the reproduction of Indian Ocean tropical tuna is not
625 specific to the NMC although some samples used for analysing the reproductive traits originate
626 from the area (Zudaire et al. 2013, 2016b; Grande et al. 2014). Temporal changes in the gonado-
627 somatic index combined with histological interpretation of preserved ovarian material and variation
628 in steroid hormones show that yellowfin and bigeye have a major peak of spawning along the
629 Seychelles-Chagos thermocline ridge during the months of November-March, i.e. the Northwest
630 monsoon season (Hassani and Stéquent 1991; Stéquent et al. 2001; Zudaire et al. 2013, 2016). A
631 second less-marked peak was observed during the Southeast monsoon in June-August (Zudaire et

632 al. 2013). Histological analysis also indicated that large mature yellowfin females have a longer
633 spawning period than the smaller mature ones (Zudaire et al. 2013). By contrast, skipjack spawn all
634 year round although the reproductive activity may be lower during inter-monsoon periods (Stéquent
635 1976; Stéquent et al. 2001; Grande et al. 2014).

636

637 Tropical tunas are mostly recruited into the purse seine fishery (~30 cm) before they reach their first
638 maturity. The reproductive traits of the 3 species show a marked gradient, from skipjack tuna
639 characterized by early maturation at around 7 months ($L_F \sim 40$ cm) and high relative batch fecundity
640 of about 136 ± 66 eggs g^{-1} body weight, to yellowfin and bigeye described by later maturity at
641 around 2.3 years ($L_F \sim 75$ cm) and 3 years ($L_F \sim 100$ cm), respectively, and lower fecundity at about
642 76 ± 40 eggs g^{-1} and 10 ± 7 eggs g^{-1} , respectively (Table 2). Maximum values of batch fecundity
643 increase with tuna size in the three tropical tunas as shown by the increasing trends in the 75% non-
644 linear quantile regression models between batch fecundity and fish standardized fork length (Fig.
645 10). The increasing maximum levels of fecundity with size appear to be mainly explained by the
646 increasing weight of gonads with fish size (Fig. 11). The high variability in fecundity observed
647 between individuals of similar size indicates that some other factors than size affect the fecundity,
648 and hence the reproductive potential of tropical tunas in the Indian Ocean. The number of eggs
649 released might depend on recently acquired energy since the three species utilize food resources
650 throughout the spawning season (i.e. income breeding strategy). The large variability observed in
651 fecundity might then reflect differences in feeding success prior to and during spawning. In
652 addition, the variability in fecundity between successive batches is poorly known while the potential
653 existence of some fish that may skip spawning due to insufficient energy for initiating oocyte
654 development has been suggested but it is difficult to demonstrate in tropical tunas (Zudaire et al.
655 2013).

656

657 Spawning frequency for the 3 species could not be determined in the Indian Ocean due to the
658 absence of postovulatory follicles in most tunas sampled while data from the Pacific indicate a
659 frequency close to daily, i.e. 1.1-1.2 days in skipjack (Hunter et al. 1986), 1.1-2 days in yellowfin,
660 and 1.4-1.6 in bigeye tuna (McPherson 1991; Schaefer 1996; Itano 2000; Sun et al. 2013). Overall,
661 the reproductive potential of the 3 species remains poorly known due to the absence of better
662 information on spawning frequency and improved understanding of regulation mechanisms in tunas
663 in relation with poor-feeding environment such as skipped spawning, delayed maturation, and fewer
664 spawning events per season or fewer eggs produced per event (McBride et al. 2015).

665

666 Recent studies based on lipid classes and profiles of fatty acids that focused on the mechanisms of
667 energy allocation in yellowfin and skipjack showed the tight linkage between environmental
668 conditions and egg production (Zudaire et al. 2014, 2015; Grande et al. 2016). Skipjack are
669 described by an income breeding strategy, i.e. they use recently acquired food resources to fuel
670 reproduction, taking advantage of nutrients critical for offspring survival that are available at the
671 spawning site (Grande et al. 2016). Female yellowfin also depend on prey availability and quality at
672 the time of spawning although they are able to store part of the energy prior to the reproduction
673 period (Zudaire et al. 2014).

674

675 Tunas aggregate for spawning in surface waters $>24^{\circ}\text{C}$ following periods of courtship behaviour
676 that have been observed for yellowfin held in captivity (Margulies et al. 2007). Experiments showed
677 that mean egg-stage duration is inversely correlated with water temperature and lasts up to a
678 maximum of 28 hours (Margulies et al. 2007). Tuna larvae usually occur in low density patches
679 near the surface, both during day and night. Historical information available from the Atlantic
680 Ocean indicates that larvae of yellowfin and bigeye might migrate to the surface during the day
681 while skipjack larvae are at the surface during the night (Richards and Simmons 1971).

682 Ichthyoplankton surveys conducted around Hawaii during 1985-1986 however showed that
683 *Thunnus* spp. larvae were mostly captured in the neuston at night but rarely in daytime, with
684 skipjack larvae occurring deeper and no clear evidence of diel vertical migration (Boehlert and
685 Mundy 1994).

686

687 Scientific ichthyoplankton surveys conducted as early as the late 1920s in the Indian Ocean
688 indicated the occurrence of skipjack and yellowfin tuna larvae in the Mozambique Channel while
689 very few larvae of bigeye tuna were found throughout the surveys (Jones and Kumaran 1963;
690 Conand and Richards 1982; Beckley and Leis 2000). Skipjack larvae predominated in the NMC and
691 tuna larvae were the most abundant during November-April (Conand and Richards 1982; Beckley
692 and Leis 2000). Although the Mozambique Channel appears to be a relatively poor feeding habitat
693 compared to other areas of the western Indian Ocean such as the Somali basin (Druon et al. 2017),
694 the warm waters (>27°C) of the area combined with mesoscale activity that enhances enrichment
695 through mixing and retention (Tew Kai and Marsac 2010) may constitute optimal environmental
696 conditions for tuna spawning (Reglero et al. 2014). New reproductive studies specifically focusing
697 on samples collected throughout the year within the NMC combined with ichthyoplankton surveys
698 would be essential to fully resolve the role of the area for tuna spawning and stocks recruitment.

699

700 Trophic ecology

701 Tunas are opportunistic predators at the apex of short food chains (Roger 1994). Tunas forage on ca.
702 45 prey families, from various micronekton assemblages composed of crustaceans (mainly the
703 pelagic crab *Charybdis smithii* and the mantis shrimp *Natosquilla investigatoris*), fishes (mainly the
704 cigarfish *Cubiceps pauciradiatus* and *Decapterus* spp) and cephalopods (mainly *Sthenoteuthis*
705 *oualaniensis*) (Potier et al. 2007, 2008a; Jaquemet et al. 2011; Potier et al. 2011; Duffy et al. 2017).
706 The proportion of each prey depends on biological parameters such as vertical behaviour, ontogeny,

707 reproduction, and the seasonal migration across regions described by different oceanographic
708 conditions and prey availability. Dissolved oxygen and temperature are key drivers constraining
709 tuna physiological abilities and vertical behaviour (Graham and Dickson 2004). Bigeye tuna is
710 tolerant to pronounced oxygen and temperature deficiencies, and commonly forages beyond the
711 scattering layer on mesopelagic preys such as myctophids and squid *S. oualaniensis* and
712 *Ornithoteuthis volatilis* (Potier et al. 2008a; Ménard et al. 2014). Yellowfin and skipjack tunas
713 prefer the oxygenated and warmer waters of the epipelagic layer (Graham and Dickson 2004).
714 Yellowfin tuna usually forage in the mixed layer on diverse prey species, including fish, crustaceans
715 and squid in almost equal part (Potier et al. 2004, 2007; Zudaire et al. 2015) while skipjack forage
716 in the surface layers, mainly on crustaceans (Grande 2013). Beyond the inter-specific differences,
717 vertical behaviour changes with ontogeny as tuna diving capacities develop with size (Holland et al.
718 1992). Until ca. 50 cm, tuna's trophic position increases with the ability to feed on bigger preys in
719 the epipelagic layer (Potier et al. 2008a; Sardenne et al. 2016). Afterwards, their trophic position
720 increases only slightly, even for bigeye and yellowfin tunas which feed more extensively on deep
721 prey when they reach 90 and 110 cm, respectively (Ménard et al. 2007; Sardenne et al. 2016).
722 Despite these differences, tropical tunas commonly form mixed chasing schools in the near surface
723 layer and in this context have a similar feeding behaviour when prey diversity is low (Potier et al.
724 2004; Fonteneau et al. 2008). As a result, food competition is strong in the near surface layer
725 between skipjack and juveniles of yellowfin tuna on FADs (Jaquemet et al. 2011; Sardenne et al.
726 2016), as well as between adult yellowfin and bigeye when occurring in free swimming schools
727 (Zudaire et al. 2015), or when tunas are attracted by a prey bloom (Fonteneau et al. 2008).

