LETTER

Impending collapse of bluefin tuna in the northeast Atlantic and Mediterranean

Brian R. MacKenzie[1,2], Henrik Mosegaard[1], & Andrew A. Rosenberg[3]

[1] National Institute for Aquatic Resources (DTU-Aqua), Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark
[2] Department of Marine Ecology, Biology Institute, University of Aarhus, c/o Charlottenlund Castle, DK-2920 Charlottenlund, Denmark
[3] Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824, USA

Keywords
Atlantic; bluefin tuna; collapse; conservation; exploitation; management; Mediterranean; recovery; recruitment; reproduction.

Correspondence
Brian R. MacKenzie, National Institute for Aquatic Resources (DTU-Aqua), Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark.
Tel: +45-3396-3300; fax: +45-3396-3333.
E-mail: brm@aqua.dtu.dk

Received: 15 September 2008; accepted 18 October 2008

doi: 10.1111/j.1755-263X.2008.00039.x

Abstract

The abundance of bluefin tuna, *Thunnus thynnus*, in the east Atlantic and Mediterranean has declined in recent decades. The International Commission for the Conservation of Atlantic Tunas (ICCAT), the regional bluefin tuna management authority, has developed a plan to promote recovery by 2022, while still permitting fishing to continue during the period 2008–2010. Here we predict that the adult population in 2011 will likely be 75% lower relative to 2005 and that quotas in some intervening years will allow the fishery to capture legally all of the adult fish. Population demographics (proportion of older fish and repeat spawners in population) indicate that buffering capacity against years of poor reproduction has been reduced. This population is at risk of collapse (90% decline in adult biomass within three generations, the criterion used by the IUCN for defining populations as *Critically Endangered*), even under the currently agreed recovery plan, unless new conservation measures are implemented in the next few years.

Introduction

A key objective of fisheries management is to maintain populations at levels where the biomass of adults does not limit the production of new young fish (Myers & Barrowman 1996; Rosenberg 2003; Beddington *et al.* 2007). This objective has proven difficult to achieve in many of the world's commercially most important fisheries: 50% and 25% of all exploited marine fish populations in the world are considered to be fully- or over-exploited, respectively (Garcia *et al.* 2005). Because effective management is difficult to implement, populations often undergo large declines and, in some cases, entire fisheries have been closed to allow populations to recover. Examples of such declines of exploited marine populations are well documented (Jackson *et al.* 2001; Hutchings & Reynolds 2004; NRC 2006; Rosenberg *et al.* 2006). Recovery following fishing closures is often slow and sometimes impossible if the depleted population is still captured incidentally in fisheries targeting other species, or if changes to habitats, the environment or food web occur, which also affect offspring survival rates (Hutchings & Reynolds 2004). The difficulties associated with preventing declines in the first place or rebuilding depleted stocks are primarily due to the difficulty of reducing fishing pressure in the face of resistance by the fishing industry to strict management controls (Rosenberg 2003; Rosenberg *et al.* 2006; Beddington *et al.* 2007).

Here we demonstrate that bluefin tuna (*Thunnus thynnus*) in the northeast Atlantic and Mediterranean (east of 45° west longitude) may also be on the way to collapse (90% decline in adult biomass within three generations, the criterion used by the World Conservation Union for defining populations as *Critically Endangered*). This population has been declining for many years (Fromentin & Powers 2005; ICCAT 2007) (Figure 1), and the biomass of adults (spawning stock biomass) is now (2006) at its lowest on record (approximately 40% of late 1950s' biomasses; Figure 1), with the steepest decline in last 5–10 years (ICCAT 2008). At these population sizes, reproductive dynamics become increasingly uncertain and are likely limited by spawner biomass (Figure 1).

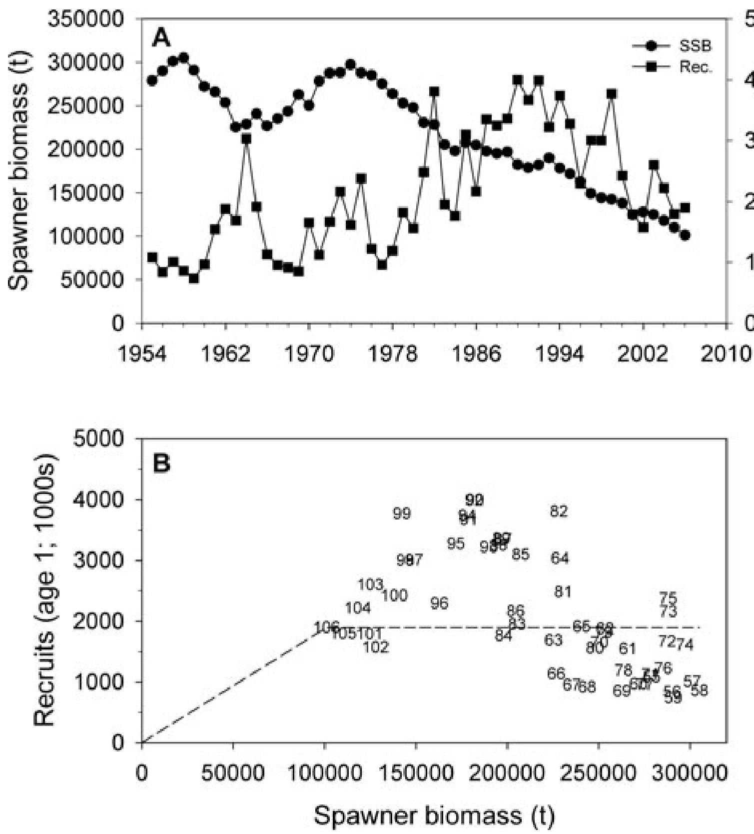

Figure 1 Temporal trends in spawner biomass and recruitment of the bluefin tuna population in the eastern Atlantic and Mediterranean, and the relationship between spawner biomass and recruitment. (A). Spawner biomass and recruitment (numbers of fish born in a given year and surviving to age 1). (B). Recruitment produced by different levels of spawner biomass. Symbols depict years corresponding to last 2 digits of birth years of recruits. Dashed line: the assumed spawner–recruit relationship used in population development scenarios 1–4. The breakpoint was estimated as the lowest observed spawner biomass (ICES 2003) (101,000 t), which occurred in 2006 (panel A); recruitment for this year is uncertain (ICCAT 2008) and was estimated as the geometric mean for the previous 5 years. See Methods for details. Input data from ICCAT (ICCAT 2008).

The spatial distribution of large, adult (> ~30–35 kg and 4–5 years) bluefin tuna has also changed since the 1950s–1970s. These size-groups were common in the Bay of Biscay (Cort & Nøttestad 2007), the North Sea and Norwegian Sea (Mather *et al.* 1995; Fromentin & Powers 2005; MacKenzie & Myers 2007), but now are rare in these areas. Bluefin tuna disappeared from the Black Sea in 1987 (Karakulak 2004) and fishery-independent surveys shows that the species is now rare in parts of the Ionian Sea (northcentral Mediterranean; Bearzi *et al.* 2006). Their disappearance from these areas has coincided with or followed the expansion of fisheries in all these regions, and generally throughout the northeastern Atlantic and Mediterranean (Mather *et al.* 1995; Fromentin & Powers 2005; ICCAT 2006b). While the causes for these disappearances require further investigation, they are consistent with fishing-induced declines of abundance (FAO 1995, 1996; ICES 2005).

The declines in biomass and contractions of geographic range indicate that the population is overexploited (FAO 1996; ICES 2005), as has been recognized by ICCAT scientists (ICCAT 2008), the EU (EU 2007, 2008), and the conservation community (WWF 2006). A recovery plan adopted in January 2007 by the International Commission for the Conservation of Atlantic Tunas (ICCAT) was implemented during 2007 (ICCAT 2006a; EU 2007). It has been developed and adopted because of concerns that the highly efficient bluefin tuna fishery may lead to commercial and local extinction throughout much of its range. The overall goal of the recovery plan is to increase spawner biomass to a level (B_{MSY}), which should support the largest long-term annual catch (i.e., maximum sustainable yield, MSY) with > 50% probability by 2022 (ICCAT 2006a). Management, which will have greatest impact on population dynamics, including the probability that biomass will increase to B_{MSY}, will be that which most directly and immediately affects fishing mortality and abundance now and in the next few years. These measures include regulations to restrict catches during the period 2007–2010 (Table 1) and to increase the minimum size of captured fish from 10 to 30 kg. This latter measure is intended to increase survival of juvenile tuna so they can reproduce at least once before capture. Recently (12 June 2008), the EU implemented short-term (6 month) emergency conservation regulations in response to new evidence of damaging fishing practices by six EU countries during the period 2007–2008 (EU 2008).

