Global population trajectories, life history strategies and vulnerability to fishing of scombrid species: implications for conservation and management

Maria José Juan Jordá

UNIVERSIDADE DA CORUÑA

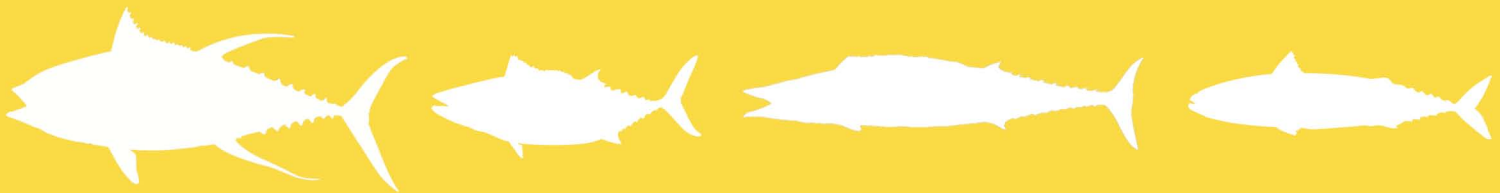**Departamento de Biología Celular y Molecular**

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Tesis doctoral

Global population trajectories, life history strategies and vulnerability to fishing of scombrid species: implications for conservation and management

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Esta tesi la dedique als meus pares,

María José i Tomás,

a la meua germana Aina

i al meu marit Tyson.

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species populations history fishing life scombrid management assessments age exploitation size data studies growth tuna mackerels fisheries biomass history stock maturity fecundity decline marine global strategies mortality longevity spawning tropical identify large annual analysis variation conservation

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Abstract

Fishing is the primary threat to marine species and ecosystems, but the details of the extent of overfishing remains fragmentary. Here, I provide new insights upon the global impacts of fishing on scombrids, which includes 51 species of tunas, Spanish mackerels, bonitos and mackerels, and advance our ability to identify, *a priori*, the characteristics of species that render them most vulnerable to overfishing. First, through a global meta-analysis of adult biomass trends, I show that scombrid populations have declined, on average, by 60% over the last half century. The decline in the total adult biomass is lower (52%) as it is buffered by a few larger sustainably fished populations. Second, I identify major gaps in biological knowledge and prioritize life history research needs, especially for the coastal scombrids. Then, I examine the diversity in their life histories, and reveal that most life history variation in scombrids can be simplified to three dimensions (governed by size, speed of life and reproductive schedule). Finally, I show that those scombrid populations with slowest life histories have experienced the largest declines in biomass and have a higher probability of being overfished. The speed of life traits - growth rate and longevity - are the best life history indicators of vulnerability to fishing. My thesis can be considered as a case-study in the importance of accounting for the varying life history strategies of species when planning conservation and management strategies.

Resumen

La pesca es la principal amenaza para las especies y ecosistemas marinos; sin embargo, la escala y el alcance de estos impactos siguen siendo inciertos. Esta tesis aporta nuevos conocimientos sobre los impactos globales de la pesca en las especies de escómbridos (51 especies de atunes, petos, bonitos y caballas), y avanza en nuestra capacidad para identificar *a priori* qué especies son más vulnerables a la sobrepesca. En primer lugar, un meta-análisis global de las tendencias en la biomasa de adultos muestra que las poblaciones de escómbridos han disminuido, en promedio, un 60% durante el último medio siglo. La disminución de la biomasa total de adultos es menor (52%), ya que está mitigada por las poblaciones más abundantes y mejor gestionadas. En segundo lugar, se identifican carencias y falta de datos biológicos para las 51 especies de escómbridos y se establecen prioridades en investigación para las especies que más lo necesitan. En tercer lugar, se examina la diversidad en las historias de vida en escómbridos, y se muestra que la mayor parte de la variación puede simplificarse en tres dimensiones (gobernadas por el tamaño máximo corporal, la velocidad de la vida y el calendario reproductivo). Por último, se muestra que las poblaciones de escómbridos con historias de vida más lentas han experimentado los mayores descensos en biomasa y tienen una mayor probabilidad de ser objeto de sobrepesca. La parámetros biológicos con unidades de medida de tiempo - la tasa de crecimiento y la longevidad - son los mejores indicadores de la vulnerabilidad de las especies a la pesca. Esta tesis se centra en los escómbridos como caso de estudio para resaltar la importancia de las distintas estrategias de vida de las especies a la hora de planificar estrategias de conservación y gestión.

Resumo

A pesca é a principal ameaza para as especies e ecosistemas mariños; con todo, a escala e o alcance destes impactos seguen sendo incertos. Esta tese aporta novos coñecementos sobre os impactos globais da pesca nas especies de escómbridos (51 especies de atúns, petos, bonitos e xardas), e avanza na nosa capacidade para identificar *a priori* qué especies son máis vulnerables á sobrepesca. En primeiro lugar, unha meta-análise global das tendencias na biomasa de adultos mostra que as poboacións de escómbridos diminuíron, en promedio, un 60% durante o último medio século. A diminución da biomasa total de adultos é menor (52%), xa que está mitigada polas poboacións máis abundantes e mellor xestionadas. En segundo lugar, identifícanse carencias e falta de datos biolóxicos para as 51 especies de escómbridos, e establécense prioridades en investigación para as especies que máis o necesitan. En terceiro lugar, examínase a diversidade nas historias de vida dos escómbridos, e móstrase que a maior parte da variación pode simplificarse en tres dimensións (gobernadas polo tamaño máximo corporal, a velocidade da vida e o calendario reprodutivo). Para rematar, móstrase que as poboacións de escómbridos con historias de vida máis lentas experimentaron os maiores descensos en biomasa, e teñen unha maior probabilidade de ser obxecto de sobrepesca. Os parámetros biolóxicos con unidades de medida de tempo - a taxa de crecemento e a lonxevidade - son os mellores indicadores da vulnerabilidade das especies á pesca. Esta tese resalta a importancia das estratexias de vida das especies para planificar estratexias de conservación e xestión.

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Chapter 1.

Introduction

Human induced impacts on marine ecosystems such as overexploitation of natural resources, eutrophication, habitat degradation, climate change and ocean acidification, are increasing and accelerating, yet our understanding of how marine ecosystems are responding to these impacts remains incomplete and uncertain (Millennium Ecosystem Assessment 2005, Sala and Knowlton 2006, Blanchard et al. 2010, Brander et al. 2010, Hoegh-Guldberg and Bruno 2010). Among all threats, fishing has been identified as the primary threat to marine species and ecosystems (Reynolds et al. 2005, Coll et al. 2008, McClenachan et al. 2012). Assessing the impacts of fishing on marine species and at the ecosystem-scale is challenging, in part because large-scale experiments and long-term manipulations in open marine systems are rarely possible (Bundy et al. 2012, Jensen et al. 2012). Therefore, existing fishery data sets collected by governments throughout the world, and biological and ecological data sets generated in hundreds of international, regional and local scientific projects within the last century, when pooled together, become a potential valuable resource of information to tackle global ecological questions by searching for patterns and processes at large spatial and temporal scales. This thesis is part of a European project entitled METAOCEANS "*Elucidating the structure and functioning of marine ecosystems through synthesis and comparative analysis*" (Metaoceans 2006). The principal motivation of METAOCEANS was to train a new generation of scientists to use novel techniques, such as meta-analysis and comparative analysis techniques, to synthesize and re-analyze vast amount of existing data under a broader perspective. The METAOCEANS project trained 14 PhD students to utilize the vast resources of existing biological, ecological and fisheries data sets, which are commonly dispersed and underutilized, and exploit them in order to advance our understanding on the functioning and structure of marine ecosystems, as well as advance our abilities to predict how marine ecosystem are responding to human impacts.

Within the METAOCEANS vision of tackling broad ecological questions by means of meta-analysis techniques, this thesis aims to provide new insights on the impacts of fishing on marine species and marine ecosystems, and advance our predictive abilities to identify which species might be most vulnerable to fishing. In the last few decades, there has been a push to manage fisheries using an ecosystem approach, where maximizing the catch of single target fish species is no longer the main focus of management, and

instead there is an urge to account for other ecosystem components to ensure a balance between exploiting marine resources and maintaining healthy ecosystems (FAO 2003, Pikitch et al. 2004, Garcia 2010, Jennings and Rice 2011). I see two main challenges in the current management of marine fisheries, which are slowing down our progress to apply ecosystem-based fisheries management on marine species:

(1) Our understanding of the impacts of fishing on marine species and marine ecosystems remains fragmentary and uncertain.

(2) Less than 1% of fish species have been properly assessed. Therefore, the biological status for the immense majority of marine fish species that are impacted directly or indirectly by fisheries is not known.

The first challenge reflects our limited understanding of the direct and indirect effects of fishing on marine species and marine ecosystems (Sala and Knowlton 2006, Crowder et al. 2008, Shin et al. 2010). On one hand, marine systems are very dynamic which makes it very hard to quantify the effects of fishing on fish populations and even harder to quantify how these impacts in turn alter the structure and function of marine ecosystems (Planque et al. 2010, Glaser et al. 2013). On the other hand, quality data to quantify the impacts of fishing on marine species and ecosystems is available for a relatively small number of species, typically only those of a high economic importance (Reynolds et al. 2005, Ricard et al. 2012). Consequently, the current global status of the word's fisheries remains fragmented and highly contested, in part because the sources and quality of the data differ among species. According to the Food and Agriculture Organization (FAO), in 2009, 57.4% of the fish stocks monitored by FAO were fully exploited (production close to their maximum sustainable limits), 29.9% were overexploited and 12.7% were non-fully exploited (FAO 2012). The FAO global fishery status assessment, which is based on official government catch statistics and expert opinion using direct indicators of the state of resources, covers approximately 600 marine fish populations distributed throughout the world. There have been also other attempts to assess the global status of fisheries using catch-based methods, which has the advantage of including a large number of species for which landing data is available (Froese et al. 2012, Pauly 2013). However, these studies have been criticized because by using catch data, as a substitute to reflect fish abundances and infer status, these catch-based methods might be exaggerating the status of world fisheries (Branch et al. 2011, Carruthers et al. 2012). Alternatively, it has been suggested that global attempts to evaluate the global state fisheries should use abundance data derived from fishery stock assessments (Polacheck 2006, Sibert et al.

2006, Branch et al. 2011). A state of the art fishery stock assessment collates a wide variety of fisheries dependent and independent data as well as data on the biology of the species, to derive abundance trajectories, determine sustainable yields, and estimate current status (Cooper 2006). Although data on fish abundances and stock assessments might be the preferred sources of information to deduce the global state of fisheries, irremediably these data and analyses are only available for a limited number of exploited populations and species. Even, the FAO global catch data set leaves out numerous fish populations and species for which there are no official statistics, notably, excluding bycatch species and species exploited by artisanal and subsistence fisheries (Zeller and Pauly 2007). This takes us to the second challenge.

Globally there are more than 15,000 marine fish species. Marine fish species and the fisheries they support, provide economic goods and ecosystem services to humanity (Millennium Ecosystem Assessment 2005). Nonetheless, less than 1% of fish species have been properly assessed (Dulvy et al. 2004, Costello et al. 2012). The biological status for the immense majority of marine fish species that are impacted directly or indirectly by fisheries is not known (Worm et al. 2009, Costello et al. 2012, Ricard et al. 2012). How many fish species are potentially overexploited and ultimately threatened with extinction? Understanding what species might be most at risk and the development of methods to identify *a priori* what species are most vulnerable to fishing exploitation can be very useful for guiding the management and planning effective conservation strategies (Cheung et al. 2005, Reynolds et al. 2005, Pinsky et al. 2011). One way to approach this challenge has been to understand the link between the life histories of the species and their vulnerability to fishing. The life history and ecology of a species determines, at least in part, how a species respond to exploitation. Therefore, the identification of potential biological and ecological correlates of species vulnerabilities to fishing are very useful to predict the species capacity to respond to fishing in data poor situations (Jennings et al. 1998, Dulvy et al. 2004, Reynolds et al. 2005, Hutchings et al. 2012b, Pardo et al. 2012). The biological information of a species is more readily available than fisheries dependent and independent data sets which are needed to develop fishery stock assessment models. Therefore, "rule-of-thumb" approaches based on the biology of the species have been proposed as a quick way to rapidly assess the conservation status of the species and identify those most at risk in data-poor situations, as a way to prioritize resources and efforts (Reynolds et al. 2001, Dulvy et al. 2004, Reynolds et al. 2005). The intrinsic biological characteristics of species, in combination with a measure of exposure to fishing,

might provide an opportunity to rank species according to their vulnerabilities to fishing, which forms the basis for ecological risk assessment methods (Hobday et al. 2011).

In this thesis I focus on scombrid species when addressing these two global challenges. The scombrids, which include 51 species of tunas, Spanish mackerels, bonitos and mackerels (Family Scombridae), are major components of the pelagic ecosystems being epipelagic and epi-mesopelagic predators (Collette and Nauen 1983). Scombrids occupy high trophic levels in the marine food web, consuming large quantities of prey to satisfy their high metabolic requirements (Brill 1996, Korsmeyer and Dewar 2001). Their life cycles are confined to marine open waters, although some species are associated with coral reefs and use estuarine and riverine habitats (Collette and Nauen 1983). They are widely distributed throughout the tropical, subtropical and temperate waters of the world's oceans, with a large number of species being endemic to the Indo-Pacific region. In addition to their key ecological roles as top predators in marine ecosystems, scombrid species are also economically, socially and culturally important in many fishing communities and nations throughout the world. They support important and diverse commercial fisheries throughout their distributions, ranging from large-scale industrial to small-scale artisanal fisheries, and many species are caught in recreational fisheries worldwide (Collette 2002, Pillai et al. 2002, Majkowski 2007, Di Natale et al. 2009, Miyake et al. 2010). Annual catches of scombrids have risen continuously since the 1950s, reaching 9.6 million tonnes in 2010 (FAO 2010-2013). Together, all scombrid catches contribute up to 15% of the annual total marine fish catch and are worth in excess of US$ 5 billion each year (Majkowski 2007, FAO 2009). Among scombrid species, seven species of tunas are commonly known as the principal market tunas due to their economic importance in the global markets. These include albacore (*Thunnus alalunga*), bigeye tuna (*T. obesus*), Atlantic bluefin tuna (*T. thynnus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), yellowfin tuna (*T. albacares*) and skipjack tuna (*Katsuwonus pelamis*). The principal market tunas have widespread oceanic distributions, are highly migratory, sustain highly industrialized fisheries worldwide and are a highly valued in the international trade as a commodity for the canning and sashimi industry (Collette and Nauen 1983, Majkowski 2007). The rest of scombrid species, the small tunas, bonitos, Spanish mackerels, and mackerels have in general more coastal distributions and are associated with continental shelves or oceanic islands (Collette and Nauen 1983). While the economic value of coastal scombrids is lower in the global markets, they can reach high values locally supporting a diversity of fisheries (Pillai et al. 2002, Di Natale et al. 2009). These are largely small-scale artisanal fisheries but also semi-industrial and

industrial fisheries, in both developed and developing countries (Collette and Nauen 1983, Gillett et al. 2001, Pillai et al. 2002, Majkowski 2007, Di Natale et al. 2009, Miyake et al. 2010). Hence, scombrid species are an important source of wealth and food security to fishing communities throughout the world.

There are two main reasons this thesis focuses on scombrid species. First, the impacts of fishing on pelagic species, particularly tunas, has been debated intensely in the past, giving rise to divergent views on the scale and extent of the impacts on pelagic ecosystems (Myers and Worm 2003, Hampton et al. 2005, Myers and Worm 2005a, Sibert et al. 2006). Given their economic, ecological and social importance, the scale and extent of the global fishing impacts on this important group of species are surprisingly uncertain. In 2003, one of the first syntheses brought the plight of ocean predators (mainly large tuna and billfish species) to the attention of the wider scientific community, concluding that global community biomass of large pelagic fishes had been reduced by approximately 90% from pre-industrial fisheries abundance (Myers and Worm 2003). However, this work relied heavily upon an analysis of catch and effort data from only one fishing gear type as index of abundance, resulting in an overestimation of tuna declines (Walters 2003, Hampton et al. 2005, Polacheck 2006). An alternative source of data and indicators can be found in fisheries stock assessments, which provide a more reliable estimate of population size and trajectory (Polacheck 2006, Sibert et al. 2006, Worm et al. 2009). Given the increasing availability of stock assessments in scombrid populations, it seems timely to evaluate the global development, trajectory and sustainability of this group of species, which in turn, will also provide new insights on the global impacts of fishing on marine species and marine ecosystems. Second, some scombrid species are probably among the most extensively studied species of marine fishes. Their increasing economic importance during the last 50 years has led to a relatively large number of biological studies and fisheries stock assessments. This cumulative amount of information (1) provides an opportunity to study the diversity of life history strategies in this family of fishes, which knowledge is fundamental to our understanding of how species respond to human exploitation, and (2) makes one of the longest, large-scale fisheries data sets available for testing the role of life histories and fishing in determining the population trajectories of scombrid populations and their current exploitation status. Potentially, comparative analysis of multiple species that have evolved distinct life history strategies and have different histories of exploitation can provide insights on what biological characteristics makes species more vulnerable to fishing. Comparative analysis can provide the quantitative basis to develop tools for predicting how species respond to

exploitation and identify what species are more at risk in data-poor situations (Jennings et al. 1998, Jennings et al. 1999b, Anderson et al. 2011).

Objectives

Have industrial fisheries removed 90% of the biomass of tunas? Can simple life history traits be used to diagnose those scombrid species most likely to decline and become overfished? And, what are the critical data gaps hindering the assessments and conservation in scombrid species? In this thesis, we address these questions by carrying out a global meta-analysis of biomass trends in scombrid populations in order to provide a more accurate picture of the global impacts of fishing on this group of species; and by assessing the role of their life histories in determining their population trajectories in order to advance our predictive abilities to identify which species might be most vulnerable to fishing. This thesis also has the overarching goal of exploiting and maximizing the use of existing data sets, and analyzing them using novel techniques, such as meta-analysis and comparative methods. Therefore, the development of this thesis required the *a priori* compilation of existing fisheries data and life history data for all scombrid species globally, which resulted in the construction of two data sets. One data set consists of a worldwide compilation of all available age-structured stock assessments of scombrid populations. After careful data screening, I end up with stock assessments for 26 populations of 11 species of scombrids. The second data set consists of a worldwide compilation of life history data, including information on maximum size, growth, longevity, maturity, spawning season and fecundity for the 51 species of scombrids. This life history data set includes life history information extracted from 684 life history studies.

Using the compiled data sets, I address the main objectives of this thesis in the following chapters (Figure 1.1):

In Chapter 2, I evaluate the global trajectories in adult biomass of 26 populations of scombrids from 1954 to 2006 and quantify the overall impact of fishing globally, including the extent of the impact within major oceans, major taxonomic groups and species with different life histories using mixed models. Have industrial fisheries removed 90% of the biomass of tunas globally? What is the current exploitation status of scombrids globally? I review their current exploitation status and discuss the implications for the long-term sustainability of this group of species.
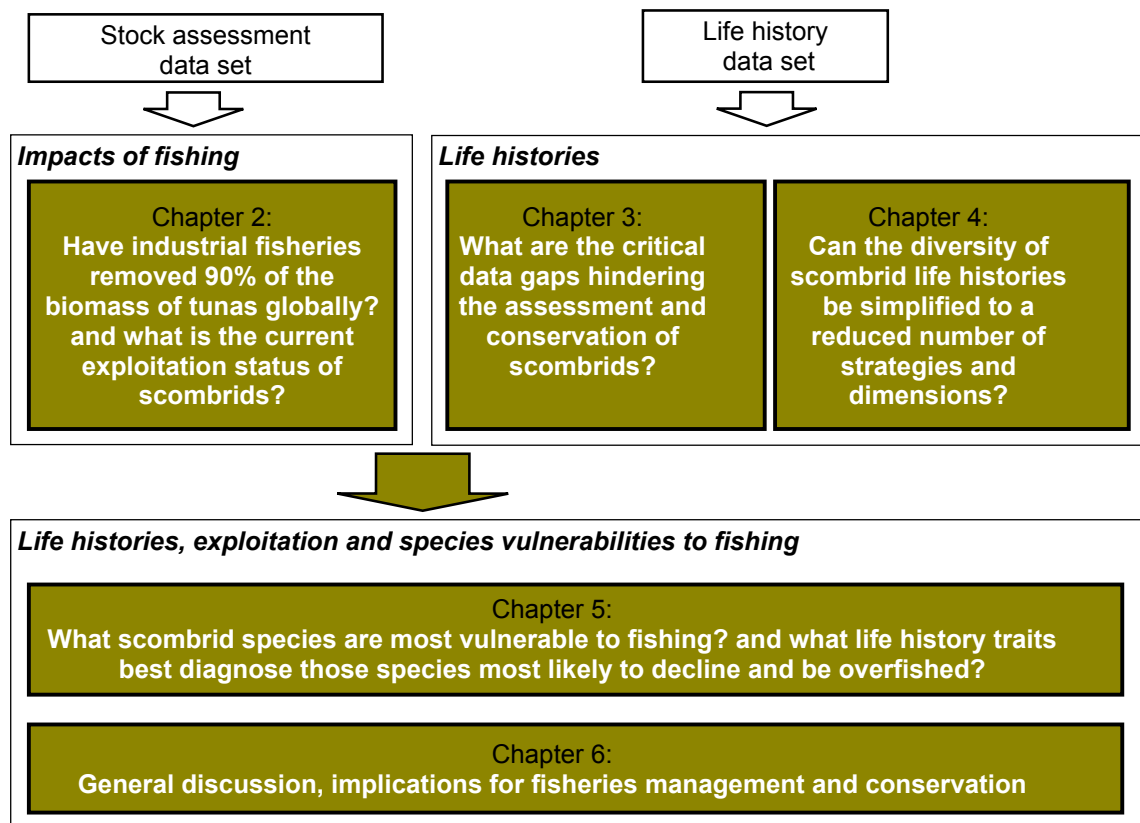
Figure 1.1   Thesis structure illustrated with a flow diagram.

Then, I turn my focus to examine the main patterns in life history variation across scombrid species and characterize their life history strategies, which is fundamental to our understanding of how species respond to human exploitation. In Chapter 3 I focus on synthesizing the life history information assembled and critically review it to identify gaps in biological knowledge across the 51 species of scombrids. Are there critical data gaps hindering the assessment and conservation of scombrid species? I make recommendations to prioritize life history research needs in scombrid species based on their biological gaps in knowledge, the importance of their fisheries and their current conservation status according to the International Union for Conservation of Nature (IUCN) Red List. Then in Chapter 4, I focus on examining the main patterns in the life history traits across scombrid species and use multivariate analyses to examine the co-variation among traits and evaluate how many principal axes of trait variation underlie scombrid life history strategies. Can the diversity of scombrid life histories be simplified to a reduced number of strategies and dimensions?

In Chapter 5, I use the ecological insights gained in Chapter 2, 3 and 4, to develop and test several *a priori* hypotheses to examine the role of life histories and fishing in determining the population trajectories and current exploitation status of scombrids using an information-theoretic approach for data analysis. What life history traits best diagnose those populations most likely to decline and be overfished? In this chapter, I aim to advance our predictive abilities to identify which populations and species might be most vulnerable to fishing.

In the final chapter, I summarize the main findings of each chapter and discuss their implication for the management and conservation of scombrid species. Then, I contextualize the implications of the main findings towards advancing the implementation of ecosystem based fisheries management in the world fisheries, and discuss the potential of future work.

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Chapter 2

Chapter 2.

Global population trajectories of tunas and their relatives[1]

Abstract

Tunas and their relatives dominate the world's largest ecosystems and sustain some of the most valuable fisheries. The impacts of fishing on these species have been debated intensively over the past decade, giving rise to divergent views on the scale and extent of the impacts of fisheries on pelagic ecosystems. We use all available age-structured stock assessments to evaluate the adult biomass trajectories and exploitation status of 26 populations of tunas and their relatives (17 tunas, 5 mackerels and 4 Spanish mackerels) from 1954 to 2006. Overall, populations have declined on average by 60% over the last half century, but the decline in the total adult biomass is lower (52%) driven by few abundant populations. The trajectories of individual populations depend on the interaction between life histories, ecology and fishing pressure. The steepest declines are exhibited by two distinct groups: the largest longest-lived highest-value temperate tunas and the smaller short-lived mackerels, both with most of their populations being overexploited. The remaining populations, mostly tropical tunas have been fished down to approximately maximum sustainable yield levels preventing further expansion of catches in these fisheries. Fishing mortality has increased steadily to the point where around 12.5% of the tunas and their relatives are caught each year globally. Overcapacity of these fisheries is jeopardizing their long-term sustainability. To guarantee higher catches, stabilize profits, and reduce collateral impacts on marine ecosystems requires the rebuilding of overexploited populations and stricter management measures to reduce overcapacity and regulate threatening trade.

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Introduction

Humans have long exploited the margins of pelagic ecosystems but only over the last half century has rapid technological development allowed fisheries to operate regularly beyond the sight of land and exploit vast populations of oceanic fishes which were relatively untouched (Myers and Worm 2003, Swartz et al. 2010). Fifty or more years later, the global impact of fishing on pelagic fishes and their ecosystems is only now beginning to be understood (Sibert et al. 2006, Worm et al. 2006). Tunas and their relatives, which include 51 species of tunas, Spanish mackerels, bonitos and mackerels (collectively known as scombrids) are major components of pelagic ecosystems, being both important predators and forage species which are widely distributed throughout the temperate and tropical epipelagic waters of the world's oceans (Table 2.S1). The majority of tunas and their relatives are highly migratory with widespread oceanic and coastal distributions; therefore their management and conservation are under the jurisdiction of several international management organizations such as the tuna Regional Fisheries Management Organizations (RFMOs) (see SI.1.3). These predators and forage fishes support some of the largest and most valuable of the world's fisheries, sustaining industrial and artisanal fisheries throughout their ranges and comprise 12% of global capture fisheries worth US$ 5 billion a year (Majkowski 2007, FAO 2010) (see SI.1.2).

Given the ecological, social and economic importance of tunas and their relatives one might expect that their status and trajectories would be closely monitored and well understood, particularly in an era of monitoring progress toward global biodiversity targets (Butchart et al. 2010). However, the scale and extent of the global fishing impacts on these important species are surprisingly uncertain (Myers and Worm 2003, Hampton et al. 2005, Majkowski 2007). In 2003, one of the first syntheses brought the plight of ocean predators (mainly tuna species) to the attention of the wider scientific community, concluding that global community biomass of large pelagic fishes had been reduced by around 90% from pre-industrial abundance (Myers and Worm 2003). However, this work relied heavily upon an analysis of catch and effort data from only one fishing gear-type resulting in an overestimation of tuna declines (Walters 2003, Hampton et al. 2005, Polacheck 2006). Alternatively, fisheries stock assessments provide a more reliable estimate of population size and trajectory and are regarded as the preferred source of information with which to assess the effects of fishing on fish populations and ecosystems (Polacheck 2006, Worm et al. 2009, Hutchings et al. 2010, Branch et al. 2011). In light of the problems with catch data, the increasing availability of stock assessments and

increasing public concern for the sustainable long-term management of natural resources it seems timely to evaluate the global development, trajectory and sustainability of tuna fisheries and their relatives.

Here we evaluate the trajectory and exploitation status of 26 populations of tunas and their relatives. First, we quantify the overall impact of fishing on adult biomass globally, including the extent of the impact within major oceans, major taxonomic groups and species with different life-history strategies using two metrics; the average annual rate of change and the total extent of decline. Second, we compare the adult biomass trajectories against the current exploitation status of each population determined by two standard biological reference points: the ratio of the current adult biomass relative to the adult biomass that would provide the Maximum Sustainable Yield (MSY) (B/B_{MSY}) and the ratio of current fishing mortality relative to the fishing mortality rate that maintains MSY (F/F_{MSY}).

Results

We assembled age-structured stock assessments with >15 years of data for 17 tuna populations (7 species), 5 mackerel populations (2 species) and 4 Spanish mackerel populations (2 species) out of the 51 species of scombrids (Figure 2.1, Figure 2.S1 and Table 2.S2). We observe that those mackerel and tuna species with the largest number of stock assessments are the most economically important species comprising 70% of the global reported catches (Figure 2.2A). In contrast, the small tunnies, Spanish mackerels and bonitos, which are mainly tropical coastal species, have a smaller number of stock assessments available. The status of these tropical coastal scombrids is mostly unknown throughout their ranges despite the importance of their commercial fisheries for many coastal fishing communities in many developed and developing countries around the world (See SI.2).

Trajectories of catches and adult biomass across tunas and their relatives.