728

729 Although a direct link between the mesoscale eddies of the Mozambique Channel and tuna diet has
730 not yet been well established (Tew Kai and Marsac 2010; Potier et al. 2014), their trophic position
731 estimated through nitrogen stable isotopes values ($\delta^{15}\text{N}$) is lower than in other regions, about 3‰

732 lower than in the rest of the western Indian Ocean (Ménard et al. 2007; Zudaire et al. 2015;
733 Sardenne et al. 2016). Shorter food chains and lower baseline values linked to the low $\delta^{15}\text{N}$ values
734 of the particulate organic matter in the Mozambique Channel were proposed to explain this
735 difference (Ménard et al. 2007; Kojadinovic et al. 2007; Lorrain et al. 2015). Recently, the
736 relationships between tuna trophic position and environmental conditions were investigated on
737 global and regional scales by adjusting for variability in baseline $\delta^{15}\text{N}$ values using a Model of
738 Ocean Biogeochemistry and Isotopes (MOBI) (Pethybridge et al. 2018). Homogeneous MOBI-
739 derived phytoplankton $\delta^{15}\text{N}$ values were obtained in the Mozambique Channel ($3.6\pm 0.2\text{‰}$) and in
740 the rest of the western Indian Ocean ($3.5\pm 0.3\text{‰}$). Hence, the lower trophic position of tropical tunas
741 in the NMC is most likely related to shorter lengths of food chains in this area compared to the
742 western Indian Ocean, i.e, tuna prey in the NMC would be about one trophic level lower than in
743 other parts of the region. Such short food chains suggest a higher sensitivity of tuna to climate
744 change through variability in baseline composition and abundance in the NMC in a context of
745 marked warming of the Mozambique Channel (Popova et al. 2016). Extended work on the spatio-
746 temporal variations of plankton biomass and stable isotope composition in the western Indian
747 Ocean, especially zooplankton, is essential to clarify tuna foraging and migrating behavior,
748 including its dependency to the NMC.

749

750 There is currently a lack of studies on the trophic ecology of tropical tuna larvae in the western
751 Indian Ocean which have been shown to feed on a diversity of species of microzooplankton (20-
752 200 μm) and to a lesser extent mesozooplankton (0.2-20 mm), mostly appendicularians in the case of
753 skipjack tuna (Young and Davis 1990; Llopiz et al. 2010). Recent surveys conducted in the
754 Mozambique Channel showed how mesoscale features shape the distribution of small copepods,
755 appendicularians, ostracods, and chaetognaths by increasing their abundance in cyclonic eddy-cores
756 and divergence areas between eddies (Huggett 2014; Lebourges-Dhaussy et al. 2014). Such

757 processes of enrichment, concentration, and retention might explain the importance of the NMC as
758 a major spawning area for skipjack, and yellowfin to a lesser extent, consistently with the ocean
759 triad that assumes that eddy motions provide a combination of physical processes particularly
760 favorable for the reproductive habitat of pelagic fishes (Bakun 2006).

761

762 Synthesis

763 Tropical tunas are active, fast swimmers that can perform large directed displacements across the
764 Indian Ocean basin throughout the year and move inside or outside large areas such as the NMC
765 within a few days. A rough scheme of spawning and feeding migrations of tropical tunas in the
766 western Indian Ocean can be hypothesized as follows. From the southwestern monsoon (June-
767 September) to the inter-monsoon (October-November), tropical tunas forage north of the equator,
768 within the seasonal upwelling that develops along the Somali coast and in the north of the
769 Seychelles Plateau. In both areas, they feed extensively on pelagic crabs (Romanov et al. 2009;
770 Grande 2013) and mantis shrimps (Potier et al. 2002; Malone et al. 2011). During the northeast
771 monsoon (December-March), most tunas in spawning activity forage between the Chagos Islands
772 and the south of the Seychelles Plateau, mainly on small fish such as *C. pauciradiatus* which
773 provide rich prey for offspring (Potier et al. 2008b; Grande 2013; Zudaire et al. 2015) and are
774 supported by high copepod biomass (Roger 1994). Skipjack remaining within the Somali region
775 appear to feed mainly on pelagic mollusks and gelatinous organisms (Grande 2013). Finally, during
776 the inter-monsoon (April-May), tunas reach the NMC and adopt a more diverse diet (Grande 2013).
777 The warm waters of the NMC offer particularly favorable feeding, spawning and nursery conditions
778 for skipjack tuna. Some yellowfin individuals are suspected to permanently reside within the NMC
779 (Ménard et al. 2007; Zudaire et al. 2015). Overall, the NMC is a key feeding area for tropical tunas
780 as it sustains their high energetic needs while the ocean productivity decreases at higher latitudes
781 during the spring inter-monsoon (Burkill et al. 1993).

783 The future of NMC tuna fisheries

784 Ocean warming

785 Tuna productivity within the NMC area is highly variable and strongly dependent on large-scale
786 ocean-atmosphere processes that affect the circulation in the Mozambique Channel in a context of
787 alarming warming (Popova et al. 2016). In particular, satellite altimetry data suggested that the
788 intensification of the mesoscale activity observed in the Mozambique Channel during 1993-2009
789 was due to an increase in the South Equatorial Current which was driven by enhanced trade winds
790 over the tropical Indian Ocean (Backeberg et al. 2012). The Mozambique Channel has been
791 identified as a warming hotspot and projections from a high-resolution global ocean model suggest
792 an increase of the mean sea surface temperature by 1-2° by 2050 and by about 4° by 2100 relative
793 to the year 2000 (Popova et al. 2016). The impact of ocean warming on tuna productivity and
794 fisheries within the NMC is extremely difficult to predict as several physical and biological
795 oceanographic processes will be affected in the future and they might modify the composition and
796 dynamics of phytoplankton and propagate up the food web to top-predators. Long-term projections
797 of tuna abundance and distribution at global scale based on environmental niche models and
798 Intergovernmental Panel on Climate Change scenarios suggest that yellowfin and skipjack might
799 become more abundant in tropical areas and in coastal areas by the 2050s (Erauskin Extramiana et
800 al. 2019). Projections from a mechanistic model accounting for both the effects of ocean warming
801 on tuna habitat and biology (i.e. growth, survival and spawning) also predict significant changes in
802 the basin-scale distribution of skipjack resulting from a reduction in habitat suitability in the
803 shallow waters of the Indian Ocean equatorial area (Dueri et al. 2014). Nevertheless, the model does
804 not seem to show any major change within the NMC (Dueri et al. 2014). Predictions of changes in
805 tuna distribution patterns should explicitly consider mesoscale and sub-mesoscale features that are

806 key drivers of tuna occurrence within the NMC (see above). In this context, coupling eddy-
807 resolving ocean models with food web and mechanistic tuna population models in specific ocean
808 regions such as the NMC seems essential to better understand the impacts of future warming on
809 tuna fisheries in the area. This will require in particular to obtain and make accessible fine-scale
810 data sets such as the high-resolution positions of high-seas fishing vessels recently made available
811 by Global Fishing Watch (Kroodsma et al. 2018).