Table 1 Settings for projection simulations of bluefin tuna population development during the period 2006–2022 in the northeast Atlantic and Mediterranean. F_{i-j} = age-specific fishing mortality for ages *i* – *j*; SQ = status quo, as represented by average for last 3 years of the most recent assessment (i.e., 2004–2006) and based on officially reported catch data (run 13 in ICCAT 2008); TAC = total allowable catch, as defined in the recovery plan (ICCAT 2006a), and is 29,500; 28,500; 27,500; and 25,500 t for 2007, 2008, 2009, and 2010, respectively. SSB_{low} (lowest observed spawner biomass) is the *SSB* below which recruitment is limited by *SSB* and above which recruitment varies independently of *SSB* (ICES 2003); SSB_{low} was estimated as the lowest observed spawner biomass (101,000 t) in the period of available data (1955–2006). See also Methods and Supporting Information for details

Scenario	Landings in 2006 and 2007	Spawner biomass–recruitment model	Fishing mortalities
1	Officially reported (30,650 t in each year)	Hockey stick; SSB_{low} = 101,000 t	2008–2010: $F_{1-3} = 0.15 * $ SQ (2004–2006); F_{4-20+} = TAC-dependent 2011–2022: $F_{1-3} = 0.15 * $ SQ (2004–2006); $F_{4-20+} = 0.5 * $ SQ (2004–2006)
2	ICCAT estimates (50,000; 60,000 t)	Hockey stick; SSB_{low} = 101,000 t	2008–2010: $F_{1-3} = 0.15 * $ SQ (2004–2006); F_{4-20+} = TAC-dependent 2011–2022: $F_{1-3} = 0.15 * $ SQ (2004–2006); $F_{4-20+} = 0.5 * $ SQ (2004–2006)
3	Officially reported (30,650 t in each year)	Hockey stick; SSB_{low} = 101,000 t	2008–2010: $F_{1-3} = 0.15 * $ SQ (2004–2006); F_{4-20+} = TAC-dependent 2011–2022: $F_{1-3} = 0.15 * $ SQ (2004–2006); $F_{4-20+} = 0.15 * $ SQ (2004–2006)
4	ICCAT estimates (50,000; 60,000 t)	Hockey stick; SSB_{low} = 101,000 t	2008–2010: $F_{1-3} = 0.15 * $ SQ (2004–2006); F_{4-20+} = TAC-dependent 2011–2022: $F_{1-3} = 0.15 * $ SQ (2004–2006); $F_{4-20+} = 0.15 * $ SQ (2004–2006)
5	ICCAT estimated (50,000; 60,000 t)	Ricker	2008–2010: $F_{1-3} = 0.15 * $ SQ (2004–2006); F_{4-20+} = TAC-dependent 2011–2022: $F_{1-3} = 0.15 * $ SQ (2004–2006); $F_{4-20+} = 0.5 * $ SQ (2004–2006)

In addition to changes in abundance and range occupied, the size and age structure of exploited fish populations often changes systematically over time (Anderson *et al.* 2008). These changes, which have not yet been investigated for bluefin tuna in the northeast Atlantic and Mediterranean, include changes in age/size composition and spawning experience (first-time vs. repeat), and can have direct and indirect effects on reproductive and recruitment potential, including individual relative fecundity and offspring viability (Lambert 1990; Marshall *et al.* 2003). These reproductive demographic changes in turn can lead to higher recruitment variability in heavily exploited fish populations compared with populations experiencing lower exploitation (Hsieh *et al.* 2006; Anderson *et al.* 2008). We hypothesize that similar changes in age/size structure have occurred for this population and that they may be another indicator that the population is overexploited.

Our study has two objectives related to the exploitation status and sustainability of this population. We first evaluate the likelihood that the new recovery plan will result in conservation of this population and an increase in its size to levels where recruitment is no longer limited by spawner abundance. We predict using forward projection population dynamics models how the population will respond to the recovery plan, and in particular whether the plan, assuming full implementation and successful compliance by the fishing industry, will lead to recovery of this population within the expected time frame. Our second objective is to quantify changes in age structure and reproductive demographics over time.

Methods

Population modeling

Model description

We used an age-structured stochastic modeling approach similar to that used in many fisheries assessment working groups of the International Council for the Exploration of the Sea (e.g., ICES Baltic Fisheries Assessment Working Group (ICES 2006)). The model is used for predicting future development of fish populations (typically over 10–20 years) under different assumptions of fishing mortality and population biology (e.g., growth rates, maturity schedules, reproduction rate). Empirically derived estimates of the uncertainty of input variables is directly included in the model so that probabilistic outputs of population variables (e.g., biomasses) are derived. We used biological and fishing mortality rate information from assessment run 13 of ICCAT (ICCAT 2008) to parameterize the model.

In brief, the modeling framework uses the starting population size at 1 January of each year and applies natural and fishing mortality rates to estimate numbers of survivors to 1 January of the following year. Annual estimates of adult biomass are derived from numbers of mature individuals multiplied by their weights-at-age. Production rate of new bluefin tuna each year (recruitment) is estimated from a functional relationship to spawner abundance. Full details of the modeling approach and the spawner biomass–recruitment relationship are described in Supporting Information.

Scenario descriptions

We simulated population abundance according to five different scenarios to evaluate how the population would develop under full implementation of the new management plan (Table 1). The scenarios we considered investigated the uncertainty of catches in 2006 and 2007, the parameterization and uncertainty of the spawner biomass–recruitment relationship, the limits on catches for 2008–2010, and the consequences of a recent increase in minimum landing size from 10–30 kg for most, but not all, bluefin tuna fisheries in the northeast Atlantic and Mediterranean. The total allowable catches (TACs) in 2007, 2008, 2009, and 2010 are 29,500; 28,500; 27,500; and 25,500 t, respectively (ICCAT 2006a).

All scenarios started in 2006 (most recent year for which abundance estimates were available for all age groups) and end in 2022, when the current recovery plan should end (ICCAT 2007). We conducted five scenarios: two scenarios used the officially reported catches for 2006 (30,650 t), which ICCAT scientists (ICCAT 2008) also assumed applied for 2007 (their assessment run 13), and three scenarios assumed the real catches estimated by ICCAT for 2006 and 2007 (50,000 and 60,000 t, respectively). Additional details of the scenario settings are given in Table 1.

We present and interpret results both for overall trends in output variables (spawner biomass, yield, and recruitment) and for output values at the end of the initial TAC period (i.e., 2011) and end of the recovery period (2022). We compared biomass declines with those used by the World Conservation Union to define extinction risk. In particular, we evaluated the probability that a decline in adult biomass of 90% would occur within three generations, and consider this decline rate to be a measure of population collapse. This decline rate is used by IUCN to define populations as *Critically Endangered* (IUCN 2006).

Trends in population demographics

We quantified changes in age/size composition and reproductive demographics that have occurred for bluefin tuna in the eastern Atlantic and Mediterranean. We calculated the mean age of spawners, and the proportion of older bluefin tuna (i.e., age $\geq$ 8 years) using annual ICCAT population numbers-at-age data (ICCAT 2008). We also estimated the proportion of the population, which was a repeat spawner: because bluefin tuna mature at ages 4–5 years (ICCAT 2008), we assumed that half of all 5-year olds were repeat spawners (i.e., 50% of the 5-year olds were mature and spawned as 4-year olds) and that all fish aged $\geq$ 6 had spawned at least once.

Results

We first consider scenarios 1 and 3, which assume officially reported catches for 2006–2007 and recovery plan catch during the period 2008–2010. In scenario 1, spawning stock biomass is estimated to be 99,000 in 2011 and increase to 210,000 t in 2022 (Figure 2A). Recruitment in 2012 and 2022 is expected to be 1.6 and 1.9 million individuals, respectively (Figure S2A). In comparison, geometric mean recruitment for 2001–2005 was 2 million (ICCAT 2008). Projected yield in 2022 is approximately 30,000 t (Figure S3A). In scenario 3, spawning stock biomass rises more sharply after the TAC period due to the lower assumed fishing mortality for ages $\geq$ 4 years. Spawner biomass could reach 335,000 t (Figure 2C), which would support yields of approximately 18,000 t even at these lower F-values (Figure S3C).

The next two scenarios (2 and 4) employ the more realistic and higher estimates of catches in 2006 and 2007 (ICCAT 2008) than those officially reported to ICCAT; otherwise settings are the same as for scenarios 1 and 3, respectively. Scenario 2 predicts a reduction of spawning stock biomass to 25,000 t in 2010 and 28,000 t in 2011 (Figure 2B). In 2010 (final year of existing recovery plan when TAC = 25,500 t), the fishery is legally able to capture all spawners, and there is a 5% chance that spawning stock biomass will fall to 2,000 t (Figure 2B). Recruitment will fall as spawning stock biomass declines in the early 2010s (Figure S2B). Low fishing mortality starting in 2011 allows spawning stock biomass to increase nearly four-fold to approximately 100,000 t in 2022 (Figure 2B).

Scenario 4 settings were similar to scenario 2 except that fishing mortality of age groups $\geq$ 4 during 2011–2022 was reduced from 50% of status quo (2004–2006) to 15% of status quo. A similar decline in spawning stock biomass until end of 2010 is therefore seen in both scenarios 2 and 4, but as expected, it increases more in the reduced fishing scenario (4) to approximately 177,000 t by 2022 (Figure 2D).

Under scenario 2, there is only approximately 50% probability that the population will recover to its size before implementation of the recovery plan, and that the population will exceed the threshold that no longer limits reproduction (defined as SSB_{low}; Figure 3). Moreover, there is < 5% probability that spawning stock biomass in 2022 will exceed the long-term mean biomass (Figure 3). In contrast, under scenario 4, assuming low fishing mortality for all age groups starting in 2008, there is approximately 80% chance that spawning stock biomass in 2022 will exceed SSB_{low}, and approximately 40% chance that it will exceed the long-term mean (Figure 3).