The annual catches of tuna and their relatives have risen continuously since the 1950s reaching 9.5 million tonnes in 2008 (Figure 2.2A). This increase in catches was achieved by halving global tuna biomass in half a century; total adult biomass summed across all monitored populations has declined globally by 52.2% from 1954 to 2006 (Figure 2.2B-C). This total extent of decline depends on the inclusion of the most abundant populations,

A

B
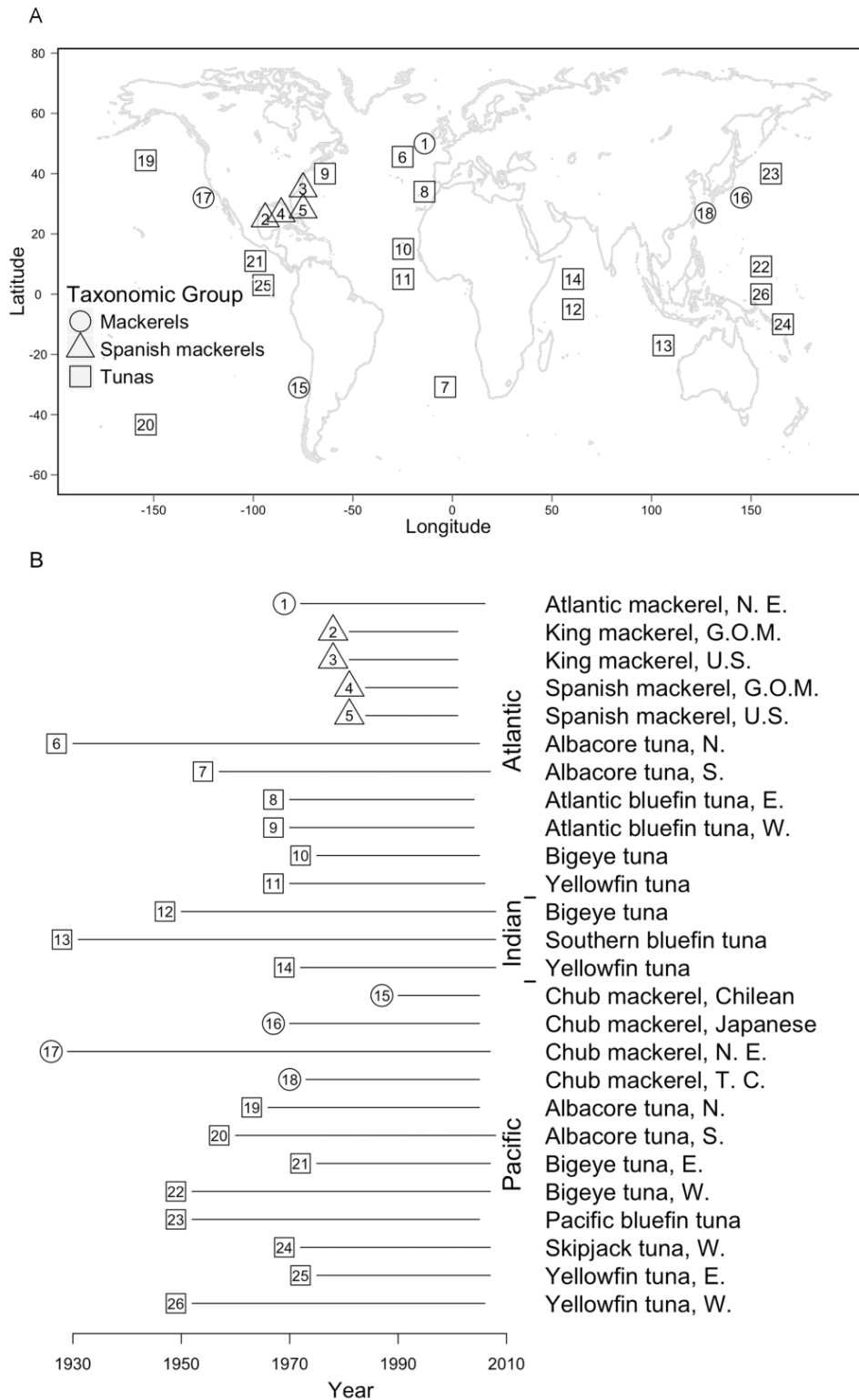
Figure 2.1   Age-structured stock assessments were available for 26 populations (11 species) of tunas and their relatives.

(A) Geographic locations. (B) Temporal span. Abbreviations for population names: N., north, S., south, E., east, W., west, N.E., northeast; U.S., United States, G.O.M., Gulf of Mexico; T.C., Tsushima Current.
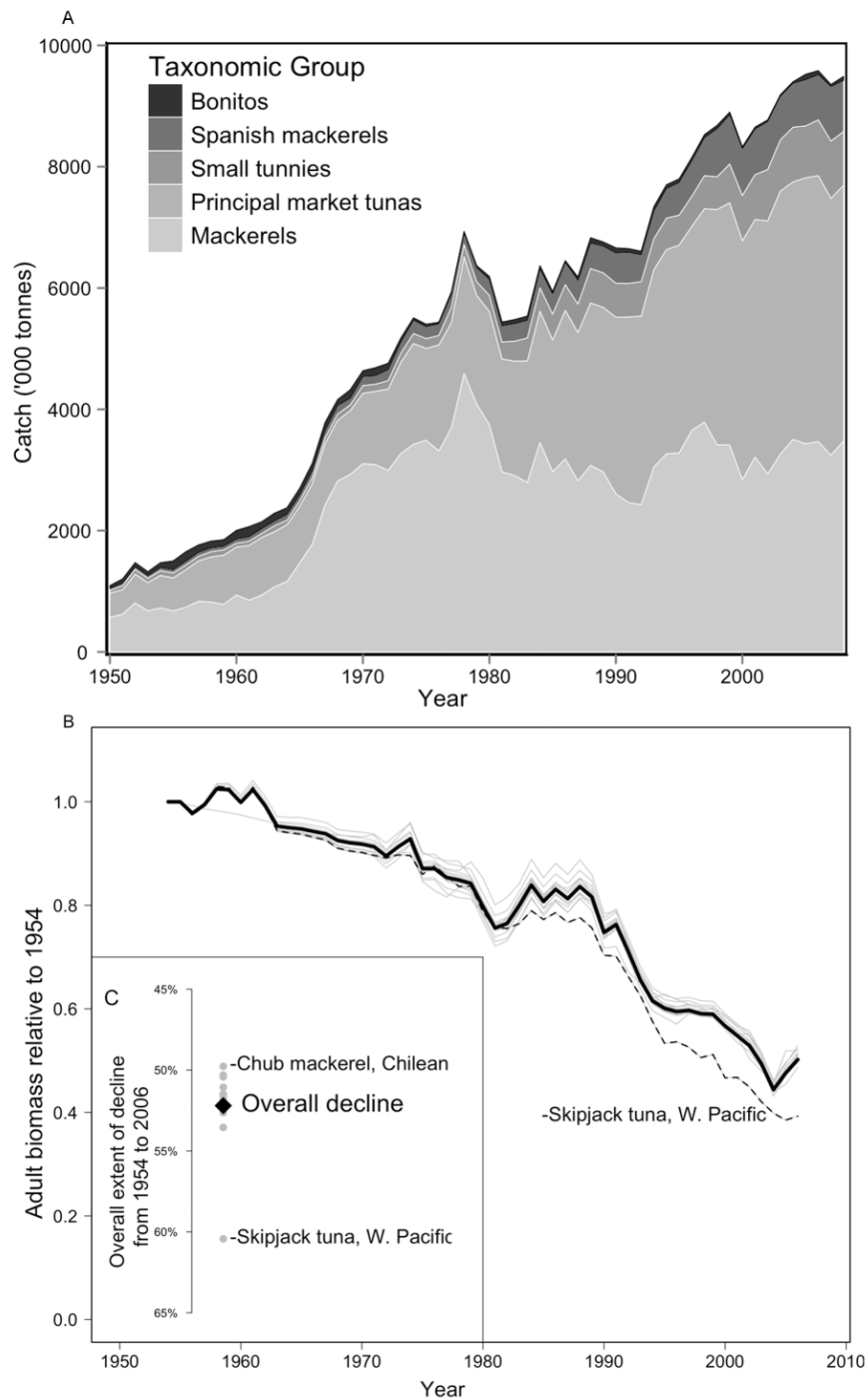
Figure 2.2 *Global catches and adult biomass trajectories of tunas and their relatives.*

(A) Catches of the major taxonomic groups of tunas and their relatives in the world from 1950 through 2008. (B) Relative adult biomass summed across 26 populations of tunas and their relatives (thick solid line), standardized to 1 in 1954. Faint grey lines and black dashed lines show the effect of excluding one population at a time from the global trend and recalculating the relative adult biomass. The dashed line show the effect of excluding the most influential population. (C) Estimated overall extent of decline in total adult biomass from 1954 to 2006 (thick solid diamond) and the effect of excluding one popualtion at at time and recalculating the total extent of decline (solid circles).

and their contribution to the overall decline can be seen by excluding one population at a time from the analysis and recalculating the overall trend (jackknifing). The overall extent of decline would have been 8.2% greater (60.4%) were it not for the inclusion of the abundant west Pacific skipjack tuna population. The overall annual rate of decline can be calculated from the yearly (i) changes in biomass ($r_{i,j}$) among populations (j), which accounts for temporal autocorrelation and the wide variation in the absolute size of populations (See Methodology Section). On average the annual rate of change in adult biomass was -1.7% y^{-1} [95 % confidence intervals (CI): -2.6 to -0.9] across the 26 populations from 1954 to 2006. This global annual rate of change is equivalent to an average decline of 59.9% across all populations within the 52 year period. Moreover, the trajectories in adult biomass of tunas and their relatives vary widely across oceans, taxonomic groups, species and life history strategies (Figure 2.3 and Figure 2.S2).

Trajectories of catches and adult biomass across tunas and their relatives.

The annual catches of tuna and their relatives have risen continuously since the 1950s reaching 9.5 million tonnes in 2008 (Figure 2.2A). This increase in catches was achieved by halving global tuna biomass in half a century; total adult biomass summed across all monitored populations has declined globally by 52.2% from 1954 to 2006 (Figure 2.2B-C). This total extent of decline depends on the inclusion of the most abundant populations, and their contribution to the overall decline can be seen by excluding one population at a time from the analysis and recalculating the overall trend (jackknifing). The overall extent of decline would have been 8.2% greater (60.4%) were it not for the inclusion of the abundant west Pacific skipjack tuna population. The overall annual rate of decline can be calculated from the yearly (i) changes in biomass ($r_{i,j}$) among populations (j), which accounts for temporal autocorrelation and the wide variation in the absolute size of populations (See Methodology Section). On average the annual rate of change in adult biomass was -1.7% y^{-1} [95 % confidence intervals (CI): -2.6 to -0.9] across the 26 populations from 1954 to 2006. This global annual rate of change is equivalent to an average decline of 59.9% across all populations within the 52 year period. Moreover, the trajectories in adult biomass of tunas and their relatives vary widely across oceans, taxonomic groups, species and life history strategies (Figure 2.3 and Figure 2.S2).

Figure 2.3   Adult biomass trajectories of tunas and their relatives within oceans.

(A-D), taxonomic and ecological groups (E-H,L) and life histories (I-L). (A,E,I) Total adult biomass in million tonnes. (B-D, F-H, J-L) Relative adult biomass across all populations (thick solid line) standardized to 1 in 1954. Faint and dashed lines show the effect of excluding one population at a time and recalculating the relative adult biomass. Dashed lines show the effect of excluding the most influential populations. The adult biomass of Spanish mackerels were eliminated from panel E because their absolute adult biomass was negligible relative to the other groups. Albacore tuna and the Atlantic, Pacific and Southern bluefin tunas are considered temperate tunas and skipjack, yellowfin and bigeye tunas are considered tropical tunas. Maximum body size of species is in table S1.

The total extent of decline in adult biomass has been greatest in the Indian Ocean with a 63.6% decline from 1954 to 2006, compared with a 49.6% and 49.2% decline in the Atlantic and Pacific Oceans respectively (Figure 2.3A-D). In the Pacific Ocean, the catches of tunas and their relatives is dominated by the abundant West Pacific skipjack tuna adult biomass which comprises 64% of the total tuna catches in the western Pacific Ocean. After excluding West Pacific skipjack the extent of decline in adult biomass in the Pacific Ocean is 66.6%. Therefore, the large observed declines in adult biomass suggest substantial impacts of fisheries in all three oceans despite the different timing in the historical expansion of industrial fisheries. Industrial fisheries, particularly targeting tuna species, started in the 1950s and 1960s in the Atlantic and Pacific Oceans while it fully developed two decades later in the Indian Ocean. We also observed the fastest annual rates of decline within the 52 year period occurred in the Indian Ocean (-3.2 % y^{-1} CI: -4.8 to -1.6) (Figure 2.3C and Figure 2.S2A), possibly due to aggressive and poorly regulated artisanal and industrial fisheries operating in a relatively lightly exploited ocean.

Of the three major taxonomic groups of tunas and their relatives, only the total adult biomass of all Spanish mackerels has recovered, increasing by 38.2% over the last half century (Figure 2.3F). The status of the four Spanish mackerel populations off the southeast coast of the US is currently healthy following the implementation of a recovery program after many years of overfishing (Ortiz 2004). Of the other two taxonomic groups, the total adult biomass of all mackerels has declined the most (58.1%) while tunas have declined by 49.1% (Figure 2.3G, L). However, after excluding the abundant west Pacific skipjack tuna, the total biomass of all tunas has decreased by 62.5% from 1954 to 2006.

The life history and ecology of fishes is intimately linked to their response to exploitation. Larger species tend to be preferentially targeted by fisheries over smaller species and may be intrinsically more sensitive to fishing due to their relatively less productive life histories (Reynolds et al. 2005). However, this ecological pattern can be overwritten by aggressive globalised fisheries (Pinsky et al. 2011). We observed that the total adult biomass of the largest species - bluefins, bigeye and yellowfin tunas, and the smallest species, the mackerels, have declined the most, 62.8% and 58.1% respectively since 1954 (Figure 2.3I-L). In addition, we only found significant and steep rates of declines in adult biomass in the largest species, -2.4% y^{-1} (CI: -3.5 to -1.4) (Figure 2.3J and Figure 2.S2A). We hypothesize that the large inter-annual variability observed in the adult biomass trends of the smallest pelagic coastal species, may be hindering the detection of significant declines in their overall annual rates of change (Figure 2.S3).

We also find that the biogeography of tuna life histories also matters. Temperate tuna populations have declined more steeply, -3.1% y^{-1} (CI: -4.2 to -1.9) than the tropical tunas, -1.7% y^{-1} (CI: -2.8 to -0.7) (Figure 2.3H and Figure 2.S2A). These rates are equivalent to an average decline of 80.2% across all the temperate tuna populations and 59.5% across all the tropical tuna populations. Temperate and tropical tuna species have biogeographically-distinct life history strategies: temperate species (bluefin and albacore tunas) are longer lived, reproduce later, have a shorter breeding season and a geographically more restricted breeding site than the tropical tuna species (yellowfin, skipjack and to some extent bigeye tuna) making them more accessible to fisheries and therefore overall less productive fisheries (Fromentin and Fonteneau 2001).

Link between the adult biomass trajectories and the current exploitation status.

Population and species trajectories depend not only on life histories and ecology, but also the level of exploitation. Here, we summarized the current exploitation status for the 21 populations for which we were able to obtain estimates of the two biological reference points, B/B_{MSY} and F/F_{MSY} (Figure 2.4A). We define "overfished" to mean that the biomass of the population has been reduced to a level less than that which would provide the MSY ($B<B_{MSY}$) and the term "overfishing" to mean that a population is being subject to a fishing effort greater than that required to produce the MSY ($F>F_{MSY}$), a definition used by the majority of the tuna RFMOs (Aranda et al. 2010). First, there are a total of four overexploited temperate tuna populations, which are "overfished" and are experiencing "overfishing": east and west Atlantic bluefin tunas, southern bluefin tuna and north Atlantic albacore tuna (Figure 2.4A). Second, there are 12 populations, mostly tropical tunas and Spanish mackerels, currently considered healthy ($B>B_{MSY}$ and $F<F_{MSY}$). Finally, there are five populations of tunas and mackerels in an intermediate state that either have biomasses below healthy levels, or a fishing mortality exceeding healthy levels, but not both ($B<B_{MSY}$ or $F>F_{MSY}$). Although the current exploitation status of tunas and their relatives can be easily categorized according to their biological reference points, it is important to highlight that the majority of tunas and their relatives, despite their assigned exploitation status, have been fished down to around MSY levels and are therefore fully exploited (Figure 2.4A and see SI.4.1). The extent of the declines in adult biomass is consistent with the current exploitation status of the populations; the populations having experienced the largest declines in biomass are either fully exploited or overexploited (Figure 2.S4, 2.S5 and see SI.4.2).

A

Overexploited

8 Atlantic bluefin tuna, E.

Overfishing (F > F$_{MSY}$)
Not Overfished (B > B$_{MSY}$)

9 Atlantic bluefin tuna, W.

15 Chub mackerel, Chilean

13 Southern bluefin tuna

22 Bigeye tuna, W. Pac.

6 Albacore tuna, N. Atl.

1
3
10
14
11 25
21
12
2

Healthy

7
4
5
26

Not Overfishing

24 Skipjack tuna, W. Pac.

20 Albacore tuna, S. Pac.

Overfished

B/B$_{MSY}$

F/F$_{MSY}$

B

Overall fishing mortality rate

-Atlantic mackerel, N.E.

-Skipjack tuna, W. Pacific

% of the population removed due to fishing

Year

Figure 2.4   *Current exploitation status and fishing mortality rate over time of tunas and their relatives.*

(A) Reference points for tunas and their relatives, current adult biomass relative to BMSY (x-axis) versus current exploitation rate relative to FMSY (y-axis). Codes follow Figure 2.1 and Table 2.S2. Colors represent the kernel density of the points. (B) Fishing mortality rate over time across tunas and their relatives. Faint grey lines and black dashed lines show the effect of excluding one population at a time and recalculating the overall fishing mortality. Dashed lines show the most influential populations. E., east; N.E., northeast; Pac., Pacific; S., south; W., west.

Discussion

The global adult biomass of tunas and their relatives has been halved over the past half century, but not without yielding considerable catches, income and food for the benefit of humanity. However, these population declines cannot continue without compromising yields in the near future: the majority of populations are fully exploited which limits the further expansion of catches from these fisheries. Currently, fisheries catch around 10%-15% of the tunas and their relatives each year globally (Figure 2.4B and see SI.3.5). The global demand for tunas and their relatives is still increasing (Allen 2010) as is the trajectory of fishing mortality (Figure 2.4B).

The largest declines in adult biomass have occurred in two groups of species with distinct life histories, the largest and less productive temperate tunas and the smallest and more productive mackerel species. Mackerels would *a priori* be considered intrinsically resilient to overfishing due to their 'fast' life histories, being fast growing, early maturing and short-lived and yet mackerels exhibit some of the steepest declines. However, it has been shown that within the last 50 years of industrial fisheries the collapse of small and fast growing pelagic species have been more frequent than in larger species (Pinsky et al. 2011)[i]. As fisheries developed in the 1950s, fisheries have preferentially targeted large biomass, shallow water species, such as small pelagics (Sethi et al. 2010). This historical patterns of fisheries development combined with the increasing global market demand of small pelagic fish for food, fishing bait, fish meal and oil (Deutsch et al. 2007), have probably contributed to their massive declines. The role of life histories is more apparent in tunas. The less-productive temperate tuna species have been impacted the most by fishing, exhibiting steeper and larger declines than the more productive tropical tuna species, suggesting that low productivity and slower life histories might be an important factor, together with catchability, accessibility and market price and demand, in determining the species vulnerability to fishing (Collette et al. 2011).

The reductions in adult biomass of tuna populations estimated in our global analysis differs from the more pessimistic interpretations of the global status of tuna fisheries described by Myers and Worm (2003). Although both studies are not strictly comparable, while Myers and Worm 2003 found a 90% decline on average in the catch per unit effort of large pelagic fish species, we found a 59.9% decline on average in adult biomass of tunas and their relatives. Notwithstanding, the gross differences both studies agree on the steep declines of three bluefin and one albacore populations which are clearly overfished with current biomasses below B_{MSY}. Instead, our results present a wide range of trajectories

across tuna populations which are more consistent with Sibert *et* al. (2006) study which reports declines ranging from 11 to 88% from baseline adult biomass across the Pacific tuna populations. Moreover our findings are consistent with those of a recent evaluation of the global conservation status of scombrid species carried out by the International Union for Conservation of Nature (IUCN) which showed that 68% (35 of 61 species) of scombrids are not considered to be threatened with extinction, but a few (5 species) have declined sufficiently to trigger listing under the IUCN Red List Threatened categories, notably the southern and Atlantic bluefin tunas (Collette et al. 2011). We caution that our estimates of total and average declines in adult biomass are almost certainly an underestimate, because fishing began long before the start of many of the time series summarized here. Stock assessments often begin years after the start of a fishery and may even be triggered by declining catches, as for example in the case of the Atlantic bluefin tuna, which was essentially fished out in the southern Atlantic in the 1960s prior to formal assessment (Fromentin and Powers 2005). Finally, we also show that globally the majority of the tunas have been already fished down to near MSY-related levels (Figure 2.S6). From a fisheries management perspective, MSY is usually obtained when the biomass of a population has been reduced by 60-70% (Hilborn 2010). Nonetheless, from a conservation perspective, the 52.2% global decline in total adult biomass and the average population declines of 59.9% across tunas and their relatives increases the probability of ecological and economic extinctions of target populations with considerable biodiversity consequences for bycatch species (Collette et al. 2011). In addition, the magnitude of these declines creates concerns about the potential unknown ecosystem effects of removing large amounts of biomass from the pelagic food webs (Polovina et al. 2009).

MSY is the explicit or *de facto* target yield level for most tuna RFMOs (Aranda et al. 2010). Given that 4 of the 26 populations are substantially below B_{MSY} (Figure 2.4A) and the others are all at target levels larger than $0.9B_{MSY}$, most fisheries managers would consider these to be extremely well managed (with the exception of the three bluefin and one albacore populations). However, there is little room for complacency. We highlight three issues to be tackled with urgency to reduce the risk of tropical tunas and other scombrid populations deteriorating in the same way as the bluefin tunas and to minimize the considerable collateral damage and biodiversity consequences of these fisheries. First, tuna productivity is apparently declining - the current estimates of MSY for some tuna populations are lower than in the past, partly a result of the increased mortality of immature tunas in the last two decades from purse seine fisheries which consequently has

decreased the maximum potential yield of the fisheries (Allen 2010). Second, their high value and global demand, and the rising fishing capacity and mortality (Figure 2.4B), is exacerbating the pressure on populations that are already fully exploited or in some cases overexploited. Management of tuna populations under the single-species approach appears to be largely successful for the less valuable tropical species, but has not been effective for high-value bluefin tunas driven by the scale of international demand for and trade of high-valued tunas. In those cases, additional measures seem to be required. Here we have a case where trade is overwhelming the, normally effective, scale of fisheries management. Hence there appears to be a role for conservation tools such as CITES (Convention on International Trade in Endangered Species) to work alongside the existing management framework to ensure the recovery and future sustainable fishing of the most exploited populations. Third, exploitation of productive species, such as tunas, at MSY is driving steep population declines and elevating the risk of extinction of some unmanaged and less productive bycatch species. Tuna fisheries are directly responsible for endangering a wide range of oceanic pelagic sharks, billfishes, seabirds, and turtles (Dulvy et al. 2008, Wallace et al. 2010).

Many of these issues could be alleviated if fisheries management organizations treated MSY as a upper limit rather than a target reference point in their management objectives, a longstanding recommendation of several international UN FAO agreements and guidelines over the last 15 years (Caddy and Mahon 1995). Most tuna RFMOs have vague management objectives and have not adopted or implemented specific targets and limits (Maunder and Harley 2006, Mooney-Seus and Rosenberg 2007). We recommend the development of well-defined management strategies involving harvest control rules and the associated decision rules that can keep the fishery within defined limits. These would potentially facilitate the creation of well-defined and specific targets and limits for each population (and therefore management objectives) improving the decision-making process and speeding the implementation of appropriate management measures (Kell et al. 2003, Maunder and Harley 2006, Mooney-Seus and Rosenberg 2007). The use of upper limits and lower targets would improve profitability and reduce the impacts on ocean biodiversity (Worm et al. 2009).

The long term sustainability of tunas and their relatives can only come from stricter management measures to treat MSY-related levels as a limit rather than a target management objective, reduce the overall fishing capacity, rebuild overexploited populations, as well as further implementing regulations to minimize the collateral impacts of these fisheries on marine ecosystems.

Methodology

Data

We compiled age-structured stock assessments with more than 15 years of data for 26 populations and 11 species of tunas and their relatives out of 51 species of scombrids (Table 2.S2 and see SI.2). We extracted the trajectories of the adult biomass, fishing mortality, and the standard biological reference points, B/B_{MSY} and F/F_{MSY}, if available from the assessments. We use the term population instead of stock.

Statistical analysis

We used two metrics to quantify fishing impacts on the population trajectories of adult biomass. First, we estimated the average annual rate of change across all the populations and its equivalent average percent decline over time globally, within oceans (Atlantic, Pacific and Indian), within the main taxonomic groups (tunas, mackerels and Spanish mackerels), within species and within groups with different life-history strategies. Second, we estimated the overall extent of decline in total adult biomass summed across all the populations over time within the same spatial and taxonomic levels. While the overall extent of decline is an indicator of ecosystem removals, it might be sensitive to the populations with the largest abundances, which we tested with a jackknife analysis. On the other hand, the estimated average annual rates of change and its equivalent average percent declines are not influenced by the few most abundant populations and can be used to address how well management is working.

Fishing impacts were quantified from 1954 to 2006 to maximize the coverage of data (Figure 2.1B). The majority of the industrial tuna fisheries began in this period, typically in the 1950s and '60s. However it should be acknowledge that prior to the 1950s there were already fisheries targeting tuna species and their relatives, in some cases for centuries such as in the case of the Atlantic bluefin tuna in the Mediterranean or skipjack in the Pacific Islands (Majkowski, 2007) and therefore our analysis does not account for these earlier effects of exploitation. In our analyses, for those time series starting after 1954, we assumed that from 1954 to the first year with data there have been no major fisheries targeting the populations and therefore the adult biomass has not changed over time. We retrospectively extended the adult biomass time series to 1954 using the mean of the first three years of data and truncated time series that began prior to 1954. For those time series finishing prior to 2006, we also extended them forward to 2006 assuming that the

most recent estimate, an average of the last three years, is projected forward to the future. This imputation approach is conservative in the sense that it is more likely to underestimate the rate and extent of decline (SI.3.1). The maximum observed body sizes of the species were used as a proxy to group species into different life histories as it correlates with other life-history traits as well as intrinsic sensitivity to fishing (Jennings and Kaiser 1998, Jennings et al. 1998). Populations with a maximum body size (measured as fork length) larger than two meters were categorized as large, between one and two meters as medium and smaller than one meter as small (Table 2.S1).

We used mixed-effect models to perform a meta-analysis of population trends in adult biomass to estimate annual rates of change within the several spatial and taxonomic levels and within populations with similar life histories. We also tested if the average annual rate of change in adult biomass across all the populations (global estimate) was accelerating or decelerating over time (See SI.3.2). Most of the time series of adult biomass showed nonlinearity and autocorrelation over time, therefore we converted the raw time series of adult biomass of each population to annual rates of change (r_i), $r_i =$ ln(AB$_{i+1}$/AB$_i$), where AB$_i$ is the adult biomass in year i (Figure 2.S7). Such differencing or taking the ratios in log-space is a common method of removing temporal autocorrelation from a time-series (Shumway and Stoffer 2006b). The annual rates of change in adult biomass r_i, was the dependent variable in the analyses of adult biomass trends. We used the following full mixed-effect model and several submodels of the full model, depending on the objective of the analysis to estimate the overall annual rates of change in adult biomass.

Level-1: $y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + \varepsilon_{ij}$ where $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2 I)$

Level-2:
$$\begin{aligned} \beta_{0j} &= \gamma_{00} + \gamma_{01}W_j + \delta_{0j} \\ \beta_{1j} &= \gamma_{10} + \gamma_{11}W_j + \delta_{1j} \end{aligned} \quad where \begin{bmatrix} \delta_{0j} \\ \delta_{1j} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_0^2 & \sigma_{01} \\ \sigma_{10} & \sigma_1^2 \end{bmatrix} \right)$$

Level 1 is a linear regression model where the intercepts and the slopes are allowed to vary by group (here populations), where j indexes the populations modeled as random effects and i indexes the years. Level 2 describes the variability of the relationship between the dependent variable y (here the annual rates of change in adult biomass) and the covariate variable X (here years) among all the populations j. Level 2 has one categorical predictor variable W which can be any of the categorical variables grouping populations geographically or taxonomically (e.g. oceans, taxonomic groups, etc.). The β's

and the γ's are the fixed effects coefficients and the δ's and ϵ's are the random effects coefficients. We assume the random effects (δ's) are normally distributed with the given variance covariance matrix and we assume that the residual errors (ϵ's) follow a $\epsilon_t \sim N(0, \sigma_\epsilon^2)$. In addition, we also estimated the average of the annual rates of change in adult biomass across all the years for each population (See SI.3.3).

We used restricted maximum likelihood to fit all the mixed models using the lme function in the NLME package in R (Pinheiro and Bates 2000). We examined the residuals of all the models and corrected for temporal autocorrelation with AR1 and AR2 processes when necessary. In addition, we allowed each population to have a different variance. The Akaike Information Criteria was used to determine the autocorrelation process and the variance structure most suitable for the time series under investigation. We show the model validation plots of one analysis although all the analyses had similar validation plots (Figure 2.S8). The significance of the fixed terms of the models were assessed by computing the confidence intervals for each fixed effect and then considering them significant if the 95% confidence intervals did not include zero.

In order to calculate the overall extent of decline in total adult biomass summed across all the populations over time within the several spatial and taxonomic levels, first, we summed the values of adult biomass across all the populations for year the 1954 and 2006 using the mean of the first and last three years of data. Second, we estimated the total percent change in adult biomass between 1954 and 2006 globally across all the populations, within each ocean, within each taxonomic group, within species and within populations with similar life histories. In addition, we also estimated the extent of decline for each individual population (See SI.3.3).

