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► **To cite this version:**

Marc Metian, Simon Pouil, André Boustany, Max Troell. Farming of Bluefin Tuna—Reconsidering Global Estimates and Sustainability Concerns. *Reviews in Fisheries Science & Aquaculture*, 2014, 22 (3), pp.184-192. 10.1080/23308249.2014.907771 . hal-03155812

HAL Id: hal-03155812

<https://hal.science/hal-03155812v1>

Submitted on 5 Sep 2023

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1 **Farming of bluefin tuna – reconsidering global estimates and sustainability concerns**

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18 **Introduction**

19 Tuna is one of the top fish commodities in the international seafood trade. In 2010, it
20 constituted 4% of global seafood production for human consumption (FAO, 2012). The tuna
21 group consists of 15 species within the Scombridae family (Graham and Dickson, 2004) and
22 in 2011 total landings reached 5.38 million tonnes (FAO, 2013). Two species, skipjack tuna
23 (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*), dominated catches with 48%
24 and 23%, respectively. Only a few tuna species are sold through the selective sushi and
25 sashimi market and the bluefin tunas, Atlantic bluefin tuna (ABT) *Thunnus thynnus*, Pacific
26 bluefin tuna (PBT) *T. orientalis*, and Southern bluefin tuna (SBT) *T. maccoyii*, are the most
27 valuable of these. Members of bluefin tunas (hereafter called BFT; Tseng et al., 2012) can
28 attain very high market prices. For example, a 222-kg specimen of PBT was sold at Tsukiji
29 market in Tokyo (Japan) for US \$1.7 million in January 2013 (BBC News, 2013). On average
30 prices are considerably lower than these every-year exceptional auctions at the beginning of
31 the year (New Year holiday season in Japan; see Kurokura et al., 2012) but the high demand,
32 overfishing, and added production costs for farming tend to increase prices (data related to
33 frozen BFT from 2002 to 2009; Miyake et al., 2010). Globally, quantities of captured BFT
34 decreased from approx. 89,000 tonnes in 1980 to less than approx. 42,000 tonnes in 2011
35 (FAO, 2013). Since 2005, the average decrease has been 10.2% per year. Thirty countries
36 regularly report catches of these species, although a small number of countries constitute the
37 bulk of landings with Japan, Australia, Mexico, Spain, Italy, and Morocco provided 83% of
38 total catches in 2011 (FAO, 2013). Continuous high demand has triggered the development of
39 BFT aquaculture (viz. live tuna, either wild caught or captive reared seed stocks, which are
40 caged and fed for a certain period of time before being harvested; Masuma et al., 2011) and
41 according to FAO (2013) BFT aquaculture constituted 18% of global BFT production in 2011

42 (global BFT production of 8,954 tonnes). However, in light of the findings of the current
43 paper these quantities seem to be significantly underestimated.

44 All bluefin tuna populations remain heavily exploited with population sizes far below pre-
45 exploitation levels. The two Atlantic bluefin populations are estimated to be at less than 20%
46 of original spawning stock biomass (ICCAT, 2009; Taylor et al., 2011) while those of SBT
47 and PBT are both estimated to be at 5% or less of unfished levels (CCSBT, 2011; ISC, 2013).
48 IUCN considers SBT and ABT as critically endangered and endangered species, respectively
49 (Collette et al., 2011).

50 This study aims at giving an overview of current bluefin tuna aquaculture and discusses its
51 linkages to fisheries by identifying direct and indirect interactions with wild fish stocks. It
52 also outlines some of the challenges for future expansion as well as pointing out significant
53 mismatch of production statistics.

54 **Tuna aquaculture – Emergence and current practices**

55 The rise of large scale commercial BFT aquaculture is relatively recent (1970s but mostly
56 1980s). According to Miyake et al., 2010, small scale commercial bluefin farming began with
57 Atlantic bluefin in Canada in the 1960s and it started in Japan in 1969 where wild juveniles of
58 PBT were used to stock near-shore net-pens where they were then fed (i.e., fattening;
59 Kurokura et al., 2012). The ABT culture spread in the Mediterranean Sea in the late 1970s
60 (Miyake et al., 2003) and in the 1980s Australia started culture of SBT (Miyake et al., 2010).
61 PBT aquaculture along the Pacific Coast of Baja California in Mexico was first introduced
62 during late 1990s (Zertuche-González et al., 2008). In complement, there have been some
63 commercial farming of other species, such as the Yellowfin tuna (*T. albacares*) and the
64 Bigeye tuna (*T. obesus*) over the last 20 years, but quantities have been irregular and minor
65 (FAO, 2013). Traditionally, the development of tuna aquaculture has been established on
66 capture-based fisheries for obtaining juveniles and sub-adults for stocking in net-pens

67 (Ottolenghi, 2008). Two distinct modes of BFT aquaculture currently exist: capture-based
68 aquaculture and closed-cycle aquaculture. According to the International Commission for the
69 Conservation of Atlantic Tunas (ICCAT, 2008), capture-based aquaculture (CBA) can be
70 classified in two ways: fattening and farming. The “fattening” consists of rearing mature
71 individuals, whose weight exceeds 30 kg, for a shorter period of time (generally between 4
72 and 9 months). The “farming” consists of immature individuals (<25 kg) that are kept over a
73 longer time period (more than a year). This sub-classification can be debated since the
74 distinction is somewhat arbitrary, nevertheless clear pattern of these two practices of capture
75 based aquaculture are observed.

76 In June 2002, a team at the Kinki University Fisheries Laboratory (Japan) became the first to
77 successfully breed tuna and raise the fry into adult tuna. According to Sawada et al. (2005),
78 over the summer of 2002, 1.63 million eggs from these fish were used for a mass rearing
79 experiment, and 17,307 juveniles were produced and transferred to an open sea net cage.
80 Worldwide, many scientific programs or commercial companies are targeting this type of
81 achievement (e.g., Mediterranean Sea and Australia) but so far only the Japanese are
82 producing BFT from larvae obtained by spawning of captive adult fish at commercial scale.

83 However, the fact is BFT aquaculture still rely on capture of individuals from the wild has
84 raised a lot of public concern as this may negatively affect wild stocks (Naylor and
85 Burke, 2005; WWF, 2006).