Scenarios 2 and 5 compare projected stock development assuming different spawner biomass–recruitment

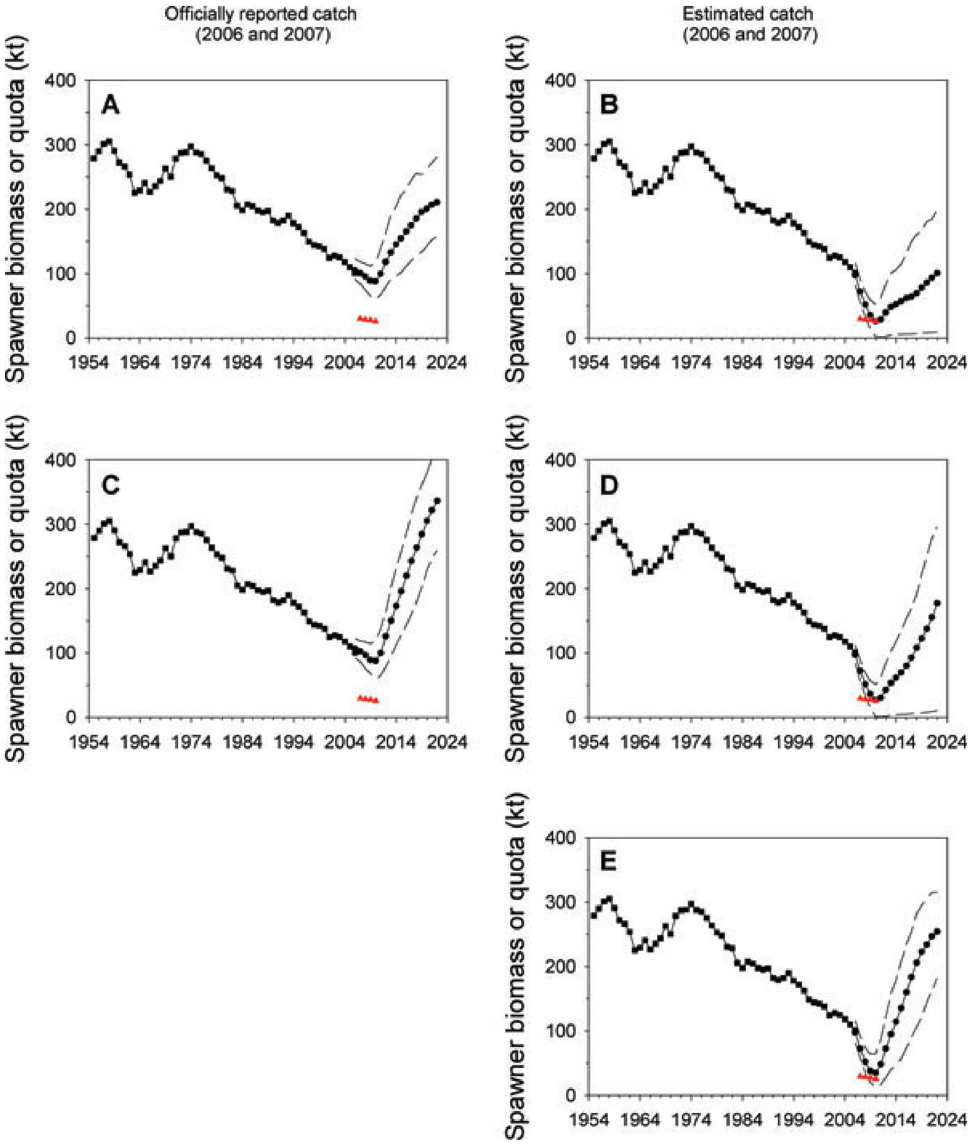

Figure 2 Projections of bluefin tuna spawner biomass under various fishing and productivity scenarios in the coming years, including those associated with total allowable catches (TACs) during the period 2008–2010. Panels A–E correspond to scenarios 1–5 as summarized in Table 1. Solid line with circles: median probability of spawner biomass; dashed lines: 5th and 95th percentiles of spawner biomass. Simulations were conducted using realistic biological inputs and levels of uncertainty in initial numbers and annual recruitment in an age-structured stochastic population model. Projections start in 2006 (final year for which officially reported catch data were available for biomass estimations) and continue until 2022 when the recovery plan objectives should be met (ICCAT 2006a; ICCAT 2007). Also shown for historical comparison (solid black line with squares) is the estimated spawner biomass during the period 1955–2006, as estimated by virtual population analysis (ICCAT 2008) (VPA), and the quota (TAC) levels associated with the recovery plan (solid red line with red triangles). For panels A–D, the breakpoint spawner biomass–recruitment relationship was used to estimate future recruitment (breakpoint = 101,000 t); for panel E, a Ricker relationship was used (see Figure S1 and Table S1 for parameters).

models (Figure S1); all other model settings were identical. Mean ± 95% confidence limits for spawner biomass in 2011 were 28,000 t (1,000–62,000 t) and 48,000 t (16,000–85,000 t) for the two scenarios, respectively (Figures 2B and 2E). Based on both models, it is likely that recruitment in next few years will be substantially reduced due to low spawner abundance (Figure S2B and E). In 2022, projected spawner biomass was 100,000 and 254,000 t, respectively (Figures 2B and 2E).

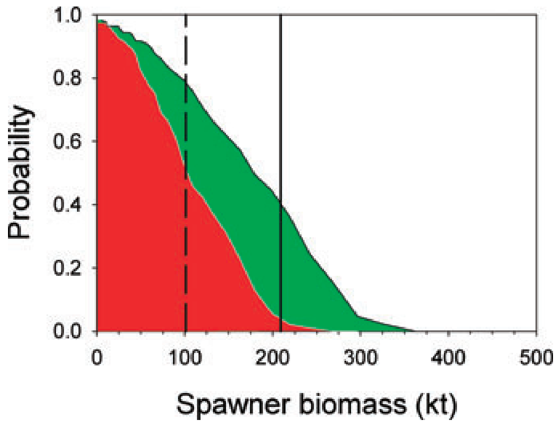

Figure 3 Probability distributions ($N = 200$ estimates) from stochastic modeling scenarios that bluefin tuna spawning stock biomass (*SSB*) in the NE Atlantic and Mediterranean by 2022 will exceed the level of *SSB* below which recruitment is expected to fall sharply ($SSB_{low} = 101{,}000$ t, this level also corresponds to the last spawner biomass estimate prior to recovery plan implementation; vertical dashed line on panel), and the long-term geometric mean *SSB* during the period 1955–2006 (209,000; vertical solid line on panel). The red (left) area (scenario 2; Table 1) assumes the ICCAT recovery plan is fully and successfully implemented during the period 2008–2010 and that fishing mortality in the remaining years of the recovery plan period (2011–2022) is assumed to be reduced by 85% and 50% on age groups 1–3 and 4+, respectively, relative to the fishing mortalities estimated for 2004–2006 using officially reported catch data. The green (right) area (scenario 4) used similar settings as scenario 2, except that fishing mortality was reduced by 85% on all age groups during the period 2011–2022. Both scenarios assume that catches in 2006 and 2007 were 50,000 and 60,000 t, respectively (ICCAT 2008). See Table 1, Methods, and Supporting Information for scenario settings and modeling details.

Several population-level indicators of age structure and reproductive demographics have declined since the start of available datasets in 1955. The mean age of mature bluefin tuna has declined since the mid-1980s and the proportion of age $\geq$ 8 years has declined, especially since the late 1970s (Figure 4A). The share of repeat spawners in the population has declined and remained generally low since the mid- to late 1980s (Figure 4B).

Discussion

The recent decline of this bluefin tuna population is primarily a result of high exploitation for too many years (ICCAT 2008). Scientific advice by ICCAT scientists and some conservation organizations has not been fully implemented by nations that exploit this population; in cases where the advice has been partly followed (e.g., quotas or fishing capacity reduced but not sufficiently to prevent decline), it has not been effectively enforced. Evidence of weak implementation and enforcement of regulations are reports of illegal fishing (e.g., capture of undersized specimens, failure to report catches, fishing outside closed seasons or areas) summarized by ICCAT scientists and others (ICCAT 2008; WWF 2006), even during the recovery plan period itself (EU 2008). Given the history of fish population collapses elsewhere, and their ecological and socio-economic consequences (Hutchings & Reynolds 2004; Beddington *et al.* 2007), it is perhaps surprising that authorities responsible for managing this population have not been more rigorous in supporting effective conservation measures. We hypothesize that authorities have been unable or unwilling to resist political pressure by the bluefin tuna fishing industry to implement recommended measures, as has been the case in many other jurisdictions for other species (Rosenberg 2003; Rosenberg *et al.* 2006; Beddington *et al.* 2007). These difficulties are particularly acute for economically valuable species such as bluefin tuna whose long-distance and high-seas migratory behavior exposes the species to fishing fleets of a large number of nations inside and beyond the territorial waters of single nations. Hence, enforcement of regulations is difficult and compliance is incomplete (ICCAT 2008).

The expected biomass trajectory, together with the declines in indicators of stock status (discussed below), is alarming: a management plan, which has been developed to promote recovery of a population, will cause it to fall to record lows and could result in both fish population and fisheries collapse. The current ICCAT and EU recovery plan as presently implemented (similar to scenario 2) is predicted to reduce the adult population close to small sizes (i.e., 50% and 5% probabilities that spawning stock biomass = 25,000 and 2000 t in 2010) within one generation of the stock, given realistic fishing mortality rates and biological uncertainty, including that related to recruitment. Even if a near-complete ban on all bluefin tuna fishing in the northeast Atlantic and Mediterranean were implemented immediately in 2008 and enforced until 2022 (scenario 4), the population will probably fall to record lows in the next few years, unless environmental conditions promote exceptionally high recruitment. In the coming years, the existing quota would allow capture of most, or all, adults; this situation makes population sustainability sensitive to the success of individual year classes and reduces buffering capacity against a series of years when environmental conditions reduce offspring survival.