Acknowledgements

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Supplementary Information

SI.1 Background on tunas and their relatives

SI.1.1Taxonomy

The Scombridae family comprises 51 epipelagic species, commonly known as tunas, bonitos, Spanish mackerels (also known as seerfishes) and mackerels, which are distributed throughout tropical and temperate oceans. The currently accepted classification of the family Scombridae is largely based on morphological studies, and is composed of two subfamilies, four tribes, fifteen genera and the fifty-one species (Table 2.S1). All the species except one belong to the subfamily *Scombrinae* which is divided in four tribes *Thunnini* (tunas), *Sardini* (bonitos), *Scomberomorini* (Spanish mackerels) and *Scombrini* (mackerels) (Collette 1999). The butterfly kingfish (*Gasterochisma melampus*) comprises a monotypic subfamily *Gasterochismatinae.*

SI.1.2 Fisheries

Scombrid species have long been targeted by mainly artisanal fishing communities throughout the world and until the 1940s most of the fishing occurred in coastal areas. The main industrialized fisheries for scombrids started between the 1940s and 1960s, particularly targeting the tuna and mackerel species. These fisheries expanded rapidly, operating nowadays in most latitudes of all oceans. The annual catches of scombrids have grown continuously rising from 1.1 million tonnes in 1950 to 9.5 million tonnes in 2008 (Figure 2.2A main text). The tunas (tribe *Thunnini*) includes the most economically important group of species known as the *principal market tunas*, which are albacore (*Thunnus alalunga*), bigeye tuna (*T. obesus*), Atlantic bluefin tuna (*T. thynnus*), Pacific bluefin tuna (*T. orientalis*), southern bluefin tuna (*T. maccoyii*), yellowfin tuna (*T. albacares*) and skipjack tuna (*Katsuwonus pelamis*). The principle market tunas are oceanic, highly migratory and are among the largest and fastest top predators of the high seas. They are the most economically important species due to their predominance in the global fish exports and their intensive international trade for canning and sashimi (Miyake et al. 2004). The catches of principal market tunas have increased continuously from less than 0.2 mt in the 1950s to over 4.2 mt in 2008 (Figure 2.2A main text). Skipjack and yellowfin tunas account for the greatest proportion of the principal market tuna world catches in terms of yield (3.5 mt in the year 2008) and most of these catches are directed to the canning industry (FAO 2009). Atlantic, Pacific and southern bluefin tunas contribute

little in terms of total catches in weight, but are very important in terms of their individual economic value. The principal fishing methods used by the industrial fleets, are purse seine, longline, bait boat (or pole and line) and trolling. Each gear is designed to target different species at different depths. Purse seine and baitboat are used to catch fish close to the surface, for example skipjack or juveniles of yellowfin, albacore, and bluefin. The longline fisheries usually target the largest and oldest individuals found at greater depths, for example adult bigeye, yellowfin and bluefin tunas. In the recreational sector, the principal fishing methods used involved mostly surface trolling, and baitboat fishing, while the artisanal fisheries use a great variety of methods such us gillnets, beach seines, bait-boat, handlines, harpoons and traps. In the tropical tuna fisheries, the catch by purse seiners using floating platforms to attract schools of tuna, called fish aggregating devices (FADs), has increased gradually since the 1990s resulting in an increased in the mortality of immature tunas globally. While purse seiners using FADs mainly target skipjack tuna, they do not discriminate among tropical tuna species, causing an increase in the mortality of immature yellowfin and bigeye tunas (Allen 2010). In the temperate tuna fisheries, the purse seiners have also been increasingly catching juveniles of Atlantic, Pacific and southern bluefin tunas to fulfill the demand of the tuna farming industry where tuna are fattened before being sold in the global markets (Fromentin and Powers 2005, Cyranoski 2010, Mylonas et al. 2010). At present, there are more than 80 nations with tuna fisheries, and in the Indian and Pacific Ocean tuna fisheries are still growing in many coastal developing countries (ISSF 2010).

Spanish mackerels, bonitos and mackerels which are species with low economic value relative to the principal market tuna species and are targeted largely by small scale industrial and artisanal fisheries throughout their ranges. The small tunny species (Tribe *Thunnini* other than the principal market tunas), Spanish mackerels (tribe *Scomberomorini*), mackerels (tribe *Scombrini*) and bonitos (tribe *Sardini*) are generally smaller coastal species associated with continental shelves. They are important forage fish that mediate the flow of energy from primary producers to top predators (Bakun 2006). The catches of scombrids other than the principal market tuna have also increased significantly since the early 1950s. In the year 2008 around 5.2 mt of mackerels, Spanish mackerels, bonitos and small tunas were caught worldwide (Figure 2.2A main text). The most important species of scombrids other than the principal market tunas in terms of weight: chub mackerel *Scomber japonicus* (~2 million tonnes), Atlantic mackerel *Scomber scombrus* (~ 600.000 tonnes), Spanish mackerels not specified (~500000 tonnes), Short mackerel *Rastrelliger brachysoma* (~310 000 tonnes), Indian mackerel not specified

(~300000 tonnes), kawakawa *Euthynnus affinis* (~280 000 tonnes), Indian mackerel *Rastrelliger kanagurta* (~280 000 tonnes), longtail tuna *Thunnus tonggol* (~277 000 tonnes), frigate and bullet tunas *Auxis thazard and A. rochei* (~230 000 tonnes) and narrow-barred Spanish mackerel *Scomberomorus commerson* (~220 000 tonnes) (FAO 2008). These catches are possibly under-reported in all the taxonomic groups (Watson and Pauly 2001), particularly even more for the small tunnies, bonitos and Spanish mackerels.

SI.1.3 Fisheries management

Several and diverse international and inter-governmental organizations have been created to manage scombrid species due to their highly migratory nature, their widespread oceanic and coastal distributions, as well as their economic importance for many countries. There are currently five Regional Fisheries Management Organizations (RFMOs) whose mandates include the management and conservation of tuna and tuna-like species in their areas of jurisdiction. The term tuna and tuna-like species includes the tunas (tribe *Thunnini* which comprise the principal market tunas and the small tunny species), the bonitos (tribe *Sardini*), the Spanish mackerels (tribe *Scomberomorini*) and the billfishes which all belong to the suborder Scombroidei (Majkowski 2007). Therefore, all the species of the family Scombridae, except the mackerels (tribe *Scombrini*), are considered tuna and tuna-like species. The five RFMOs, also known as tuna commissions, are the International Commission for the Conservation of Atlantic Tunas (ICCAT), the Indian Ocean Tuna Commission (IOTC), the Inter-American Tropical Tuna Commission (IATTC), the Western and Central Pacific Fishery Commission (WCPFC) and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT). The CCSBT is the only tuna RFMO that is in charge of only a single tuna species (the southern bluefin tuna). In addition, the International Scientific Committee (ISC) for Tuna and Tuna-like species in the North Pacific Ocean conducts fisheries research on tuna and tuna-like species in the North Pacific Ocean and cooperates with other tuna RMFOs in the region. Thus, the tuna commissions are not only mandated to manage and conserve the principal market tuna species but also smaller tunny species, bonitos and Spanish mackerels that are harvested within their jurisdiction. Commonly, the tuna commissions concentrate most of their effort, resources, and personnel into managing the principal market tuna species and billfishes giving less priority to the rest of species. Although the ICCAT and IOTC have working groups on the small tuna species, generally, the lack of fisheries data and insufficient biological knowledge paralyzes any attempt to carry out stock assessment evaluations (Majkowski 1998, 2007).

There are some exceptions in the usage of the term tuna and tuna-like species by the tuna RFMOs. The mandate of the WCPFC is the only commission that uses the term of Highly Migratory Fish instead of the term tuna and tuna-like species. The Highly Migratory Fish Stocks term refers to the species listed in Appendix I in the Article 64 of the UN Convention of the Law of the Sea (UNCLOS). This term includes some of the scombrid species (the principal market tunas, blackfin tuna, *Thunnus atlanticus,* bullet tuna, *Auxis rochei*, frigate tuna, *Auxis thazard,* little tunny, *Euthynnus alletteratus,* and kawakawa, *Euthynnus affinis*), billfishes, dolphinfishes, oceanic sharks and sauries. Although the WCPFC is mandated to manage and conserve all species of Highly Migratory Fish Stocks within the Convention Area, except sauries. Thus, the term Highly Migratory Fish Stocks does not include the bonitos, Spanish mackerels and some of the small tunnies (black skipjack, *Euthynnus lineatus*, longtail tuna, *Thunnus tonggol*, and slender tuna, *Allothunnus fallai*) that probably constitute Straddling Stocks under UNCLOS. Finally, all the tuna RFMOs recognize the obligation to manage and conserve the harvested species but also to conserve the associated and dependent species that are taken incidentally during the tuna fishing activities (Allen 2010). Small tunny species, Spanish mackerels and bonitos are commonly discarded by longliners and purse-seine tuna fisheries (Lawson 1997). Finally, we would like to point out that there are other intergovernmental fisheries organizations such as the Caribbean Regional Fisheries Mechanism which have defined strategic objectives and management plans and have recently started to evaluate the status of some coastal scombrid species in the Caribbean Sea.

Mackerel species are not under the mandate of any of the tuna RMFOs. The fisheries of mackerels are more localized, often their distributions occur either in regions where the continental shelf extends beyond the Exclusive Economic Zone limit or in coastal regions where the productivity is very high (upwelling regions) which extends their distributions in to the high seas; therefore, the mackerels are considered Straddling Stocks (and not Highly Migratory Fish Stocks). Straddling Stocks under the Article 63 of UNCLOS, are "the same stock or stocks of associated species [which] occur both within the exclusive economic zone and in an area beyond and adjacent to the zone" (Majkowski 1998). Therefore, neighboring coastal states and fishing entities should coordinate the management and conservation of these populations and usually intergovernmental regional organizations are set up for this purpose. Although, there are some intergovernmental regional organizations in charge of evaluating the stock status of mackerels, for example, International Council for the Exploration of the Sea (ICES) which provides scientific advice for the northeast Atlantic mackerel stock, most of the time the

mackerels species are evaluated separately by each individual countries (e. g. Japan & China). A combination of insufficient information with which to clearly delimit population distributions and the lack of institutional arrangements among neighboring countries to jointly manage resources leads individual states to carry out independent fisheries research for their fish populations in the best case scenarios.

SI.2 Stock assessment data

SI.2.1 Data sources and data selection

We conducted a global literature search to locate the most important commercial fisheries for scombrid species, with the primary aim of identifying: 1) what populations could potentially be under scientific review or management plans, possibly supported with stock assessments, and 2) what institutions were in charge of their evaluation, management and conservation. Next, to compile the most updated stocks assessments and their respective reports, we contacted many institutions worldwide, from international, to inter-governmental, as well as national fisheries institutions and individual scientist, which were in charge of the evaluations of any scombrid species. There are several stock assessment modeling approaches varying in complexity and data requirements, from simple surplus production models to sophisticated statistical catch-at-age models. Since we were interested in gathering population estimates of abundance at age, biomass at age and fishing mortality rates at age from the assessments, we limited our data collation to only those stock assessments that used age-structured models, either of the Virtual Population analysis family (e.g. Independent Catch Analysis, ICA, used for Northeast Atlantic mackerel) or Statistical Catch At Age family (e.g Multifan-CL applied to various tuna populations). The standard biological reference ratios, the current adult biomass relative to which would provide the Maximum Sustainable Yield (MSY) (B/B_{MSY}) and current fishing mortality relative to the fishing mortality rate which maintains MSY (F/F_{MSY}) were also extracted from the stock assessments, when available.

The data collection yielded stock assessments varying in quality, methodology used, temporal coverage and data availability. We did not include in our analysis stock assessments that 1) were considered unreliable by the scientist undertaking them, 2) were outdated (prior to 2000), 3) were not carried out with age-structured stock assessment models, like biomass dynamic models, or 4) provided estimates of population biomass for a time period shorter than 15 years.

SI.2.2 Uncertainties and caveats of stock assessments

Although data obtained from stock assessments are generally regarded as the preferred source of information with which to assess the effects of fishing on fish populations and ecosystems (Polacheck 2006, Worm et al. 2009, Hutchings et al. 2010, Branch et al. 2011), there are many sources of uncertainty surrounding the stock assessment models which might create some unknown bias in the data outputs. The uncertainties surrounding stock assessments may arise by a combination of several factors such as the variety of data sources used, the numerous inputs needed, or the limited knowledge about the dynamics of the population, all of which are very complex to quantify. All this uncertainty is commonly characterized in observation errors and model errors, both leading to estimation errors in the results of the stock assessments(FAO 2001). Observation error may arise because of measurement errors (e.g. in the weight and length of the catches) or sampling errors (e.g. in the surveys). Model error may occur because of the lack in knowledge of the biology of fish or the inability of the models to model all the processes that affect the dynamics of a fish stock. Many of these uncertainties can be identified and quantified in the stock assessment evaluations using several types of models and their respective sensitivity analysis to test different hypothesis and model assumptions. Therefore, in any stock assessment evaluation it is very common to find the results of several models with their respective sensitivity analysis all of which attempts to characterize the status of a population and the uncertainty associated. During the data compilation of this study, when several stock assessment models and several variations of the models (sensitivity runs) were available for one population, we used the base-case model specified in the stock assessment report to extract the estimates of biomass and fishing mortality over time or as advised by the stock assessment scientist. In our analysis we did not take into account the uncertainties associated with the estimates of biomass, fishing mortality rates and biological reference points extracted from the stock assessments. We merely summarize the consensus choices of the stock assessment teams as to the best parameter settings. Nonetheless, we acknowledge that the uncertainties in model outputs may be creating some unknown biases in our results. We therefore highlight the importance of consulting the original assessments reports when seeking information on the uncertainties surrounding the status of the individual populations.

We also attempted to compile the most recent available stock assessments for scombrid populations around the world. However, we are aware that some populations have been re-evaluated throughout the development of the present work. In the case of the biological

reference points, we extracted them from the most recent stock assessments up to February 2011 to present the most updated exploitation status of tunas and their relatives (Table 2.S2). We definitely encourage future studies to update this work every few years including the most updated information possible to reassess the global status of scombrids. Maybe the consortium of tuna RFMOs under the Kobe agreement could be responsible for continuously updating this type of analysis for the species under their mandate.

SI.2.3 Description of stock assessment data and identification of data gaps

After the data screening, we ended up with stock assessments for 26 populations (11 species) of scombrids, comprised of: 17 principal market tunas (7 species), 5 mackerels (2 species) and 4 Spanish mackerels (2 species) out of a total of 51 species of scombrids which we included in our analysis (Table 2.S2). By geographic regions, we were able to obtain information for 11 populations in the Altlantic Ocean, 12 populations in the Pacific Ocean, 2 populations in the Indian Ocean and 1population in the Southern Ocean (Figure 2.1 main text). The small number of exploited species evaluated with age-structure stock assessments in the Indian Ocean stands out since 34 species of scombrids are found in the Indo-Pacific region and 23 of those are endemic to the region. Next, we summarize the data availability and accessibility by taxonomic group.

Among the four major taxonomic groups of scombrids, the tunas (tribe *Thunnini*), particularly the principal market tunas, have been largely assessed and their status is generally known. There are 23 populations of principal market tunas (7 species) managed by the five tuna RFMOs. Seventeen of the 23 populations are currently evaluated with age-structure stock assessment models (Table 2.S2). The rest of the populations are either 1) evaluated with surplus production models (Indian Ocean Albacore tuna and East and West Atlantic Skipjack tuna populations), 2) evaluated based on several indicators of stock status due to the difficulties of developing proper stock assessment models for these populations (Indian Ocean and East Pacific Skipjack tuna populations) or 3) have not been evaluated yet (Mediterranean albacore tuna populations, although its assessment is planned for the year 2011).

We are not aware of any formal quantitative stock assessment evaluations using age-structured models for any of the rest of the tuna species. In general terms, the status of the small tunny species is poorly known around the world. The fisheries targeting small tunny species usually involved mostly developing countries, which have limited resources for research, monitoring and management capacity (Majkowski 1998). Yet, we would like

to highlight recent efforts to evaluate the status of several coastal scombrids with simpler stock assessment models. First, the blackfin tuna stock distributed off the coast of Brazil has been recently evaluated (De Nóbrega et al. 2009). Second, the longtail tuna stock distributed off the northern coast of Australia has also been evaluated (Griffiths 2010). Third, the FAO has recently carried out two workshops to review fisheries data, update and carry our stock assessments for fish resources in the South and Southeast Asia region. During these workshops many coastal small tunny spcies (e.g. *Auxis* sp. and *Euthynnnus* sp.), tropical mackerels species (*Rastrelliger* sp.) and tropical Spanish mackerels (*Scomberomorus* sp.) were evaluated using several stock assessment methods specific for data-poor populations (FAO 2010a, 2010b).

The mackerels (tribe *Scombrini*) include the temperate mackerels (*Scomber* sp.) that are usually evaluated with formal quantitative stock assessments and their status is generally known and the tropical mackerels (*Rastrelliger* sp.) that are either not evaluated or evaluated with simple stock assessments methods and therefore, their status is generally unknown or highly uncertain. The temperate mackerels species sustain one of the largest commercial fisheries worldwide, particularly the Chub mackerel which is among the ten most fished species in the world (FAO 2009). Consequently, some temperate mackerel populations have been relatively well monitored and evaluated by national and intergovernmental fisheries organizations. We were able to obtain reliable age-structure stock assessments for five mackerel populations (Table 2.S2). In addition to the mackerels populations included in our analysis, it is worth mentioning other temperate mackerels populations that are currently being managed with age-structured stock assessments, but for several reasons, we did not include them in our analysis. First, we did not include in the analysis two blue mackerels populations (*Scomber australasicus*) distributed along the coastal waters of Japan (Japanese blue mackerel and Tsushima Current blue mackerel) because the stock assessment evaluation covered less than 15 years of data (Kawabata et al. 2009, Yukami et al. 2009). Second, we did not include the northwest Atlantic mackerel stock (*Scomber scombrus*) distributed along the east coast of the USA and Canada. In the recent past the USA and Canadian governments have evaluated this stock separately (NEFSC 2006, DFO 2008). However, the stock is currently being assessed as a larger geographic unit in a joint assessment between the USA and Canadian governments. The joint stock assessment report only became available after the paper was written (TRAC 2010). Finally, we are not aware of any formal quantitative stock assessment evaluations for any of the tropical mackerel species (*Rastrelliger* sp.) in the Indian Ocean. However, the data availability and the status of some mackerels fisheries

have been recently evaluated with simple stock assessment methods in several countries in the South East Asia region (FAO 2010a, 2010b).

The Spanish mackerels (tribe *Scomberomorini*) has the largest number of species (18 species) and with some notable exceptions, the status of the large majority of the species is very uncertain or little known. For our analysis, we were only able to collect reliable quantitative stock assessments for four *Scomberomorus* populations (2 species) that sustain important fisheries in the southeast coast of the United States (NMFS 2003, Ortiz 2004). This is worrying given the importance of the Spanish mackerels fisheries worldwide, especially in the Indo-west Pacific region, where eleven of the eighteen species are found and sustain important fisheries throughout their distributions (Collette and Nauen 1983). Although we were not able to obtain reliable and complete formal quantitative stock assessment evaluation for four *Scomberomorus* populations, it is worth mentioning several cases where Spanish mackerel species have been evaluated in the past or are currently being evaluated at least in some regions throughout their distributions. First, the are several populations of the narrow-barred Spanish mackerel (*Scomberomorus commerson*) and spotted mackerel (*Scomberomorus munroi*), the most important commercial Spanish mackerels species in Australia, that are currently being assessed with age-structure stock assessment models (Welch et al. 2002, Mackie et al. 2003, Begg et al. 2006, Buckworth et al. 2007). However these populations were not included in our analysis because they did not provide the type of data needed for our analysis or the time coverage of the assessment data was too short or not available to us. Second, there are several species of Spanish mackerels (*Scomberomorus commerson, S. niphonius, S. brasiliensis*) whose populations have been evaluated in the past with simple stock assessment methods, for example, in Thailand (Cheunpan 1988), South East Asia region (FAO 2010a, 2010b), India (Yohannan et al. 1992, Pillai et al. 1996), Oman (Siddeek and Al-Hosni 1998, Ben-Meriem et al. 2006), southern Arabian Gulf (Grandcourt et al. 2005), Djibouti(Bouhlel 1985), Japan (Nagai et al. 1996), Brazil(De Nóbrega 2002). However, we did not use these stock assessments evaluations either because 1) they were very outdated (prior to 2000), 2) the results were highly uncertain, 3) were not evaluated with age structure models or 4) they were inaccessible. The development of age-based stock assessments models would particularly benefit and ease the management of Spanish mackerels since many of the species can reach relatively large sizes and are relatively long-lived compared with other scombrid species such as the tropical mackerels and the small tunny species.

Lastly, the status of the bonitos (tribe *Sardini*), composed of seven coastal species, is unknown throughout the world. We are not aware of any stock status evaluations of any type for any of the bonito species distributed around the world.

Based on our global literature search and findings, we can conclude that accurate and reliable formal quantitative stock assessment evaluations and fisheries advice are unknown or highly uncertain for most of the scombrid species, with the notable exception of the principal market tunas and some temperate mackerel species. We are aware that the coverage of this study in terms of the number of commercially important populations identified and number of stock assessments obtained is not exhaustive. However, to our knowledge, we identified and compiled the majority of formal quantitative age-structured assessments expanding at least 15 years of data available worldwide for scombrid populations. Nevertheless, the compilation is evolving and new assessments will be incorporated into the data set for future analysis. We welcome institutions and individual scientist to contact us and share information about the status of scombrid species not covered by this study.

SI.2.4 Major conclusions on stock assessment data compilation and recommendations

We summarize the global status and biomass trajectories of 26 populations (11 species) of scombrids using population estimates from age-structured models prepared by stock assessment scientists. By limiting the data to age-structured models we could evaluate both the effects of fishing on the adult biomass of scombrid populations over time, but at the cost of being able to include only the most important commercial species of scombrids. Thus, some of the taxonomic groups, the Spanish mackerels and the bonitos and many regions are clearly underrepresented in the analysis. However, the 26 populations of scombrids included in this analysis expanded the number and coverage of scombrids previous accounted in past studies (Sibert et al. 2006, Worm et al. 2009, Hutchings et al. 2010).

The 26 populations of 11 species of scombrids evaluated with formal quantitative age structure stock assessments collated in this study seems small given the fact that scombrid species sustain some the largest fisheries in the world. All the species of scombrids, except slender tuna (*Allothunnus fallai*), plain bonito (*Orcynopsis unicolor*) and butterfly kingfish (*Gasterochisma melampus*), are targeted by industrial and/or small-scale fisheries throughout their ranges. The disparity between the existing number of populations being exploited and those that could be included in this analysis can be

attributed to two reasons. First, there are a large number of scombrid populations for which virtually no data are available and for which no scientific advice or analysis of their status is currently carried out. Second, some of these data are not openly available, and some of them are simply not open to scrutiny and analysis, in the case of both fisheries data and assessment results.

It appears the current structure of tunas RFMOs might not be appropriate or lacking in capacity to provide quantitative scientific advice for many small tunas, bonitos and Spanish mackerels, and some of them might not even be under the remit of any international organization despite populations that usually stretch across national boundaries. The widespread perception that small tuna fisheries are irrelevant in terms of catches or revenues has been reversed in the Mediterranean and Black Seas (Di Natale et al. 2009) and is probably the case for many other regions of the world. Coastal scombrids, although low in economic value for the global markets, sustain and feed many of the coastal fishing economies in many developed and developing countries around the world. Therefore, a review of existing frameworks and their suitability for the needs of some species might be needed in order to identify gaps in the mandates of existing management bodies, identify opportunities for further collaboration across states and fisheries organizations, and promote international efforts to better quantify the status and outlook of more coastal scombrids other than the principal market tuna species. We highlight the present collaborations between ICCAT and the Caribbean Regional Fisheries Mechanism and ICCAT and the General Fisheries Commission for the Mediterranean to improve the knowledge on the sustainable exploitation of small scombrid fisheries.

An issue of open access is also of relevance here. Stock assessments or catch statistics could not be obtained for some stock assessments for which they are known to exist. Contacts with the relevant scientific or management bodies proved unsuccessful. One of the major impediments for global analysis is that there are no global repositories of fisheries data under common formats and containing the multiple sources of information related to fishing (e.g. catch statistics, stock assessments inputs and outputs, economic data, etc…) as is the case for many biological and physical oceanographic datasets (e.g World Ocean Database). The creation of global fisheries repositories has been proposed many times (e.g. Hutchings and Baum 2005) with no immediate measurable results; however, there are some recent ongoing initiatives to compile all fish stock assessments globally (Worm et al. 2009, Hutchings et al. 2010). In addition, the five tuna RFMOs have also started a dialog to create common initiatives to organize and standardize several types of fisheries data from all the tuna commissions into common formats to facilitate the

accessibility of data to all the stakeholders and exchange of knowledge (Joint-Tuna-RFMOs 2010). These types of initiatives and others should be pursued in the short term. Large global unbiased fisheries datasets would definitely benefit and motivate more analyses needed to evaluate the global status of marine fish resources and quantify impacts of fishing on marine species and ecosystems.

SI.3 Statistical analysis

SI.3.1 Data assumptions

We quantified fishing impacts on adult biomass from 1954 to 2006 because the majority of the data available started after the 1950s and finished in 2006 (Figure 2.1B main text). Yet an approach was needed to estimate the adult biomass for those populations for which biomass started after 1954 and/or finished prior to the year 2006. For those time series starting after 1954 we extended the adult biomass backwards using the mean of the first three years of data. Thus, we assumed that from 1954 to the first year with data there have been no major fisheries targeting these populations and therefore the adult biomass has not changed over time. This is a conservative approach where we are likely underestimating some of the impacts of fishing because fishing began long before the start of many of the time series summarized here. The first year in a stock assessment does not usually correspond with the start of the fishery, thus stock assessments may often not capture well past declines.

For those time series finishing prior to 2006, we extended them forward to 2006 using two different approaches. For most populations we only needed to extend them for a few years, the majority of the times one or two years. In the first approach, we used an average of the last three years to project the biomass forward up to 2006, therefore assuming no change in biomass. In the second approach, we used the model-estimated average annual rate of change of each individual population to project the adult biomass forward, therefore, assuming biomass of the last few years follows a trend based on past data. Both assumptions are plausible since recent fishing mortality for the majority of the populations has not been reduced over the past few years. In addition, by projecting forward using the average rate of change of each population we are also assuming that the statistical properties, such as the mean and variance of the rate of change, do not themselves change over time, which might not be the case in some of the time series. Therefore, this second approach might have created some bias in the estimated declines, although small, since we are projecting forward only for a few years into the future. This

assumption would not have been appropriate for medium and long-term projections, but seems reasonable enough in this case. We obtained very similar results using both approaches; therefore our results are robust to the choice of method.

SI.3.2 Estimation of the average annual rate of change in adult biomass across all populations over time

We tested if the average annual rate of change in adult biomass across all the populations (global estimate) was accelerating or decelerating over time using a submodel of the full mixed model (full model shown in the main text). The submodel consisted in keeping the covariate X (year) and eliminates the covariate W from the full mixed model. By keeping the covariate X (year) in the model we are interested in the overall global trend and we could test if the covariate year is significantly different from zero. A slope significantly different from zero indicates that the average annual rate of change in biomass has been changing over time, either accelerating and becoming more negative (negative rate) or accelerating and becoming more positive (positive trend) over time. Our data suggest that the global rate has been constant over time (γ_{10} =-0.00027, P =0.19), therefore, it has neither decreased nor increased across all the populations. At present, the majority of populations have been fished roughly around MSY levels (Figure 2.4A main text) and therefore the majority of the populations are currently fully exploited. We would expect in the near future to see a deceleration in the average annual rate of decline in order to fulfill with the international biodiversity commitments and fisheries targets of maintaining populations at MSY and when necessary to halt and reverse declines and recover populations to the level that would generate MSY.

SI.3.3 Estimation of the average annual rate of change and extent of decline in adult biomass for each population

We estimated the average of the annual rates of change in adult biomass across all the years for each population using a generalized least-squares model of the form $Y_i = b_o + e_i$. Y_i, the dependent variable, are the annual (i) rates of change in adult biomass of each population, b_0, the intercept, is interpreted as the average annual rate of change in adult biomass across all the years (Figure 2.S5A) and e_i are the residual errors. For these analyses, we used the raw time series of adult biomass of each population and therefore the time series of each population differ in time coverage and time span (Figure 2.1B main text). We used maximum likelihood to fit all the generalized least-square models using the gls function in the NLME package in R (Pinheiro and Bates 2000). We examined the residuals of all the models and corrected for temporal autocorrelation with AR1 and AR2

processes when necessary. In addition, we also estimated the extent of decline for each individual population as follows: $(1-\exp(b_o *n))*100$ where b_o is the model estimated average annual rate of change for each individual population and n is the length of the time series of each individual population (Figure 2.S5B).

SI.3.4 Estimation of the average rate of change in adult biomass within species

While we used mixed effects models to perform a meta-analysis of population trends in adult biomass to estimate annual rates of change globally, within oceans, within the main taxonomic groups and within distinct life history strategies, we did not use mixed effect models to estimate the average rates of change within species because the number of populations within each species was too low (a maximum of 4 populations per species). To estimate trends in the average annual rate of change of adult biomass from 1954 to 2006 within species, first, we estimated the average of the annual rates of change in adult biomass from 1954 to 2006 for each population using a generalized least-squares model of the form $Y_i = b_o + e_i$ (see Section 3.2). Second, we combined the single population average annual rate of change estimated in the first step within each species using weights according to the inverse of the standard errors of the estimates (Figure 2.S2A).