812

813 Access to fishing grounds

814 The future of the NMC tuna fisheries is also dependent on the accessibility to the fishing grounds at
815 a time when there is no ongoing fishing agreement between the EU and the coastal countries and
816 IOTC members are debating about the criteria of catch allocation (IOTC 2019). Following the
817 presidential elections in Madagascar in late 2018, the negotiation process of fisheries access
818 agreements with the EU will likely resume in 2019. The renewal of a fishing agreement between the
819 EU and Comoros might take more time as the country has been identified as non-cooperating third
820 country under the EU's regulation to fight and deter illegal, unreported and unregulated fishing.
821 Finally, the conditions imposed to the EU fishing vessels by Mozambique for accessing the national
822 waters are considered inapplicable by the fishing companies. No EU FPA has ever been developed
823 with Tanzania but some Memoranda of Understanding exist with the purse seine fishing companies
824 and EU vessels might be able to seasonally operate within the Tanzanian EEZ if an agreement is
825 found with the government. Information on fishing agreements between Asian longline fisheries
826 and the NMC coastal countries as well as data on operational costs of high seas fishing fleets would
827 be extremely useful to assess the distribution of benefits and fairness of the agreements. The
828 negotiation of both public and private fishing agreements would likely benefit from improved data
829 collection, increased transparency, and active collaboration between the NMC countries to generate
830 leverage and influence distant water fishing nations.

831

832 **Conclusions**

833 The pelagic zone of the NMC offers a favourable habitat for tunas which seasonally migrate in the
834 area for both feeding and spawning, benefiting from mesoscale-driven enrichment and increased
835 prey abundance. With an annual catch of about 10000 mt in recent years by coastal fisheries, tuna
836 and tuna-like species represent an important component of food security for the low-income
837 countries bordering the NMC, i.e. Madagascar, Mozambique, Comoros, and Tanzania. The NMC is
838 also a major tuna fishing ground for high seas fishing fleets which annually export an average catch
839 of more than 20000 mt of about 100 million USD value to the tuna can and sashimi markets of
840 high-income countries.

841

842 The contribution of tuna caught by the artisanal fisheries to the welfare and economy of the least
843 developed countries bordering the NMC is poorly understood and studied. Acknowledging the lack
844 of data available to properly assess the economic dependence of Coastal States on fishery resources
845 and impacts of fishery resource rents in terms of income, investments and jobs, the IOTC recently
846 recommended a pilot study to (i) evaluate what socio-economic data are collected and available and
847 (ii) propose a suite of socio-economic indicators that would describe the respective CPCs economic
848 and social aspects of fisheries (IOTC Res. 18/09). Such information is essential for the Coastal
849 States as the economic dependence on tuna resources is one of the criteria that is under
850 consideration for tuna catch allocation (IOTC 2019). In data-poor situations, developing and
851 conducting fisher surveys to collect individual-level data on fishing practices, effort, catch, costs,
852 and revenues has been shown to be an efficient approach for assessing the socio-economic
853 importance of small-scale fisheries in the south-west of Madagascar (Barnes-Mauthe et al. 2013).
854 Some fisher surveys have been conducted in some NMC countries but they remain limited and do
855 not include any extrapolation at the national level (Ranaivoson and Ranaivoarison 2013). In the

856 Seychelles where a good fisheries monitoring system is in place, a national satellite account for tuna
857 fisheries has been recently developed and shown to better reflect the contribution of fisheries to the
858 gross domestic product when pre- and post-harvest activities are accounted for (Bistoquet et al.
859 2018). Overall, improving monitoring systems and collecting information on the socio-economic
860 dimension of coastal fisheries and their fisheries-related sectors (e.g. whole sale, transport) through
861 dedicated surveys is crucial to assess the dependence of NMC coastal populations on tuna resources
862 and empower NMC countries to more involvement in the management of tuna stocks with IOTC.

863

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865 **References**

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917 Fig. 10. Relationship between batch fecundity and standardized fish length (fork length divided by
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922 Fig. 11. Relationships between gonad weight (g) and total weight (kg) for Indian Ocean skipjack
923 (SKJ), bigeye (BET), and yellowfin (YFT). Lines indicate 10% (dashed), 50% (solid) and 90%
924 (dotted) non-linear quantile regression models fitted to the data.

925 **TABLES**

926 Table 1. Contribution of the Exclusive Economic Zone (EEZ) of each country to the Northern Mozambique Channel (NMC). Total surface area and
927 area within the NMC are given in km².

EEZ	Area (km ²)	Area within NMC (km ²)	Part within NMC (%)	Contribution (%)
Comoros	164781	164781	100	21
Madagascar	1239905	253493	20	33
Mayotte	63011	63011	100	8
Mozambique	566114	180960	32	24
Tanzania	241445	106997	44	14

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931 Table 2. Summary of the main biological features of Indian Ocean tropical tunas. Observations of maximum size available from IOTC. Growth:
 932 Eveson et al. (2015). Maturity and fecundity: Grande et al. (2014), Zudaire et al. (2013, 2016). Natural mortality: Fu and Fiorellato (2017), Langley et
 933 al. (2015, 2016). † Constant value used in the grid of skipjack assessments (Fu and Fiorellato 2017)

Function	Feature	Parameter	Definition	Notation	Unit	SKJ	YFT	BET
Growth	Lifespan	Maximum length	Maximum fork length observed in the wild	L_{Fmax}	cm	100	200	206
		Maximum weight	Maximum total weight observed in the wild	W_{Tmax}	kg	30	165	207
		Longevity	Maximum age	A_{max}	y	7	9	15
	Growth	Growth rate	Initial growth coefficient of the stanza growth	K_I	y^{-1}	1.41	0.21	0.06
Reproduction	Maturity	Length at maturity	Fork length at which 50% of the females are mature, i.e. ovaries are classified in developing phase following the presence of oocytes in cortical alveolar stage as the most advanced developmental stage	L_{Fmat}	cm	40	75	102
		Weight at maturity	Total weight at which 50% of the females are mature	W_{Tmat}	kg	1.3	8.9	25
		Age at maturity	Age at which 50% of the females are mature	A_{mat}	y	0.6	2.3	3
	Fecundity	Batch fecundity	Average number of oocytes (million) in the stages of hydration, germinal vesicle migration and breakdown in the ovary	F_B	eggs	0.28±0.15	3.22±1.78	0.72±0.56
		Relative batch fecundity	Ratio between batch fecundity and gonad-free weight of the fish	F_{RB}	eggs g^{-1}	136±66	76±40	10±7
Mortality	Natural	Annual rate [†]	Natural mortality rate	M	y^{-1}	0.8 [†]	0.54-1.34	0.25-0.8

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937 Table 3. Summary table of the main characteristics of the past protocols under the Fisheries

938 Partnership Agreement between the European Union and Comoros, Madagascar, and Mozambique.

939 Financial contributions were calculated as an average of the annual payments.

Country	Comoros	Madagascar	Mozambique
Start date	2014-01-01	2015-01-01	2012-02-01
End date	2016-12-30	2018-12-31	2015-01-31
Number of purse seiners	42	43	44
Number of longliners	20	81	45
Annual total contribution (€)	600000	1526875	980000
Annual sectoral support (€)	300000	700000	460000
Annual access right	300000	826875	520000
Reference tonnage (mt)	6000	15750	8000
Shipowners contribution (€/mt)	55	65	35