At the projected low biomasses, recruitment will become severely impaired due to (1) low numbers of spawners (Myers & Barrowman 1996; ICCAT 2007), (2) potential Allee effects on reproductive success (Frank & Brickman 2000), and (3) increased risk of recruitment failures due to adverse environmental conditions (Brander 2005). In particular, there is a 25% chance that the

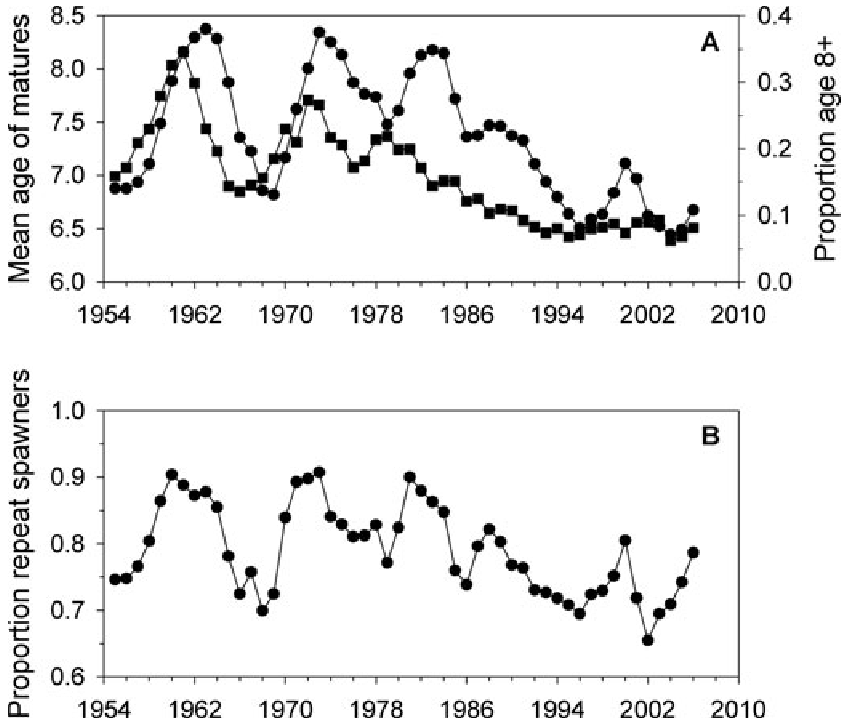

Figure 4 (A). Mean age of mature bluefin tuna (left axis and circles) and proportion of bluefin tuna aged 8 and older among all bluefin in the population older than age 1 (right axis and squares). (B). Proportion of mature bluefin tuna which have spawned at least once in their lifetimes. Data from ICCAT (ICCAT 2008).

expected decline (scenario 2) in biomass between 1999 (spawning stock biomass = 142,000 t) and 2010 (25th percentile = 14,000 t) will be 90% under the agreed recovery plan management measures. Given that a decline > 90% within three generations (= 12–15 years for this population) is one of the criteria for a population to be listed as *Critically Endangered* on the World Conservation Union's Red List (IUCN 2006), the current recovery plan (which allows high catches during the period 2008–2010) ironically could justify a species-at-risk listing, rather than a sustainably managed population. Furthermore, our calculations demonstrate that reproduction will be limited by spawner abundance (i.e., SSB < SSB_{low} = 101,000 t) for many years to come. The status of the eastern bluefin tuna population may therefore reach that of the population in the West Atlantic, which is now extremely low and also in danger of collapse (Safina & Klinger 2008).

Alternative scenarios could be constructed to evaluate various fishing mortalities and compliance levels on recovery, but our overall results and conclusions regarding the decline of the population would not change; in general, higher fishing mortality or implementation failure will prolong population decline and subsequent recovery. In particular, the trajectory after 2010 is uncertain because there presently are no recovery-specific TAC regulations in place following the expiration of the current TAC schedule.

Our projections of biomass development depend, as do all fish population projections, on the recruitment–spawner biomass relationship. We used two such models; both demonstrate that the population will decline to record lows in the next few years under the recovery plan. Our analyses indicate that the hockey–stick model follows the recent recruitment pattern more closely than the Ricker model (see Supporting Information). In addition, the hockey stick model has superior management implications: in particular, meta-analyses based on 100s of fish populations show that it generally does not overestimate maximum reproductive rates at low population sizes, as do alternative models (Barrowman & Myers 2000), and therefore does not overestimate the resilience of the population to declining biomass. These characteristics are particularly important for the specific case of bluefin tuna because the population is in rapid decline, the spawner biomass–recruitment relationship is uncertain, a recovery plan is in place, yet implementation of the management measures and compliance by the fishing industry is difficult (ICCAT 2006b; EU 2007, 2008). Using the hockey stick model for management decisions under these circumstances is therefore more consistent with the precautionary approach to fisheries management (FAO 1995, 1996; ICES 2003).

Other indicators of population status have changed. Age structure and reproductive demographics for the population have shifted to configurations that likely reduce reproductive potential and increase vulnerability of the remaining population to additional stressors, such as ecosystem variability. Although the contribution of different ages to recruit production, parent–offspring relationships and frequency of skipped (nonannual) spawning for bluefin tuna remain to be fully investigated, changes in reproductive demographics like those documented here can lead to a reduction in reproductive and recruitment potential and increased recruitment variability in many other fish species (Marshall *et al.* 2003; Anderson *et al.* 2008). The narrowing and displacement of age structure toward younger individuals with less spawning experience is a common feature in exploited fish populations (Anderson *et al.* 2008). When the population is eventually allowed to recover, recruit production per spawner will likely be lower, and population recovery will probably take longer, than for a population of the same biomass composed of older, more experienced spawners.

The declines in abundance and age structure may also be factors responsible for the disappearance of bluefin tuna from formerly occupied areas in the northeast Atlantic and Mediterranean. For example, many other fish species expand (or contract) their geographic ranges when abundant (or rare) (MacCall 1990; Garrison 2001; Bakun 2005), probably as a response to density-dependent feedbacks as local carrying capacity is reached (Matsukawa 2006). A rebuilding population could reoccupy former areas of the distributional range.

The existing recovery plan, whose progress is scheduled to be assessed in 2008 by ICCAT (ICCAT 2006a), therefore needs rapid adjustment to minimize the rate of further decline especially in 2008–2010. Some other evaluations of the recovery plan using different fishing and biological assumptions also show that the recovery plan objective may not be met (BFT species group 2007) and that implementation success of the new fishery regulations will be critical for achieving the plan objective (Fromentin 2007). Experience with collapses of other fish populations and their recoveries shows that (1) cessation of fishing is the single most effective measure available for promoting the rebuilding of most collapsed fish populations (Rosenberg 2003; Beddington *et al.* 2007), (2) recovery sometimes requires many decades even when exploitation has been greatly reduced, and (3) recovery tends to occur fastest when conservation plans are implemented soon after declines become evident and over short periods (Hutchings & Reynolds 2004; Shertzer & Prager 2007).

A modified recovery plan (i.e., no or little bluefin tuna fishing of any kind for several years) in the northeast Atlantic and Mediterranean urgently needs to be implemented to reduce the risk of population collapse. Implementing major reductions in fishing mortality for this population is difficult (EU 2008); however, past experience with recovery successes shows that fishing mortalities need to be very low in order to promote recovery (Hutchings & Reynolds 2004; Rosenberg *et al.* 2006; Beddington *et al.* 2007). A retrospective analysis by ICCAT showed that fishing mortality since 2003–2004 was three-fold higher than that which would lead to MSY (ICCAT 2007, 2008), and similar difficulties with implementation of fishing restrictions for species (cod *Gadus morhua*, herring *Clupea harengus*, etc.) in other jurisdictions are common (Rosenberg 2003; Beddington *et al.* 2007). Nevertheless, delaying implementation for bluefin tuna will mean that this species in the NE Atlantic and Mediterranean will take longer to recover and become more susceptible to collapse, possibly within one generation. Such a fishing-induced collapse would be an ecological disaster for the population, a fisheries management failure by and for the fishing industry, managers and regulatory agencies, and socio-economic hardship for those depending on the population for livelihoods. Given the slow recovery rate of other collapsed fish populations, many years or even decades may be necessary before a sustainably exploitable population could be reestablished (Hutchings & Reynolds 2004). Moreover, a fishing-induced collapse would contradict the intentions of international agreements such as the FAO Code Of Conduct for Responsible Fisheries Including the Precautionary Approach (FAO 1995, 1996) and the Conventions on Biodiversity (UN 1992), and Sustainable Development (UN 2002), which many signatories of ICCAT and the EU have otherwise adopted.

Acknowledgments

We thank Eskild Kirkegaard, Irene Mantzouni, Jerry Scott, Morten Vinther, and the ICCAT Secretariat for assistance, editors and anonymous reviewers for comments and suggestions, and our late colleague and friend, Ransom A. Myers, for inspiration. This work is a contribution to the History of Marine Animal Populations project of the Census of Marine Life and to two EU Networks of Excellence (MarBEF [publication MPS-08053]; Eur-oceans).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Methods (description of modelling approach)

Spreadsheet file for modelling population dynamics.

Figure S1. Spawner biomass–recruit relationship with fitted recruitment models (hockey stick; Ricker).

Figure S2. Historical and simulated projected recruitment for bluefin tuna in the northeast Atlantic and Mediterranean.

Figure S3. Historical and simulated projected landings of bluefin tuna in the northeast Atlantic and Mediterranean.

Table S1. Input biological data for population modeling.

Table S2. Statistical results of spawner biomass–recruitment analyses.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

References

Anderson, C.N.K., Hsieh, C.H., Sandin, S.A. *et al*. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835–839.