SI.3.5 Estimation of the average fishing mortality over time across all the populations

In order to estimate what percentage of tunas and their relatives are caught each year by fisheries, we used the matrices of fishing mortality at age over time for each population from the stock assessments. For each population, we then calculated the weighted average fishing mortality across all ages, using the abundances by age. Then we estimated an average annual fishing mortality rate across all the populations ($F_{overall}$) by taking a weighted average of the average annual fishing mortality rates of each population, weighting them by the total number of individuals in each population. Finally, we used the estimated average annual fishing mortality rate across all the populations ($F_{overall}$) to calculate the annual percent removal of fish due to fishing using the Baranov catch equation, $(F/(F+M))*(1-\exp(-(F+M)))$, where F is the instantaneous fishing mortality rate and M is natural mortality rate (Figure 2.4B main text). We estimated that currently fisheries catch around 10%-15% of the tunas and their relatives each year globally ($F_{2003-2005}$ = 0.16 and using a natural mortality rate of 0 to 0.85, Figure 2.4B main text). The complete matrix of fishing mortality at age over time was only available for 21 of the 26 populations under study. The matrix of fishing mortality at age over time was not available or harvest rates were provided instead, for the following populations: Pacific bluefin tuna,

Japanese chub mackerel, Tsushima current chub mackerel and Southern bluefin tuna. Therefore these populations were not included in the analysis.

SI.4 Population trajectories in adult biomass and their current management status

SI.4.1 Current management status of tunas and their relatives according to the reference points (B/B$_{MSY}$ and F/F$_{MSY}$)

The biological reference points, B/B$_{MSY}$ and F/F$_{MSY}$, were available for twenty-one out of the twenty-six populations of tunas and their relatives (15 tuna populations, 4 Spanish mackerel populations and 2 mackerel populations) (Table 2.S2). For the remainder of the populations, these reference points were either not estimated as part of the assessment process (some mackerel populations) or were considered highly uncertain by the assessment scientists and were not included (Pacific bluefin tuna and North Pacific albacore tuna). We define "overfished" to mean that the biomass of the population has been reduced to a level less than that which would provide the MSY (B<B$_{MSY}$) and the term "overfishing" to mean that a population is being subject to a fishing effort greater than that required to produce the MSY (F>F$_{MSY}$), a definition used by the majority of the tuna RFMOs (Aranda et al. 2010). According to the biological reference points, the current status of the four Atlantic Spanish mackerels is healthy with adult biomasses above B$_{MSY}$ and current fishing mortalities below F$_{MSY}$ (Figure 2.4A and Table 2.S2). Among the 15 tuna populations with biological reference points, eight populations are sustainably exploited with biomasses above B$_{MSY}$ and fishing mortality lower than F$_{MSY}$. Only the west Pacific bigeye tuna is being subject to a fishing effort greater than that required to produce the MSY. Four tuna populations, all temperate tunas, are overexploited with current biomasses being below B$_{MSY}$ and experiencing excessive fishing mortalities (F$_{current}$ > F$_{MSY}$). Finally, two tuna populations, the south Atlantic albacore tuna and Atlantic yellowfin tuna, are overfished with current biomasses below B$_{MSY}$ but are not experiencing overfishing (F$_{current}$ < F$_{MSY}$). Therefore, three distinct exploitation categories are evident in the tuna populations (Figure 2.S6). On one extreme, the "Good" category comprises moderately exploited and successfully managed populations: west Pacific skipjack and south Pacific albacore. On the other extreme, the "Ugly" category comprises the populations that are overexploited and managed poorly: eastern and western Atlantic bluefins and Southern bluefin. Finally, in the "Fully-exploited" category separating these two extremes, the majority of the populations circle MSY. The reference points of two tuna populations, the Pacific Bluefin tuna and the north Pacific albacore tuna, were considered

highly uncertain by the assessment scientists and were not included. Finally, only two of the five mackerel populations had estimates of biological reference points. The northeast Atlantic mackerel is considered healthy with current biomass at B_{MSY} and fishing mortality rates lower than F_{MSY} (ICES 2009). The current biomass of the Chilean Chub mackerel is above B_{MSY} and the current fishing mortalities are higher than F_{MSY} (Canales 2006). The reference points B_{MSY} and F_{MSY} were not estimated as part of the stock assessment process for the Japanese chub mackerel and the northeast Pacific chub mackerel. However, since 2003 there are measures to reduce fishing mortality and recover the Japanese chub mackerel population to healthy levels (Ishida et al. 2009). For the northeast Pacific mackerel, the exploitation rate is currently low. This fishery collapsed in the 1960s and recovered afterwards. The current biomass still remains very low relative to its historical peaks due to a combination of historical fishing pressure and unfavorable oceanographic conditions (Crone et al. 2009).

We would like to highlight the current exploitation status of tuna populations and their relatives can be easily categorized according to their standard biological reference points, although it is important to take into account two points. First, there is uncertainty associated to the estimated reference points. Second, the reference points for the majority of the majority of tunas and their relatives, despite their assigned exploitation status, are roughly at MSY. Most of the populations are considered fully exploited, thus the expansion of the catches in these fisheries is limited.

SI.4.2 Link between population trajectories and their current management status

There is a consistent link between the population trajectories in adult biomass and their current exploitation status (Figs. S4 and S5). First, there are a total of four overexploited populations, all temperate tunas, with current biomasses below target levels ($B<B_{MSY}$) and experiencing excessive fishing mortalities ($F>F_{MSY}$). These overexploited populations have exhibited the steepest rate of decline, -3.7%y^{-1} (CI: -5.2 to -2.1) and on average have declined by 85.7% from 1954 to 2006 (s S4A and S5C). These overexploited populations have also experienced a large extent of decline in total adult biomass, a 84.8% since1954 (Figure 2.S5D). Second, there are 12 healthy populations, mostly tropical tunas and Spanish mackerels, which are healthy with biomass levels above target levels ($B>B_{MSY}$) and fishing mortality rates not exceeding F_{MSY} ($F<F_{MSY}$). These healthy exploited populations have decreased at a rate of -1.1 % y^{-1} (CI: -2.1 to -0.1) and have declined on average by 43.9% since 1954 (Figure 2.S4C and S5C). The overall extent of decline in total adult biomass in these 12 healthy populations has been 42.8% since1954 (Figure

2.S5D). Finally, there are six populations of tunas and mackerels that either have biomasses below healthy levels, or fishing mortalities are exceeding healthy levels, but not both ($B<B_{MSY}$ or $F>F_{MSY}$). These populations have decreased at a rate of -2.1% y^{-1} (CI: -3.7 to -0.6) and experienced an average decline of 67.7% since 1954 (Figs. S4B and S5C). They have also experienced an extent of decline in total adult biomass of 58.7% since 1954, similar to that exhibited by the overexploited populations (Figure 2.S5D).

We found the link between the trajectories of adult biomass and their current management status remains at the population levels (Figure 2.S5A-B). However, there are some discrepancies between the trajectories of the individual populations and their current management status; populations exhibiting the largest declines are not always considered currently as being unsustainably exploited and *vice versa*. First, two chub mackerels (the Chilean and the north east Pacific populations) have experienced the steepest and most variable declines, yet their exploitation statuses are not currently considered overexploited. In the case of the Chilean chub mackerel, the most recent current biomass (2006) was still considered within safe levels but close to unsuitable levels if the exploitation rates were not reversed (Canales 2006). For the northeast Pacific mackerel, the exploitation rate is currently low due to the collapse of the important commercial fishery it once supported. Although the stock collapsed in the mid- 1960s and recovered afterwards, the current biomass still remains very low relative to its historical peaks due to a combination of historical fishing pressure and unfavorable oceanographic conditions (Crone et al. 2009). Second, the south Pacific albacore is deemed healthy despite having experienced one of the largest declines. The large declines may be partly spurious due to a poorly fit stock assessment model resulting in overestimates of the adult biomass in the earlier periods (Hoyle et al. 2008). Last, the current management status for the eastern Atlantic bluefin tuna is overexploited, despite relatively small declines in adult biomass compared to the other overexploited populations. This may be due to a shifted baseline perspective as the population estimates start only in the 1970s. The eastern Bluefin tuna has a long history of exploitation and mismanagement accompanied with substantial quantities of illegal, unreported and unregulated fishing in the recent history which makes it difficult to estimate the historical population trajectory (ICCAT 2009, 2010).

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Supplementary Figures
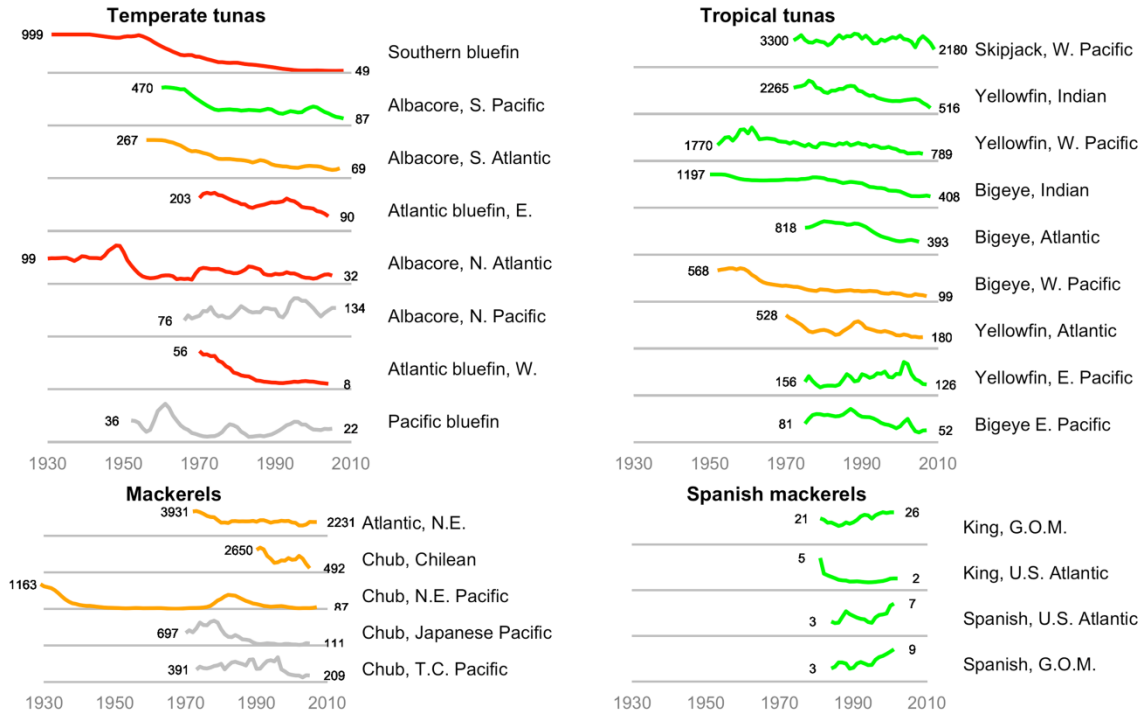
Figure 2.S1 ***Trajectories of adult biomass (1000 tonnes) for 26 populations of tunas and their relatives (11 species).***

The values indicate initial and final adult biomass estimates. The horizontal grey lines delineate a biomass of zero. Abbreviations for population names: N., north, S., south, E., east, W., west, N.E., northeast; U.S., United States, G.O.M., Gulf of Mexico; T.C., Tsushima Current. Population trajectories are colored according to their exploitation status: Red - populations are overfished ($B<B_{MSY}$) and experiencing overfishing ($F>F_{MSY}$). Orange - populations are overfished or experiencing overfishing ($B<B_{MSY}$ or $F>F_{MSY}$, not both) and Green - populations are not overfished ($B>B_{MSY}$) and are not experiencing overfishing ($F<F_{MSY}$). Population trajectories for which reference points were unavailable are colored in grey (See SI Section 4). Populations are plotted in descending rank order of abundance at former levels, with the least abundant at the bottom.
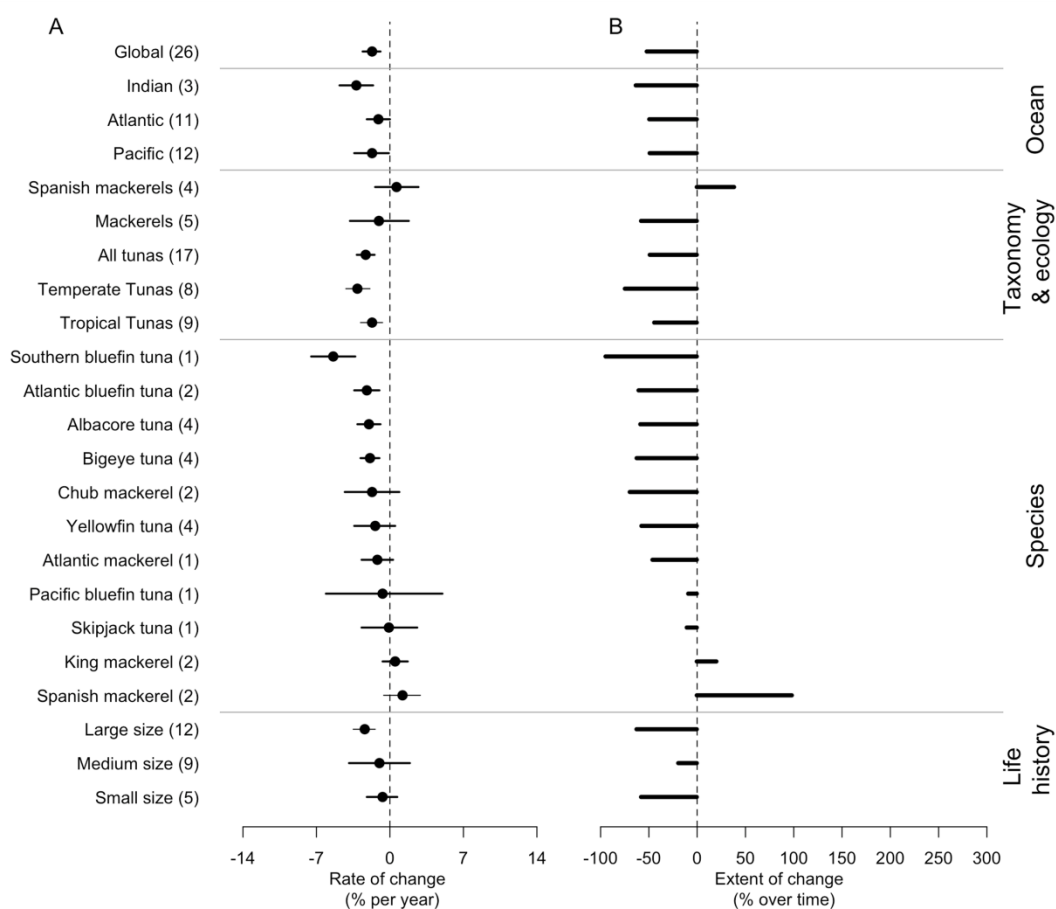
Figure 2.S2 ***Meta-analysis of fishing impacts on adult biomass globally, within major oceans, within the major taxonomic groups, ecological groups, species and life history strategies using maximum body size as a proxy.***

(A) Average annual rates of change in adult biomass (average % per year ± 95% confidence intervals) from 1954 to 2006. (B) Overall extent of decline or recovery in total adult biomass from 1954 to 2006. Number of populations within each category is shown between brackets. Albacore and bluefin tunas are considered temperate tunas and skipjack, yellowfin and bigeye tunas are considered tropical tunas. Species were grouped according to their maximum body size (Large >2m FL, Medium >1 and <2 m FL and Small <1m FL) which we used as a proxy to describe life-history strategies. Maximum body size of species is in Table 2.S1.
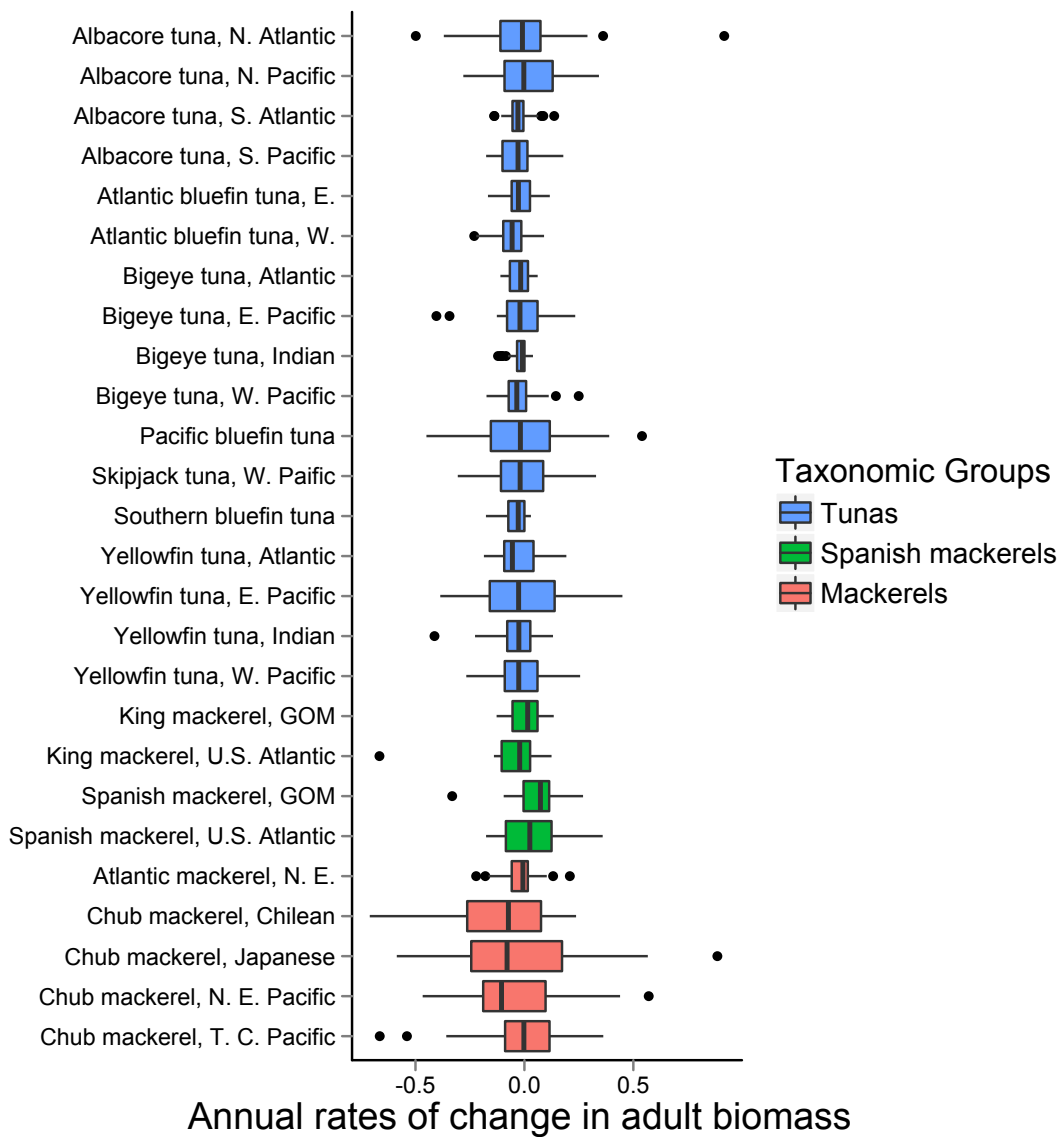
Figure 2.S3 *Box plots of the annual rates of change (r_i) in adult biomass for the 26 populations of tunas and their relatives.*

Mackerel populations exhibit greater inter-annual variability. Figure 2.S7 shows the time series of the annual rates of change (r_i) for each population. Abbreviations for population names: E., east; GOM, Gulf of Mexico; N., north; N.E., northeast; S., south; T.C., Tsushima Current; U.S., United States; W., west.
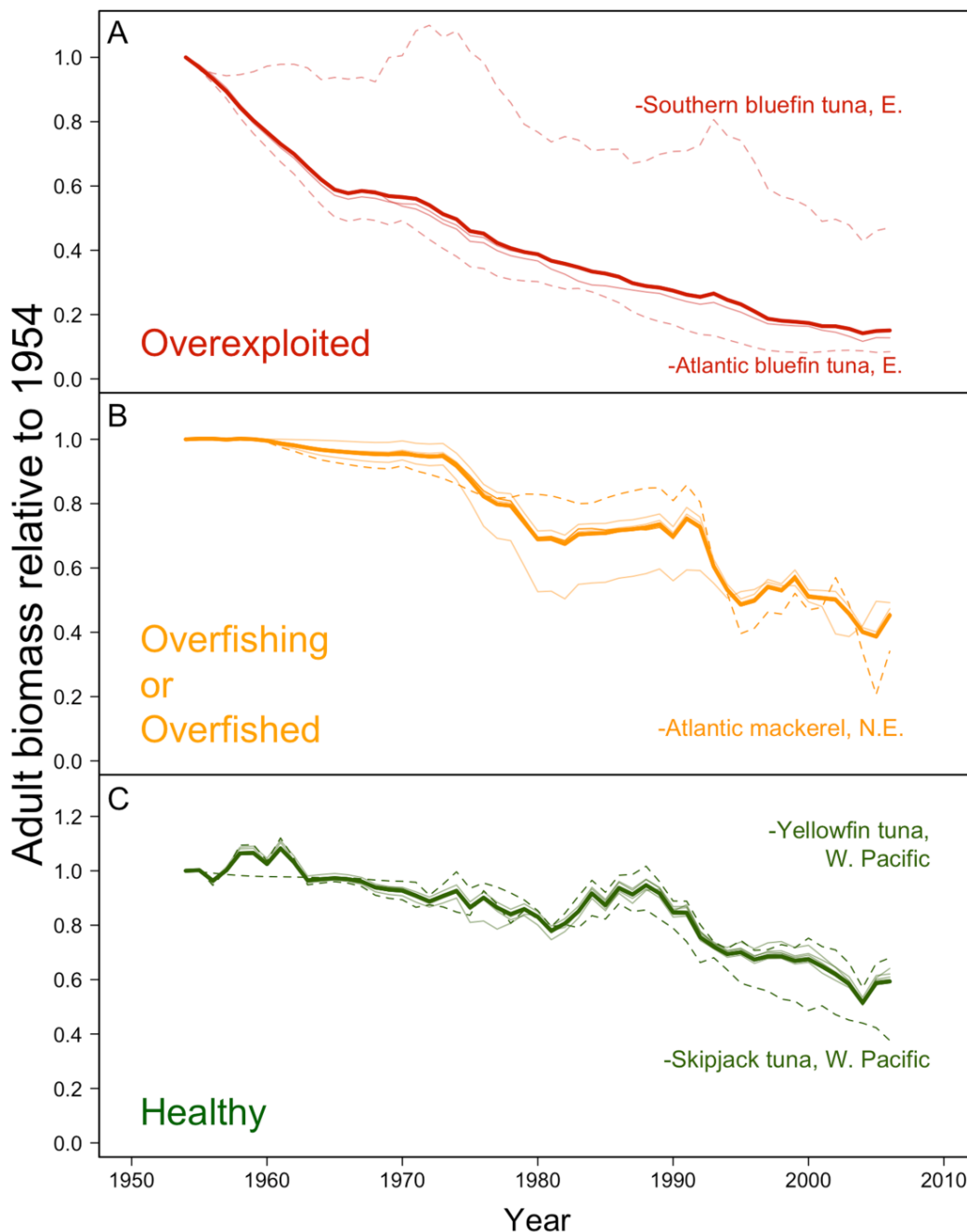
Figure 2.S4   Relative adult biomass trajectories (thick solid line) of tunas and their relatives within each exploitation status category, standardized to 1 in 1954.

Faint and dashed lines show the effect of excluding one population at a time from the overall trend and recalculating the relative adult biomass. Dashed lines delineate the most influential populations. Trajectories are colored according to the exploitation status of populations: Red – overexploited - populations are overfished ($B<B_{MSY}$) and experiencing overfishing ($F>F_{MSY}$). Orange - populations are overfished or experiencing overfishing ($B<B_{MSY}$ or $F>F_{MSY}$, not both) and Green – healthy - populations are not overfished ($B>B_{MSY}$) and are not experiencing overfishing ($F<F_{MSY}$). E., east; N.E., northeast; W., west.
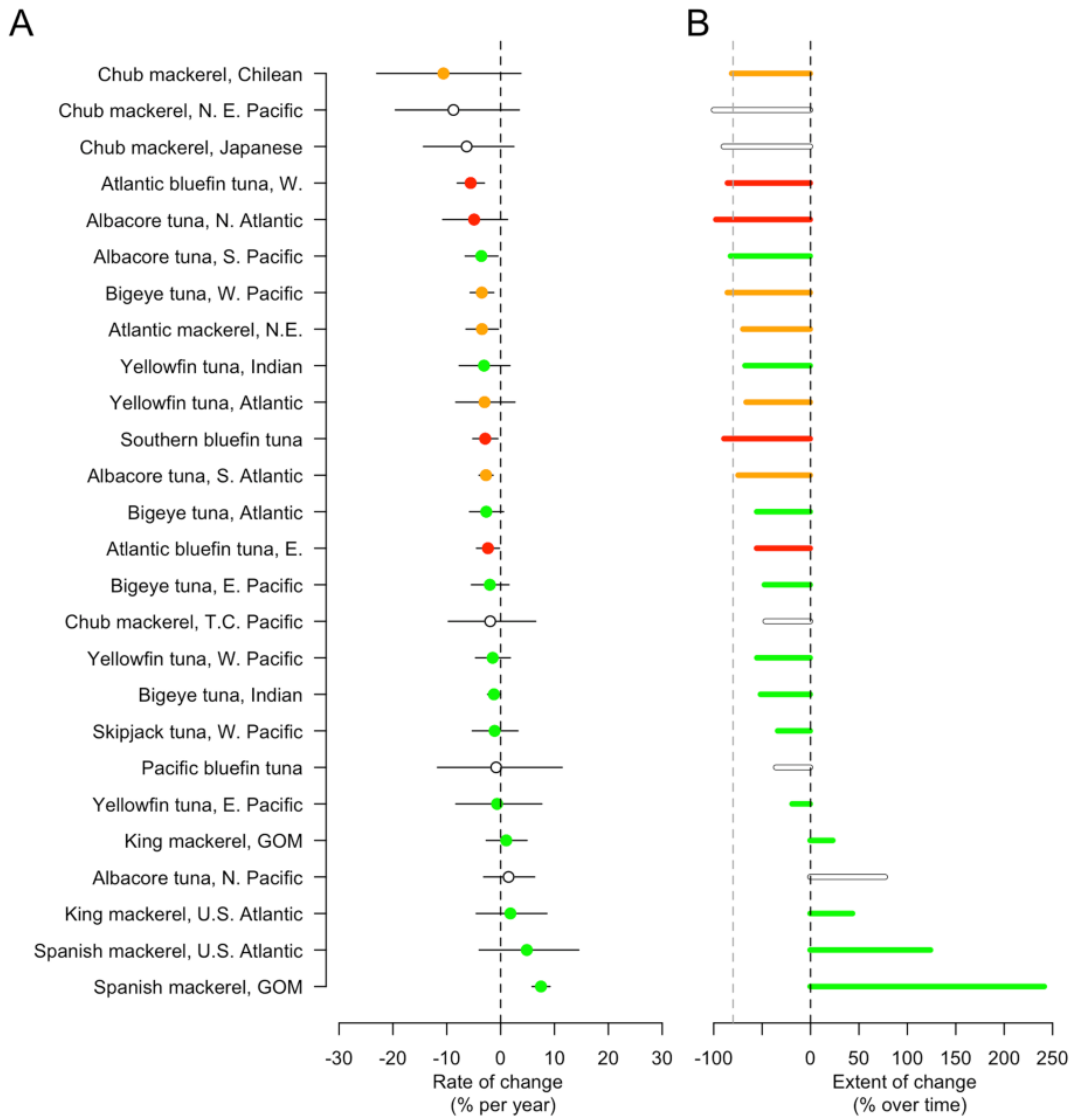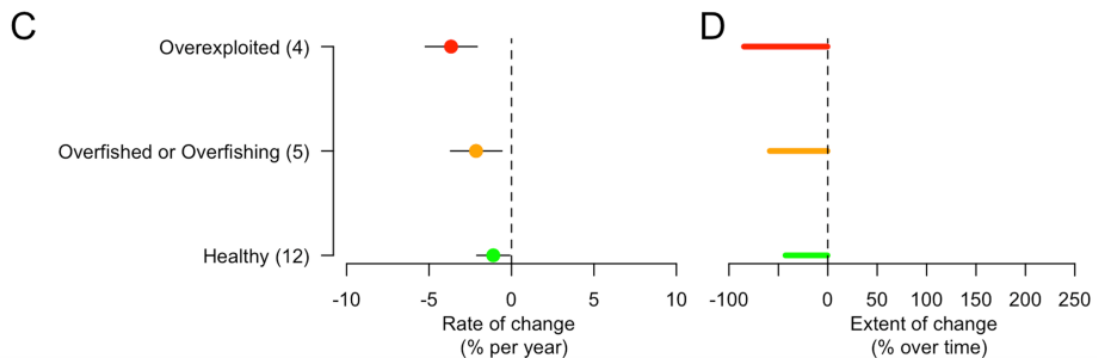
Figure 2.S5   *Population trajectories in adult biomass and link with their current exploitation status.*