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943 **FIGURES**

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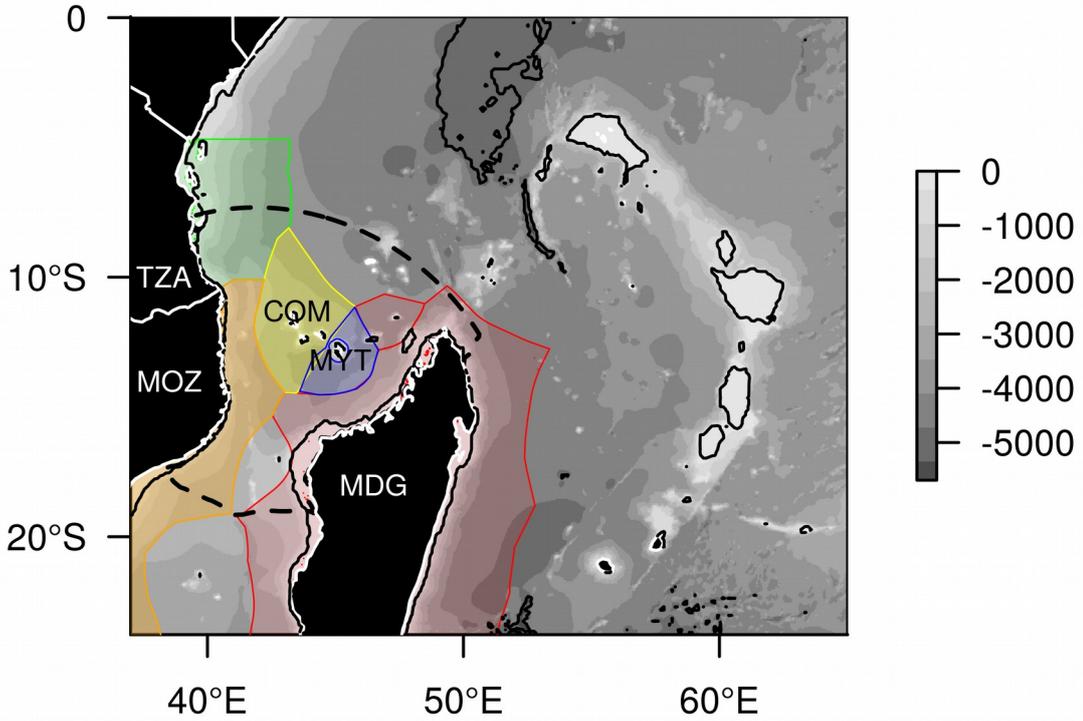


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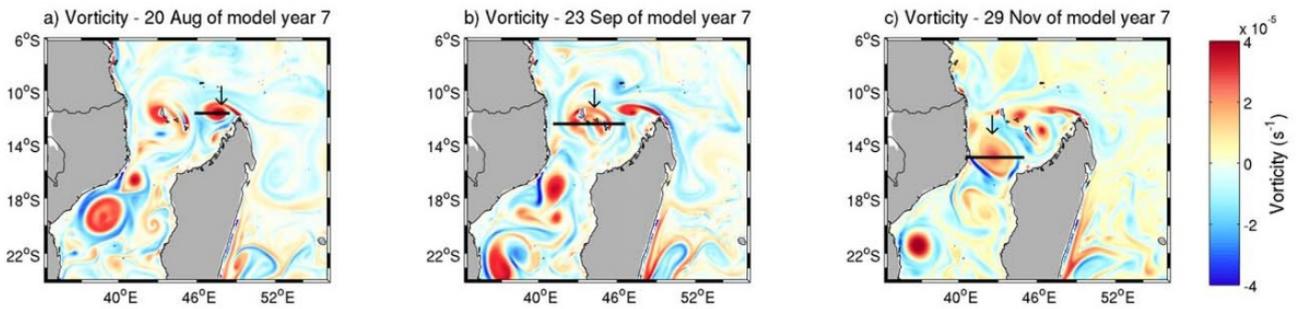


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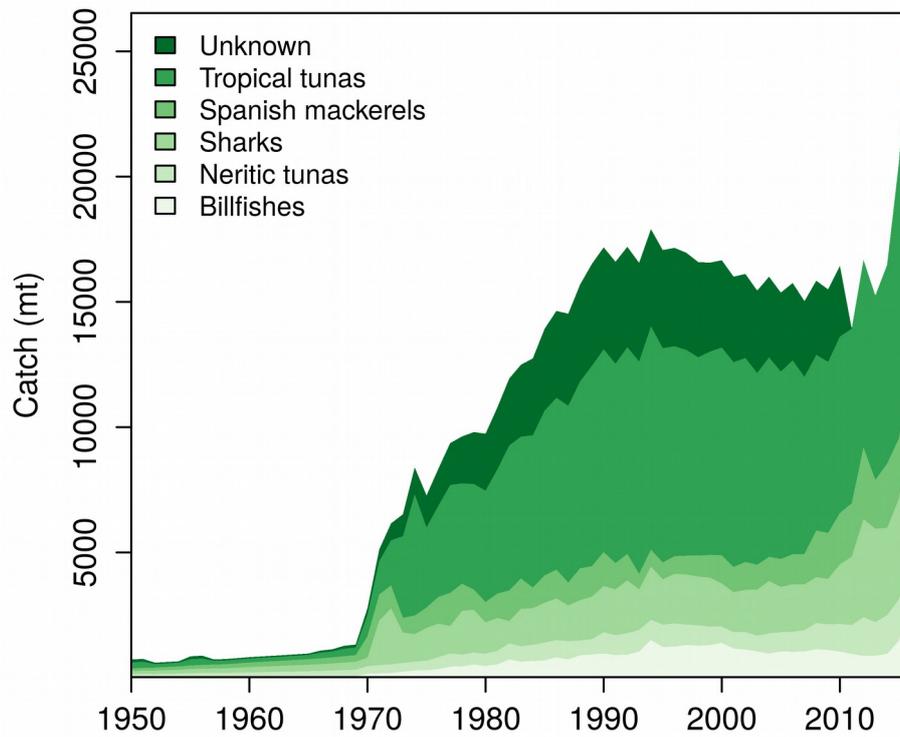


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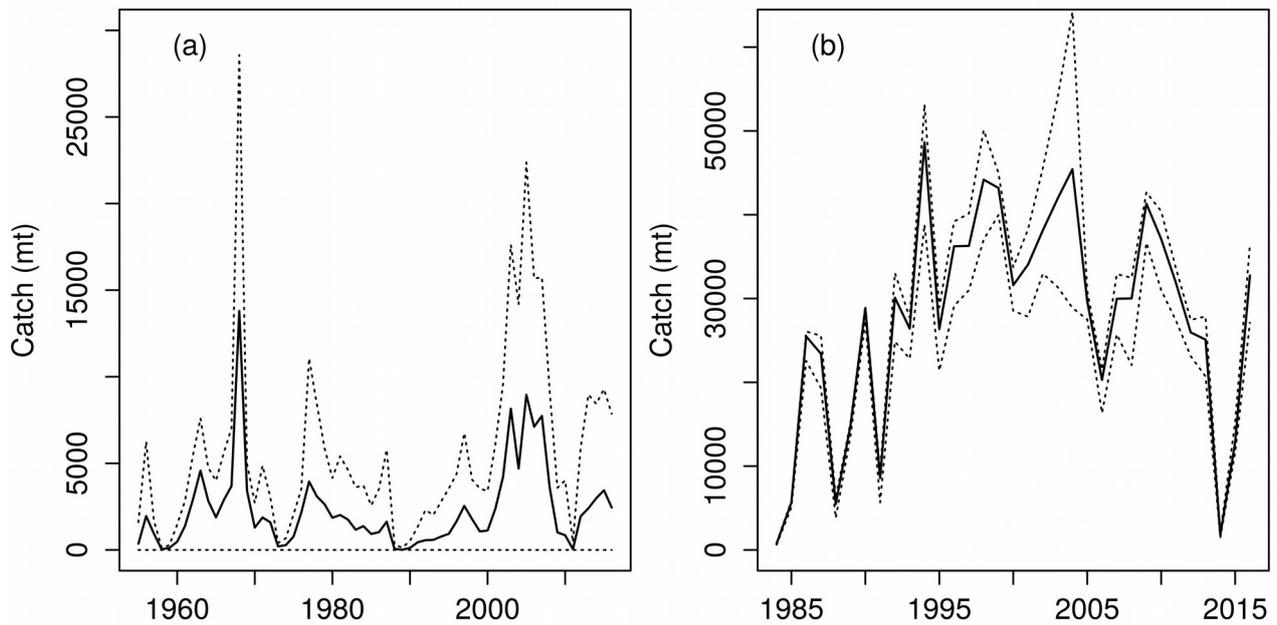


Fig. 4. Annual time series of tropical tuna catch of high seas (a) longliners and (b) purse seiners within the Northern Mozambique Channel (NMC). Solid line indicates estimates based on assumption of evenly distribution of the public-domain gridded catch intersected with NMC area. Dotted lines represents the uncertainty on catch estimated through lower and higher bounds based on assumptions of exclusion and inclusion of all catches intersected by NMC boundaries, respectively.