Bakun, A. (2005) Seeking an expanded suite of management tools: Implications of rapidly-evolving adaptive response mechanisms (e.g., "school-mix feedback"). *Bull Mar Sci* **76**, 463–483.

Barrowman, N.J., Myers, R.A. (2000) Still more spawner-recruitment curves: the hockey stick and its generalizations. *Can J Fish Aquat Sci* **57**, 665–676.

Bearzi, G., Politi, E., Agazzi S., Azzellino, A. (2006) Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biol Conserv* **127**, 373–382.

Beddington, J.R., Agnew, D.J., Clark, C.W. (2007) Current problems in the management of marine fisheries. *Science* **316**, 1713–1716.

BFT species group (2007) Eastern Atlantic and Mediterranean bluefin: moving in a good direction and how long will it take to get there? *ICCAT/SCRS/2007/169* 1–7.

Brander, K.M. (2005) Cod recruitment is strongly affected by climate when stock biomass is low. *ICES J Mar Sci J Conseil* **62**, 339–343.

Cort, J.L., Nøttestad, L. (2007) Fisheries of bluefin tuna (*Thunnus thynnus*) spawners in the northeast Atlantic. *Col Vol Sci Pap ICCAT* **60**, 1328–1344.

EU (2007) Council regulation (EC) No. 643/2007 of June 11 2007 amending Regulation (EC) No. 41/2007 as concerns the recovery plan of bluefin tuna recommended by the International Commission for the Conservation of Atlantic Tunas. *Off J Eur Union* L 151/1, 1–16.

EU (2008) Commission regulation (EC) 530/2008 of June 12, 2008 establishing emergency measures as regards purse seiners fishing for bluefin tuna in the Atlantic Ocean, east of 45 W longitude, and in the Mediterranean Sea. *Off J Eur Union* **L155**, 9–10.

FAO. (1995) *FAO code of conduct for responsible fisheries*. Pages 1–49. Food and Agricultural Organisation of the United Nations, Rome, Italy. Available at: http://www.fao.org (accessed 22 November, 2008).

FAO (1996) Precautionary approaches to fisheries. Part 2: guidelines on the precautionary approach to capture fisheries and species introductions. *FAO Fish Tech Pap* **350**, 1–54.

Frank, K.T., Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Can J Fish Aquat Sci* **57**, 513–517.

Fromentin J.-M. (2007) An attempt to evaluate the recent management regulations of the East Atlantic and Mediterranean bluefin tuna stock through a simple simulation model. *ICCAT/SCRS/2007/147* 1–8.

Fromentin J.-M., Powers, J.E. (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish Fish* **6**, 281–306.

Garcia, S., Boucher, J., Cury, P. *et al*. (2005) Workshop 10—Report of the debates and proposed priority actions. In R. Barbault, J.P. LeDuc, editors. UNESCO, Paris.*Proceedings of the International Conference on Biodiversity, Science and Governance, Paris, 24–28 January, 2005*.

Garrison, L.P. (2001) Spatial patterns in species composition in the northeast United States continental shelf fish community during 1966–1999. Pages 513–537 in G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, D. Witherell, editors. University of Alaska Sea Grant College Program AK-SG-01–02, Fairbanks, AK. *Spatial processes and management of marine populations (Proceedings of the Symposium on Spatial Processes and Management of Marine Populations, October 27–30, 1999, Anchorage, Alaska)*.

Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nature* **443**, 859–862.

Hutchings, J.A., Reynolds, D.A. (2004) Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* **54**, 297–309.

ICCAT. (2006a) Recommendation by ICCAT to establish a multi-annual recovery plan for bluefin tuna in the eastern Atlantic and Mediterranean. 06–05, pp. 1–14.

ICCAT. (2006b) Report of the 2006 Atlantic bluefin tuna stock assessment session (Madrid, Spain—June 12 to 18, 2006). ICCAT SCRS/2006/013, 1–137. ICCAT, Madrid, Spain.

ICCAT. (2007) Report of the standing committee on research and statistics (SCRS) , Madrid, Spain, October 1 to 5, 2007. 1–216. 2007. ICCAT, Madrid, Spain.

ICCAT. (2008) Report of the 2008 Atlantic bluefin tuna stock assessment session, Madrid, Spain, June 23 – July 4, 2008. 1–161. ICCAT, Madrid, Spain.

ICES (2003) Report of the study group on precautionary reference points for advice on fishery management. *ICES CM 2003/ ACFM: **15*** 1–81.

ICES. (2005) Ecosystem effects of fishing: impacts, metrics and management strategies. Copenhagen, ICES. *ICES Coop Res Rep* **272**, 1–187.

ICES (2006) Report of the Baltic Fisheries Assessment Working Group. *ICES CM 2006/ACFM:24*.

IUCN. (2006) Guidelines for using the IUCN's red list categories and criteria (version 6.2, December 2006). Pages 1–60 *IUCN Species Survival Commission*. IUCN, Gland, Switzerland and Cambridge, U.K.

Jackson, J.B.C., Kirby, M.X., Berger, W.H. *et al*. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.

Karakulak, F.S. (2004) Catch and effort of the bluefin tuna purse-seine fishery in Turkish waters. *Fish Res* **68**, 361–366.

Lambert, T.C. (1990) The effect of population structure on recruitment in herring. *J Conseil* **47**, 249–255.

MacCall, A. (1990) *Dynamic biogeography of fish populations*. Washington Sea Grant, Seattle, WA.

MacKenzie, B.R., Myers, R.A. (2007) The development of the northern European fishery for north Atlantic bluefin tuna (*Thunnus thynnus*) during 1900–1950. *Fish Res* **87**, 229–239 (doi:10.1016/j.fishres.2007.01.013).

Marshall, C.T., O'Brien, L., Tomkiewicz, J. *et al*. (2003) Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *J Northw Atl Fish Sci* **33**, 161–190.

Mather, F.J., Mason, J.M., Jones, A.C. (1995) US Department of Commerce, NOAA, NMFS, Southeast Fisheries Science Center. *Historical document: life history and fisheries of Atlantic bluefin tuna* 370, 1–165. NOAA Technical Memorandum NMFS-SEFSC-370.

Matsukawa, Y. (2006) Carrying capacity and survival strategy for the Pacific bluefin tuna, *Thunnus orientalis*, in the Western Pacific. *Fisheries Oceanography* **15**, 104–112.

Myers, R.A., Barrowman, N.J. (1996) Is fish recruitment related to spawner abundance? *Fish Bull* **94**, 707–724.

NRC (2006) *Dynamic changes in marine ecosystems. Fishing, food webs and future options. Committee on Ecosystem Effects of Fishing: Phase II—assessments of the extent of change and the implications for policy.* National Academy Press, Washington, DC.

Rosenberg, A.A. (2003) Managing to the margins: the overexploitation of fisheries. *Front Ecol Environ* **1**, 102–106.

Rosenberg, A.A., Swasey, J.H., Bowman, M. (2006) Rebuilding US fisheries: progress and problems. *Front Ecol Environ* **4**, 303–308.

Safina, C., Klinger, D.H. (2008) Collapse of bluefin tuna in the western Atlantic. *Conserv Biol* **2**, 243–246.

Shertzer, K.W., Prager, M.H. (2007) Delay in fishery management: diminished yield, longer rebuilding, and increased probability of stock collapse. *ICES J Mar Sci J Conseil* **64**, 149–159.

UN. (1992) *UN convention on biological diversity*, Rio deJaneiro, Brazil. Available at: http://www.cbd.int. 1–31. New York, United Nations.

UN. (2002) *UN report of the world summit on sustainable development*, Johannesburg, South Africa. A/conf. 199/20, 1–173. New York, United Nations.

WWF. (2006) The plunder of bluefin tuna in the Mediterranean and East Atlantic in 2004 and 2005—uncovering the real story. World Wide Fund for Nature, Rome.

Editor: Corey Bradshaw

Impending collapse of bluefin tuna in the northeast Atlantic and Mediterranean (Supporting information)

Brian R. MacKenzie, Henrik Mosegaard, Andrew A. Rosenberg

Supporting information

Modelling approach

We used an age-structured stochastic modelling approach similar to that used in many fisheries assessment working groups of the International Council for the Exploration of the Sea (e. g., ICES Baltic Fisheries Assessment Working Group (ICES 2006)). The model is used for evaluating development of fish populations in future time periods (typically 10-20 years) under different assumptions of fishing mortality and population biology (e. g., growth rates, maturity schedules, reproduction rate, natural mortality rates). Empirically-derived estimates of the uncertainty of key input variables is directly included in the model so that probabilistic outputs of population variables (e. g., biomasses) are derived. In the case of bluefin tuna in the northeast Atlantic and Mediterranean, we used biological and fishing mortality rate information from assessment run 13 of ICCAT (ICCAT 2008).

The modelling framework uses the starting population size at January 1 of each year and applies natural and fishing mortality rates to estimate numbers of survivors to January 1 of the following year. Estimates of adult biomass at January 1 are derived from numbers of mature individuals multiplied by their weights-at-age.

Natural mortality rates, weights, and probability of maturity data are available on age-specific basis (ICCAT 2006b) (see Table S1); the age range we used was 1-20+ (Fromentin & Kell 2007). We assumed, as does ICCAT (ICCAT 2006b), that these traits are constant over time, partly because there is presently no evidence of temporal trending.