(A) Average annual rate of change in adult biomass (mean ± 95% confidence intervals) for each population including the entire time span of the time series (see Figure 2.1B for time span). (B) Overall extent of decline or recovery in adult biomass for each population from the first to the last year of available data (see SI.3.3). (C) Average annual rate of change in adult biomass (mean ± 95% confidence intervals) from 1954 to 2006 within each exploitation status category. (D) Overall extent of decline or recovery in total adult biomass from 1954 to 2006 within each exploitation status category. The vertical dashed line in panel B delineates an extent of decline of 85%. Population trajectories are colored according to their exploitation status: Red - populations are overfished ($B<B_{MSY}$) and experiencing overfishing ($F>F_{MSY}$). Orange - populations are overfished or experiencing overfishing ($B<B_{MSY}$ or $F>F_{MSY}$, not both) and Green - populations are not overfished ($B>B_{MSY}$) and are not experiencing overfishing ($F<F_{MSY}$). Population trajectories for which reference points were unavailable are shown with white solid circles and lines (See SI Section 4). Abbreviations for population names: E., east; GOM, Gulf of Mexico; N., north; N.E., northeast; S., south; T.C., Tsushima Current; U.S., United States; W., west.
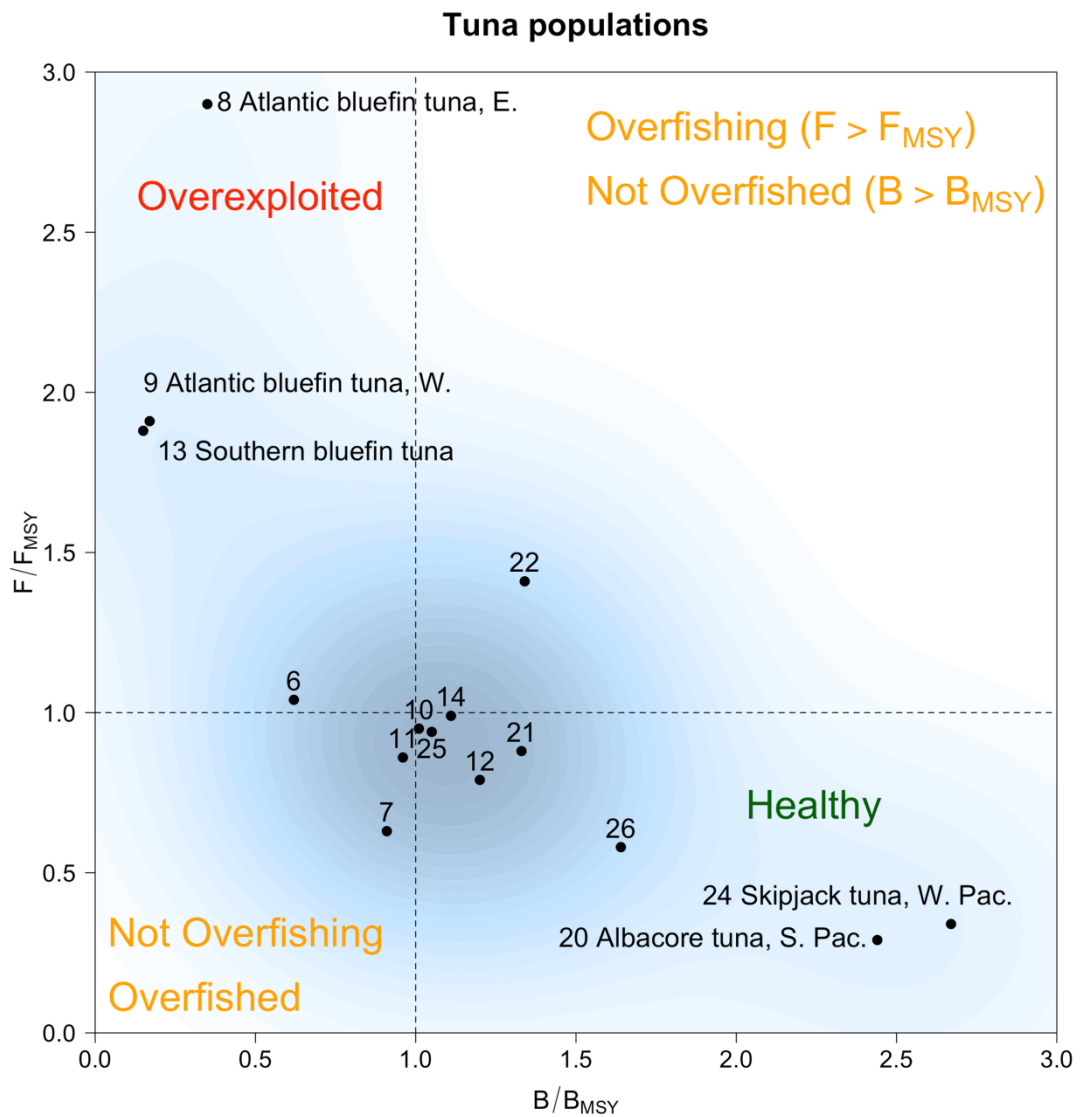
Tuna populations

Figure 2.S6 *Current adult biomass relative to B_{MSY} (x-axis) versus current exploitation rate relative to F_{MSY} (y-axis) reference points for tuna populations.*

Codes follow Figure 2.1 and Table 2.S2. Colors represent the density of the points (the probability of occurrence) as calculated with a kernel density function. The reference points of two tuna populations were not available; Pacific bluefin tuna and North Pacific albacore tuna (See SI Section 4). E., east; Pac., Paci!c; S., south; W., west.

A
Temperate tuna populations

B   Tropical tuna populations

C   Mackerel and Spanish mackerel populations
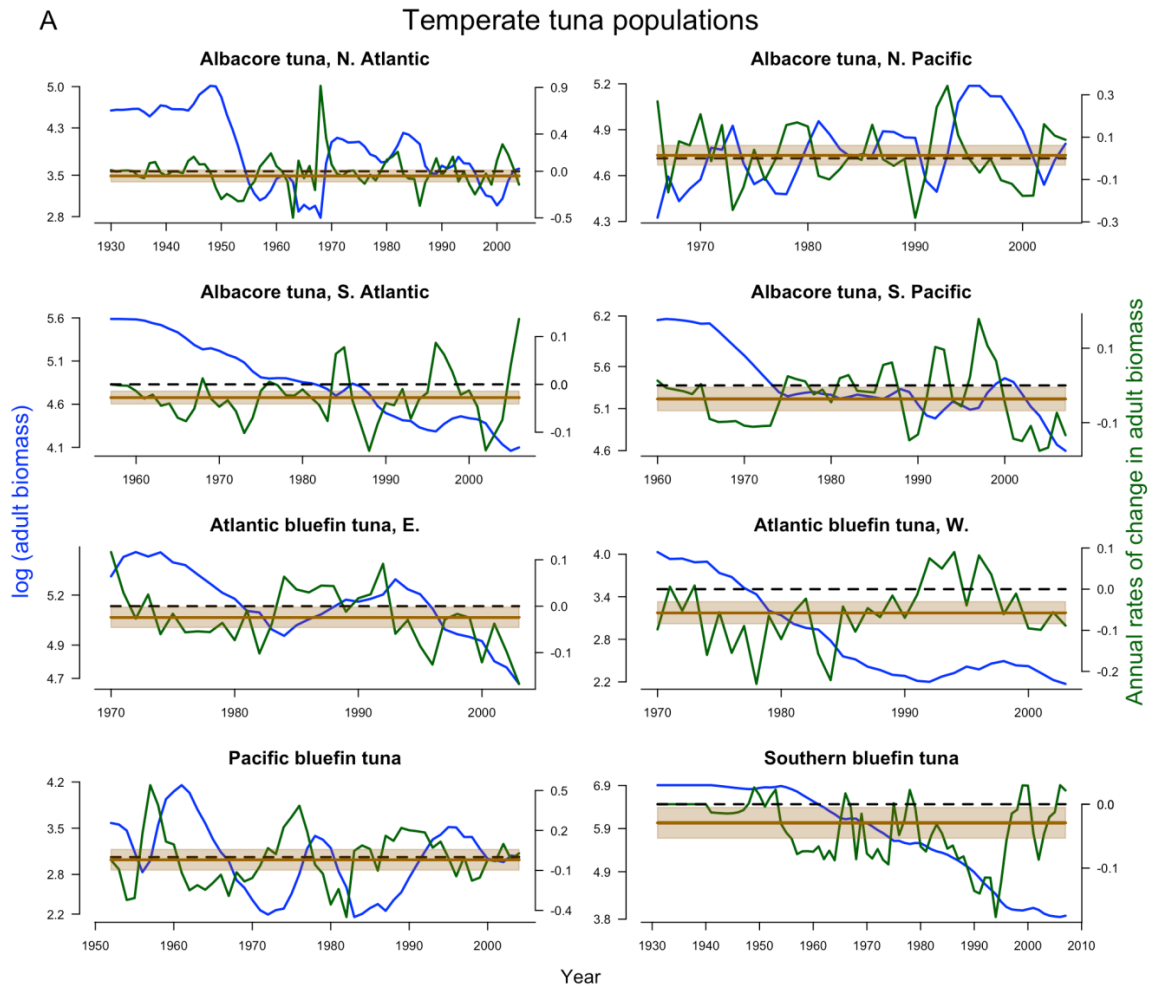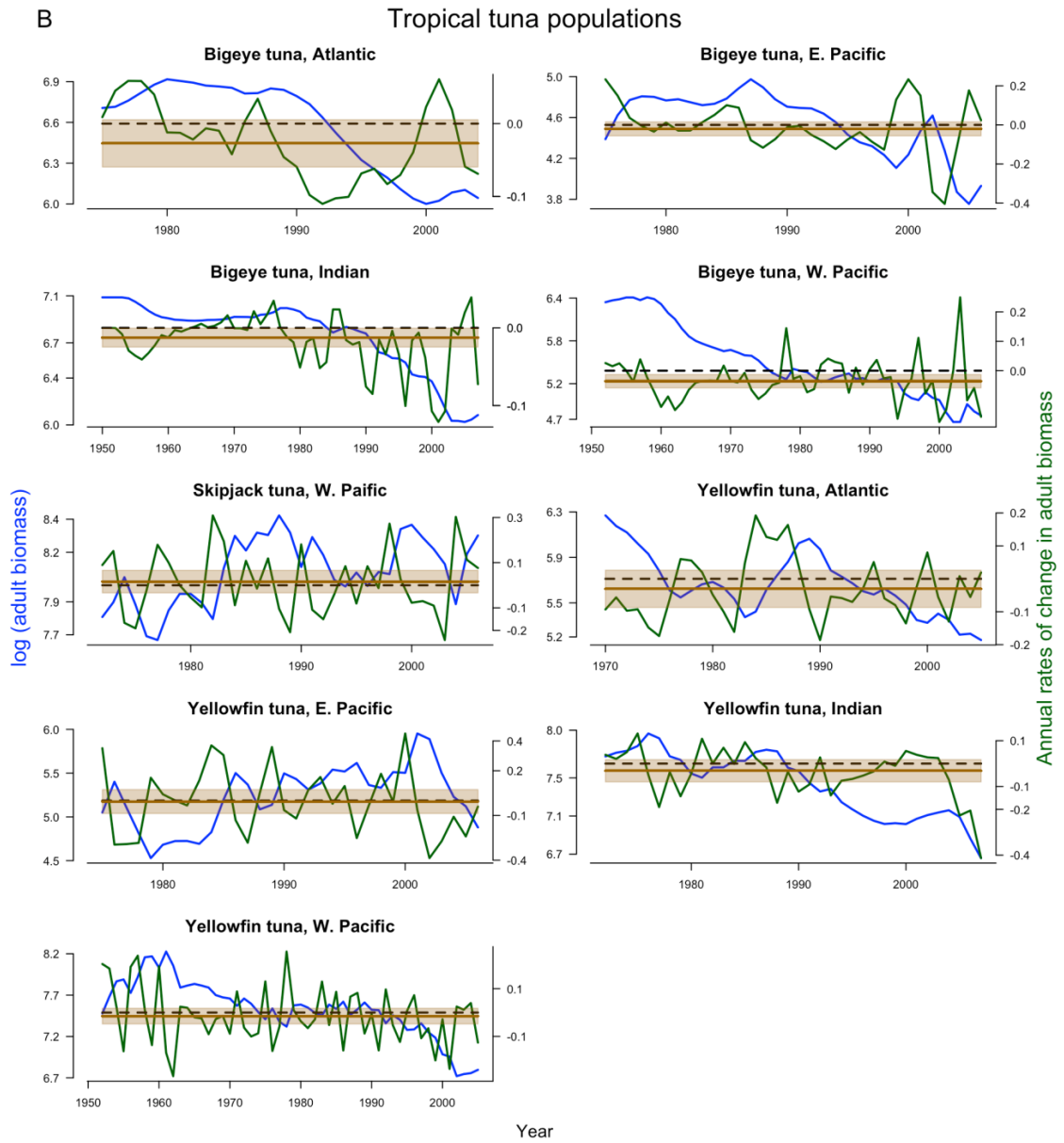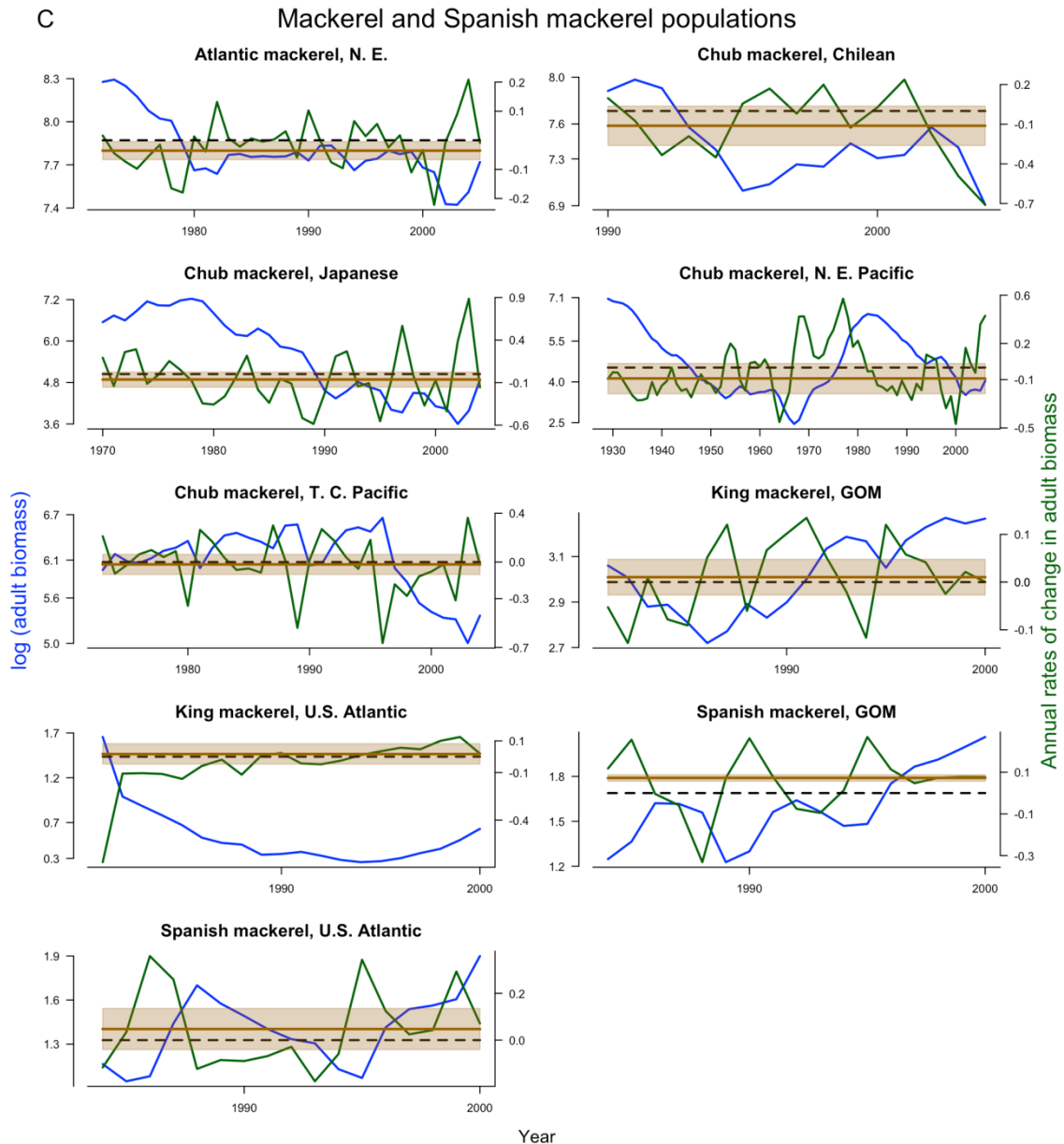
Figure 2.S7A *Time series of adult biomass on the logarithmic scale (left y-axis, blue solid line) and time series of the annual rates of change (year-on-year rate of change) in adult biomass (right y-axis, green solid line) in scombrid populations.*

(A) Scombrid populations of temperate tunas. (B) Scombrid populations of tropical tunas. (C) Scombrid populations of mackerels and Spanish mackerels. We converted the time series of adult biomass of each population to annual rates of change (r_i) as $r_i = \ln(AB_{i+1}/AB_i)$, where AB_i is adult biomass in year i, to allow for nonlinear trends and reduce autocorrelation. The annual rates of change in adult biomass r_i, was the dependent variable in the analyses of biomass trends. The model-estimated average annual rate of change (brown solid line) and its confidence intervals (shaded brown polygon) are also shown. Abbreviations for population names: E., east; GOM, Gulf of Mexico; N., north; N.E., northeast; S., south; T.C., Tsushima Current; U.S., United States; W., west.
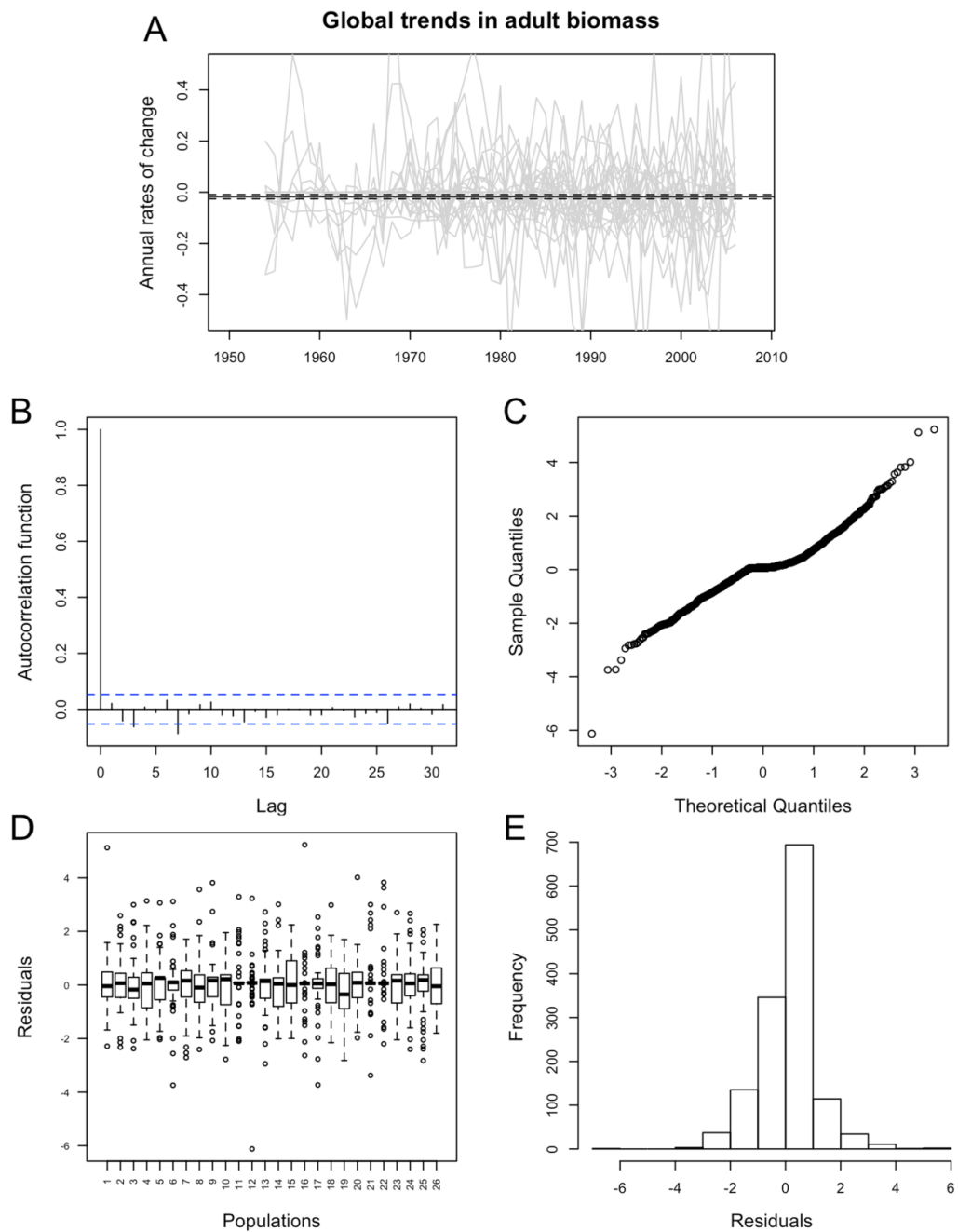
Figure 2.S8   Results and validation analysis from the meta-analysis of trends in adult biomass across tuna populations and their relatives (global estimate) using a mixed-effects model.

(A) Solid and dashed black lines indicate the overall fixed-effect average annual rate of change and 95% confidence intervals, respectively, in adult biomass across all 26 populations. Grey lines represent the time series of annual rates of change for the 26 populations. (B–E) Validation plots of the final model. Autocorrelation function with 95% confidence intervals (dashed blue horizontal lines).

Supplementary Tables

Table 2.S1   List of scombrid species (Family Scombridae) with their maximum body sizes and geographic distributions. (*) Principal market tunas.

Subfamily and Tribe	Latin name	Common name	Maximum size (cm)	Geographic distribution
Subfamily Scombrinae				
Tribe Thunnini (tunas)	*Thunnus alalunga**	Albacore tuna	140	Cosmopolitan
	Thunnus albacares*	Yellowfin tuna	239	Cosmopolitan
	Thunnus atlanticus	Blackfin tuna	108	Western Atlantic Ocean
	Thunnus maccoyii*	Southern bluefin tuna	245	Southern Oceans
	Thunnus obesus*	Bigeye tuna	228	Cosmopolitan
	Thunnus thynnus*	Atlantic bluefin tuna	426	Atlantic Ocean
	Thunnus orientalis*	Pacific bluefin tuna	300	Pacific Ocean
	Thunnus tonggol	Longtail tuna	145	Indian Ocean, Indo-Pacific region, Western Pacific Ocean
	Katsuwonus pelamis*	Skipjack tuna	110	Cosmopolitan
	Euthynnus affinis	Kawakawa	100	Indian Ocean, Indo-Pacific region
	Euthynnus alletteratus	Little tunny	106	Atlantic Ocean, including the Mediterranean and Black Seas
	Euthynnus lineatus	Black skipjack	84	Eastern Pacific Ocean
	Auxis rochei	Bullet tuna	50	Cosmopolitan
	Auxis thazard	Frigate tuna	65	Cosmopolitan
	Allothunnus fallai	Slender tuna	105	Southern Oceans

Subfamily Scombrinae				
Tribe Sardini (bonitos)	*Cybiosarda elegans*	Leaping bonito	45	Indo-Pacific region
	Gymnosarda unicolor	Dogtooth tuna	248	Indian Ocean, Indo-Pacific region. The distribution is disjoint, found primarily around reefs.
	Orcynopsis unicolor	Plain bonito	130	Eastern Atlantic Ocean including Mediterranean Sea
	Sarda australis	Australian bonito	180	Indian and Pacific Oceans
	Sarda chiliensis	Eastern Pacific bonito	102	Eastern Pacific Ocean
	Sarda orientalis	Indo-Pacific bonito	102	Indian Ocean and Western Pacific Ocean
	Sarda sarda	Atlantic bonito	91	Atlantic Ocean including Mediterranean Sea
Subfamily Scombrinae	*Acanthocybium solandri*	Wahoo	239	Cosmopolitan
Tribe Scomberomorini (Spanish mackerels)	*Scomberomorus brasiliensis*	Serra Spanish mackerel	125	Western Atlantic Ocean
	Scomberomorus cavalla	King mackerel	173	Western Atlantic Ocean
	Scomberomorus commerson	Narrow-barred king mackerel	240	Indian Ocean and Western Pacific Ocean. Recently found in Mediterranean Sea along the Northern African countries.
	Scomberomorus concolor	Monterey Spanish mackerel	77	Eastern Central Pacific Ocean
	Scomberomorus guttatus	Indo-Pacific king mackerel	76	Indian Ocean and Western Pacific Ocean
	Scomberomorus koreanus	Korean seerfish	150	Indian Ocean and Western Pacific Ocean

Scomberomorus lineolatus	Streaked seerfish	80	Indian Ocean and Indo-Pacific region
Scomberomorus maculatus	Atlantic Spanish mackerel	91	Western Atlantic Ocean
Scomberomorus multiradiatus	Papuan seerfish	35	Restricted to the Gulf of Papua and Timor Sea in the Indo-Pacific
Scomberomorus munroi	Australian spotted mackerel	104	Indo-Pacific region restricted to Northern Australia and Papua New Guinea
Scomberomorus niphonius	Japanese Spanish mackerel	100	Northwest Pacific
Scomberomorus plurilineatus	Kanadi kingfish	120	Western Indian Ocean along the Eastern African Coast
Scomberomorus queenslandicus	Queensland school mackerel	100	Indo-Pacific region restricted to Northern Australia and Papua New Guinea
Scomberomorus regalis	Cero	164	Western Atlantic Ocean
Scomberomorus semifasciatus	Broad-barred king mackerel	120	Indo-Pacific region restricted to Northern Australia and Papua New Guinea
Scomberomorus sierra	Pacific sierra	99	Eastern Pacific Ocean
Scomberomorus sinensis	Chinese seerfish	218	Western Pacific Ocean
Scomberomorus tritor	West African Spanish mackerel	98	Eastern Atlantic Ocean including the Mediterranean Sea
Grammatorcynus bicarinatus	Shark mackerel	112	Indo-Pacific region
Grammatorcynus bilineatus	Double-lined mackerel	100	Indian Ocean and Indo-Pacific region. It is not clear if the distribution is continuous, at least around the Indian Ocean.

Subfamily Scombrinae			
Tribe Scombrini (mackerels)	*Rastrelliger brachysoma*	Short mackerel	35	Indo-Pacific region
	Rastrelliger faughni	Island mackerel	20	Indo-Pacific region
	Rastrelliger kanagurta	Indian mackerel	35	Indian Ocean and Western Pacific Ocean
	Scomber australasicus	Spotted chub mackerel	44	Indo-West Pacific region
	Scomber japonicus	Chub mackerel	62	Indian and Pacific Oceans
	Scomber scombrus	Atlantic mackerel	60	North Atlantic Ocean
	Scomber colias	Atlantic chub mackerel	63	Atlantic Ocean including Mediterranean Sea
Subfamily Gasterochismatinae	*Gasterochisma melampus*	Butterfly kingfish	164	Southern Oceans

Table 2.S2 *Populations of tunas and their relatives analyzed and sources of stock assessments and management reference points.*

Code	Ocean	Taxonomic group	Species Latin name	Population common name	Sources of the stock assessments	B/B_{MSY}	F/F_{MSY}	Source of the reference points
1	Atlantic	Mackerels	*Scomber scombrus*	Atlantic mackerel, North East	(1)	1.13	1.07	(2)
2	Atlantic	Spanish mackerels	*Scomberomorus cavalla*	King mackerel, Gulf of Mexico	(3)	1.50	0.83	(4)
3	Atlantic	Spanish mackerels	*Scomberomorus cavalla*	King mackerel, U.S. Atlantic	(5)	1.34	1.00	(4)
4	Atlantic	Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, Gulf of Mexico	(5)	1.07	0.60	(5)
5	Atlantic	Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, U.S. Atlantic	(5)	1.44	0.65	(5)
6	Atlantic	Tunas	*Thunnus alalunga*	Albacore tuna, North Atlantic	(6)	0.62	1.04	(7)
7	Atlantic	Tunas	*Thunnus alalunga*	Albacore tuna, South Atlantic	(6)	0.91	0.63	(7)
8	Atlantic	Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, East	(8)	0.35	2.90	(9)
9	Atlantic	Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, West	(8)	0.15	1.88	(9)
10	Atlantic	Tunas	*Thunnus obesus*	Bigeye tuna, Atlantic	(10)	1.01	0.95	(11)
11	Atlantic	Tunas	*Thunnus albacares*	Yellowfin tuna, Atlantic	(12)	0.96	0.86	(12, 13)
12	Indian	Tunas	*Thunnus obesus*	Bigeye tuna, Indian	(14)	1.20	0.79	(15)
13	Indian	Tunas	*Thunnus maccoyii*	Southern bluefin tuna	(16)	0.17	1.91	(16)
14	Indian	Tunas	*Thunnus albacares*	Yellowfin tuna, Indian	(14)	1.11	0.99	(15)
15	Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, Chilean	(17)	2.78	2.07	(17)
16	Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, Japanese	(18)			
17	Pacific	Mackerels	*Scomber japonicus*	Chub mackerel,	(19)	<1	<1	(20)

18	Pacific	Mackerels	*Scomber japonicus*	North East Pacific Chub mackerel, Tushima Current Pacific	(21)			
19	Pacific	Tunas	*Thunnus alalunga*	Albacore tuna, North Pacific	(22)			
20	Pacific	Tunas	*Thunnus alalunga*	Albacore tuna, South Pacific	(23)	2.44	0.29	(24)
21	Pacific	Tunas	*Thunnus obesus*	Bigeye tuna, East Pacific	(25)	1.33	0.88	(26)
22	Pacific	Tunas	*Thunnus obesus*	Bigeye tuna, West Pacific	(27)	1.34	1.41	(28)
23	Pacific	Tunas	*Thunnus orientalis*	Pacific bluefin tuna	(29)			
24	Pacific	Tunas	*Katsuwonus pelamis*	Skipjack tuna, West Pacific	(30)	2.67	0.34	(30)
25	Pacific	Tunas	*Thunnus albacares*	Yellowfin tuna, East Pacific	(31)	1.05	0.94	(32)
26	Pacific	Tunas	*Thunnus albacares*	Yellowfin tuna, West Pacific	(33)	1.64	0.58	(34)

Supplement Information: References for Table 2.S2

1. ICES (2007) Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy (WGMHSA).

2. ICES (2009) Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy (WGMHMSA).

3. Ortiz M (2004) Stock assessment analysis on Gulf of Mexico king mackerel. SEDAR5- 2004 NMFS SEFSC Miami Lab Sustainable Fisheries Division Contribution 2004-004.