86 BFT aquaculture in the Mediterranean Sea and Australia is mainly based on “fattening” but
87 “farming” is also practiced, especially in Croatia where fish (5–25 kg of body weight) are
88 kept for more than 20 months (Tičina et al., 2005). In Mexico, “fattening” is the only practice,
89 whereas both methods of capture-based aquaculture exist in Japan, where “farming” is
90 dominant using juveniles weighing around 150 and 500 grams. These individuals are raised
91 for three to four years before being sold (Ikeda, 2003). By definition, the juveniles should

92 come from capture fisheries (Ikeda, 2003), but as mentioned previously, a non-negligible part
93 of PBT production is based on juveniles from captive brood stock kept in Kinki University
94 facilities (40,000 fingerlings produced in 2009; JFS, 2010). Japan seems to be the only
95 country producing tuna from closed cycle systems at a commercial level (named “Kindai”
96 bluefin) but its profitability may be questionable as it involves a costly production process.
97 Fish for fattening or farming are caught by purse-seine vessels and then transferred into
98 transport cages (called towing pens), which are being towed to land and where the fish enters
99 larger rearing pens. Depending on location of capture relative to location of the rearing pens,
100 transport cages may need to be towed for very long distances at low speeds (around 1.8–
101 2.8 km h⁻¹ to minimize stress and can take up to 20 days; FAO/GFCM/ICCAT, 2005;
102 Glencross et al., 2002; Zertuche-Gonzalez et al., 2008; Mylonas et al., 2010). The fattening
103 process increases total mass and fat content, which substantially improve the selling price
104 especially at the Japanese market (Katavić et al., 2003a; Roy et al., 2009).
105 Periods of catch and harvesting depend on the regions where the fish are produced. In the
106 Mediterranean Sea, the harvesting period begins when prices are higher during the many
107 Japanese festivities in December (Ottolenghi, 2008). Harvesting can also take place during
108 periods when landing from wild fisheries are low as this also triggers market prices. Farmers
109 may however be forced to sell when market prices are inauspicious due to high production
110 costs (Tičina et al., 2005).

111 **Bluefin tuna statistics**

112 UN FAO statistics are the main source of comprehensive global fishery statistics. Capture
113 fisheries data from FAO have been accused of providing erroneous data (Pauly and
114 Zeller, 2003; Tesfamichael and Pauly, 2011), but the present aquaculture data seems to better
115 reflect actual production (Trujillo et al., 2012; Campbell and Pauly, 2013). However, the
116 bluefin tuna statistics that FAO receives from the Regional Fisheries Management

117 Organizations (RFMOs) seem unreliable for farmed BFT. Miyake et al. (2003) showed that
118 volumes calculated from tuna trade do not match with official volumes reported by countries
119 (imports recorded by the Japanese custom services vs. imports of farmed tuna recorded
120 through the Bluefin Tuna Statistical Documents; BTSD). Kurokura et al. (2012) also found
121 that FAO statistics do not provide a comprehensive aggregate of aquaculture tuna production
122 worldwide. Figure 1 shows the large discrepancy for bluefin tuna aquaculture production in
123 2009 between FAO and national statistics of major producing countries. FAO reported
124 approximately 12,000 tonnes and national sources more than 30,000 tonnes. The difference
125 can be even larger at the country level, e.g., the Maltese national statistics showing
126 approximately four times higher quantities than FAO. The imbroglio of statistics is not recent
127 and the discrepancy has increased in recent years (Figure 2). The fact that tuna aquaculture
128 involves both a fishing phase and a farming phase is probably causing confusion with respect
129 to documenting and reporting correct volumes of fish (Miyake et al., 2003). This is something
130 that the scientific committee within ICCAT has expressed concern about for the
131 Mediterranean region (ICCAT, 2005).

132 Eurostat (2013) and national sources confirm the situation of under-reporting and the global
133 underestimation of BFT farming estimates is worrying and specifically so concerning
134 numbers from Japan, the Mediterranean Sea, and Australia. Japan has in various documents,
135 including the scientific literature and media, been identified as a producer of farmed BFT
136 (e.g., Kumai et al., 2011; Business Line, 2013; Minato-Tsukiji, 2013) but FAO report no
137 farmed BFT. Japanese documents reveal a Japanese production of around 8000 tonnes
138 produced in 2009 (Kumai et al., 2011). This value is in accordance with the first official
139 volumes recently released for 2012 by the Japanese Ministry of Agriculture, Forestry and
140 Fisheries (9600 tonnes; MAFF, 2013) with the official numbers of farms allowed to practice
141 BFT aquaculture are to date between 129 and 140 farms.

142 Expansion of tuna fattening operations in the Mediterranean Sea involves a large number of
143 countries and actors actively involved in BFT capture fisheries and farming operations.
144 Bregazzi (2007) reported that only a third of the Mediterranean BFT production was
145 presented by FAO statistics (approx. 10,000 vs. 28,450 tonnes). National statistics of farmed
146 BFT were also not available for all Mediterranean countries or data were not detailed at the
147 group or species level, e.g., Cyprus, Malta, or Turkey. In 2003, 66% of the declared quotas
148 were put into farms and much of the fishing was targeting juvenile BFT, something that risks
149 causing declines in wild stocks (Sumaila and Huang, 2012). In addition, due the uncertainties
150 in statistics there is also a risk of underreporting, i.e., “tuna laundering” (Miyake
151 et al., 2003). Table 1 shows a nonexhaustive comparison of reported volumes of farmed BFT
152 in Mediterranean Sea from various sources (FAO, Eurostat and National reports or database).
153 Statistics from FAO and Eurostat differ and some national reports do also not match with one
154 of the two supranational organizations statistics. Only the Portuguese statistics are totally in
155 line with FAO or Eurostat. Libya, who has one farming facility registered to ICCAT, was not
156 reporting quantities to FAO (even before the 2011 civil war) whereas WWF (2006) reported
157 3107 tonnes in 2004. Eurostat reported a quantity for France (12, 19, 504, and 235 tonnes for
158 the year 2002, 2003, 2004, and 2005, respectively) but no farming activity been reported to
159 ICCAT.

160 Farming of SBT is currently the single most valuable sector of South Australia's aquaculture
161 industry (Clarke and Ham, 2009). Over the past decade the farming sector has grown to the
162 point where around 98% of the Australian SBT quota is now from farming (Clarke and
163 Ham, 2009). This is a unique situation, which simplifies the general management of the SBT
164 stock, as capture fisheries for direct landings is only minor. Figure 3 shows Australian
165 aquaculture and fisheries statistics for the last ten years and how they differ according to the
166 sources: it is clear that FAO data (FAO, 2013) differ from National statistics (DAFF, 2013)

167 and also from the RFMO data set (CCSBT, 2013) in terms of landings. National statistics
168 provided quantities of “tuna” without mentioning the species, something that actually
169 confuses the visualization of capture fisheries data since other tuna species (albacore and
170 yellowfin tuna) are caught by the Australia fleet and landed in Australia. Nevertheless, as
171 SBT almost exclusively is being caught for aquaculture, the capture fisheries landing reported
172 for SBT by FAO do not agree with catch reported to CCSBT (>2 times higher than what is
173 landed; CCSBT, 2013). The aquaculture production reported by the National authorities
174 implicitly refers to SBT only and the number was up to two times higher than that reported by
175 FAO for SBT (Figure 3). The volume of catch provided by the CCSBT (2013) could explain
176 this difference as the volumes are in line with FAO fisheries landings. In addition, the
177 Commission for the Conservation of Southern Bluefin Tuna (CCSBT; the RFMO in charge of
178 Southern Bluefin tuna), has for the last two years reported farmed volumes and volumes
179 landed for trade (based on BTSD). If calculating initial quantity before the fattening process
180 using these landing data (see Figure 3; based on a biomass gain between 50–100% and
181 assuming no mortality; Ottolenghi, 2008), the results obtained are in accordance with reported
182 volumes catch for aquaculture provided by CCSBT.

183 The large difference between statistics reported from various sources is difficult to explain.
184 This might be due to misreporting, unreporting, failing “vertical” information transfer,
185 different conversion factors used at different reporting stages or as stated earlier confusion
186 related to separating between catch vs. landings/harvesting.