The starting population size in numbers by age (except for age 1) in our model was that estimated by ICCAT for the final year (2005) of run 13 of its 2006 assessment (ICCAT 2008). The numbers of age 1 in the last year of virtual population analyses (VPA) are typically more uncertain than previous years (Shepherd 1999); we therefore used the geometric mean of the last 5 available yearclasses (i.e., 1999-2003) as an estimate of recruitment for 2004. Annual age-specific fishing mortality rates are also available from ICCAT (ICCAT 2008). We used an average of the three most recent assessment years (i.e., 2004-2006) as default fishing mortality rate in model simulations.

The production of new young bluefin tuna (recruitment) can theoretically be estimated using historical functional relationships between annual recruitment and spawner biomass. However for bluefin tuna in the northeast Atlantic and Mediterranean, this relationship is uncertain (ICCAT 2008). Much of the uncertainty in the spawner-recruit relationship is due to the spawner and recruit data, which are based on commercial catch data whose quality has deteriorated in the past 5-10 years (ICCAT 2008). Additional uncertainty is due to the influence of undetermined ecosystem conditions (e. g., predation) which have affected recruitment over the past range of spawner biomass. Uncertainty in the spawner-recruit relationship for eastern Atlantic-Mediterranean bluefin tuna could perhaps be reduced in future if catch data quality were improved (ICCAT 2008) and new research clarified recruitment processes for this population (Garcia *et al.* 2006; Mariani *et al.* 2008).

Nevertheless the population is believed to have declined (EU 2007; EU 2008; ICCAT 2008), and, when spawner biomass is sufficiently reduced, recruitment clearly must decline such that the underlying curve either passes through the origin, or intercepts the x-axis (e. g., if Allee effects become important (Frank & Brickman 2000)). In addition, there is empirical evidence that low levels of fish spawner biomass generally, and specifically for bluefin tuna (western Atlantic population (Brown *et al.* 2002)), produce fewer recruits (Myers & Barrowman 1996; ICES 2003).

Attempts to fit three of the most common models (Ricker, Beverton-Holt, hockey-stick regression) to the data showed that only the Ricker model explained a low amount of variation (Table S2; Figure S1). The parameter estimates and model predictions are uncertain (Figure S1). In addition, the residual variation displayed important temporal variations: for example, the model overestimates recruitment every year after 1999 (Figure S1). Moreover we conducted a retrospective analysis of the ability of the Ricker model to forecast future recruitment by fitting the model to only the data for 1955-1999, and then comparing its predictions with the subsequent 7 year classes (2000-2006). This analysis also showed that the model overestimated recruitment in each subsequent year. Using this model therefore overestimates the recent productivity dynamics of the stock and therefore underestimates the probability of stock decline as spawner biomass is reduced.

Given the uncertainty of the precise form of the spawner-recruit relationship for eastern Atlantic-Mediterranean bluefin tuna, we assumed a simpler relationship in which recruitment is similar to the long-term average (1955-2006) when spawner biomass exceeds the lowest observed SSB (= 101,000 t, hereafter referred to SSB_{low}), but declines linearly to the origin when $SSB < SSB_{low}$ (Figure 1). This model has the advantage that its predictions pass through the cluster of recruitments since 1999 (i.e., both positive and negative residuals). Although the model does not explain much variation over the entire time series, we use it in simulations because of its superior ability to explain recent (post-1999) data (which are characterized by low spawner biomasses, where it is more critical to have proper representation of population dynamics). The hockey-stick approach involving use of SSB_{low} as a breakpoint spawner biomass level is widely accepted among fisheries scientists and managers when stock-recruitment data are uncertain, yet management advice is needed for conservation of populations: the approach has been applied to many other fish populations worldwide and is consistent with major international fishery agreements such as the Precautionary Approach for management of fish stocks (FAO 1995; FAO 1996; ICES 2003). For comparison purposes, we also implemented the Ricker model (Table 1) in one of our simulations.

The applied age-specific fishing mortalities (F) for all years is the mean age-specific F for the last 3 years in the ICCAT VPA assessment. This fishing pattern was expected to change in 2007, when the legal minimum landing size increased to 30 kg from 10 kg for most but not all bluefin tuna fisheries in the northeast Atlantic and Mediterranean. Thirty-kg tuna are approximately 3-4 years old (ICCAT 2008), so from 2008 onwards the fishing mortality for ages 1-3 was set to 15% of the level during 2004-2006 to represent catches allowed by some fleets under the recovery plan, potential noncompliance by the fishing industry with the new regulations and bycatch during fisheries for other species.

ii) Incorporation of biological uncertainty:

The inputs to our population development model are approximations of real values and therefore uncertain to varying degrees. We included past observed estimates of variability of the most important inputs when conducting model simulations. For initial numbers–at-ages 1-20+ (i.e., in

2006), we assumed a coefficient of variation (CV) of 0.30 (Restrepo 2007). Numbers-at-age were then estimated from a random lognormal distribution based on observed numbers-at-age and their variability. Numbers-at-ages 2-20+ in subsequent years were estimated based on annual estimates of natural and fishing mortality. Numbers of age 1 in each year were estimated based on the hockey-stick stock-recruitment relationship described above (Scenarios 1-4) or the Ricker model (Scenario 5).

Uncertainty in recruitment was simulated by sampling randomly from a log-Gaussian distribution fitted to historical time series of recruitment.

For the hockey stick model, if simulated $SSB_i > SSB_{low,}$ then

$$R_i \sim LN(\overline{\ln R}, \sigma^2_{\ln R})$$

where

R_i = expected recruitment in projected year *i*,

$\overline{\ln R}$ = mean of ln R,

$\sigma^2_{\ln R}$ is the variance of ln R (= 0.242).

If $SSB_i < SSB_{low}$, then

$$\frac{SSB_{low}}{SSB_i} * R_i \sim LN(\overline{\ln R}, \sigma^2_{\ln R})$$

For the Ricker model (R = 69.2*S*$e^{-0.0000089*S}$; Table S2), predicted recruitment was calculated from a log-gaussian distribution with variance of ln residuals, $\sigma^2_{\ln res}$, (= 0.152).

All calculations were conducted in a spreadsheet. Simulations of stock development for each set of inputs (see below and Table 1 for specification) were repeated 200 times to generate distributions of spawner biomass, recruitment and fishing yield. These distributions used the random variations associated with the initial population sizes and the spawner biomass – recruitment relationships. Based on these distributions we estimated percentiles (5, 10, 25, 50, 75, 90, 95) to quantify the uncertainty of our population projections, and the risk that population size would remain low, given realistic levels of variability in key biological inputs.

We also consider how catch uncertainty (i.e., uncertainty in the total landings) affect population projections. This topic is addressed under “Scenario descriptions”.

iii) Scenario descriptions

We simulated population abundance according to five different scenarios to evaluate how the population would develop under full implementation of the new management plan (Table 1). The scenarios we considered investigated the uncertainty of catches in 2006 and 2007, the parameterisation of the spawner biomass-recruitment relationship, the limits on catches for 2008-2010 due to the recovery plan, and the consequences of a recent increase in minimum landing size from 10 to 30 kg for most but not all bluefin tuna fisheries in the northeast Atlantic and Mediterranean. The Total Allowable Catches (TACs) in 2007-2010 are 29,500, 28,500, 27,500 and 25,500 t, respectively (ICCAT 2006a).

All scenarios started in 2006 (most recent year for which abundance estimates were available for all age-groups) and end in 2022. The choice of end year was defined based on the final year in the current recovery plan for this population (ICCAT 2007): we wished to estimate the trajectory of population development during the whole recovery plan period. We conducted 5 scenarios: 2 scenarios used the officially reported catches for 2006 (30,650 t), which ICCAT scientists also assumed applied for 2007 (their assessment run 13), and 3 scenarios assumed the real catches estimated by ICCAT for 2006 and 2007 (50,000 and 60,000 t respectively).

Scenarios 1 and 3 assume that landings in 2006 and 2007 equalled those officially reported to ICCAT for 2006; several EU countries had not reported their catch for 2007 in time for the June 2008 assessment meeting, so ICCAT scientists assumed official catches in 2007 were similar to those in 2006 (ICCAT 2008). In 2008-2010, we assumed that catches would follow the agreed TAC and allowed the age-specific fishing mortalities to reflect those catch levels. However, because fishing mortality rates differ among age-groups, we restrict the relative age-specific pattern of fishing mortalities (known as “selection pattern” in fisheries science) to represent the average during 2004-2006 (last three years of assessment based on official catch data). In 2008-2010, however, we assumed that *relative* fishing mortality on ages 1-3 would be 85% lower than during 2004-2006 (based on officially reported catch data) because of the implementation of new minimum size restrictions during 2007; this size restriction, in combination with the agreed TAC in 2008 (28,500 t), essentially shifts fishing pressure to older age groups for 2008-2010. Starting in 2011, we assumed that fishing mortality of ages 1-3 would continue to be 15% of the levels during 2004-2006. For scenarios 1 and 3 we assumed that fishing mortality of ages $\geq$ 4 would be 50 and 15%, respectively of that during 2004-2006.

Scenarios 2 and 4 had identical settings as scenarios 1 and 3 except that we assumed that catch in 2006 and 2007 were those estimated by ICCAT scientists (ICCAT 2008) (50,000 and 60,000 t, respectively). These scenarios consider therefore how catch uncertainty in the recent two years could affect perception of population development in coming years.

Scenarios 1-4 all used the hockey stick spawner–recruitment relationship with breakpoint at 101,000 t. Scenario 5 used the Ricker model; other settings for scenario 5 are identical to those for scenario 2. Hence the sensitivity of population projections using the two stock-recruitment models are directly comparable for scenarios 2 and 5.