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5. NMFS (2003) Stock assessment analysis on Spanish and king mackerel stocks. Prepared for the 2003 Mackerel Stock Assessment Panel Meeting.Southeast Fisheries Science Center, Miami, Florida, United States.

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Chapter 3

Chapter 3.

The conservation and management of tunas and their relatives: setting life history research priorities [1]

Abstract

Scombrid species (tunas, bonitos, Spanish mackerels and mackerels) support important fisheries in tropical, subtropical and temperate waters around the world, being one of the most economically- and socially-important marine species globally. Their sustainable exploitation, management and conservation depend on accurate life history information for the development of quantitative fisheries stock assessments, and in the fishery data-poor situations for the identification of vulnerable species. Here, we assemble life history traits (maximum size, growth, longevity, maturity, fecundity, spawning duration and spawning interval) for the 51 species of scombrids globally. We identify major biological gaps in knowledge and prioritize life history research needs in scombrids based on their biological gaps in knowledge, the importance of their fisheries and their current conservation status according to the International Union for Conservation of Nature Red List. We find that the growth and reproductive biology of tunas and mackerel species have been more extensively studied than for Spanish mackerels and bonitos, although there are notable exceptions in all groups. We also reveal that reproductive biology of species, particular fecundity, is the least studied biological aspect in scombrids. We identify two priority groups of species, including 32 species of scombrids, and several populations of principal market tunas, for which life history research should be prioritized following the species-specific life history gaps identified in this study in the coming decades. By highlighting the important gaps in biological knowledge and providing a priority setting for life history research in scombrid species this study provides guidance for management and conservation and serves as a guide for biologists and resource managers interested in the biology, ecology, and management of scombrid species.

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Introduction

Life history information such as growth, age and maturity are fundamental determinants of the population dynamics of fishes and underpin the sustainable exploitation and management of species (Beverton and Holt 1959, King and McFarlane 2003, Winemiller 2005). As a result, in the last fifty years there has been considerable effort devoted to the analysis of fish life histories. However, even in the era of powerful databases, e.g. FishBase, this information often remains scattered, incomplete and not readily accessible (Zeller 2005, Froese and Pauly 2012). Here, we compile life history studies for the 51 species of the family Scombridae, commonly known as tunas, bonitos, Spanish mackerels and mackerels (Table 3.1 and Figure 3.1). We aim to promote the best use of the existing life history information, synthesize the current knowledge on life history traits across species and identify priority biological research needs in an effort to inform management and conservation of this important group of species in the coming decades.

Scombrid species sustain some of the most important fisheries in the world. They support diverse commercial fisheries throughout their distributions, ranging from large-scale industrial to small-scale artisanal fisheries, and many species are caught in recreational fisheries worldwide (Table 3.S1). Annual catches of scombrids have risen continuously since the 1950s, reaching 9.6 million tonnes in 2010 (FAO 2010-2013). Together, all scombrid catches contribute up to 15% of the annual total marine fish catch and are worth in excess of US$ 5 billion each year (Majkowski 2007, FAO 2009). Scombrids are epipelagic predator and prey species and are widely distributed in coastal and oceanic waters throughout the tropical, subtropical and temperate waters of the world's oceans. The majority of the species are found in marine open waters and some are associated with estuarine and riverine habitats and coral reefs (Collette and Nauen 1983). Among the fifteen species of tunas (Thunnini), seven species are known as the principal market tunas due to their economic importance in the global markets (see list of species in Table 3.1). The principal market tunas have widespread oceanic distributions, are highly-migratory, sustain highly-industrialized fisheries worldwide and are a highly-valued international trade commodity for canning and sashimi (Collette and Nauen 1983, Majkowski 2007, Collette et al. 2011). The rest of scombrid species, the small tunas, bonitos, Spanish mackerels, and mackerels have in general more coastal distributions and are associated with continental shelves or oceanic islands (Table 3.1). While the economic value of coastal scombrids is lower in the global markets, they can reach high values locally supporting a diversity of fisheries. These are largely small-scale artisanal fisheries but also
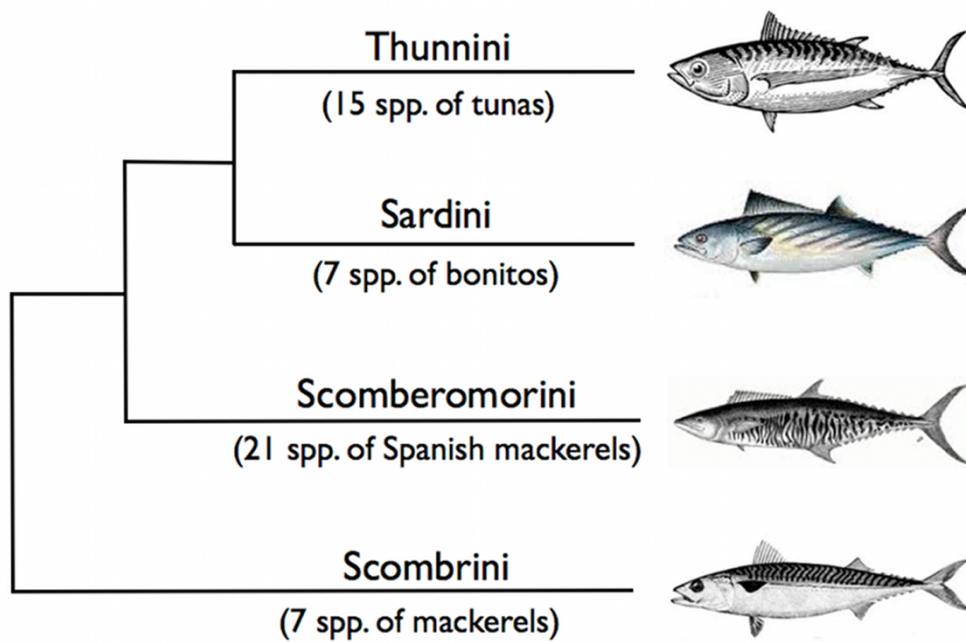
Figure 3.1   **Phylogeny of the family Scombridae showing the four tribes of the subfamily Scombrinae (Collette et al. 2001).**

The subfamily Gasterochismatinae, which has only one species, butterfly kingfish *Gasterochisma melampus,* is not shown.

Table 3.1 **List of scombrid species including their taxonomic classification, maximum body size (Lmax), climate, environment and geographic distributions. (*) Principal market tuna.**

Taxonomic group	Latin name	Common name	L_{max}	Climate	Environment	Geographical distribution
Tribe Thunnini (tunas)	*Thunnus alalunga	Albacore tuna	135	Subtropical	Oceanic	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea
	*Thunnus albacares	Yellowfin tuna	231	Tropical	Oceanic	Atlantic, Pacific and Indian oceans
	Thunnus atlanticus	Blackfin tuna	104	Tropical	Neritic	Western Atlantic Ocean
	*Thunnus maccoyii	Southern bluefin tuna	245	Temperate	Oceanic	Southern waters of the Atlantic, Pacific and Indian oceans
	*Thunnus obesus	Bigeye tuna	236	Subtropical	Oceanic	Atlantic, Pacific and Indian oceans
	*Thunnus thynnus	Atlantic bluefin tuna	427	Temperate	Oceanic	Atlantic Ocean
	*Thunnus orientalis	Pacific bluefin tuna	300	Temperate	Oceanic	Pacific Ocean
	Thunnus tonggol	Longtail tuna	145	Tropical	Neritic	Northern Indian Ocean, Indo-Pacific region, Western Pacific Ocean
	*Katsuwonus pelamis	Skipjack tuna	111	Tropical	Oceanic	Atlantic, Pacific and Indian oceans
	Euthynnus affinis	Kawakawa	100	Tropical	Neritic	Indian Ocean, Indo-Pacific region
	Euthynnus alleteratus	Little tunny	108	Tropical	Neritic	Atlantic Ocean, including the Mediterranean and Black seas
	Euthynnus lineatus	Black skipjack	86	Tropical	Neritic	Eastern Pacific Ocean
	Auxis rochei	Bullet tuna	48	Tropical	Neritic	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea
	Auxis thazard	Frigate tuna	62	Tropical	Neritic	Atlantic, Pacific and Indian oceans
	Allothunnus fallai	Slender tuna	105	Temperate	Oceanic	Southern waters of the Atlantic, Pacific and Indian oceans
Tribe Sardini (bonitos)	Cybiosarda elegans	Leaping bonito	45	Tropical	Neritic, associated with coral reefs	Western Pacific Ocean restricted to the southern coast of Papua Guinea and northern Australia
	Gymnosarda unicolor	Dogtooth tuna	186	Tropical	Neritic	Disjoint distribution in the Indian Ocean and Indo-Pacific region
	Orcynopsis unicolor	Plain bonito	130	Subtropical	Neritic	Eastern Atlantic Ocean including Mediterranean Sea
	Sarda australis	Australian bonito	108	Subtropical	Neritic	Southwest Pacific Ocean in south western Australia and northern New Zealand
	Sarda chiliensis	Eastern Pacific bonito	101	Subtropical	Neritic	Eastern Pacific Ocean
	Sarda orientalis	Indo-Pacific bonito	102	Subtropical	Neritic	Indian and Pacific Oceans
	Sarda sarda	Atlantic bonito	97	Subtropical	Neritic	Atlantic Ocean including Mediterranean Sea
Tribe Scomberomorini (Spanish mackerels)	Acanthocybium solandri	Wahoo	238	Tropical	Oceanic, associated with coral reefs	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea
	Scomberomorus brasiliensis	Serra Spanish mackerel	125	Tropical	Neritic	Western Atlantic Ocean
	Scomberomorus cavalla	King mackerel	159	Tropical	Neritic	Western Atlantic Ocean
	Scomberomorus commerson	Narrow-barred king mackerel	240	Tropical	Neritic	Indian Ocean and Western Pacific Ocean. Recently found in the Mediterranean Sea along the northern African countries.

Species	Common name		Temperature	Habitat	Distribution
Scomberomorus concolor	Monterey Spanish mackerel	77	Subtropical	Neritic	Eastern Central Pacific Ocean. Current distribution is restricted to the northern part of the Gulf of California.
Scomberomorus guttatus	Indo-Pacific king mackerel	87	Tropical	Neritic, associated with estuaries	Northern Indian Ocean and Indo-Pacific region
Scomberomorus koreanus	Korean seerfish	150	Tropical	Neritic	Northern Indian Ocean and northwestern Pacific Ocean
Scomberomorus lineolatus	Streaked seerfish	98	Tropical	Neritic	Northern Indian Ocean and Indo-Pacific region
Scomberomorus maculatus	Atlantic Spanish mackerel	80	Subtropical	Neritic	Northwestern Atlantic Ocean
Scomberomorus multiradiatus	Papuan seerfish	35	Tropical	Neritic, associated with estuaries	Restricted to the Gulf of Papua and Timor Sea in the Indo-Pacific
Scomberomorus munroi	Australian spotted mackerel	103	Tropical	Neritic	Indo-Pacific region restricted to northern Australia and Papua New Guinea
Scomberomorus niphonius	Japanese Spanish mackerel	103	Temperate	Neritic	Northwest Pacific Ocean
Scomberomorus plurilineatus	Kanadi kingfish	120	Subtropical	Neritic	Western Indian Ocean along the Eastern African Coast
Scomberomorus queenslandicus	Queensland school mackerel	100	Tropical	Neritic, associated with estuaries	Indo-Pacific region restricted to northern Australia and Papua New Guinea
Scomberomorus regalis	Cero	94	Tropical	Neritic	Western Atlantic Ocean
Scomberomorus semifasciatus	Broad-barred king mackerel	120	Tropical	Neritic	Indo-Pacific region restricted to northern Australia and Papua New Guinea
Scomberomorus sierra	Pacific sierra	99	Tropical	Neritic	Eastern Pacific Ocean
Scomberomorus sinensis	Chinese seerfish	248	Subtropical	Neritic, associated with estuaries	Northwestern Pacific Ocean
Scomberomorus tritor	West African Spanish mackerel	97.5	Tropical	Neritic, associated with estuaries	Eastern Atlantic Ocean including the Mediterranean Sea
Grammatorcynus bicarinatus	Shark mackerel	122	Subtropical	Neritic, associated with coral reefs	Southwestern Pacific restricted to the northern coast of Australia
Grammatorcynus bilineatus	Double-lined mackerel	100	Subtropical	Neritic, associated with coral reefs	Northern Indian Ocean and Indo-Pacific region with a disjoint distribution
Tribe Scombrini (mackerels)					
Rastrelliger brachysoma	Short mackerel	34.5	Tropical	Neritic, associated with estuaries	Indo-Pacific region
Rastrelliger faughni	Island mackerel	30.9	Tropical	Neritic	Indo-Pacific region
Rastrelliger kanagurta	Indian mackerel	39.6	Tropical		Indian Ocean, Indo-Pacific region and Western Pacific Ocean
Scomber australasicus	Spotted chub mackerel	55	Subtropical	Neritic	Western Pacific Ocean and northwestern Indian Ocean
Scomber japonicus	Chub mackerel	63	Subtropical	Neritic	Northwest Pacific Ocean and Eastern Pacific Ocean
Scomber scombrus	Atlantic mackerel	60	Temperate	Neritic	Northwest Atlantic Ocean and Northeast Atlantic Ocean including the Mediterranean Sea
Scomber colias	Atlantic chub mackerel	63	Subtropical	Neritic	Eastern Atlantic Ocean including Mediterranean Sea
Subfamily Gasterochismatinae					
Gasterochisma melampus	Butterfly kingfish	195	Temperate	Oceanic	Southern waters of the Atlantic, Pacific and Indian oceans

semi-industrial and industrial fisheries, in both developed and developing countries (Table 3.S1). Hence, they are an important source of wealth and food security to local fishing communities (Collette and Nauen 1983, Gillett et al. 2001, Majkowski 2007, Di Natale et al. 2009). Given the global scale and magnitude of scombrid fisheries and their economic and social importance for many coastal countries, a global review of the life history studies of scombrids seems essential to evaluate the biological knowledge of this important group of species and set the research agenda for the coming decades.

Two recent global evaluations have provided a global picture of the current exploitation and conservation status of scombrid species. One evaluation quantified global fishing impacts on fishery-assessed population of scombrids showing the adult biomass of scombrids (including 26 populations of 11 of the 51 species) have decreased on average by 60% over the past fifty years (Juan-Jordá et al. 2011). It also revealed that the fisheries for the majority of these scombrid populations are currently fully exploited worldwide, suggesting that the further expansion of sustainable catches from these fisheries in the short term are limited. By assembling all the available, long-term and reliable stock-assessment fishery evaluations of scombrid populations globally, this study focused on the most economically-important principal market tunas and mackerels. However, it also exposed that the large majority of scombrid populations and species lack reliable and up-to-date formal quantitative stock assessments of the long-term impacts of fishing on population biomasses. Consequently, the current exploitation status remains unknown or highly uncertain for the majority of scombrid species worldwide. The other global evaluation summarized the conservation status for scombrids species using the International Union for Conservation of Nature (IUCN) Red List criteria, hence, ranking species in terms of their relative risk of global extinction (Collette et al. 2011). Of the 51 species of scombrids, 68% (35 of 51 spp.) were listed under the Least Concern IUCN Red List category, having a relatively low risk of global extinction. Sixteen percent (8 spp.) had declined sufficiently in biomass to trigger listing under the Threatened or Near Threatened categories having relatively higher risk of global extinction. Lastly, 16% (8 spp.) of scombrids were listed under the Data Deficient category, meaning these species have insufficient information to evaluate their global conservation status. These two global evaluations together revealed that the impacts of fishing and the exploitation status for the majority of scombrid populations and species remains unknown or is highly uncertain globally and highlighted which species are in need of further protection and management. Consequently, the global life history dataset assembled and synthesized in this study will

become particularly useful for those scombrid populations and species for which their exploitation and conservation status is unknown. In an era where stock assessments are expensive and data intensive and where it is unlikely that there will ever be sufficient information to develop long-term quantitative stock assessments for all exploited species, the knowledge of life history parameters can provide a starting framework in support of management (King and McFarlane 2003).

In this study we first compile a data set of life history traits (maximum size, growth, longevity, maturity, spawning season and fecundity) for the 51 species of scombrids on a global scale. Second, we synthesize the life history information assembled and critically review it to identify gaps and priorities in biological knowledge across the species. Third, we recommend and prioritize life history research needs in scombrid species based on their biological gaps in knowledge, the importance of their fisheries and their current conservation status according to the IUCN Red List of Threatened Species. The present study does not represent a complete synthesis of all available life history information; rather we focus on reviewing the available growth and reproductive studies for the adult stages of the species, which are the essential information that generally feeds quantitative fisheries stocks assessment models and forms the basis of their management and conservation.

Methods

We assembled life-history data for the 51 species of scombrids on a global scale from a wide range of published literature including: scientific journals, reports and theses published in English, Spanish, French, Portuguese, Italian and any other language that provided an English summary. We reviewed and included in the data set only the original studies, excluding review articles. By reviewing only original information, we avoided propagating widely-used but poorly-supported or erroneous parameter estimates. From each life history study, we extracted the trait estimates reported for females, males, and both sexes combined along with the sample sizes and the method used to estimate each of the life history traits. We transformed standard lengths or total lengths into fork lengths using published length conversion equations. The data set includes studies up to November 2012.

The data set includes 684 studies (Appendix C) from which we extracted the following life history information: (1) Maximum length (L_{max}, cm) of the fish observed from each life

history study; (2) Growth information derived from the von Bertalanffy growth function, $L_t = L_\infty (1-e^{-k(t-to)})$, where L_t is the length at age t in years, L_∞ is asymptotic length in cm - the mean size the individuals in the population would reach if they were to grow indefinitely; growth coefficient k (year^{-1}) expresses the rate at which the asymptotic length is approached and t_o is defined as the hypothetical age in years that fish would have at zero length; (3) Longevity or maximum observed age (T_{max}, years) extracted from growth and aging studies; (4) Length and age maturity estimates where we distinguished between length and age at first maturity (L_m, cm; T_m, years; which is the length and age at maturity first reached by an individual in a sample) and length and age at 50% maturity (L_{m50}, cm; T_{m50}, years; which is the maturity at which 50% of the individuals are matured in the sample); (5) Duration of the spawning season (Spw_{season}, months); and (6) Fecundity metrics including estimates of batch fecundities (absolute average batch fecundities $F_{average}$ as the average number of oocytes across all sampled females, and relative batch fecundities, F_{rel}, as the average number of oocytes per gram across all sampled females) and spawning intervals (Spw_{int}, the average number of days between spawning). We further discuss later how we filtered fecundity studies based on the accuracy of various methodologies to estimate fecundity.

We used standard plots for basic descriptive statistics to synthesize the life history information assembled and critically review it to identify gaps and priorities in biological knowledge for each scombrid species. In the analysis, we preferentially used the female estimates whenever the traits were reported separately for sexes in the studies. Additionally, we reviewed the life history information for the seven species of principal market tunas at the population level (see list of species in Table 3.1). The principal market tunas are oceanic species with worldwide distributions, and some species are composed of various populations, with one or two populations in each ocean. Due to their widespread distributions and economic importance, the principal market tunas are managed as 23 independent management units or tuna stocks, here referred as populations, by five Regional Fisheries Management Organizations. Therefore, we also reviewed the life history information and identified gaps and priorities for the 23 populations in the seven species of principal market tunas, a distinction we deem relevant given the scale of their management. All data management, manipulation and plots were done using the R statistical software, v.2.14.2 (R Development Core Team 2012) and the packages ggplot2 (Wickham 2009) and VennDiagram (Chen and Boutros 2011). The life history data set is available upon request from the corresponding author.

Results and Discussion

Below we first synthesize and critically review the biological knowledge on growth and reproductive traits for the 51 species of scombrids. Then, we identify and propose priority life history research for scombrid species based on their biological gaps in knowledge, the importance of their fisheries throughout their distributions and their current conservation status according to the IUCN Red List of Threatened Species

Biology of scombrids: Current knowledge, data gaps and data concerns

Growth and longevity

Growth and age are the most important life history attributes in fish stock assessments, as they are influential in the evaluation of population productivity and have large impacts on the evaluation of population status (Restrepo et al. 2011). The importance of growth and age studies is reflected in the life history research conducted to date in scombrid species. There are a total of 547 von Bertalanffy growth curves in the data set and growth has been studied in 41 of 51 species of scombrids and in all 23 populations of principal market tunas (Figure 3.2 and 3.3). We find scombrid species have evolved different strategies for growth, attaining different asymptotic sizes (L_∞) in their lifetimes and managing to reach those asymptotic sizes at different rates (k) (Figure 3.4). Thus, the L_∞ and k coefficients vary greatly between scombrid species ranging from 24.4 cm and 2.3 y^{-1}, respectively, in the short mackerel (*Rastrelliger brachysoma*) to 309.7 cm and 0.12 y^{-1}, respectively, in the Atlantic bluefin tuna (*Thunnus thynnus*). While, the von Bertalanffy growth parameters, L_∞ and k, are fundamental to describe the growth trajectories of individual species, it is not straight-forward to use L_∞, which represents size, and k, which has time dimensions (y^{-1}), by themselves to compare multiple growth curves and growth rates across multiple species (Pauly 1979). Instead, a metric linking change in size or weight of a species with time is needed to describe growth patterns across multiple species (Pauly 2010). Therefore, we used two complementary approaches to describe the growth patterns in scombrid species. First, we used the von Bertalanffy k parameter, which conveys how fast a species reaches its maximum body size to differentiate between "fast growing" and "slow-growing" species given a maximum body size. Second, we used the growth performance index, initially developed by Pauly 1979, and defined as $\varnothing'=\log_{10}k+2\log_{10}L_\infty$, which is a metric with dimensions of size and time, to differentiate between species that have "high growth performances" from species having "low growth performances"

regardless of their maximum body size (Munro and Pauly 1983). A species with a high index of growth performance would rapidly reach a large maximum body size in a short time span and therefore would have both relatively high k and L_∞ values compared to species with low growth performances. However, because the growth performance index is the product of combining information from two parameters, L_∞ and k, a high index of growth performance could also be the result of having only a high L_∞, thus, it does not necessarily imply fast growth rates (a high k) to reach L_∞. Yet, the species with the highest growth performances will have both relatively high L_∞ and k. In addition, we also used the auximetric plot, which is a double logarithmic plot of the parameters k and L_∞ (Pauly 1979, Pauly 1991) to portray and visualize what are "fast vs slow growing" species given a maximum body size and species with "high vs low growth performances" (Figure 3.5A). By plotting k vs L_∞, which are inversely related, in the auximetric plot, the growth space utilized by fishes can be represented (Pauly 1979, 2010). Different population of a same species will tend to form a cluster of points, describing the "growth space" of the species, and the cluster of points will grow in size as higher taxonomic levels (e.g. genera and families) are represented in the auximetric plot.

Scombrids are among the fastest growing species of all fishes. All scombrid species have relatively high k values (a mean k of 0.48 y^{-1}) given their maximum size when compared to the rest of fish species, exhibiting rapid growth toward their maximum body size (Figure 3.5A). Among all scombrid species, the fastest growing species (k values > 0.7 y^{-1}) given their maximum body size are the three tropical Indian mackerels, Indian mackerel (*Rastrelliger brachysoma*), Island mackerel (*R. faughni*) and short mackerel (*R. kanagurta*), the Indo-Pacific king mackerel (*Scomberomorus guttatus*) and frigate tuna (*Auxis thazard*) (Figure 3.4). Moreover, the three bluefin tuna species (*Thunnus thynnus, T orientalis,* and *T. maccoyii*) and two Spanish mackerels (Monterey Spanish mackerel *Scomberomorus concolor* and Serra Spanish mackerel *S. brasiliensis*) are the slowest growing species (k <0.2 y^{-1}) among scombrids. We also found that the growth performance index Ø' in scombrids is among the highest in fish species, indicating not only that scombrids have relatively high k values given their maximum body size, but they also have both relatively high k and L_∞ values, being able to grow very fast to large body sizes compared to the rest of fish species (Figure 3.5). Note how the growth space of scombrids species is located towards the top right quarter of the auximetric plot, although there are some exceptions (Figure 3.5A). Four tuna species, yellowfin, Atlantic bluefin, Pacific bluefin and bigeye tuna (*Thunnus albacares, T. thynnus, T. orientalis* and *T. obesus*, respectively) have the largest growth performances indices (Ø'> 4) among

A

B

Figure 3.2   ***Life history information in scombrid species.***

Information includes life history estimates of Von Bertalanfy growth parameters, longevity, length and age at 50% maturity, duration of spawning season, average batch fecundity, relative batch fecundity and spawning interval. (A) Number of life history trait estimates in the dataset for all the species combined. (B) Number of scombrid species with at least one life history trait estimate (grey). There are 51 species in the family Scombridae.

A

Species	Growth	Longevity	Length at maturity	Age at maturity	Spawning season	Average batch fecundity	Relative batch fecundity	Spawning interval	Group
Thunnus thynnus	16	11	4	5	3		1	1	Tunas
Thunnus orientalis	4	3		1	1	1		1	
Thunnus maccoyii	14	7	2	2	2	1	1	1	
Thunnus obesus	25	12	8	2	5	3	3	3	
Thunnus albacares	37	9	12	1	10	6	6	6	
Thunnus tonggol	12	3	5	2	7				
Thunnus alalunga	42	18	1	1	8	2	2	2	
Katsuwonus pelamis	45	11	14	2	10	4	4	2	
Euthynnus alletteratus	11	13	4	1	10				
Allothunnus fallai		1			1				
Thunnus atlanticus	10	8	2		5				
Euthynnus affinis	15	1	4	1	13	1			
Euthynnus lineatus	1		3		4	3	3	3	
Auxis thazard	16	1	4		8				
Auxis rochei	6	6	3	1	9	1	1		
Gymnosarda unicolor	1		1		2				Bonitos
Orcynopsis unicolor	1	1	1	1	2				
Sarda australis									
Sarda orientalis	3		1		3				
Sarda chiliensis	4	6	2	1	6				
Sarda sarda	10	10	1		9	1	1		
Cybiosarda elegans									
Scomberomorus sinensis									Spanish mackerels
Scomberomorus commerson	34	12	10	6	11	1			
Acanthocybium solandri	9	3	3	2	8	2	1	2	
Scomberomorus cavalla	30	22	6	4	9	1	1	1	
Scomberomorus regalis			2		1				
Scomberomorus koreanus	1								
Scomberomorus brasiliensis	7	5	2		6				
Grammatorcynus bicarinatus									
Scomberomorus semifasciatus	6	1	1		2				
Scomberomorus plurilineatus	2	2	1	2					
Scomberomorus niphonius	2	3			3	1		1	
Scomberomorus munroi	7	7	3	1	5				
Scomberomorus queenslandicus	4	4	2		2				
Grammatorcynus bilineatus					1				
Scomberomorus sierra	8	5	2	2	1				
Scomberomorus lineolatus	2				1				
Scomberomorus tritor	1		2		3				
Scomberomorus guttatus	9	2	1		2				
Scomberomorus maculatus	7	8	2		5	1	1		
Scomberomorus concolor	3	3	2	2	3				
Scomberomorus multiradiatus									
Scomber japonicus	37	19	42	35	23	3	3	2	Mackerels
Scomber colias	28	20	7	4	10				
Scomber scombrus	25	12	30	26	11		1		
Scomber australasicus	12	10	1		7	1	1	1	
Rastrelliger kanagurta	46	5	11	2	15				
Rastrelliger brachysoma	31	1	7	1	13				
Rastrelliger faughni	5								

Figure 3.3 Synthesis of life history information in scombrid species.