187 **Bluefin aquaculture within the context of allowable catches**

188 In order to improve BFT stocks and thus capture fisheries, RFMOs are in charge of the tuna
189 stocks, including BFT. RFMOs provide the framework by which member states come to
190 agreement on conservation and management measures, and the implementation of those
191 measures occurs at the country level (Boustany, 2011). The RFMOs also constitutes a

192 mechanism to monitor compliance by Member States and to collect fishery data (without
193 enforcement). Four RFMOs are responsible for the management of bluefin tuna fisheries; the
194 organization of each RFMO differs, but decisions are usually made by consensus.
195 Consequently, enacting major changes to fisheries management is a gradual and often difficult
196 process. Differences also exist in how the science of population assessments is conducted and
197 used in management (Boustany, 2011).

198 Most RFMOs define a total allowable catch (TACs) each year for their region and thus for
199 each member country within the region defined by RFMOs. Nations must ensure compliance
200 with quotas by their fishing fleet (Aranda et al., 2012). However, nongovernmental
201 organizations believe that these measures are insufficient for ensuring sustainable stocks
202 (WWF, 2006; Greenpeace, 2006). RFMO decisions, however, do not always follow scientists'
203 recommendations and, for example, ICCAT set in 2010 for the first time their TACs within
204 the range recommended by scientists (IFREMER, 2013). Another problem is the existence of
205 illegal, unreported and unregulated (IUU) tuna catches. Tuna "laundering" activities have
206 been documented by commercial transactions analysis (Bregazzi, 2007; Polacheck, 2012).

207 Another potential problem in obtaining accurate statistics is the difference between weight of
208 captured fish and weight at harvest after fattening period. Quotas (or TAC) assigned to
209 countries are based on biomass and they are supposed to cover total tuna mortality caused by
210 that nation – due to fishing, farming, and bycatch mortality. The amount "charged" to the
211 quota for fish put into cage operations is calculated based on size at capture and not size at
212 harvest at the farm. This is problematic, as fish destined for farming are not being measured.
213 Fish for aquaculture swim from the purse seine net into the tow pen, and later from the tow
214 pen directly into the net pen. The sizes and weight of farmed fish at capture are instead
215 estimated by back-calculating from size at harvest at the farm, considering time in the pen and
216 estimated growth rates. Without any independent control, growth rates used in aquaculture

217 could be defective and unrealistically large, resulting in smaller estimated sizes at capture and
218 less tonnage being charged to the quota. ICCAT is currently trying to get a handle this
219 specific case (ICCAT, 2013b).

220 Currently, the only way to know the sizes of the fish being transferred to the net-pen is to
221 estimate an average length/weight and number of fish by eye. Even if underwater video
222 recording sometimes is used this is an imprecise method (Lovatelli, 2005). However, some
223 current efforts are made (viz. ICCAT funded research) through innovation and technology
224 involving, e.g., dual lasers and sonar to estimate length and number of fish (Espinosa
225 et al., 2011), but these technologies are still not common practice.

226 **Role of aquaculture for increasing sustainability of BTF fisheries**

227 Development of aquaculture stands as an economic alternative route for supplying seafood
228 and it also has the potential to relieve pressure on fish stocks (Naylor et al., 2000). To what
229 extent that this really is happening is difficult to say, and it will depend on where and how
230 aquaculture is performed and to an even larger extent how the fisheries and aquaculture are
231 being governed. Compared to many other aquaculture species bluefin tuna aquaculture still
232 rely on wild BFT stocks for both juveniles and adults, and also to a large extent on small
233 pelagic fish used as feeds (Figure 4). In addition to the feed aspect, the time the fish spend in
234 towing pens imply extra energy cost on tugboats that need to be included in any economic and
235 environmental performance model (such as Life Cycle Assessment model; see LCA example
236 related to fisheries in Hospido and Tyedmers, 2005).

237 Feeding ratio for tuna range between 2% and 10% of total tuna biomass (Lovatelli, 2005) and
238 this varies with physiological stage of the tuna, among countries and season (lower rates with
239 lower temperatures). Literature indicates a feed conversion between 10:1 to 20:1 (10–17:1 for
240 Australia, 12:1 for Mexico 10–20 for Japan, and 10–20:1 for Mediterranean, with 15–20:1 in
241 Croatia; Ikeda, 2003; Katavić et al., 2003b; Lovatelli, 2005; Fernandes et al., 2007; Zertuche-

242 Gonzalez et al., 2008). Using the data available for each producing countries (Feed
243 Conversion Ratios, biomass gains, mortality rates, and the national reports for 2009), we were
244 able to back calculate an initial biomass of tuna caught for aquaculture of 14,000–18,000
245 tonnes (not a volume per year since the period of farming varies from countries to countries).
246 A rough estimation of small pelagic fish needed as feed for BFT aquaculture can also be made
247 by estimating biomass gain, duration of farming and farmed volumes (hereto 2009 quantities
248 of farmed bluefin tuna and assuming 100% dependence on small pelagic fish): the global
249 quantity of small pelagic fish needed would range between 178 and 362 thousand tonnes (the
250 100% assumption providing thus the maximum amount required). These fish mainly
251 originates from local/regional fisheries and possibly to less extent also from more distant
252 fisheries (fresh or frozen) that can be provided from local or global market (see Figure 4).
253 There is an ongoing debate about the sustainability of using fish to feed farmed fish and the
254 aquaculture industry is aware of future limitation for this resource and is, therefore, putting a
255 lot of effort into finding alternative feed ingredients (Watanabe, 2002; Klinger and
256 Naylor, 2012). However, tuna farming may prove challenging out from this perspective as it
257 still depends on very large inputs of raw fish resources per output.

258 The high dependency on raw fish resources is a matter of concern also for the tuna
259 aquaculture industry and compound feeds suited for tuna are under development (Mourente
260 and Tocher, 2009). Compound feeds could reduce the dependence on small pelagic stocks
261 through inclusion of alternative protein and fatty acid sources that can fit the nutritional
262 requirement of blue fin tuna in captivity (Fauvel and Suquet, 2004; Smullen, 2009; for more
263 specific details on feeding farmed tuna, see the review made by Mourente and Tocher, 2009).
264 The fact that BTF is a top carnivorous species that requires large inputs of marine based
265 proteins constitutes a challenge for reducing its dependency on fish resources (Naylor and
266 Burke, 2005). It should also be noted that besides fish also squids are used as feeds for BFT,

267 particularly during the few days before slaughter (e.g., in Tunisia; Hattour, 2011). One way to
268 reduce feed usage would be to shorten the production time and provide a smaller fish than
269 usual to the market. But to what extent this is possible will mainly depend on the acceptance
270 of consumers (e.g., tastes, preferences, willingness to pay, etc.).

271 In 2002, the General Fisheries Commission for the Mediterranean (GFCM) called for the
272 establishment of a Working Group, to be convened jointly with the ICCAT, with a mandate to
273 develop practical guidelines to address known problems, with emphasis on fishing and
274 farming statistics, and to propose needed research to address these problems
275 (FAO/GFCM/ICCAT, 2005). ICCAT also ruled in 2003 that each country is required to report
276 authorized farming facilities and has established a list of these, which, amongst other
277 information, also includes farming capacity (ICCAT, 2013a). FAO/GFCM/ICCAT (2005)
278 pointed out that the critical phase for obtaining accurate estimated of catch is the period when
279 fish are transferred from the fishing gear to the transport and/or farming cages.