We present and interpret results both for overall time trends in output variables (spawner biomass, yield and recruitment) and for output values at the end of the initial TAC period (i.e., 2011) and end of the recovery period (2022).

Supporting tables

Table S1. Input biological values used for population modelling of bluefin tuna in the northeast Atlantic and Mediterranean. Numbers data are for 2006 for ages 2-20+ or geometric mean from years 2002-2006 (yearclasses 2001-2005) for age 1. The coefficient of variation of the numbers-at-age was 0.3 and was used in population simulations. Fishing mortalities are averages for 2004-2006 based on officially reported catch data. Data sources: ICCAT (ICCAT 2008) for numbers, maturity and mortalities (assessment run 13; V. Restrepo (NOAA, USA, pers. comm.) for weights.

Age	Numbers	Weight (kg)	Prob. mature	Natural mortality	Fishing mortality
1	1964315	5.4	0	0.49	0.275
2	1116760	12.8	0	0.24	0.446
3	790262	23.4	0	0.24	0.508
4	309505	37.2	0.5	0.24	0.156
5	245404	53.5	1	0.24	0.143
6	271083	71.9	1	0.20	0.158
7	208771	92.0	1	0.175	0.228
8	170280	113.2	1	0.15	0.280
9	121435	135.0	1	0.125	0.370
10	20081	157.2	1	0.10	0.370
11	21819	179.4	1	0.10	0.370
12	16982	201.4	1	0.10	0.370
13	17337	222.8	1	0.10	0.370
14	12478	243.6	1	0.10	0.370
15	11242	263.6	1	0.10	0.370
16	10768	282.8	1	0.10	0.370

17	4095	301.0	1	0.10	0.370
18	4610	318.3	1	0.10	0.370
19	1793	334.6	1	0.10	0.370
20+	7310	349.9	1	0.10	0.370

Table S2. Statistical results of attempts to fit spawner biomass-recruit models for bluefin tuna in the eastern Atlantic and Mediterranean. $R^2_{adj.}$ = explained variation, adjusted for number of fitted parameters in model; P = probability of making a Type I error; N = 34 year classes (1955-2006 (ICCAT 2008)). Parameter estimates for the Ricker model are shown with standard error.

Model	Equation	$R^2_{adj.}$	P
Ricker	$R = 69.2 \pm 12.4 \cdot S \cdot e^{-0.0000089 \pm 0.0000009 \cdot S}$	0.34	< 0.0001
Beverton-Holt	$R = S / (a + b \cdot S)$	Could not be fit	--
Hockey-stick regression	$R = a \cdot S$ if $S < S_{break}$; $R = a \cdot S_{break}$ if $S > S_{break}$	Could not be fit	--

Supporting figure captions:

Figure S1. Relationship between spawner biomass and recruitment for bluefin tuna in the eastern Atlantic and Mediterranean during 1955-2006 (symbols denote yearclasses according to last 2 digits of birthyears). The thick solid line shows the hockey stick model with a breakpoint at the lowest observed spawner biomass (101,000 t). This model was used in scenarios 1-4. The thin solid line is the fitted curve from the Ricker model ($R = 69*S*e^{-0.0000089*S}$); dashed lines show the model fit given the uncertainty ($\pm$ 2 standard errors) of the steepness parameter, a (= 69), from this model. The Ricker model was used in scenario 5.

Figure S2. Historical and simulated future recruitment and 95% confidence limits for the five scenarios corresponding to those described in Table 1 and Figure 2. Recruitment data for 1955-2006 from ICCAT (ICCAT 2008).

Figure S3. Historical and simulated future fishery landings and 95% confidence limits for the five scenarios corresponding to those described in Table 1 and Figure 2. Data sources from ICCAT (ICCAT 2008).

Ricker curve fitted using raw data and ± 2 SE of alpha parameter.

$R = 69.2 \pm 12.4 * S * e^{-0.0000089 \pm 0.0000009*S}$

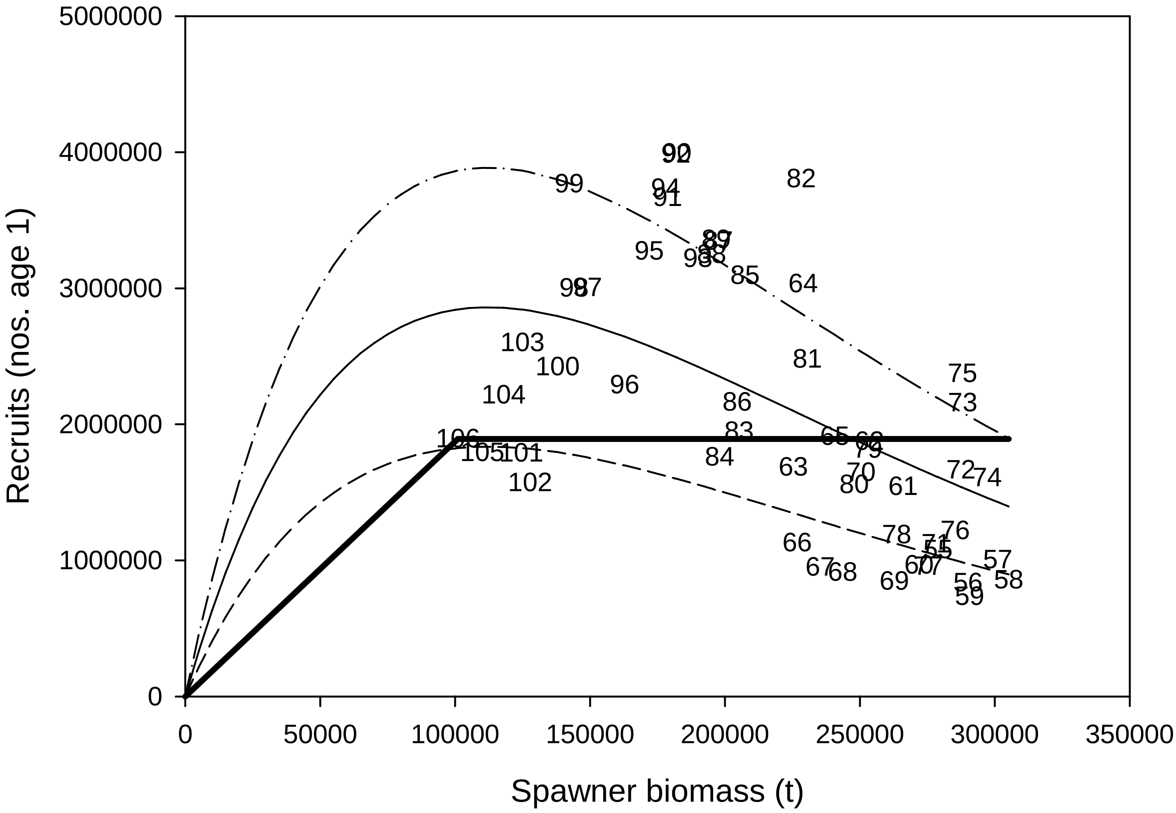

Figure S1.

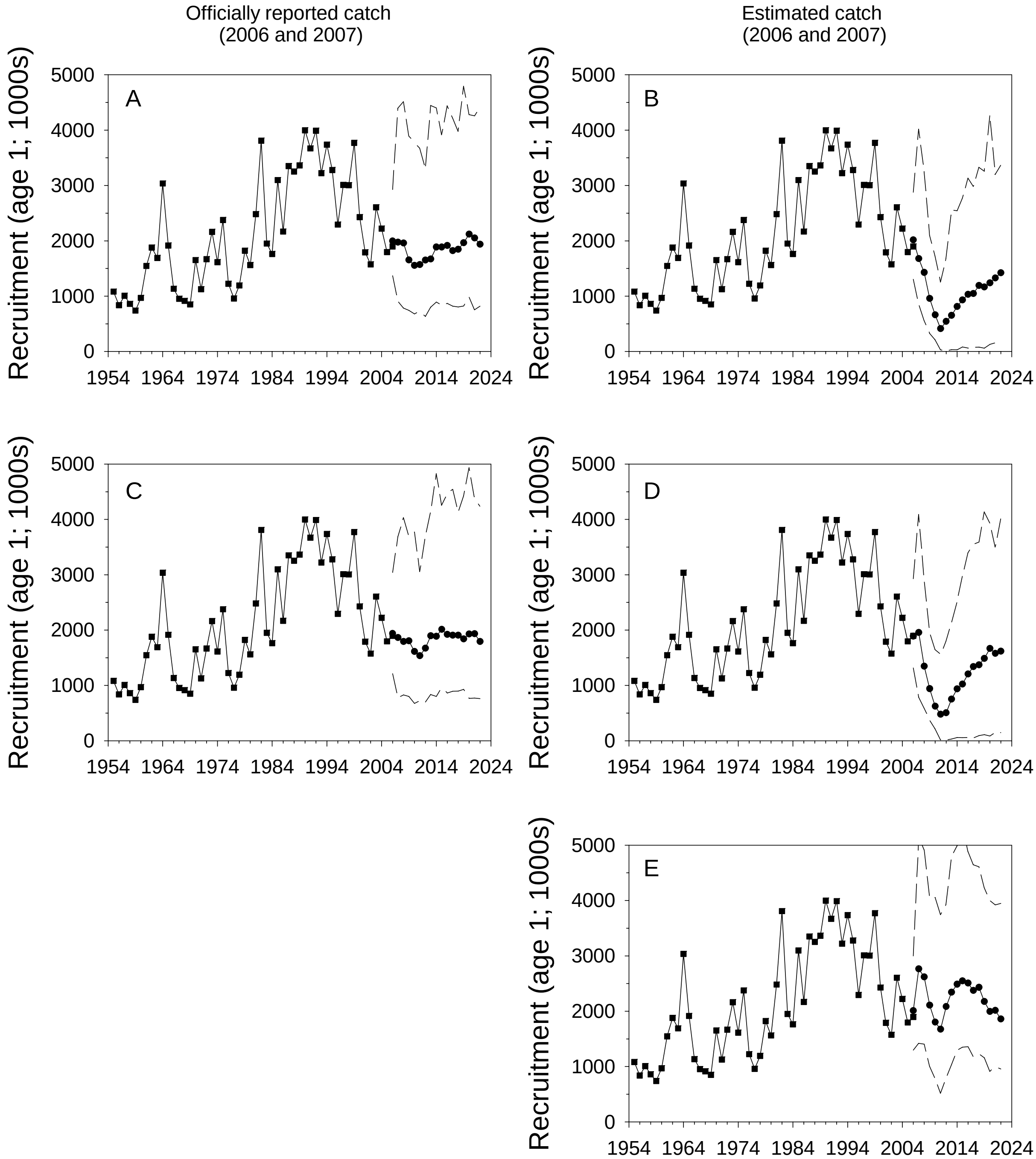
Officially reported catch
(2006 and 2007)
Estimated catch
(2006 and 2007)
A
B
C
D
E
Recruitment (age 1; 1000s)
0
1000
2000
3000
4000
5000
1954
1964
1974
1984
1994
2004
2014
2024