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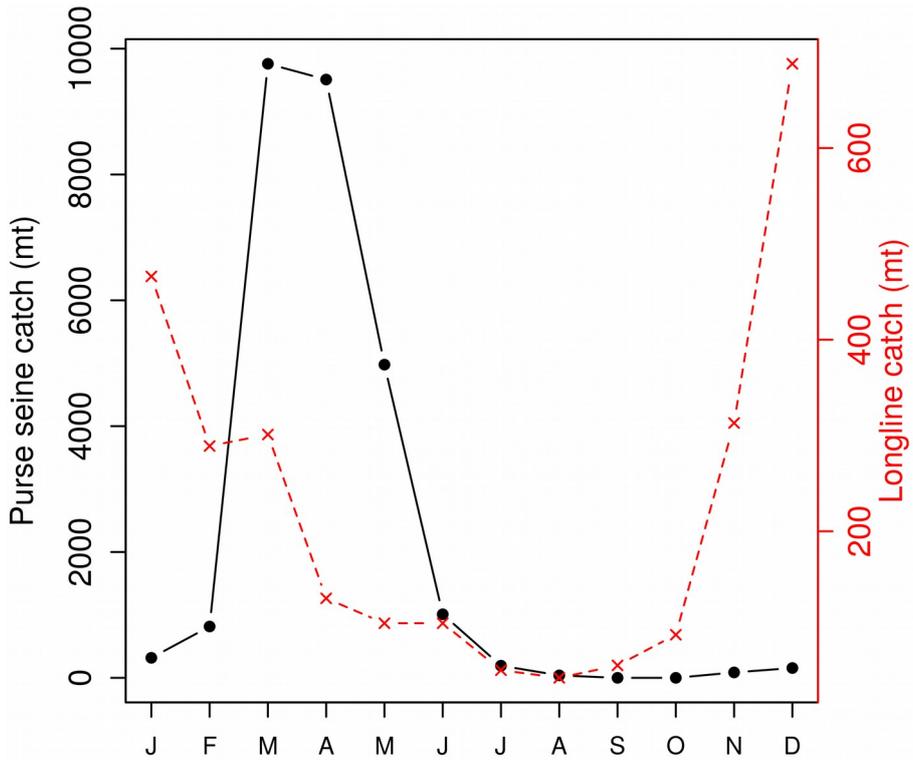


Fig. 5. Mean annual monthly catch (mt) of tropical tunas by high seas purse seiners (black solid line with dots) and longliners (red dashed line with crosses) during 2007-2016.

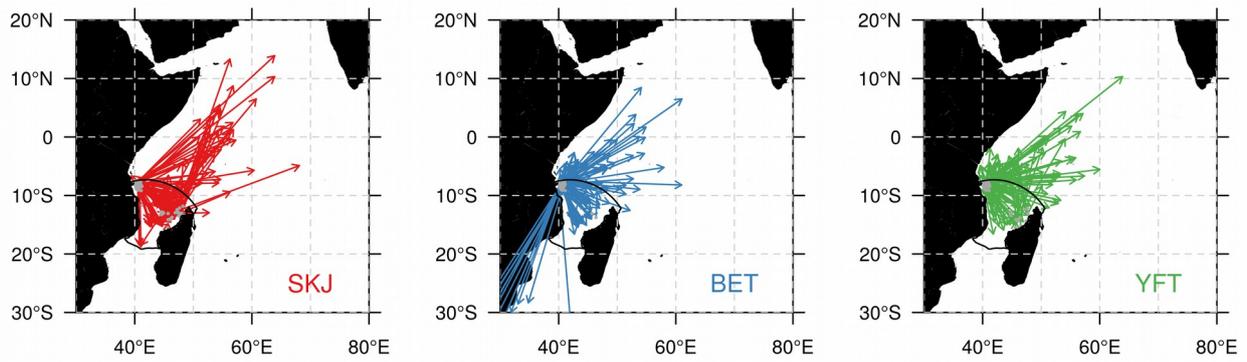


Fig. 6: Linear trajectories between tagging and recovery positions of skipjack (SKJ; $n = 135$), bigeye (BET; $n = 119$), and yellowfin (YFT; $n = 108$) tagged with dart tags within the Northern Mozambique Channel (solid black line). Positions of tagging are indicated with grey open circles. The number of mark-recaptures was sub-sampled for readability.

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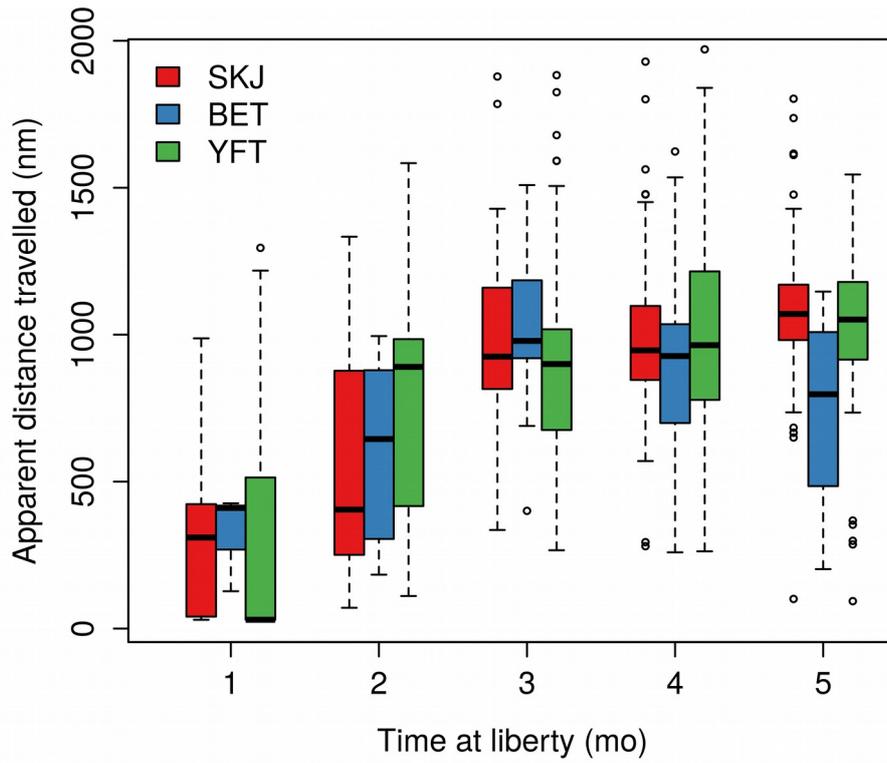
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980 *Fig. 7: Distribution of apparent distance travelled (nm) by month during the*
981 *first 5 months at liberty of tropical tunas tagged with dart tags within the*
982 *Northern Mozambique Channel. SKJ = skipjack; BET = bigeye; YFT =*
983 *yellowfin.*