280 **Conclusions and recommendations**

281 Drivers for investing in tuna farming are to provide fish outside the fishing season when the
282 supply from capture fisheries is limited and being able to supply a fattier fish to the market
283 (Roy et al., 2009). The main challenges for improved sustainability involve closing the live
284 cycle in captivity and develop feeds based on alternative protein sources to fish. There is also
285 a need to improve management of BFT capture fisheries with respect to increasing
286 transparency of fishing volumes allocated for aquaculture. A roadmap for BFT aquaculture in
287 the Mediterranean Sea was presented 8 years ago by FAO, GFCM, and ICCAT
288 (FAO/GFCM/ICCAT, 2005). Besides ICCAT RFMOs only a few improvements have been
289 made since then and there is a need to extend also to other BFT producing regions.

290 As it has been done for Chinese fisheries (FAO, 2012), Japan and other countries should
291 revise their statistics of BFT aquaculture production, leading to harmonization of the data.

292 This should, however, be a collective effort between the producing countries and various
293 official supranational organizations (e.g., FAO, Eurostat, and RFMOs). Such harmonization
294 will help the scientific stock assessment and thus facilitate for sustainable quotas or TACs.
295 This would also have to involve better estimation of fish (sizes and weights) caught for
296 aquaculture. Maybe more than a need for simple innovations in term of technology used to
297 accurately quantify fish, there is a need for increased transparency in on-farm management
298 and also on-board fishing boats.

299 A potential action at the national level and in addition to already existing measure to keep
300 track of the licenses delivered for the BFT farms (see Figure 5 for the global number of tuna
301 farms) would be to act on the allowed capacity of the registered farms. A reduction or an
302 increase of their authorized volume capacities (max amount of fish authorize to farm) when
303 the scientific recommendation for the TAC fluctuates: decrease of the National TAC would
304 imply a restriction of the farming capacities. This would be a similar action already done for
305 ITQ decided for the bluefin tuna vessels (seen, e.g., in France or in Spain). This raises the
306 question of how the current authorization for farming tuna is provided since these numbers
307 are significantly larger than production quantities. As an example, farming capacities in
308 Mediterranean Sea is over 60,000 tonnes (Figure 5; ICCAT, 2013a) which is larger than the
309 global reported landing of bluefin tuna worldwide in 2010 (viz., 41,664 tonnes; FAO, 2013).
310 This overcapacity of tuna farms has increased around the Mediterranean by approximately
311 20,000 tonnes since 2004–2005 (WWF, 2006) whereas the ICCAT TAC has been declining in
312 recent years (from 32,000 tonnes to the current 12,900 tonnes; ICCAT, 2003, 2012). If
313 appropriate system is in place, production through aquaculture could potentially improve
314 overall record keeping as farming activities should theoretically be easier to monitor and to
315 get accurate estimates from compared to current wild capture/direct landings fisheries.

316 **Acknowledgments**

317 The authors thank Kazuhito Watanabe for his help getting data. MM and AB are Nippon
318 Foundation Senior Nereus Fellows.

319 **References**

320 Aranda, M., H. Murua, and P. D. Bruyn. Managing fishing capacity in tuna regional fisheries
321 management organisations (RFMOs): development and state of the art. *Mar.*
322 *Policy*, **36**: 985–992 (2012).

323 Barazi-Yeroulanos, L. Regional synthesis of the Mediterranean marine finfish aquaculture
324 sector and development of a strategy for marketing and promotion of Mediterranean
325 aquaculture (MedAquaMarket). Studies and Reviews General Fisheries Commission for
326 the Mediterranean. No. 88. Rome: FAO (2010).

327 BBC News. Japan bluefin tuna fetches record \$1.7m. Available
328 from <http://www.bbc.co.uk/news/world-asia-20919306> (2013).

329 Boustany, A. *Bluefin Tuna: The State of the Science*. Washington, DC: Ocean Science
330 Division, Pew environment Group (2011).

331 Bregazzi, R. M. *The Plunder of Bluefin Tuna in the Mediterranean and East Atlantic during*
332 *2006 and 2007*. Madrid: Advanced Tuna Ranching Technology (2007).

333 Business Line. Japan to ban expansion of bluefin tuna farms. Available
334 from [http://www.thehindubusinessline.com/news/international/japan-to-ban-expansion-](http://www.thehindubusinessline.com/news/international/japan-to-ban-expansion-of-bluefin-tuna-farms/article4034539.ece)
335 [of-bluefin-tuna-farms/article4034539.ece](http://www.thehindubusinessline.com/news/international/japan-to-ban-expansion-of-bluefin-tuna-farms/article4034539.ece) (2013).

336 Campbell, B. and D. Pauly. Mariculture: a global analysis of production trends since
337 1950. *Mar. Policy*, **39**: 94–100 (2013).

338 CBS. Croatian Bureau of Statistics. Available from http://www.dzs.hr/default_e.htm (2013).

339 CCSBT. Southern Bluefin Tuna Data. Catch Documentation Scheme (CDS) Harvest report
340 (January 2010 to December 2011 inclusive); Subset of the Annex 2a Report of the

341 CCSBT Trade Information Scheme 2002–2009; Global Southern Bluefin Tuna Catch
342 By Flag 1952–2011. Available from <http://www.ccsbt.org/site/data.php> (2013).

343 Clarke, S. and J. Ham. Aquafin CRC – Southern Bluefin Tuna Aquaculture Subprogram:
344 coordination, administration and facilitation. FRDC Final Report (Project No. 2004/216).
345 SARDI Aquatic Sciences. *SARDI Research report series No. 329* (2009).

346 Collette, B. B., K. E. Carpenter, B. A. Polidoro, M. J. Juan-Jorda, A. Boustany, D.
347 J. Die, C. Elfes, W. Fox, J. Graves, L. Harrison, R. McManus, C. Minte-
348 Vera, R. Nelson, V. Restrepo, J. Schratwieser, C.-L. Sun, M. Brick
349 Peres, C. Canales, G. Cardenas, S.-K. Chang, W.-C. Chiang, N. de
350 Oliveira Leite, H. Harwell, R. Lessa, F. L. Fredou, H. A. Oxenford, R. Serra, K.-
351 T. Shao, R. Sumalia, S.-P. Wang, R. Watson, and E. Yanez. High value and long life—
352 Double jeopardy for tunas and billfishes. *Science*, **333**: 291–192 (2011).

353 Commission for the Conservation of Southern Bluefin Tuna – CCSBT. Report of the
354 Sixteenth Meeting of the Scientific Committee. 19–28 July
355 2011. Bali, Indonesia (2011).

356 Department of Agriculture, Fisheries and Forestry – DAFF. Australian Fisheries Statistics
357 (1991–2011) Australian government. Available
358 from http://www.daff.gov.au/abares/publications_remote_content/publication_series/australian_fisheries_statistics (2013).