(A) Number of estimates for each life history trait within the main four taxonomic groups of scombrids (tunas, bonitos, Spanish mackerels and mackerels). Within each taxonomic group, the species are plotted in ascending rank order of body size, with the smallest species at the bottom (See Table 3.1 for maximum body size). The Butterfly kingfish (*Gasterochisma melampus*), the only species in the subfamily Gasterochismatinae, is not included. The only life history trait recorded for this species is maximum length, being 195 cm (Kohno 1994). (B) Number of estimates for each life history trait for the 23 populations of seven principal market tunas. The area of the grey circle is proportional to the number of estimates available for each trait.
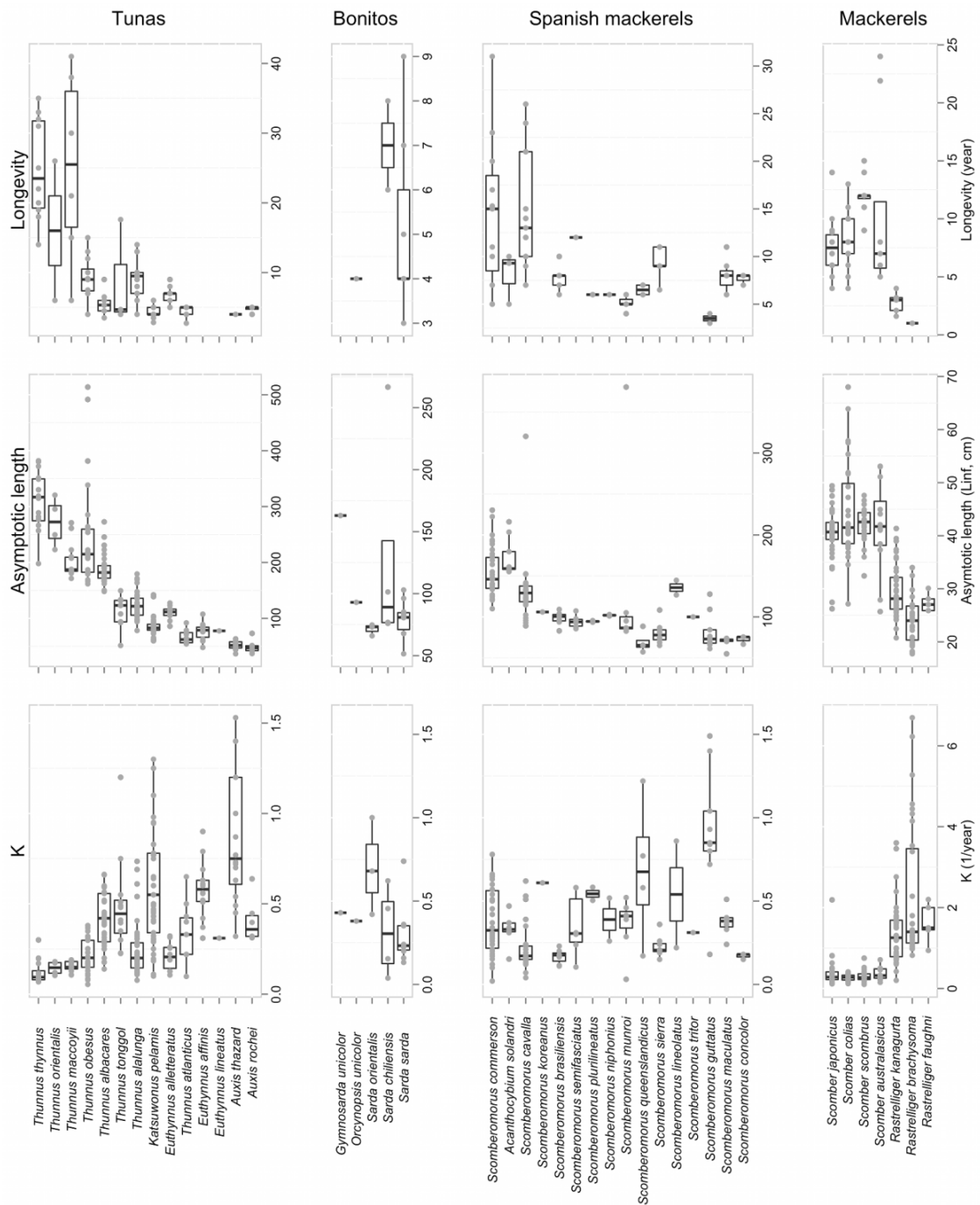
Figure 3.4   Von Bertlanffy growth parameters – K (y⁻¹) and asymptotic length L∞ (cm), and longevity estimates in scombrid species.

Within each taxonomic group, the species are plotted in ascending rank order of body size, with the smallest species at the bottom (See Table 3.1 for maximum body size).
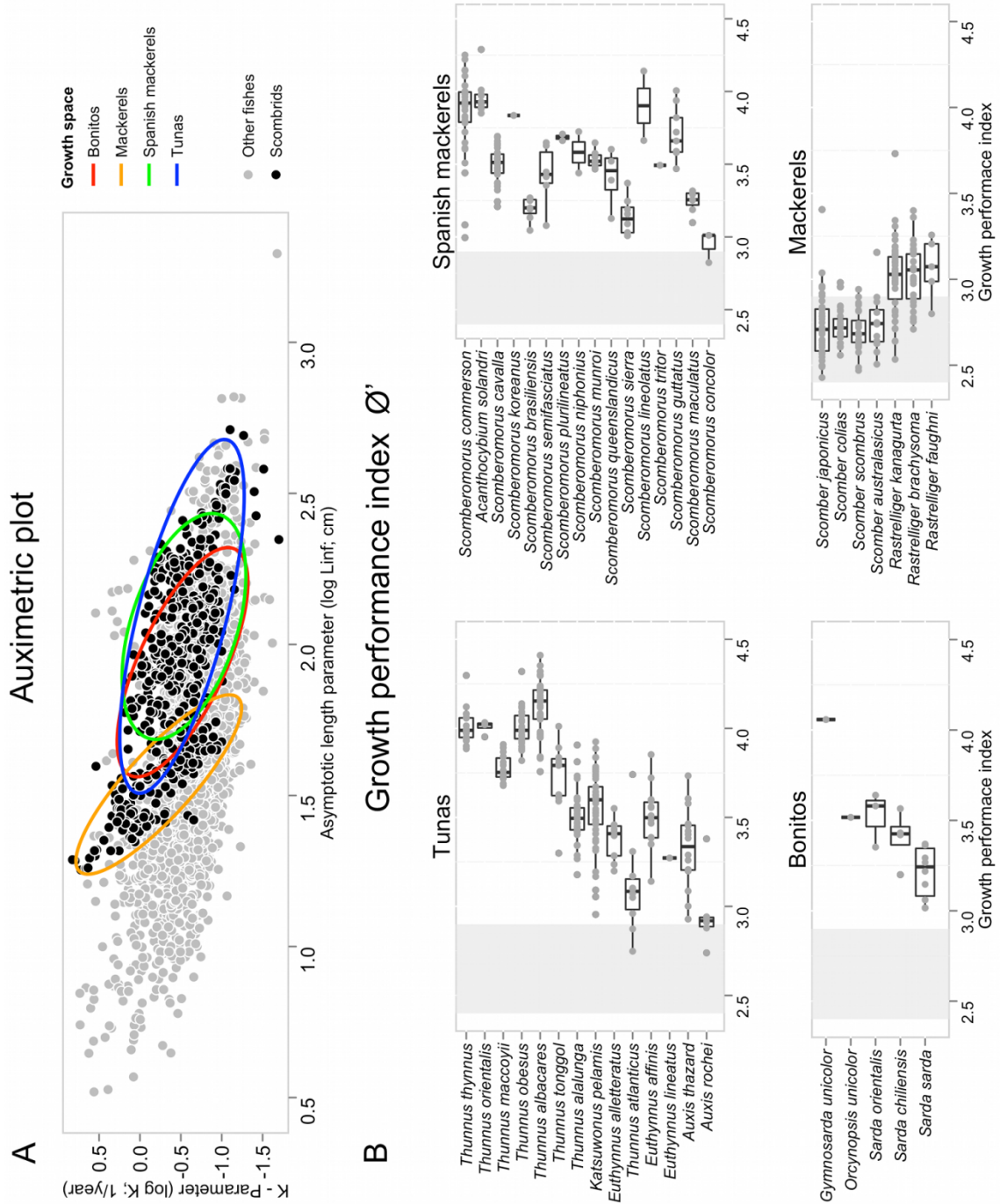
Figure 3.5   Growth performances in scombrid species including all fishes in FishBase, illustrating the high growth performances of scombrids.

(A) Auximetric plot comparing the growth performance of scombrid species (black circles) with that of fishes in general (grey circles). Fish data extracted from FishBase as August 2012. The growth space for the main four taxonomic groups of scombrids, tunas, bonitos, Spanish mackerels and mackerels, are also illustrated (colored ellipse curves). **(B)** The growth performance index Ø' (defined as Ø'=$\log_{10}k+2\log_{10}L_\infty$) of scombrid fishes compared with the average growth performances in fishes in FishBase (average growth performance is 2.7 ± 0.3, grey band area).

scombrids, followed by dogtooth tuna (*Gymnosarda unicolor*), wahoo (*Acanthocybium solandri*) and the narrow-barred Spanish mackerel (*Scomberomorus commerson*) (Figure 3.5B). On the other hand, the four temperate mackerel species, Chub mackerel (*Scomber japonicus*), Atlantic mackerel (*S. scombrus*), Atlantic chub mackerel (*S. colia*s) and blue mackerel (*S. australasicus*) have the lowest growth performances among scombrid species (Ø'< 2.7). Scombrids are among the fastest growing species of all fishes. All scombrid species have relatively high *k* values (a mean *k* of 0.48 y^{-1}) given their maximum size when compared to the rest of fish species, exhibiting rapid growth toward their maximum body size (Figure 3.5A). Among all scombrid species, the fastest growing species (*k* values > 0.7 y^{-1}) given their maximum body size are the three tropical Indian mackerels, Indian mackerel (*Rastrelliger brachysoma*), Island mackerel (*R. faughni*) and short mackerel (*R. kanagurta*), the Indo-Pacific king mackerel (*Scomberomorus guttatus*) and frigate tuna (*Auxis thazard*) (Figure 3.4). Moreover, the three bluefin tuna species (*Thunnus thynnus, T orientalis,* and *T. maccoyii*) and two Spanish mackerels (Monterey Spanish mackerel *Scomberomorus concolor* and Serra Spanish mackerel *S. brasiliensis*) are the slowest growing species (*k* <0.2 y^{-1}) among scombrids. We also found that the growth performance index Ø' in scombrids is among the highest in fish species, indicating not only that scombrids have relatively high *k* values given their maximum body size, but they also have both relatively high *k* and *L*$_\infty$ values, being able to grow very fast to large body sizes compared to the rest of fish species (Figure 3.5). Note how the growth space of scombrids species is located towards the top right quarter of the auximetric plot, although there are some exceptions (Figure 3.5A). Four tuna species, yellowfin, Atlantic bluefin, Pacific bluefin and bigeye tuna (*Thunnus albacares, T. thynnus, T. orientalis* and *T. obesus*, respectively) have the largest growth performances indices (Ø'> 4) among scombrids, followed by dogtooth tuna (*Gymnosarda unicolor*), wahoo (*Acanthocybium solandri*) and the narrow-barred Spanish mackerel (*Scomberomorus commerson*) (Figure 3.5B). On the other hand, the four temperate mackerel species, Chub mackerel (*Scomber japonicus*), Atlantic mackerel (*S. scombrus*), Atlantic chub mackerel (*S. colia*s) and blue mackerel (*S. australasicus*) have the lowest growth performances among scombrid species (Ø'< 2.7). Yet, scombrid species have among the highest growth performances of all fishes with an average Ø' values of 3.4, while the average Ø' for the rest of marine fishes is 2.7 (Figure 3.5B). What explains the high growth rates and high performances of scombrid species? Pauly's theory of growth in fishes states that the oxygen supply, and therefore the gill surface area, is the limiting factor of growth in fishes (Pauly 1979, 1981, 2010). The gill structure of scombrids is among the most advanced in fishes. All scombrid species have disproportionally large gill surface areas relative to their body weights, and

tuna species have the largest gill surface areas among all scombrids, permitting high rates of the oxygen acquisition to maintain those high rates of growth (Wegner et al. 2010). Pauly's work on growth in fishes starting in the 1980s already noticed that tuna species had relatively high growth rates and large gill sizes compared with the rest of teleost fishes, directing him to investigate the positive relationship between that gill surface area of fishes, hence supply of oxygen, and their maximum growth rates (Pauly 1979, 1981).

Longevity is a difficult parameter to estimate in fishes, as it depends on the accuracy of the growth methods and age-validation techniques and is an important parameter to consider when managing exploited populations (Campana 2001, Cailliet and Andrews 2008). Longevity estimates were available for 41 of the 51 species of scombrids and in all 23 populations of principal market tunas (Figure 3.2 and 3.3). We find that the average longevity across all scombrid species is 12.2 years, making scombrids medium-lived species when compared to the rest of fishes, according to the life history productivity classification of the American Fisheries Society(Musick 1999). However, longevity estimates vary greatly across scombrid species (Figure 3.4). On one extreme, the shortest-lived tropical mackerels (short mackerel *Rastrelliger brachysoma* and Indian mackerel *R. kanagurta)* have longevities of 1 and 4 years, respectively. On the other extreme, the southern bluefin tuna (*Thunnus maccoyii)* with a maximum estimated longevity of 41 years, Atlantic bluefin tuna (*T. thynnus)* (35 years) and narrow-barred Spanish mackerel (*Scomberomorus commerson)* (31 years) are the longest-lived species of scombrids.

Growth and longevity have not been studied in nine scombrid species. In addition, we find that the estimates of the von Bertalanffy growth parameters, L_∞ and k, the growth performance index Ø', and longevity vary substantially within some scombrid species (Figure 3.4 and 3.5). This variation can be attributed mainly to two factors: (1) the life histories of species may vary with average temperature and seasonality at different latitudes within their distributions (Jennings and Beverton 1991), and (2) the accuracy of the aging and growth approaches used, and the power of the validation methods employed, if any (Campana 2001). The von Bertalanffy growth curves of scombrids were estimated using a variety of aging methods including direct methods such as calcified structures (vertebrae, spines, scales and otoliths) and indirect methods such as modal analysis of length frequencies and tagging studies, or by various combinations of several of these methods (Figure 3.S1). While it is not the objective of this study to quantify how much variation in growth might be due to environmentally driven intraspecific variability within species and how much by differences in aging techniques, we compared estimates

of *k*, the growth performance index Ø' and longevity between several aging techniques, and observed that some of the differences can be attributed to the ageing approaches employed (Figure 3.S2). This analysis should ideally be carried out at species level, to better determine the effect of different aging techniques on growth estimates and to identify what methods are more consistent leading to more accurate age and growth estimates for each species. Moreover, while we cannot disentangle easily the effect of aging techniques on growth and age estimations, we can easily use the growth performance index Ø' to identify potential inaccurate growth curves for each individual species. Given that the Ø' values for a given species or taxonomically related group of species should be normally distributed around the mean Ø' of the taxonomic unit, values further away from the mean of the distribution must be interpreted with increasing caution (Munro and Pauly 1983). Therefore, we consider the scombrid growth curves depicted as outliers in the boxplots in figure 3.5B potentially unreliable and we advise caution in their use.

Reproductive biology

Information on the full reproductive biology of a species, including length and age at maturity, spawning season and fecundity-length schedules are also essential to fish management in order to calculate the reproductive potential of species and to conduct proper stock assessments (Schaefer 2001). We first provide an overview of the maturity studies in scombrids followed by an overview of the fecundity studies. Length at maturity estimates, calculated as the length at which 50% of the sampled individuals have matured, were available for 38 of the 51 species and 16 of the 23 principal market tuna populations (Figure 3.2 and 3.3). While at first we observe that small scombrid species tend to mature at smaller sizes than larger body scombrids, we also find that scombrids reach maturity at similar proportional sizes, at around half of their maximum length, typically at 44.7% of the maximum length (Figure 3.6). Multiple studies have documented the relative constancy of the ratio L_{m50}/L_{max} within most families of fish and other taxonomic groups (Beverton and Holt 1959, Beverton 1963). Yet, it has also been documented that smaller species tend to reach maturity at larger sizes relative to their maximum body sizes while larger species tend to mature at relatively smaller sizes. This pattern can also be discerned in Figure 3.6 where, for example, the smallest scombrid for which maturity information exists, the short mackerel (*Rastrelliger brachysoma*), matures at 16.7 cm (at 50% of its maximum body size) and the largest scombrid, the Atlantic bluefin tuna (*Thunnus thynnus*), matures at 155.2 cm (at 36 % of its maximum body size, combining information for both eastern and western population). Moreover, we find that

estimations of age at first maturity are scarcer in scombrid species (Figure 3.2 and 3.3). Reproductive studies only estimated age at 50% maturity or reported age at 50% maturity by converting length at maturity to age using a Von Bertalanffy growth equation for 25 species of scombrids (Figure 3.7). With the limited information available, we find that scombrids appear to mature early in life compared to their maximum life span, at around one quarter of the way through their lifespan (at 25.4 % of the maximum age across all the species) (Figure 3.7). Extreme values in the distribution are provided by Australian spotted mackerel (*Scomberomorus munroi),* which matures at 0.3 years (at 5% of the maximum age), while southern bluefin tuna (*Thunnus maccoyii)* reaches maturity at 11 years old (at 27% of the maximum age).

Understanding the fecundity in scombrid fishes is challenging because they are batch spawners, spawning multiple times during the spawning season and have what is called indeterminate fecundity. Indeterminate fecundity refers to species whose annual potential fecundity is not fixed before the spawning season, since unyolked oocytes continue to be produced, matured and spawned during the spawning season, while determinate fecundity refers to species for which annual potential fecundity is fixed before the spawning season (Murua and Saborido-Rey 2003). In order to estimate the potential annual fecundities of scombrids, three measurements are required, batch fecundity (number of eggs released per spawning), spawning frequency, and the duration of the spawning season (Hunter et al. 1985, Schaefer 2001, Murua and Saborido-Rey 2003). In addition, the ovaries of all scombrid species are considered asynchronous, meaning that oocytes of all stages of development are present in the ovary simultaneously without a distinctive oocyte size class (Schaefer 2001, Murua and Saborido-Rey 2003). This is characteristic of species with protracted spawning season, where oocyte development depends on the food available in the environment (Murua and Saborido-Rey 2003).

Therefore, histological analysis of ovarian tissue is needed to accurately measure batch fecundity in scombrids since there is a critical moment along all the stages of oocyte maturation when batch fecundity can be estimated (Schaefer 2001). At the final stages of oocyte maturation, beginning with migratory-nucleus phase and followed by hydration, which results in a clear hiatus or size break along the distribution of oocytes, batch fecundity can be derived by counting the number of hydrated oocytes in ovaries. While a more detailed description on the methods to derive accurate batch fecundities in scombrid species can be found in Schaefer et al. (2001) and Murua and Saborido-Rey (2003), what we need to know here is that only ripe, pre-spawning females, with hydrated oocytes in
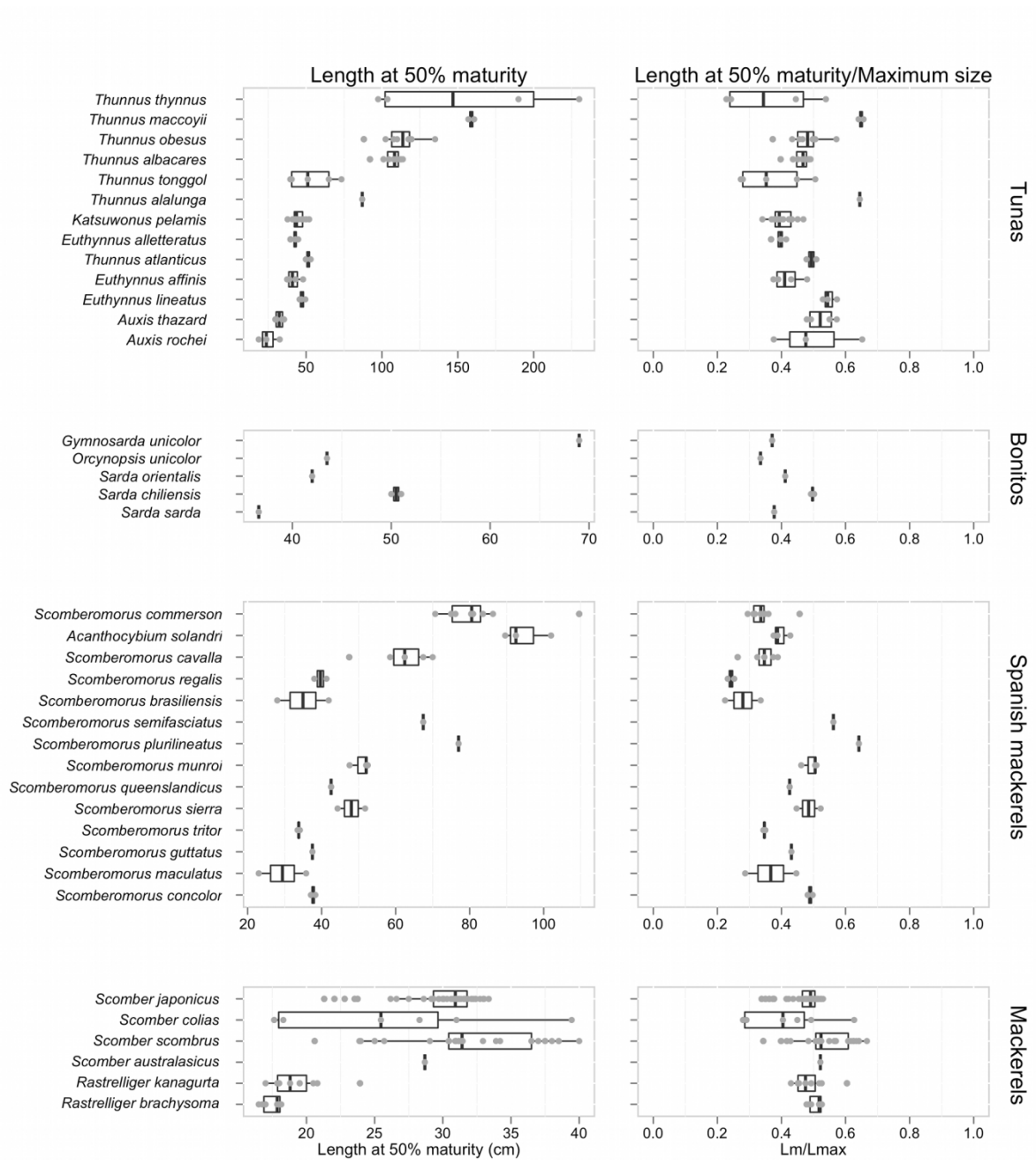
Figure 3.6   *Length at 50% maturity estimates and the ratio length at 50% maturity/maximum body size for scombrid species.*

Within each taxonomic group, the species are plotted in ascending rank order of body size, with the smallest species at the bottom (See Table 3.1 for maximum body size).
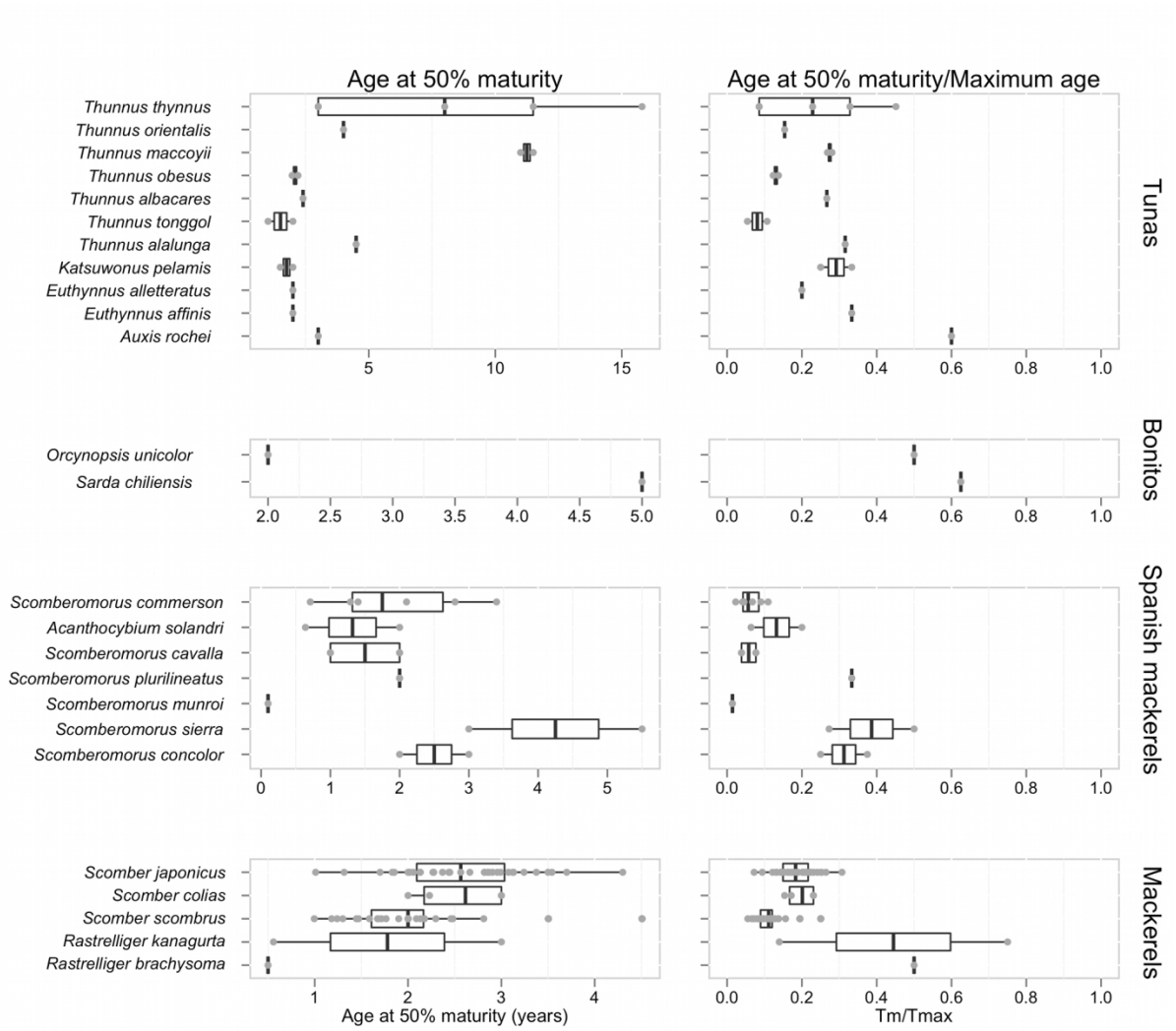
Figure 3.7   Age at 50% maturity estimates and the ratio age at 50% maturity/maximum body size for scombrid species.

Within each taxonomic group, the species are plotted in ascending rank order of body size, with the smallest species at the bottom (See Table 3.1 for maximum body size).

their ovaries can be used to estimate batch fecundity accurately by means of histological analysis.

After reviewing 134 studies of fecundity in scombrid species we could only identify 33 studies using accurate methodologies that clearly stated that the species studied was a batch spawner, had indeterminate fecundity, reported asynchronous development of oocytes in the ovaries, used histological analysis, and estimated batch fecundity based on the count of the number of migratory-nucleus or hydrated oocytes in the ovary (Schaefer 2001). Unfortunately most of the fecundity studies of scombrid species conducted in the last 50 years used inaccurate methodologies, for example, by wrongly assuming determinate fecundity or overestimating fecundity by counting oocytes before reaching the hydration stage. This concern was already raised by Schaefer et al 2001, which reviewed the reproductive biology studies of tunas, but those concerns can be further extended to all scombrid species. Furthermore, we had to exclude from our analysis the majority of fecundity studies for Atlantic mackerel (*Scomber scombrus)* for which total annual fecundity, instead of batch fecundity, is routinely estimated, given that this species is managed in the Northeast Atlantic Ocean under the assumption of a determinate fecundity pattern. The accuracy of this assumption is, however, being revised (ICES 2011, 2012).