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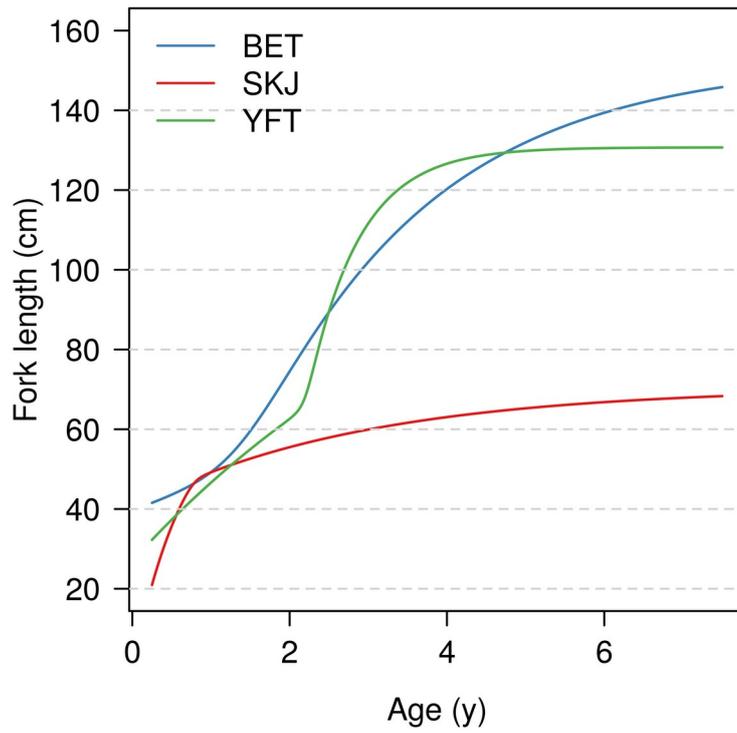


Fig. 8: Mean growth curves in fork length (cm) for bigeye (BET), yellowfin (YFT), and skipjack (SKJ) tuna derived from integrated statistical models (Eveson et al. 2015).

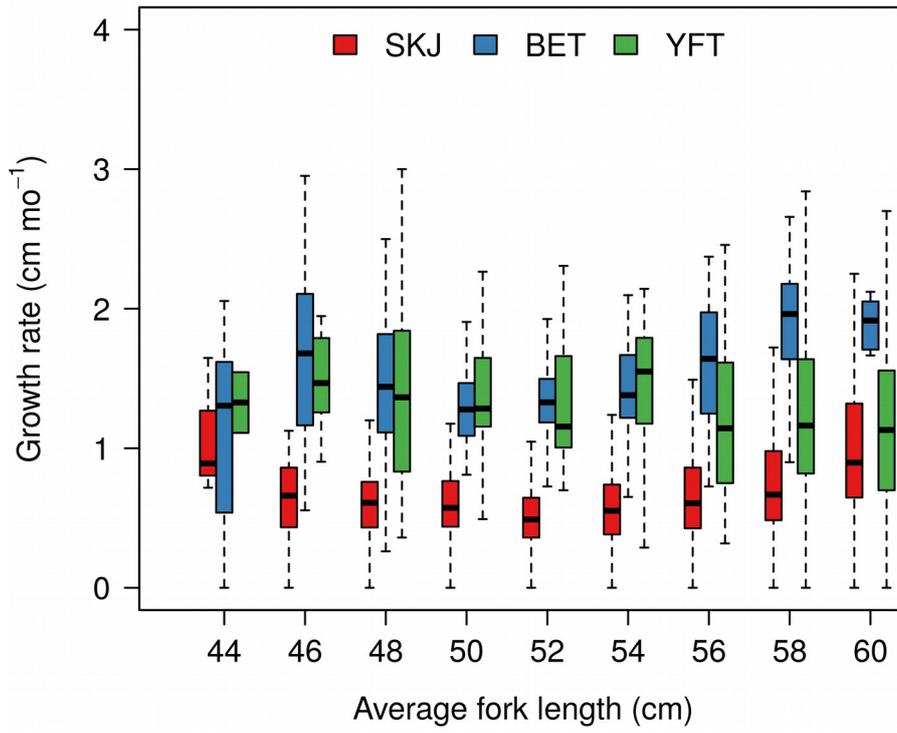


Fig. 9. Distribution of individual growth rates (cm mo⁻¹) as a function of average length between tagging and recapture for skipjack (SKJ) and juveniles of bigeye (BET) and yellowfin (YFT) tagged with dart tags within the Northern Mozambique Channel.

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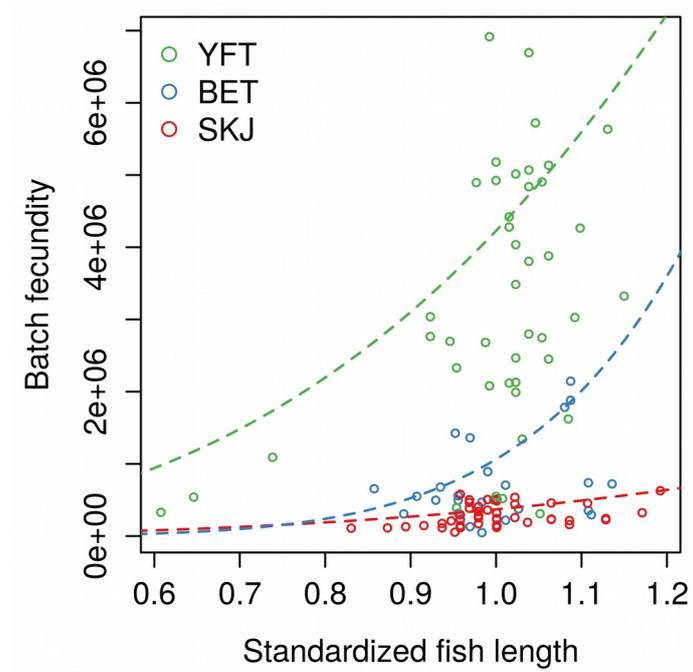


Fig. 10: Relationship between batch fecundity and standardized fish length (fork length divided by the mean) for Indian Ocean yellowfin (YFT; Zudaire et al. 2013), bigeye (BET; Zudaire et al. 2016), and skipjack (SKJ; Grande et al. 2014). Dashed lines indicate non-linear 75% quantile regression models fitted to each data set.

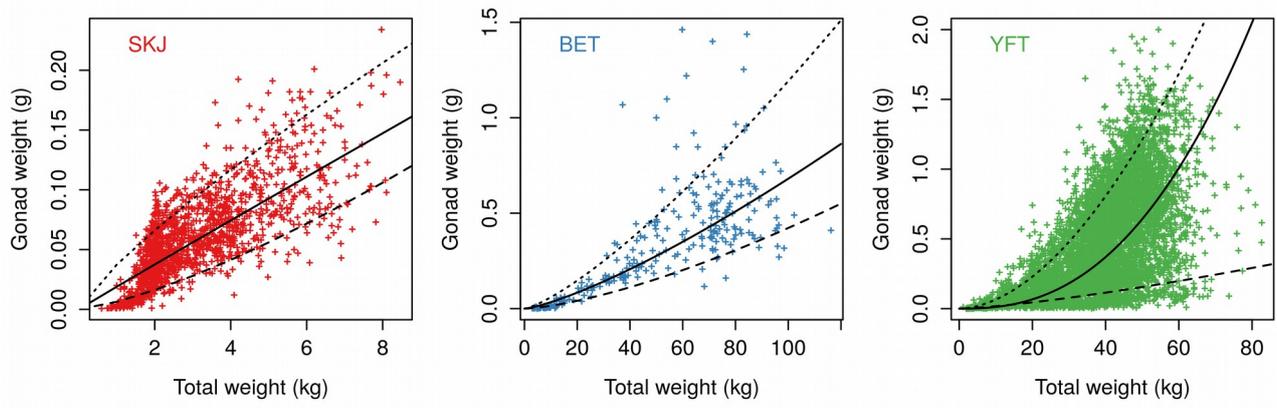


Fig. 11: Relationships between gonad weight (g) and total weight (kg) for Indian Ocean skipjack (SKJ), bigeye (BET), and yellowfin (YFT). Lines indicate 10% (dashed), 50% (solid) and 90% (dotted) non-linear quantile regression models fitted to the data.