359
360 DGPA. Directorate-General of Fisheries and Aquaculture of Portugal. Available
361 from <http://www.dgrm.min-agricultura.pt/xportal/xma-in?xpid=dgrm> (2013).

362 Espinosa, V., E. Soliveres, A. Cebrecos, V. Puig, S. Sainz-Pardo, and F. de la
363 Gándara. Growing monitoring in sea cages: TS measurements issues. **In:** *Proceedings*
364 *of the 34th Scandinavian Symposium on Physical Acoustics*, Geilo 30 January–2
365 February, 2011 (2011).

366 Eurostat. Eurostat Fisheries database. Last update 09.07.2013 Available
367 from <http://epp.eurostat.ec.europa.eu/portal/page/portal/fishe-ries/data/database> (2011).

368 FAO (Food and Agriculture Organization). The State of World Fisheries and Aquaculture.
369 FAO Fisheries and Aquaculture Department. Rome: FAO (2012).

370 FAO (Food and Agriculture Organization). Fishstat Plus: Universal Software for Fishery
371 Statistical Time Series. Aquaculture Production: Quantities 1950–2011, Aquaculture
372 Production: Values 1984–2011; Capture Production: 1950–2011; Commodities
373 Production and Trade: 1950–2010. Rome: FAO Fisheries Department, Fishery
374 Information, Data and Statistics Unit (2013).

375 FAO/General Fisheries Commission for the Mediterranean/International Commission for the
376 Conservation of Atlantic Tunas. Report of the third meeting of the Ad Hoc
377 GFCM/ICCAT Working Group on Sustainable Bluefin Tuna Farming/Fattening
378 Practices in the Mediterranean. Rome, 16–18 March 2005. FAO Fisheries Report. No.
379 779. Rome: FAO (2005).

380 FAO/NASO EN. FAO - National Aquaculture Sector Overview English version. Available
381 from: http://www.fao.org/fishery/countrysector/naso_tunisia/en (2013).

382 FAO/NASO FR. FAO - National Aquaculture Sector Overview French version. Available
383 from http://www.fao.org/fishery/countr-ysector/naso_tunisia/fr (2013).

384 Fauvel, C., and M. Suquet. Fish domestication, what about bluefin tuna? *INRA Prod.*
385 *Anim.*, **17**(3): 183–187 (2004).

386 Fernandes, M, M. Angove, T. Sedawie, and A. Cheshire. Dissolved nutrient release from solid
387 wastes of southern bluefin tuna (*Thunnus maccoyii*, Castelnau)
388 aquaculture. *Aquaculture Res.*, **38**: 388–397 (2007).

389 Graham, J. B., and K. A. Dickson. Tuna comparative physiology. *J. Exp. Biol.*, **207**: 4015–
390 4024 (2004).

391 Glencross, B., S. Clarke, and J. Buchanan. Temporal growth patterns of farmed juvenile
392 southern bluefin Tuna, *Thunnus maccoyii* (Castelnau) fed moist pellets. *J. World*
393 *Aquacult. Soc.*, **33**(2): 138–145 (2002).

394 Greenpeace. *Where have All the Tuna Gone?* Greenpeace. Greenpeace International (2006).

395 Hattour, A. Bluefin tuna (*Thunnus thynnus thynnus* L. 1758) in Tunisian waters: state of the
396 art, fishing and fattening activities. *Bulletin de l'Institut National des Sciences et*
397 *Technologies de la Mer de Salammbô*, **38**: 5–19 (in French) (2011).

398 Hospido, A., and P. Tyedmers. Life cycle environmental impacts of Spanish tuna
399 fisheries. *Fish. Res.*, **76**(2): 174–186 (2005).

400 ICCAT. Report for biennial period, 2002–03 Part I (2002) Vol. 1 (2003).

401 ICCAT. ICCAT Report for the biennial period, 2004–2005, Part II (2005), Vol. 2 (2005).

402 ICCAT. Recommendation amending the Recommendation by ICCAT to establish a
403 multiannual recovery plan for bluefin tuna in the eastern Atlantic and Mediterranean.
404 Madrid (2008).

405 ICCAT. Extension of the 2009 SCRS Meeting to Consider the Status of Atlantic Bluefin Tuna
406 Populations with Respect to CITES Biological Listing Criteria. Madrid, Spain, October
407 21–23, 2009. Doc. No. PA2-604/2009 (2009).

408 ICCAT. Recommendation by ICCAT amending the recommendation by ICCAT to establish a
409 multi-annual recovery plan for Bluefin tuna in the Eastern Atlantic and Mediterranean
410 (2012).

411 ICCAT. ICCAT record of BFT farming facilities. Available
412 from <http://www.iccat.int/en/ffb.asp> (2013a).

413 ICCAT. Report of the 2013 Bluefin Meeting on Biological parameters reviews. Available
414 from <http://www.iccat.es/Documents/Meetings/Docs/2013->
415 [BFT_BIO_ENG.pdf](http://www.iccat.es/Documents/Meetings/Docs/2013-BFT_BIO_ENG.pdf) (2013b).

416 IFREMER. Le thon rouge Atlantique. *IFREMER Press release*. Paris. 6p. (in French).
417 Available
418 from http://wwz.ifremer.fr/institut_eng/content/download/41835/569837/file/13_01_28
419 [_DP_Thon_rouge.pdf](#) (2013).

420 Ikeda, S. Market and domestic production of cultured tuna in Japan- cultured tuna in the
421 Japanese market. *CIHEAM Cahiers Options Méditerranéennes*, **60**: 83–84 (2003).

422 International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific
423 Ocean – ISC. Stock assessment of Pacific bluefin tuna in 2012. Pacific Bluefin Tuna
424 Working Group. Available
425 from [http://isc.ac.affrc.go.jp/pdf/Stock_assessment/Stock%20Assessment-](http://isc.ac.affrc.go.jp/pdf/Stock_assessment/Stock%20Assessment%20of%20Pacific%20Bluefin%20Assmt%20Report%20-%20May15.pdf)
426 [nt%20of%20Pacific%20Bluefin%20Assmt%20Report%20-%20May15.pdf](#) (2013).

427 Japan For Sustainability – JFS. Toyota Tsusho, Kinki University to Commercialize World's
428 First Complete Bluefin Tuna Farming. Posted: 23 december 2010 Available
429 from <http://www.japanfs.org/en/pages/030453.html> (2010).

430 Katavić, I., V. Franičević, and V. Tičina. Bluefin tuna (*Thunnus thynnus* L.) farming on the
431 Croatian coast of the Adriatic Sea: Present stage and future plans. *CIHEAM Cahiers*
432 *Options Méditerranéennes*, **60**: 101–106 (2003b).

433 Katavić, I., V. Tičina, L. Grubišić, and V. Franičević. Tuna farming as a new achievement in
434 mariculture of Croatia, pp. 10–20. **In:** *Workshop on Farming, Management and*
435 *Conservation of Bluefin Tuna 13* (Oray, I. K., and F. S. Karakulak,
436 Eds.). Istanbul, Turkey: Turkish Marine Research Foundation (2003a).

437 Klinger, D., and R. Naylor. Searching for solutions in aquaculture: charting a sustainable
438 course. *Annu. Rev. Environ. Res.*, **37**: 247–276 (2012).