Figure S2

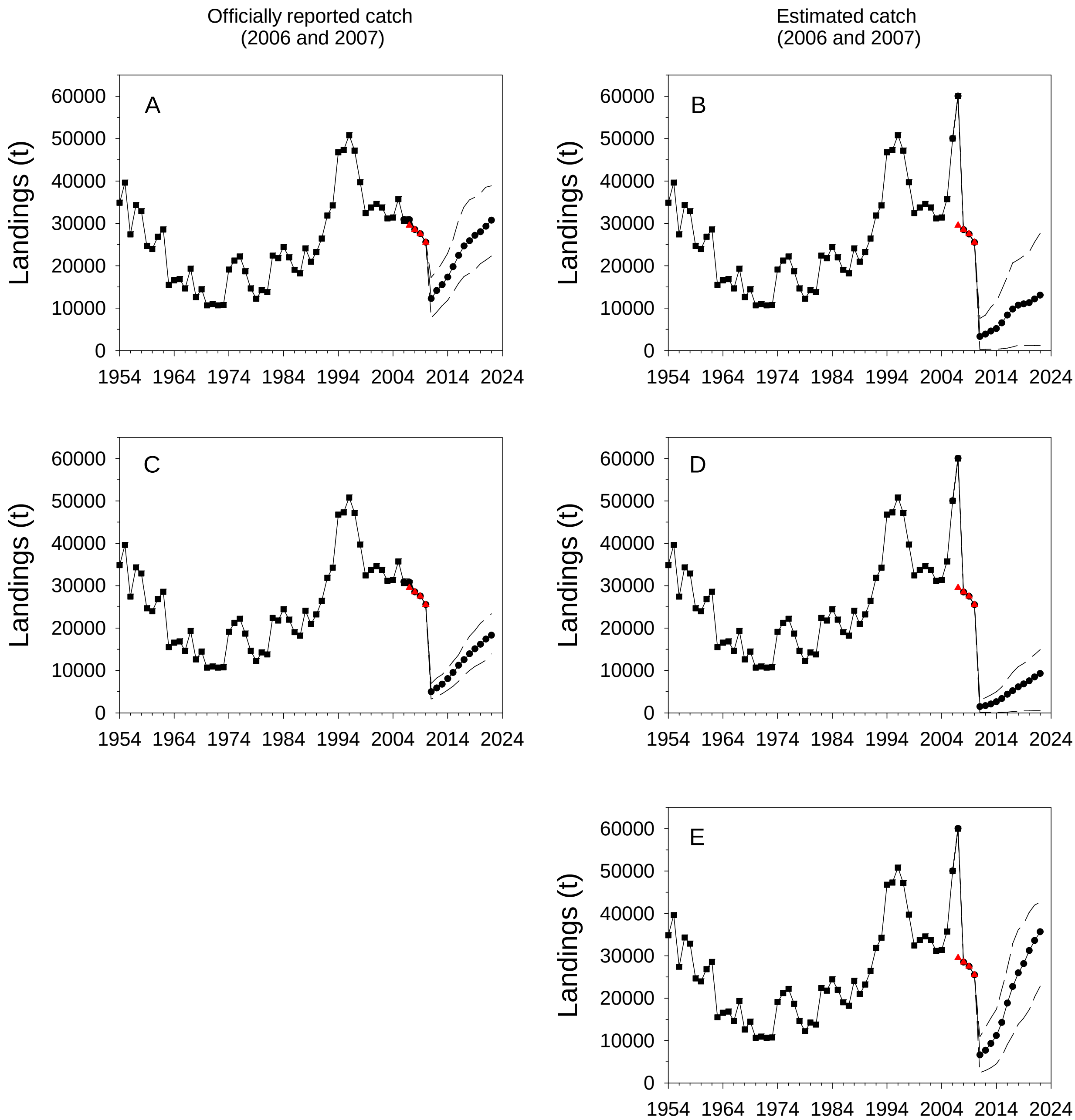
Officially reported catch
(2006 and 2007)
Estimated catch
(2006 and 2007)
A
B
C
D
E
Landings (t)
0
10000
20000
30000
40000
50000
60000
1954
1964
1974
1984
1994
2004
2014
2024

Figure S3

References

Brown C.A., Porch C.E., Scott G.P. & Turner S.C. (2002) Correlation between the North Atlantic Oscillation index and stock-recruitment trends of west Atlantic bluefin tuna (*Thunnus thynnus*). *Col.Vol.Sci.Pap.ICCAT* 54, 953-963

EU (2007) Council regulation (EC) No. 643/2007 of June 11 2007 amending Regulation (EC) No. 41/2007 as concerns the recovery plan of bluefin tuna recommended by the International Commission for the Conservation of Atlantic Tunas. *Official Journal of the European Union (13.6.2007)* L 151/1, 1-16

EU (2008) Commission regulation (EC) 530/2008 of June 12, 2008 establishing emergency measures as regards purse seiners fishing for bluefin tuna in the Atlantic Ocean, east of 45 W longitude, and in the Mediterranean Sea. *Official Journal of the European Union (13.6.2008)* L155, 9-10

FAO. FAO Code of Conduct for Responsible Fisheries (available at http://www.fao.org). 1-49. 1995. Rome, Italy, Food and Agricultural Organisation of the United Nations.

FAO (1996) Precautionary approaches to fisheries. Part 2: Guidelines on the precautionary approach to capture fisheries and species introductions. *FAO Fisheries Technical Paper* 350, 1-54

Frank K.T. & Brickman D. (2000) Allee effects and compensatory population dynamics within a stock complex. *Can.J.Fish.Aquat.Sci.* 57, 513-517

Fromentin J.-M. & Kell L.T. (2007) Consequences of variations in carrying capacity or migration for the perception of Atlantic bluefin tuna (*Thunnus thynnus*) population dynamics. *Can.J.Fish.Aquat.Sci.* 64, 827-836

Garcia A., Cortes D., Ramirez T., Fehri-Bedoui R., Alemany F., Rodriguez J.M., Carpena A. & Alvarez J.P. (2006) First data on growth and nucleic acid and protein content of field-captured

Mediterranean bluefin (*Thunnus thynnus*) and albacore (*Thunnus alalunga*) tuna larvae: a comparative study. *Sci.Mar.(Suppl.2)* 70, 67-78

ICCAT. Recommendation by ICCAT to establish a multi-annual recovery plan for bluefin tuna in the eastern Atlantic and Mediterranean. 06-05, 1-14. 2006a.

ICCAT. Report of the 2006 Atlantic bluefin tuna stock assessment session (Madrid, Spain - June 12 to 18, 2006). ICCAT SCRS/2006/013 , 1-137. 2006b. Madrid, Spain, ICCAT.

ICCAT. Report of the standing committee on research and statistics (SCRS), Madrid, Spain, October 1 to 5, 2007. 1-216. 2007. Madrid, Spain, ICCAT.

ICCAT. Report of the 2008 Atlantic bluefin tuna stock assessment session, Madrid, Spain, June 23 - July 4, 2008. 1-161. 2008. Madrid, Spain, ICCAT.

ICES (2003) Report of the study group on precautionary reference points for advice on fishery management. *ICES CM 2003/ ACFM: 15* 1-81

ICES (2006) Report of the Baltic Fisheries Assessment Working Group. *ICES CM 2006/ACFM:24*

Mariani P., MacKenzie B.R., Iudicone D. & Botte V. (2008) Modelling retention and dispersion mechanisms of bluefin tuna (*Thunnus thynnus*) eggs and larvae in the northwest Mediterranean Sea (Balearic area). *Prog.Oceanogr.(submitted)* x, x

Myers R.A. & Barrowman N.J. (1996) Is fish recruitment related to spawner abundance? *Fish.Bull.* 94, 707-724

Restrepo V.R. Personal communication from Dr. Victor Restrepo, ICCAT scientist (presently at NOAA, USA). 2007.

Shepherd J.G. (1999) Extended survivors analysis: An improved method for the analysis of catch-at-age data and abundance indices. *ICES J.Mar.Science* 56, 584-591