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1017 Supplementary Online Materials

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1019 **The key role of the Northern Mozambique Channel**

1020 **for Indian Ocean tropical tuna fisheries**

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1032 **Materials & Methods**

1033 The IOTTP was conducted during 2002-2009 through several small-scale tagging projects and a

1034 larger regional component, the Regional Tuna Tagging Project (RTTP), to improve knowledge on

1035 the population dynamics of tropical tunas and strengthen the quality of management advices derived

1036 from stock assessments (Murua et al. 2015). More than 200000 tropical tunas were tagged with

1037 plastic dart tags and released in various areas of the western Indian Ocean, including the

1038 Mozambique Channel and along the coast of Tanzania where about 130000 tunas were tagged

1039 between July 2005 and August 2007 (Hallier and Fonteneau 2015). In addition, 6 pop-up tags were

1040 deployed on yellowfin tunas during the tagging operations off the coast of Tanzania in July-August

1041 2007 but failed to transmit. Here, we used the mark-recapture data set of skipjack and juveniles of

1042 yellowfin and bigeye tunas (<80 cm) tagged with dart tags within the NMC to (i) analyse their
1043 horizontal movements during the first 5 months at liberty inferred from tagging and recovery
1044 positions and (ii) estimate their growth rates. In both cases, we selected tunas tagged during the
1045 RTTP operations and characterized by reliable information on geographic position, species
1046 identification and length at both tagging and recapture events. A small number of growth rates
1047 values were found to be inconsistent with tuna growth. We therefore removed 188 mark-recapture
1048 data that had growth rates larger than the 97.5% quantile value of 4.28 cm mo⁻¹ and lower than the
1049 2.5% quantile of 0 cm mo⁻¹, i.e. excluding all fish showing apparent shrinkage between tagging and
1050 recapture (**Table S1**). For the analysis of growth rates, we finally selected the tunas of average fork
1051 length between tagging and recapture in the range 44-60 cm to balance the sampling design
1052 between the 3 species. First, we modelled the apparent distance travelled (D ; nm) as a function of
1053 species (S), average length between tagging and recapture (L_F ; cm), month of tagging (M_T) and time
1054 at liberty (T ; d) with generalized additive models (GAMs). GAMs make no a priori assumptions
1055 about the nature of the associations between predictors and response variables by using local
1056 smoothers (Hastie and Tibshirani 1990). Second, we modelled the growth rate (G ; cm mo⁻¹) between
1057 tagging and recapture as a function of S , L_F , T , and M_T to describe and compare the growth of the
1058 three tropical tuna species when they mostly occur in association with floating objects. In both
1059 cases, spline function smoothers were used for modelling the effects of length (L_F) and time at
1060 liberty T . Interaction between species S and length L_F was included in each model and tested for
1061 significance. Model fitting and automatic selection of the degrees of freedom for the regression
1062 splines were performed using the generalized cross-validation method (Wood and Augustin 2002)
1063 implemented in the mgcv package in R version 3.3.1 (R Core Team 2016). The assumption of
1064 Gaussian error distributions was checked through the residuals. Each covariate was added to the
1065 model following a stepwise approach and selection of the best model was based upon the Akaike
1066 information criterion (AIC). Model predictions of daily distance travelled were made in the month

1067 of May for (i) an average length of 56.9 cm corresponding to the average fork length between
1068 tagging and recapture observed in the data set to compare the horizontal movements between the 3
1069 tuna species and (ii) for values of fork length of 40, 50, and 60 cm for each species to illustrate the
1070 influence of size on the extent of the movements. Model predictions of growth rates were made
1071 using a time at liberty of 1 day to account for the smoothing effect of duration at liberty (Gaertner et
1072 al. 2010).

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1074 **References**

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1077 **List of figures**

1078 Fig. S1. Predictions of daily apparent distance travelled (nm) during the first 5 months of liberty for
1079 skipjack (SKJ), bigeye (BET) and yellowfin (YFT) tagged with dart tags within the Northern
1080 Mozambique Channel in the month of May and of average size between tagging and recovery of
1081 56.9 cm fork length. Dashed lines indicate mean \pm standard error.

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1083 Fig. S2. Predictions of daily apparent distance travelled (nm) during the first 5 months of liberty for
1084 skipjack (SKJ), bigeye (BET) and yellowfin (YFT) tagged with dart tags within the Northern
1085 Mozambique Channel in the month of May and of average size between tagging and recovery of 40,
1086 50, and 60 cm fork length. Dashed lines indicate mean \pm standard error.

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1088 Fig. S3. Predictions of growth rates (cm mo^{-1}) for bigeye (BET), yellowfin (YFT), and skipjack
1089 (SKJ) tagged with dart tags within the Northern Mozambique Channel in the month of May. Dashed
1090 lines indicate mean \pm standard error.

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1092 **List of tables**

1093 Table S1. Description of the data sets used for modelling the apparent distance travelled between
1094 tagging and recovery locations in the first five months of liberty and average daily growth rates for
1095 skipjack, bigeye, and yellowfin tuna. L_T = Fork length at tagging. L_R = Fork length at recovery.

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1097 Table S2. Comparison of statistical models used for modelling (i) the horizontal movements during
1098 the first five months of liberty and (ii) the growth rates of skipjack and juveniles of yellowfin and
1099 bigeye tagged with dart tags within the North Mozambique Channel. Model formula, proportion of
1100 variance explained (adjusted r-squared), and difference in value of the Akaike information criterion
1101 (ΔAIC) relative to a one parameter constant model. D = apparent distance travelled (nm); G =

1102 growth rate (cm mo^{-1}); S = species (skipjack, bigeye or yellowfin); T = time at liberty (d); M_T =
1103 month of tagging; L_F = average fork length between tagging and recapture (cm); s = spline function
1104 smoother.

1105 **Figures**

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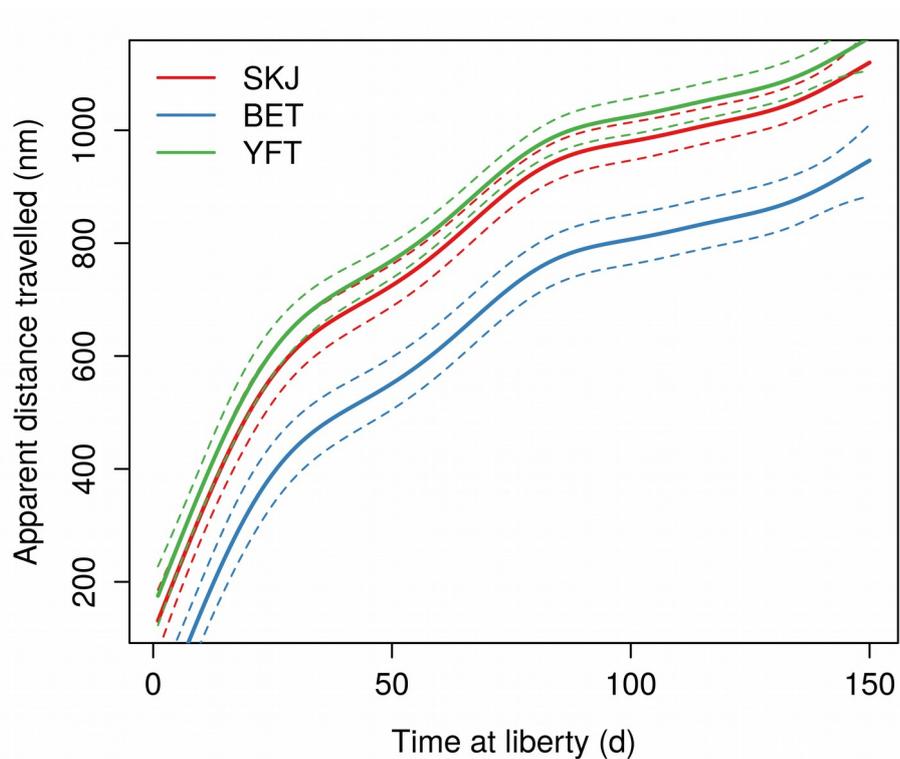
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Fig. S12: Predictions of daily apparent distance travelled (nm) during the first 5 months of liberty for skipjack (SKJ), bigeye (BET) and yellowfin (YFT) tagged with dart tags within the Northern Mozambique Channel in the month of May and of average size between tagging and recovery of 56.9 cm fork length. Dashed lines indicate mean \pm standard error.