439 Kumai, H., M. Arimoto, S. Ono, and N. S. Gakkai. Bluefin tuna aquaculture industry -
440 business development and technology development. Fisheries science series No 168

441 (Suisangaku Shirīzu 168 - in Japanese). ISBN - 78-4769912439:
442 Kōseishakōseikaku, Tokyo (2011).

443 Kurokura, H., A. Takagi, Y. Sakai, and N. Yagi. Tuna goes around the world on
444 sushi. *Aquacult. Econ. Manage.*, **16**(2): 155–156 (2012).

445 Lovatelli, A. Report of the Third Meeting of the Ad Hoc GFCM/ICCAT Working Group on
446 Sustainable Bluefin Tuna Farming/Fattening Practices in the Mediterranean. Rome, 16–
447 18 March 2005. FAO Fisheries Report. No. 779. Rome: FAO (2005).

448 MAGRAMA. Ministerio de Agricultura, Alimentación y Medio Ambiente. Available
449 from <http://www.magrama.gob.es/es/> (2013).

450 MANREC. Ministry of Agriculture, Natural Resources and Environment of Cyprus. Available
451 from <http://www.moa.gov.cy> (2013).

452 Masuma, S., T. Takebe, and Y. Sakakura. A review of the broodstock management and
453 larviculture of the Pacific northern bluefin tuna in Japan. *Aquacult.*, **315**: 2–
454 8 (2011). [Crossref],

455 Ministry of Agriculture, Forestry and Fisheries – MAFF. Fishery production statistics survey.
456 Available
457 from http://www.maff.go.jp/j/tokei/kouhyou/kaimen_gyosei/index.html#y. Bluefin tuna
458 fish farms list (in Japanese). Available
459 from http://www.jfa.maff.go.jp/j/tuna/taiheiyou_kuromaguro/pdf/kuromaguro_itiran.pdf
460 (2013).

461 Minato-Tsukiji. Japan's 2011 domestic shipment of farmed bluefin tuna amounted to 9,044
462 tons. Available from http://www.minato-tsukiji.com/news_detail_5423.html (2013).

463 MiPAAF. Ministero delle Politiche Agricole Alimentari e Forestali. Available
464 from <http://www.politicheagricole.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/311>
465 (2013).

466 Miyake, P., J. M. De la Serna, A. Di Natale, A. Farrugia, I. Katavić, N. Miyabe,
467 and V. Tičina. General review of bluefin tuna farming in the mediterranean
468 area. *Collective Volume of Scientific Papers ICCAT*, **55**(1) (2003).

469 Miyake, M. P., P. Guillotreau, C.-H. Sun, and G. Ishimura. Recent developments in the tuna
470 industry: Stocks, fisheries, management, processing, trade and markets. FAO Fisheries
471 and Aquaculture Technical Paper 543. Rome: FAO (2010).

472 Mourente, G., and D. R. Tocher. Tuna nutrition and feeds: current status and future
473 perspectives. *Rev. Fish. Sci.*, **17**(3): 373–390 (2009).

474 Mylonas, C. C., F. De La Gándara, A. Corriero, and A. B. Ríos. Atlantic bluefin tuna
475 (*Thunnus thynnus*) farming and fattening in the Mediterranean sea. *Rev. Fish.*
476 *Sci.*, **3**(18): 266–280 (2010).

477 Naylor, R. L. and M. Burke. Aquaculture and ocean resources: Raising tigers of the
478 sea. *Annual Rev. Environ. Resour.*, **30**: 185–218 (2005).

479 Naylor, R. L., R. J. Goldberg, J. H. Primavera, N. Kautsky, M. C.
480 M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney, and M. Troell. Effect of
481 aquaculture on world fish supplies. *Nature*, **405**: 1017–1024 (2000).

482 Ottolenghi, F. Capture-based aquaculture of bluefin tuna, pp. 169–182. **In:** *Capture-based*
483 *Aquaculture: Global Overview* (Lovatelli, A. and P. F. Holthus,
484 Eds.). Rome: FAO (2008).

485 Pauly, D., and D. Zeller. The global fisheries crisis as a rationale for improving the FAO's
486 database of fisheries statistics, pp. 1–9. **In:** *Fisheries Centre Research Report*
487 *11*, Vancouver, BC: The Fisheries Center, University of British Columbia (2003).

488 Pedersen, E., and R. Ito. Marine aquaculture of pacific bluefin tuna *Thunnus orientalis* in
489 Ensenada, Baja California Mexico: A sustainable approach. **In:** *Aquaculture 2010*
490 *Meeting*, San Diego, CA: World Aquaculture Society (2010).

491 Polacheck, T. Assessment of IUU fishing for Southern Bluefin Tuna. *Mar. Policy*, **36**: 1150–
492 1165 (2012).

493 Roy, B. C., M. Ando, K.-I. Kawasaki, and Y. Tsukamasa. Comparison of lipid and fatty acid
494 composition in different flesh cuts of farmed fed, farmed fast and wild Pacific Bluefin
495 tuna (*Thunnus orientalis*), pp. 50–54. **In: Proceedings of the 2 Global COE Program**
496 *Symposium of Kinki University, 2009 “Sustainable Aquaculture of the Bluefin and*
497 *Yellowfin Tuna – Closing the Life Cycle for Commercial Production”* (2009).

498 Sawada, Y., T. Okada, S. Miyashita, O. Murata, and H. Kumai. Completion of the pacific
499 bluefin tuna *Thunnus orientalis* (Temminck et Schlegel) life cycle. *Aquacult.*
500 *Res.*, **36**: 413–421 (2005).

501 Smullen, R. A. world first for Tuna: formulated feed success for Southern Bluefin
502 Tuna, *Thunnus maccoyii*, pp. 59–61. **In: Proceedings of the 2 Global COE Program**
503 *Symposium of Kinki University, 2009 “Sustainable Aquaculture of the Bluefin and*
504 *Yellowfin Tuna – Closing the Life Cycle for Commercial Production”* (2009).

505 Sumaila, U. R. and L. Huang. Managing bluefin tuna in the Mediterranean Sea. *Mar.*
506 *Policy*, **36**: 502–511 (2012).

507 Taylor, N. G., M. K. McAllister, G. L. Lawson, T. Carruthers, and B. A. Block. Atlantic
508 bluefin tuna: a novel multistock spatial model for assessing population biomass. *PLoS*
509 *ONE*, **6**(12): e27693 (2011).

510 Tesfamichael, D. and D. Pauly. Learning from the past for future policy: approaches to time-
511 series catch data reconstruction. *Western Indian Ocean J. Mar. Sci.*, **10**(1): 99–
512 106 (2011).

513 Tičina, V., I. Katavić, L. Grubišić, N. Skakelja, and V. Franičević. Farming northern bluefin
514 tuna (*Thunnus thynnus* L.) in the Adriatic Sea. Meeting Word Aquaculture
515 2005. Bali (2005).

516 Trujillo, P., C. Piroddi, and J. Jacquet. Fish farms at sea: the ground truth from Google
517 Earth. *PloS ONE*, **7**(2): e30546 (2012).

518 Tseng, M.-C., J. Chuen-Tan, P. J. Smith, and Y.-H. Hung. Interspecific and intraspecific
519 genetic diversity of *Thunnus* species, pp. 63–82. **In: Analysis of Genetic Variation in**
520 *Animals* (Caliskan, M., Ed.), Rijeka, Croatia: InTech (2012).

521 Watanabe, T. Strategies for further development of aquatic feeds. *Fish. Sci.*, **68**(2): 242–
522 252 (2002).

523 World Wild Fund - WWF. *The Plunder of Bluefin Tuna in the Mediterranean and East*
524 *Atlantic in 2004–2005: Uncovering the Real Story*. Rome: WWF Mediterranean
525 Programme Office (2006).

526 Zertuche-González, J. A., O. Sosa-Nishizaki, J. G. Rodriguez, R. D. Simanek, C. Yarish,
527 and B. A. Costa-pierce. *Marine science assessment of capture-based tuna (Thunnus*
528 *orientalis) aquaculture in the Ensenada region of northern Baja California,*
529 *Mexico*. Stanford: University of Connecticut (2008).

530

531 **Figure captions**

532 Figure 1. Bluefin tuna aquaculture production in 2009: comparison between FAO data and
533 national statistics (or other sources).

534 Figure 2. Global trends of bluefin tuna farming 2002–2011: FAO data and national statistics
535 (or other sources).

536 Figure 3. Australian case study for Southern bluefin tuna aquaculture viewed from different
537 sources of statistics.

538 Figure 4. Schematic vision of bluefin tuna production and dependence to wild stocks of tuna
539 and small pelagic fish (1) capture fisheries, (2) fattening, (3) farming (4), and full cycle
540 production.

541 Figure 5. Geographic distribution of bluefin tuna farms (number of farms and reported
542 farming capacities; data from ICCAT, 2013a; CCSBT, 2013; MAFF, 2013; Pedersen and Ito,
543 2010).

544

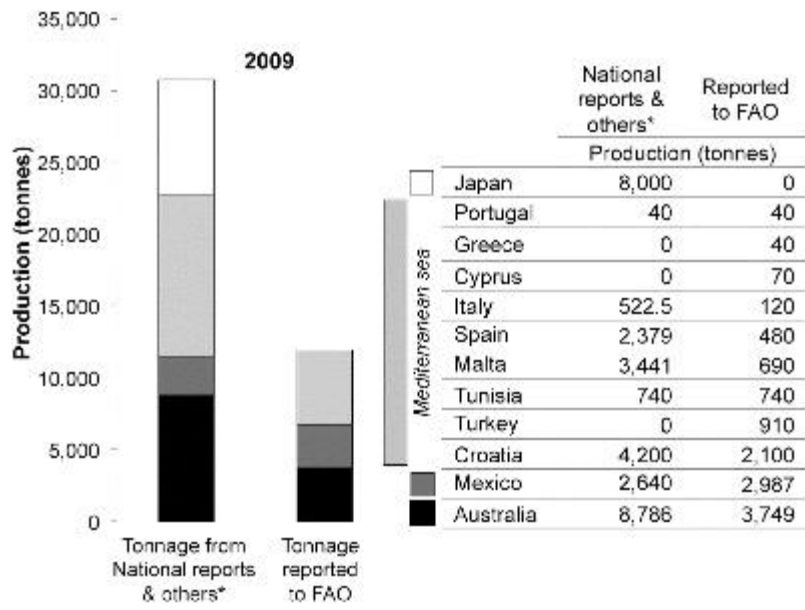
545 Table 1 Production of the Mediterranean Sea's countries (in tonnes) from various sources

Country	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Sources
Croatia	202	302	575	782	1910	1710	3350	2090	1860	2100	1680	1610	FAO
	202	302	575	782	920	747	—	—	3711	4200	3368	3223	EUROSTAT
	—	—	—	—	—	—	—	4180	3711	4200	—	—	CBS (2013)
Cyprus	0	0	—	—	270	296	210	190	130	70	10	—	FAO
	—	—	—	—	—	247	1030	940	1020	—	—	—	EUROSTAT
Greece	—	—	—	—	—	1480	1000	1000	1000	0	0	—	MANREC (2013)
	0	0	0	0	0	0	210	110	180	40	90	95	FAO
	—	—	—	—	—	60	—	—	—	—	—	—	EUROSTAT
Italy	0	61	323	222	431	458	370	860	370	120	20	—	FAO
	0	61	323	222	431	458	1163	2577	344	23	20	435	EUROSTAT
Malta	—	—	—	—	1000	1800	1163	1262	343.9	522.5	—	—	MiPAAF (2013)
	0	0	0	0	0	0	840	940	1010	690	990	960	FAO
	—	—	—	—	—	—	6069	6813	5035	3441	4955	1759	EUROSTAT
Portugal	—	—	—	—	—	1	12	13	22	40	—	—	FAO
	:	:	:	:	:	1	12	13	22	40	—	—	EUROSTAT
	—	—	—	—	—	1	12	13	22	40	0	—	DGPA (2013)
Spain	740	890	980	740	1280	670	510	820	640	480	360	575	FAO
	546	714	—	—	—	—	—	—	3217	2379	1793	2866	EUROSTAT
	—	—	5185	5194	6296	3364	2572	4076	3217	2379	1793	2866	MAGRAMA
	—	—	—	3687	6423	3700	2939	3102	—	—	—	—	MedAquaMarket
Tunisia	0	0	5	152	44	213	450	430	420	740	350	70	FAO
	0	0	0	—	—	—	511	519	600	380	373	329	FAO/NASO FR
	—	—	—	250	260	476	450	430	420	740	—	—	Campbell and Pauly, 2013
Turkey	—	—	—	—	1300*	1500*	—	—	—	—	—	—	FAO/NASO EN
	0	0	0	0	440	390	390	870	710	910	580	100	FAO
	—	—	—	—	440	390	82	148	—	—	—	—	EUROSTAT

546 FAO: Food and Agriculture Organisation (FAO, 2013); Eurostat: Eurostat Fisheries database (Eurostat, 2013).

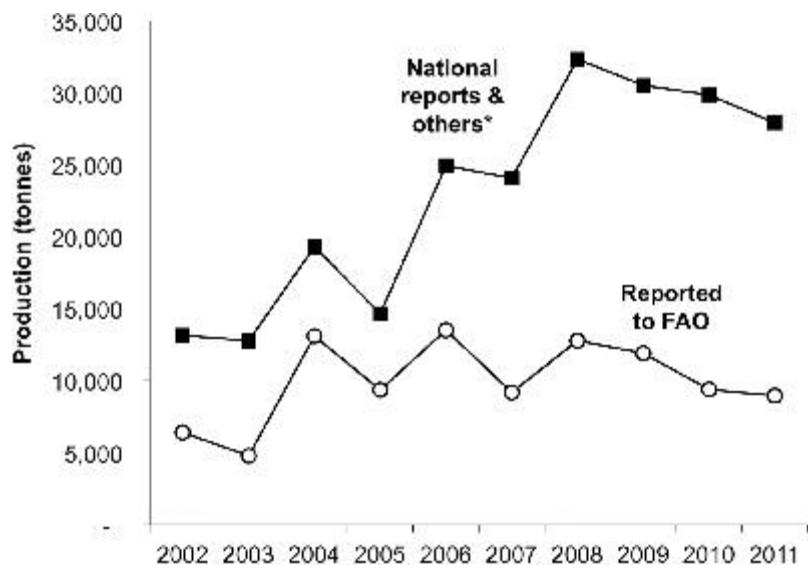
547 MedAquaMarket: Mediterranean marine finfish aquaculture sector and development of a strategy for marketing and
548 promotion of Mediterranean aquaculture; see Barazi-Yeroulanos, 2010).549 *According to FAO6 NASO EN, this is the total quantity of bluefin tuna fattening cages; the value-added to
550 production by fattening is estimated at 250 tonnes in 2003 and 260 tonnes in 2004 and 476 tonnes in 2005.