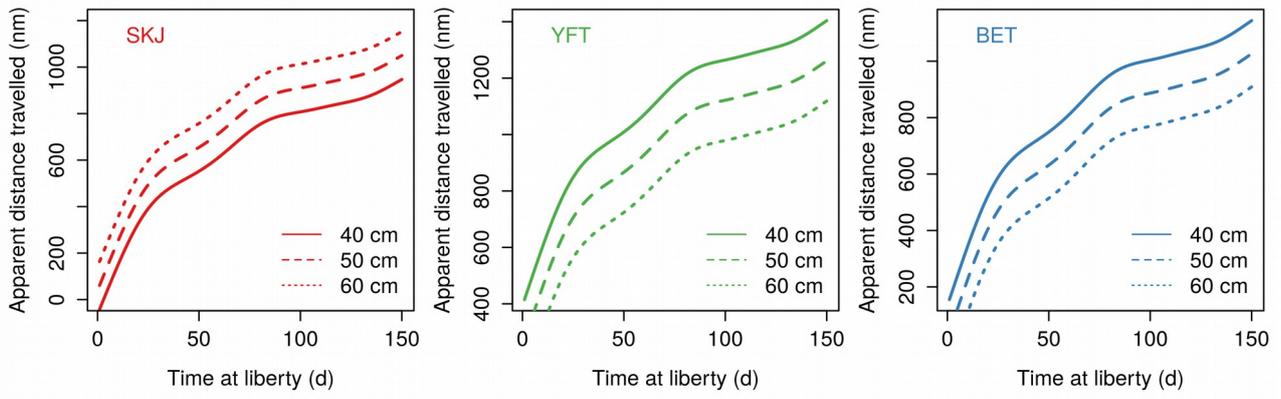


Fig. S13. Predictions of daily apparent distance travelled (nm) during the first 5 months of liberty for skipjack (SKJ), bigeye (BET) and yellowfin (YFT) tagged with dart tags within the Northern Mozambique Channel in the month of May and of average size between tagging and recovery of 40, 50, and 60 cm fork length. Dashed lines indicate mean \pm standard error.

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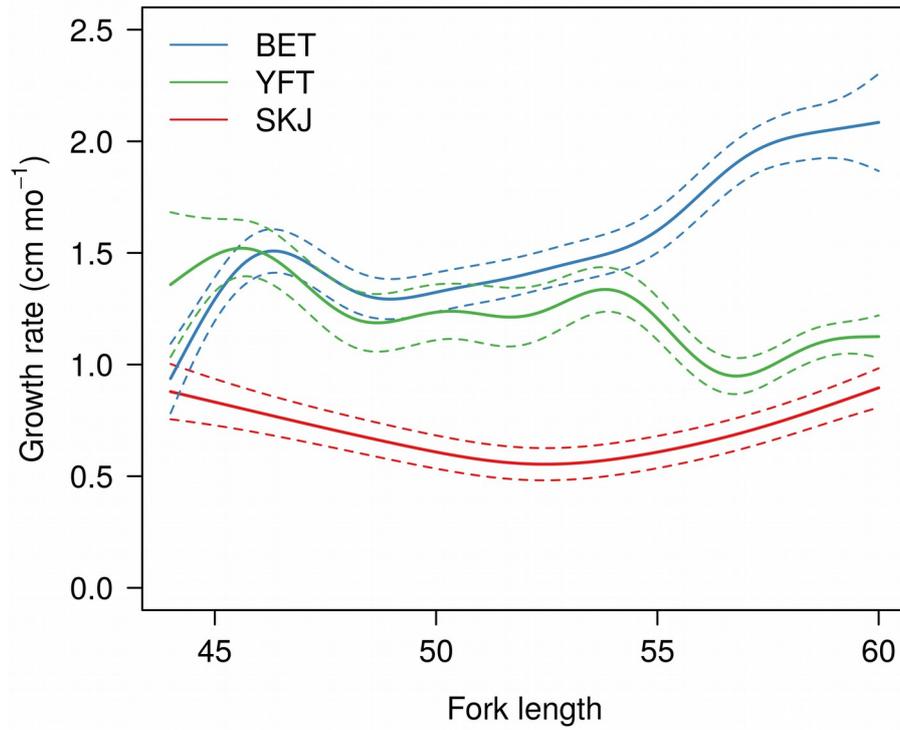


Fig. S14. Predictions of growth rates (cm mo⁻¹) for bigeye (BET), yellowfin (YFT), and skipjack (SKJ) tagged with dart tags within the Northern Mozambique Channel in the month of May. Dashed lines indicate mean \pm standard error.

1147 **TABLES**

1148 Table S1. Description of the data sets used for modelling the apparent distance travelled between
 1149 tagging and recovery locations in the first five months of liberty and average daily growth rates for
 1150 skipjack, bigeye, and yellowfin tuna. L_T = Fork length at tagging. L_R = Fork length at recovery.

Species	Fish number	Range L_T (cm)	Mean \pm SD L_T (cm)	Range L_R (cm)	Mean \pm SD L_R (cm)
Distance travelled					
BET	93	41-70	50.2 (\pm 8.4)	42-81	55.7 (\pm 9.9)
SKJ	270	43-68	53.6 (\pm 3.4)	43-67	56 (\pm 3.9)
YFT	424	33-71	57.1 (\pm 5.4)	42.2-110	60.8 (\pm 6.3)
Growth rates					
BET	364	37-58	46.1 (\pm 2.8)	44-78.2	57 (\pm 5.7)
SKJ	1236	38-59	50.7 (\pm 3.5)	45-69	56.5 (\pm 3.7)
YFT	348	39-60	53.9 (\pm 4.7)	46-68.6	58.3 (\pm 3.8)

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1154 Table S2. Comparison of statistical models used for modelling (i) the horizontal movements during
 1155 the first five months of liberty and (ii) the growth rates of skipjack and juveniles of yellowfin and
 1156 bigeye tagged with dart tags within the North Mozambique Channel. Model formula, proportion of
 1157 variance explained (adjusted r-squared), and difference in value of the Akaike information criterion
 1158 (Δ AIC) relative to a one parameter constant model. D = apparent distance travelled (nm); G =
 1159 growth rate (cm mo^{-1}); S = species (skipjack, bigeye or yellowfin); T = time at liberty (d); M_T =
 1160 month of tagging; L_F = average fork length between tagging and recapture (cm); s = spline function
 1161 smoother.

Model	Adjusted r ²	Δ AIC
Model 1: Distance travelled		
$D \sim S + T + M_T$	0.317	-289.7
$D \sim S + s(T) + M_T$	0.387	-369.8
$D \sim S + s(T) + L_F + M_T$	0.403	-389.2
$D \sim S + s(T) + s(L_F) + M_T$	0.418	-404.5
$D \sim S + s(T) + L_F + M_T + L_F:M_T$	0.429	-402.7
Model 2: Growth rate		
$G \sim S + L_F + M_T + T$	0.407	-1005.6
$G \sim S + L_F + M_T + s(T)$	0.411	-1013.3
$G \sim S + s(L_F) + M_T + s(T)$	0.426	-1054
$G \sim S + s(L_F):T + M_T + s(T)$	0.456	-1149.6

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