551



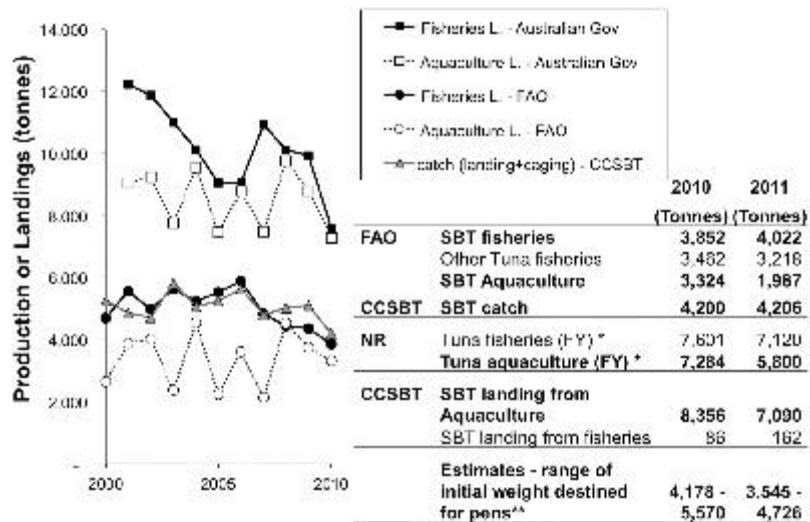
552

553 Figure 1



554

555 Figure 2

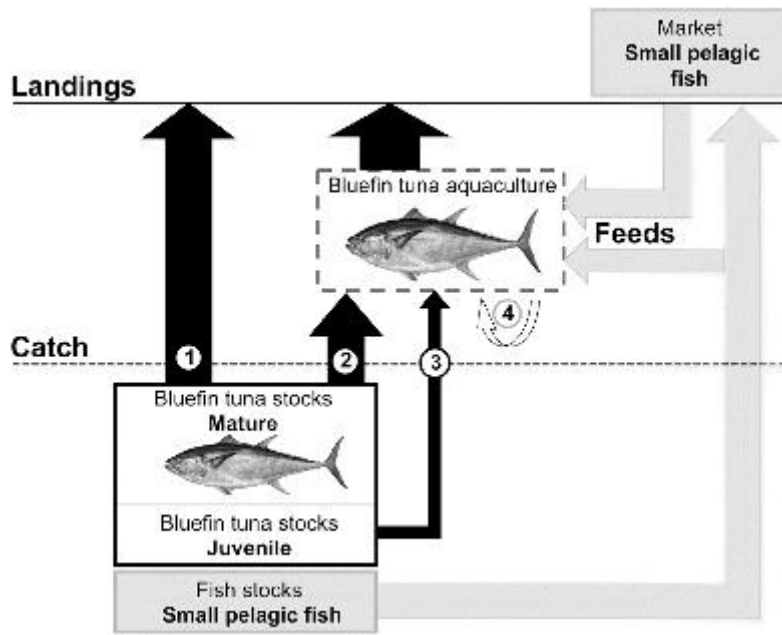


* Not defined at the species level, FY stands for Fiscal year viz. 09-10 & 10-11

** Based on CCSBT, a biomass gain between 50-100% and no mortality hypothesis

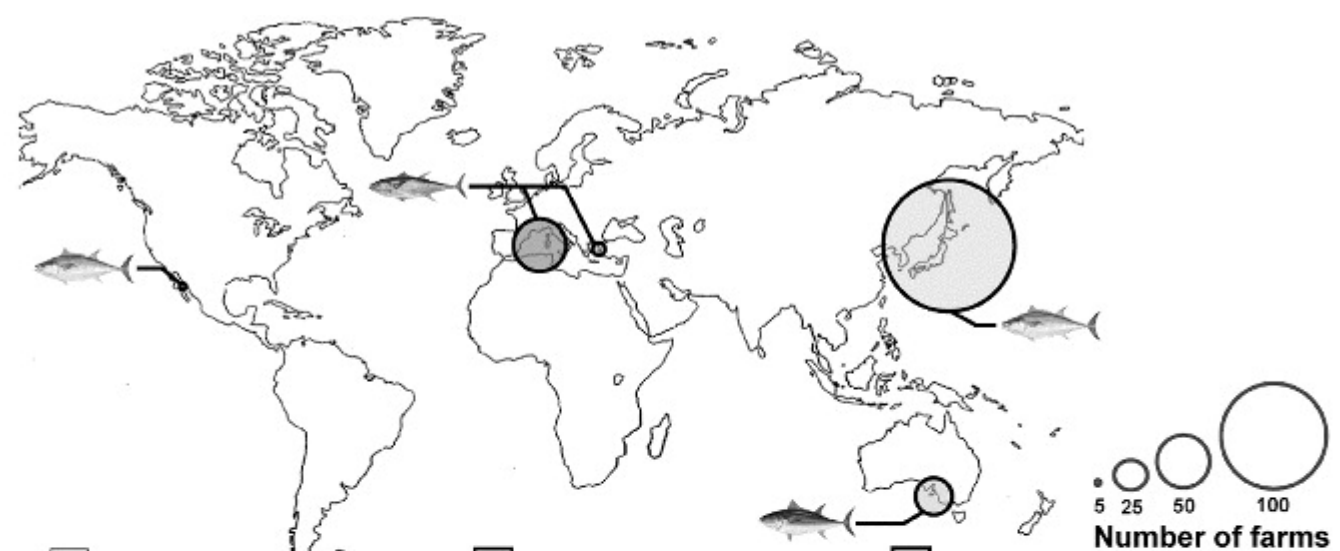
556

557 Figure 3



558

559 Figure 4



Country	Number of farms	Farming capacity (t)	Country	Number of farms	Farming capacity (t)	Country	Number of farms	Farming capacity (t)
Mexico	5 (active)	n.c.	Croatia	4	7,430	Japan	125 (up to 140)	n.c.
			Cyprus	3	3,000	Australia	35	49 266
			Spain	17	11,852			
			Greece	2	2,100			
			Italy	14	12,600			
			Malta	8	12,300			
			Libya	1	1,000			
			Tunisia	5	1,867			
			Turkey	12	8,660			

Global **potential capacities** reported : **110,0075 tonnes** (Japan & Mexico's p.c. not communicated)
 Global number of BFT aquaculture : **227 farms** (43% with potential capacities reported)

560 Figure 5