Absolute average batch fecundities, relative batch fecundities and spawning frequencies were available for 17, 15 and 13 species of scombrids, respectively (Figure 3.2 and 3.3). Estimates of average absolute batch fecundities vary greatly across scombrid species, ranging from 69,000 oocytes in blue mackerel (*Scomber australasicus)* to 16 million eggs in Pacific bluefin tuna (*Thunnus orientalis),* which is mainly driven by the different body sizes of the species (Figure 3.8A). The average relative batch fecundity (number of oocytes per gram) is a better metric to compare fecundity among species of different sizes. The number of oocytes per gram in scombrids ranges from 38 in bigeye tuna (*Thunnus obesus)* to 242 in bullet tuna (*Auxis rochei). S*maller scombrids tend to have higher mass-specific fecundities, spawning a greater number of oocytes per gram of body mass than bigger scombrid species (Figure 3.8B). The time between successive spawning events in scombrid species varies between every 1.1 days in southern bluefin tuna (*Thunnus maccoyii*) to every 6.5 days in blue mackerel (*Scomber australasicus*), and smaller scombrids tend to have greater spawning intervals between spawning events than larger body scombrids, although there are more some exceptions (Figure 3.8C). Finally, tropical species have generally longer spawning seasons (an average of 6 months), than their subtropical (5 months) and temperate (3.5 months) relatives (Figure 3.8D),
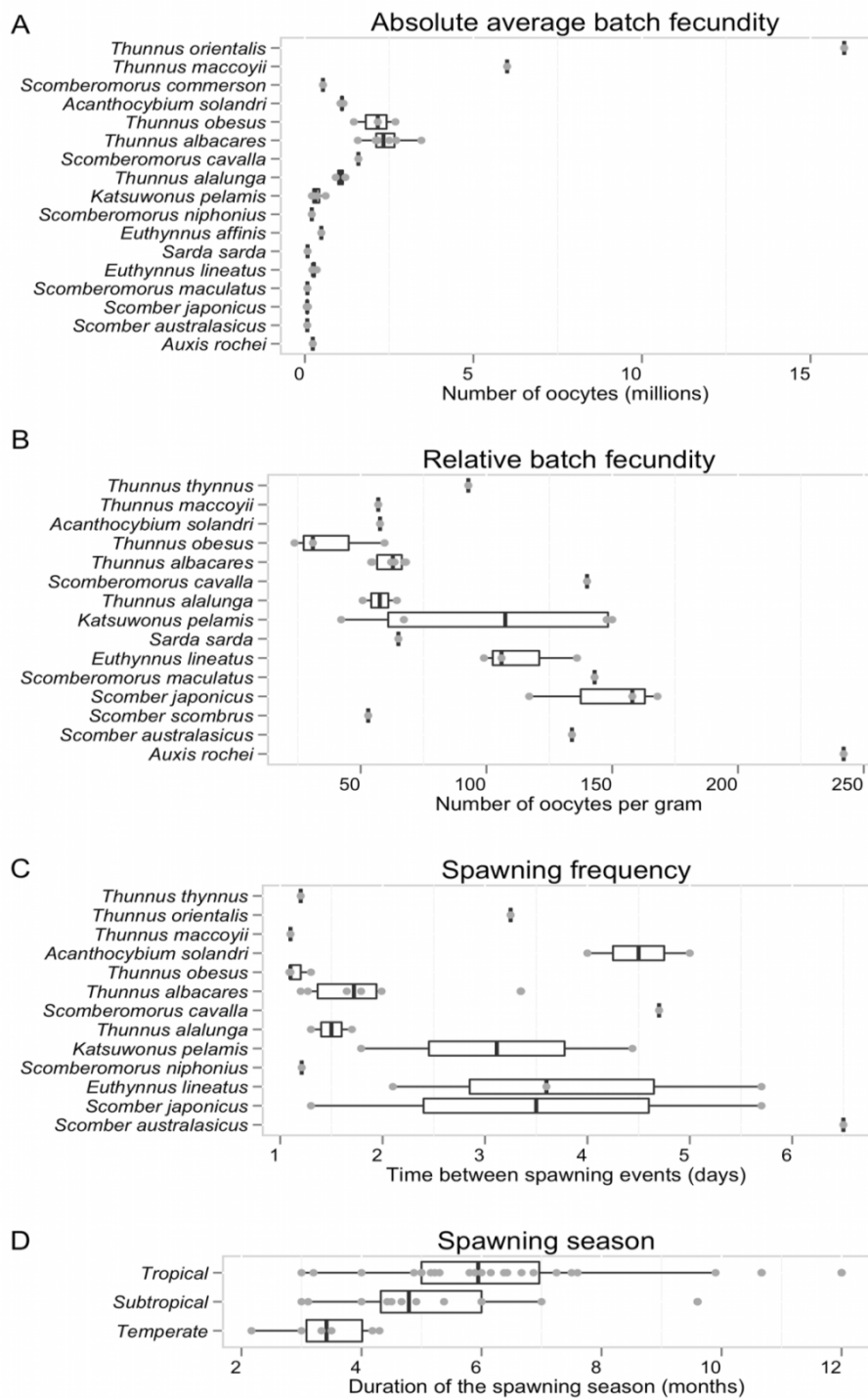
Figure 3.8   Batch fecundity estimates for scombrid species.

(A) Absolute average batch fecundity. **(B)** Relative average batch fecundity. **(C)** Duration of spawning season of scombrid species by type of climate (find species climate in Table 3.1). In all the figures, the species are plotted in ascending rank order of body size, with the smallest species at the bottom (See Table 3.1 for maximum body size).

suggesting an association between spawning duration and the type of environment that species inhabit.

Information on the full reproductive biology, including length and age at maturity, batch fecundities, spawning duration and frequency, is incomplete for most scombrid species, and around half of the populations of the principal market tunas (Figure 3.2 and 3.3). The length at 50% maturity and spawning season is unknown for 13 and 9 species of scombrids, respectively. More worrying, fecundity studies with accurate methodologies are lacking for 34 of the 51 species of scombrids. We also find that estimates of length at 50% maturity are less variable than growth estimates, suggesting that there is more uniformity among the methods (Figure 3.6). However, some species show large variability among studies, calling for some detailed examinations. Given the relative constancy of the ratio L_{m50}/L_{max} within scombrid species, we find this ratio particularly useful to identify those species and studies that need further examination. For example, the estimates of length at 50% maturity and the ratio L_{m50}/L_{max} vary greatly among studies for the species Atlantic bluefin tuna (*Thunnus thynnus)*, longtail tuna (*T. tonggol)* and Atlantic chub mackerel (*Scomber colias)*. In the case of Atlantic bluefin tuna (*T. thynnus)*, the different lengths at maturity of the eastern and western Atlantic populations might be driving some of the observed variation. It has been hypothesized that the different histories of exploitation for the two populations might explain some of the differences (ICCAT, 2009). The large differences in length at 50% maturity for longtail tuna (*Thunnus tonggol)* and Atlantic chub mackerel (*Scomber colias)* could be driven by the different methodologies employed in the studies or perhaps be an environmental-driven response of the species within its distribution. Finally, we also see some discrepancies in the estimates of relative fecundity within some species, for example the relative fecundities of skipjack tuna (*Katsuwonus pelamis)* differ greatly among studies.

Setting priorities in life history research and future directions

We assembled, summarized and critically reviewed the available biological knowledge on growth, maturity and fecundity for the 51 species of scombrids. We revealed that one third of species (17 spp.) have reasonable information on growth, maturity and fecundity and we refer to them as data-rich species. Half of the species (26 spp.) lack information on either growth, maturity or fecundity, and eight species have no information at all on growth, maturity or fecundity, for which we know little more than their maximum body sizes and their overall distributions. We refer to them as data-poor species. Additionally, by comparing the life history information across the four major taxonomic groups of

scombrids, we found that the biology of tunas and mackerel species have been more extensively studied than for Spanish mackerels and bonitos, although there are notable exceptions in all the taxonomic groups. Moreover, we also revealed that reproductive biology of species, particular fecundity, is the least-studied biological aspect when compared with growth and maturity.

Although we would ideally encourage any biological studies to fill all life history data gaps of scombrid species identified in this study (Figure 3.3), instead we identify and propose a set of priorities for research based on the following criteria: (1) their biological life history data gaps, (2) the importance of their fisheries throughout their distributions and (3) their current conservation status according to the IUCN Red List of Threatened species. We assigned the highest priority rank for life history research to those species that have: (1) biological data gaps, (2) are targeted by commercial fisheries, and (3) are listed as Threatened, or Near Threatened or Data Deficient on the IUCN Red list. Similarly, we assigned the second highest priority to those species that have biological data gaps in knowledge and are also targeted by commercial fisheries throughout their ranges. Therefore, we differentiated between data-poor and data-rich species, between species targeted and non-targeted by commercial fisheries, and between species listed as Threatened, Near Threatened and Data Deficient from those listed as Least Concern in the IUCN Red List. (Table 3.S2). Threatened species are those listed as Critically Endangered, Endangered, and Vulnerable in the IUCN Red List (IUCN 2010). Species in the Data Deficient category are species for which there is insufficient information to evaluate their risk of extinction, and they may or may not be Threatened. Because of the risk associated with the uncertainty in their status, we treated them together with species in the Threatened categories as high priority in life history research (Table 3.S2).

Based on our criteria we identified two groups of species for which life history research should be prioritized in the coming decades. The first priority group is made up of ten scombrid species for which we identified large life history-data gaps, are currently targeted by commercial fisheries throughout their distributions and are listed as Threatened, Near Threatened or Data Deficient (Figure 3.9). These species include six Spanish mackerels (*Scomberomorus sinensis, S. plurilineatus, S. munroi, S. niphonius, S. guttatus, S. concolor*), one tuna (*Thunnus tonggol*) and the three tropical mackerels *(Rastrelliger kanagurta, R. brachysoma and R. faughni*). For these species the full reproductive biology is unknown or very poorly known. This is particularly true for the Chinese seerfish (*Scomberomorus sinensis)* and the Japanese Spanish mackerel (*S. niphonius),* two important commercial species off the coast of Japan, Korea and China (Ni and Kwok

1999, Seikai National Fisheries Research Institute 2001, Obata et al. 2008, Xianshi 2008). While for *S. niphonius* we lack any length or age at maturity and fecundity estimates, for Chinese seerfish there is no data on maturity, fecundity or growth. Given the large maximum size reported for these species (*S. sinensis* ~ 240 cm and *S. niphonius* 103 cm), it is likely they might be vulnerable to fishing pressure throughout its range. Moreover, all the species in our top priority list were categorized as Data Deficient, with the exceptions of Monterey Spanish mackerel (*Scomberomorus concolor)* and Australian spotted mackerel (*S. munroi)* which were listed as Vulnerable (Collette et al. 2011). For these species there is insufficient data on their biology, population status, and current threats to even conduct the IUCN assessments, yet, they sustain diverse commercial fisheries in many countries throughout their ranges (Table 3.S1). Exacerbating the poor biological knowledge of these species and unknown exploitation and conservation status, the landings of these species have increased greatly in the last decade and are usually misclassified and highly underreported throughout their ranges given the limited capacities of the countries to undertake surveillance and enforcement in fishing ports (Majkowski 2007, FAO 2010-2013, Collette et al. 2011).

The second group of species for which life history research should be prioritized in the coming decades is made up of twenty-two data-poor and commercially targeted species of scombrids (Figure 3.9). For five of these species, we know little more than their maximum size and their distributions. All of these species are currently supporting diverse commercial fisheries throughout their distributions (Table 3.S1), yet most of these species either lack proper quantitative fisheries stock assessments or those available are outdated and therefore their exploitation status is unknown or poorly known throughout their distributions (Collette et al. 2011, Juan-Jordá et al. 2011). Similar to the species in the first priority group, the landings for these scombrid species have been increasing greatly in the last decades and those landings are often misclassified and even underreported in the country fisheries statistics (FAO 2010-2013). Most of the species in the two priority groups are endemic in the Indian Ocean and Indo-Pacific region, which we identified as the region with the highest diversity of scombrid species, and the region with the largest number of data-poor scombrid species. For all these reasons, we stress life history research should be prioritized on these species following the species-specific life history gaps identified in this study (see life history data gaps in Figure 3.3) in the coming decades. Basic life history knowledge on growth, maturity and fecundity schedules has proven to be very valuable in fishery data poor situations. Several methods have been developed to manage species with a lack of long term fisheries statistics based on basic life history information

TARGETED
Acanthocybium solandri
Scomberomorus cavalla
*Katsuwonus pelamis
Euthynnus affinis
Sarda sarda
Euthynnus lineatus
Scomberomorus maculatus
Scomber japonicus
Scomber scombrus
Scomber australasicus
Auxis rochei

THREATENED, NT or DD and TARGETED
*Thunnus thynnus
*Thunnus maccoyii
Scomberomorus commerson
*Thunnus obesus
*Thunnus albacares
*Thunnus alalunga

Targeted by fisheries

Threatened NT or DD

Life history data-poor

11

6

10

22

2

DATA-POOR
Gasterochisma melampus
Allothunnus fallai

Priority species

DATA-POOR and TARGETED
*Thunnus orientalis
Gymnosarda unicolor
Scomberomorus koreanus
Orcynopsis unicolor
Scomberomorus brasiliensis
Grammatorcynus bicarinatus
Scomberomorus semifasciatus
Euthynnus alletteratus
Sarda australis
Thunnus atlanticus
Sarda orientalis

Sarda chiliensis
Grammatorcynus bilineatus
Scomberomorus queenslandicus
Scomberomorus sierra
Scomberomorus lineolatus
Scomberomorus tritor
Scomberomorus regalis
Scomber colias
Auxis thazard
Cybiosarda elegans
Scomberomorus multiradiatus

DATA-POOR and TARGETED and THREATENED, NT or DD
Scomberomorus sinensis
Thunnus tonggol
Scomberomorus plurilineatus
Scomberomorus munroi
Scomberomorus niphonius
Scomberomorus guttatus
Scomberomorus concolor
Rastrelliger kanagurta
Rastrelliger brachysoma
Rastrelliger faughni

Figure 3.9   Ven Diagram of life history research priorities in scombrid species.

We differentiated between life history data-poor and data-rich species (see definition in main text), between species targeted and non-targeted by commercial fisheries (see Table 3.S1), and between species listed as Threatened, Near Threatened (NT) and Data Deficient (DD) from those listed as Least Concern in the IUCN Red List (See Table S2). Threatened species are those listed as Critically Endangered, Endangered, and Vulnerable in the IUCN Red List. Enclosed box illustrates scombrid species with the highest priorities for life history research. (*) Highlights the principal market tuna species.

of the species, which have proved useful to rank species according to their intrinsic sensitivities to threats such as fishing and are now commonly used to identify and select sensitive species to prioritize management and efforts to protect and recover most threatened species (Dulvy et al. 2004, Reynolds et al. 2005, Pardo et al. 2012).

Only one species of principal market tuna, the Pacific bluefin tuna (*Thunnus orientalis),* was included in the priority species list. However, the life history review for the 23 principal market tuna populations revealed that there are multiple tuna populations for which the reproductive biology, including length and age at maturity and fecundity schedules, is still poorly known (Figure 3.3B). Particularly, the reproductive biology of albacore tuna (*Thunnus alalunga)* and Pacific bluefin tuna (*T. orientalis)* is the most poorly known and understudied of all principal market tunas. This is remarkable given the economic importance of these species globally (Majkowski 2007, Juan-Jordá et al. 2011). It is noteworthy that only recently the first complete studies on the reproductive biology of north Pacific albacore tuna, south Pacific albacore tuna and Pacific bluefin tuna were published (Chen et al. 2006, Chen et al. 2010, Farley et al. 2012). Although for these tuna species there are several old studies reporting estimates of length at first maturity instead of length at 50% maturity, we believe these estimates must be used with caution, and we do not report them here, because they are highly variable and might not represent length at maturity for the populations as a whole (Schaefer 2001). Therefore, we recommend prioritizing research on the reproductive biology including maturity and fecundity studies for Pacific bluefin tuna, and populations of Albacore tuna, other than the northern and southern Pacific populations.

Up to now, we focused on identifying life history research priorities for specific species of scombrids. Yet, the determination of longevity and validation studies of age is one area of life history research that we believe should also be given high priority in the coming decades. Biological timings and rates, such as maximum age, age at maturation and growth rate are one of the primary axes of life history variation in vertebrates and especially scombrids (Juan-Jordá et al. 2012). The ability to accurately estimate and validate age in fishes is important for the subsequent estimation of demographic parameters of growth, mortality, longevity and age at maturity (Campana 2001, Cailliet and Andrews 2008). In light of the within-species variation observed, longevity estimates in scombrids should be used with caution and we recommend prioritizing age validation studies particularly for long-lived scombrids. To date, age validation techniques have only been applied recently to some populations and species of the genera *Thunnus*, *Scomber,* and *Scomberomorus* (e.g. Kalish et al. 1996, McIlwain et al. 2005, Chen et al. 2006, Gunn

et al. 2008, Shiraishi et al. 2008, Shimose et al. 2009). The ages and longevities of large-bodied, and potentially long-lived, species have often been underestimated in fishes, potentially causing fisheries management plans to be less successful (Cailliet and Andrews 2008). Scombrid species include some of the most valuable exploited species in the world and the sustainability benefit of valid demographic estimates would seem worth the comparatively modest outlay involved in age validation.

Finally, we highlight some of the caveats of this study and suggest future directions to address them. First, by synthesizing and identifying life history research priorities at the taxonomic unit of species, we overlooked scombrid species that have widespread distributions and therefore the possibility of multiple locally-adapted populations throughout their geographical range. While it was not the scope of the present study to review and prioritize life history research in scombrids at the population level, in part due to the large volume of work and time constraints, the population structure for the large majority of scombrids species is unknown or poorly known throughout their distributions, with few exceptions. Second, by focusing this study on the taxonomic unit of species we also overlooked the potential spatial and temporal patterns of life history variation within each scombrid species or populations. Life history traits for a given species might vary spatially in response to environmental effects and latitudinal clines (Jennings and Beverton 1991, Blanck and Lamouroux 2007) and in addition vary temporally in response to fishing-induced effects (Rochet 1998). To our knowledge, very few studies have quantified how growth and reproductive life history traits vary spatially within the species distributions (e.g. Schaefer 1987, 1998, Farley et al. 2012) or vary temporally perhaps induced by fisheries exploitation (e.g. Grégoire 1993, Watanabe and Yatsu 2006). We therefore further encourage two broad lines of research. An immediate line of research with relatively low cost could make use of the life history data set assembled here to test the intraspecific variation in the multiple life history traits across large-scale environmental effects (e.g latitude, temperature, habitat types) in scombrid species, and at the same time focus on identifying and prioritizing regional life history data-gaps for each individual species. As a second line of research, we encourage future studies to continue determining the population structure of scombrid species using multiple approaches from genetic techniques to the use of biological markers such as otolith microstructure and electronic tagging methods, in order to define geographic boundaries of populations at scales relevant for fisheries management.

Conclusions

We reviewed and synthesized the life history information on growth and reproductive biology for the 51 species of scombrids, including a population-level review for the principal market tuna species, identified major biological gaps in knowledge and prioritized life history research needs for scombrid species and principal market tuna populations given the life history gaps identified, importance of their fisheries and current conservation status according to the IUCN Red List. Given their economic and social importance and the increase in global catches and demand, scombrid species will continue to be central in future fisheries and ecological research. Globally the majority of life history research has focused, and still is focused, on the principal market tuna species and a few temperate mackerel species, giving less priority to the life history research of the rest of coastal scombrid species. We emphasize the need to continue field studies, employing proper experimental design and methodologies on the life history data-rich principal market tuna and mackerel species as needed, yet we hope to have raised attention to the urgent need for work on the life history of the smaller coastal scombrid species. Although lower in economic value in the global markets, coastal scombrid species support diverse fisheries throughout their distributions and are an important source of wealth and food security to the local fishing communities in many countries (Collette and Nauen 1983, Gillett et al. 2001, Majkowski 2007, Di Natale et al. 2009). Furthermore, we encourage future studies to use the assembled life history data set presented here to develop comparative analyses to make use of the biological knowledge on data-rich scombrid species to data-poor scombrid species with potential similar biology which could potentially have a positive effect in the quality of management advice. Last, by highlighting the important gaps in biological knowledge and providing a priority setting for life history research in scombrid species, we hope this study can serve as a guide for fish biologists and resource managers interested in the biology, ecology and management of scombrid species, particularly in areas of the world where the information is lacking, inadequate or outdated.

Acknowledgements

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Supplementary Figures
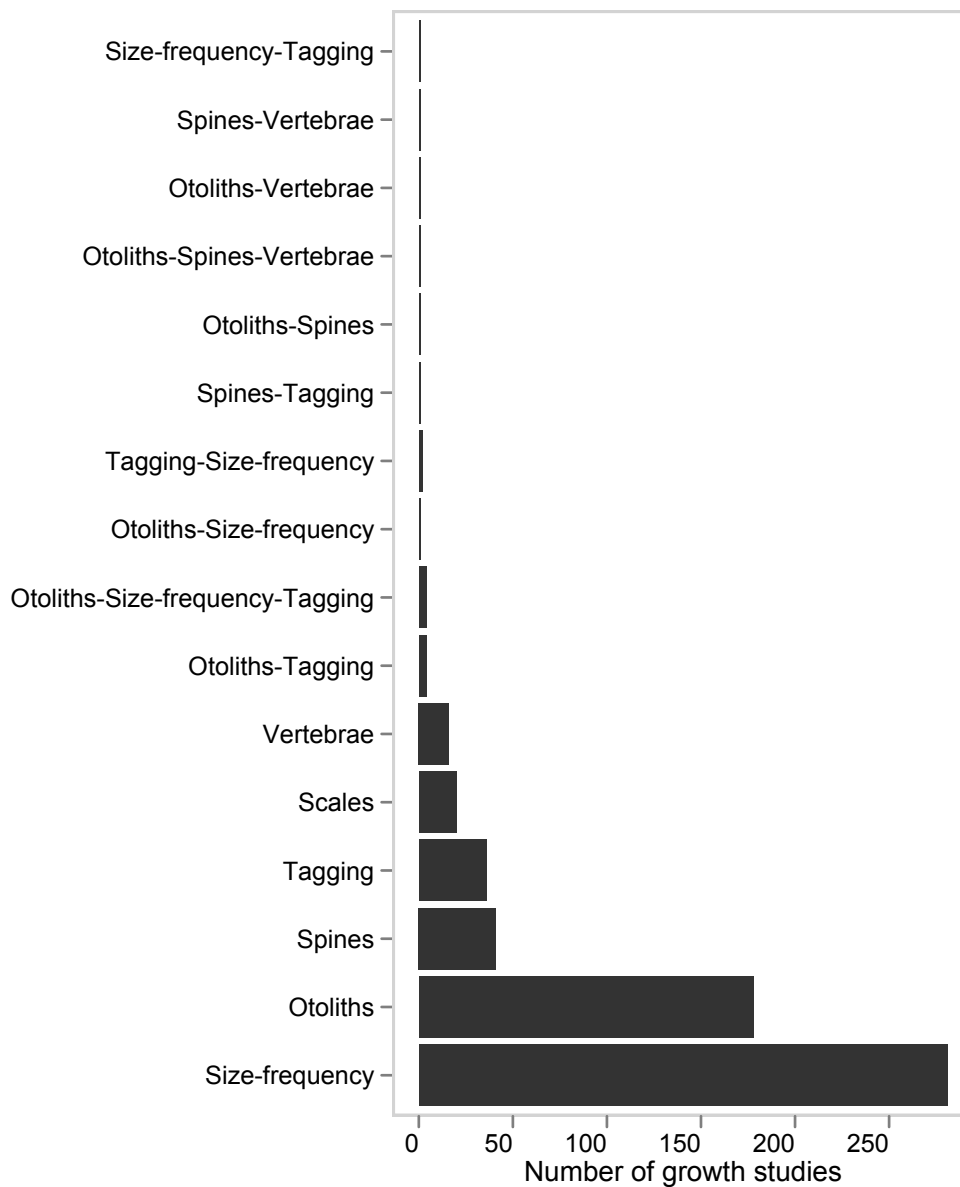
Figure 3.S1 **Number of studies to estimate age and growth by method type in scombrid species.**

Aging methods including direct methods such as calcified structures (vertebrae, spines, scales and otoliths) and indirect methods such as modal analysis of length frequencies and tagging studies, or by various combinations of several of these methods.

Growth performance index Ø' by aging and growth methods
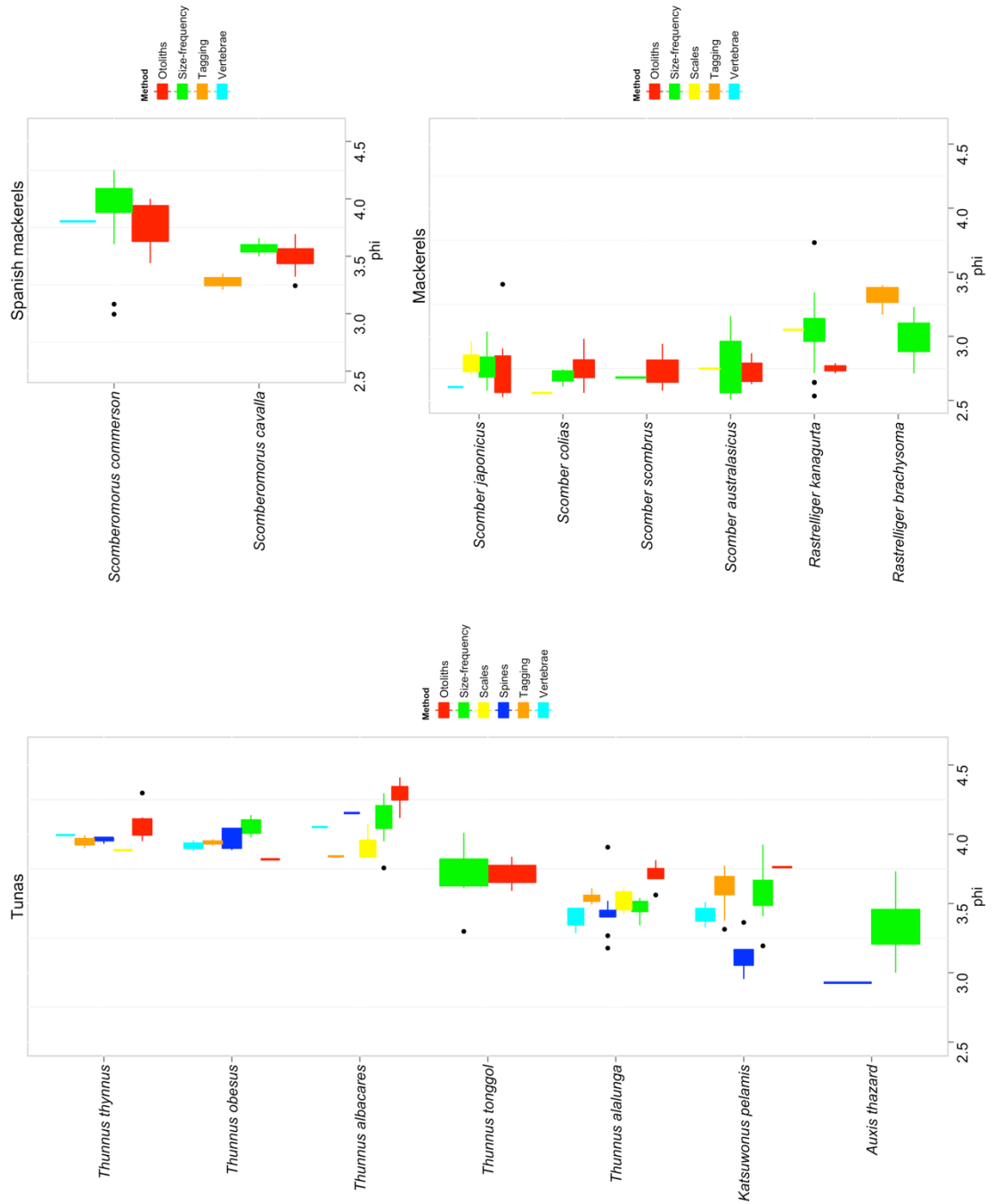
Von Bertalanffy growth parameter K by aging and growth methods
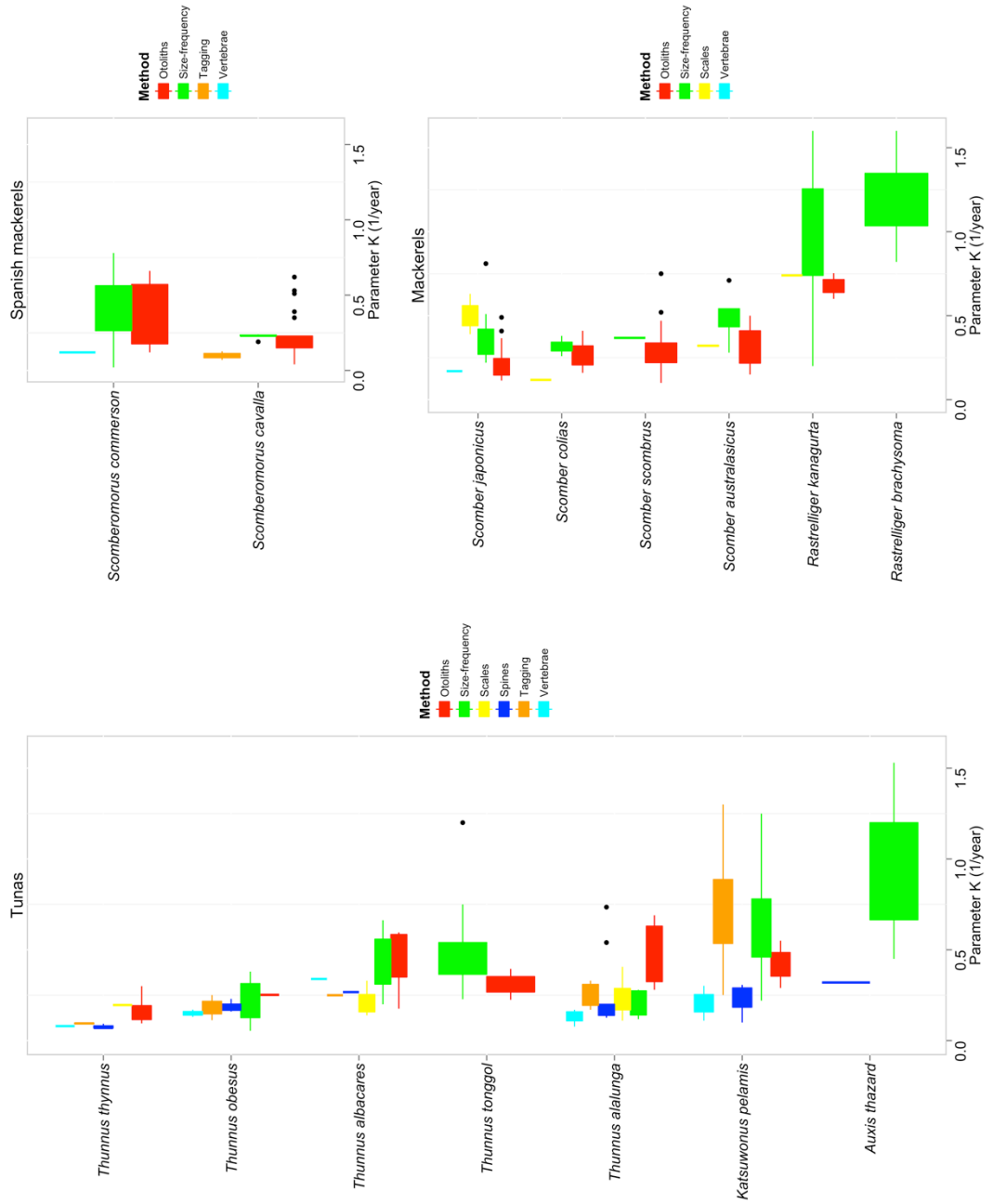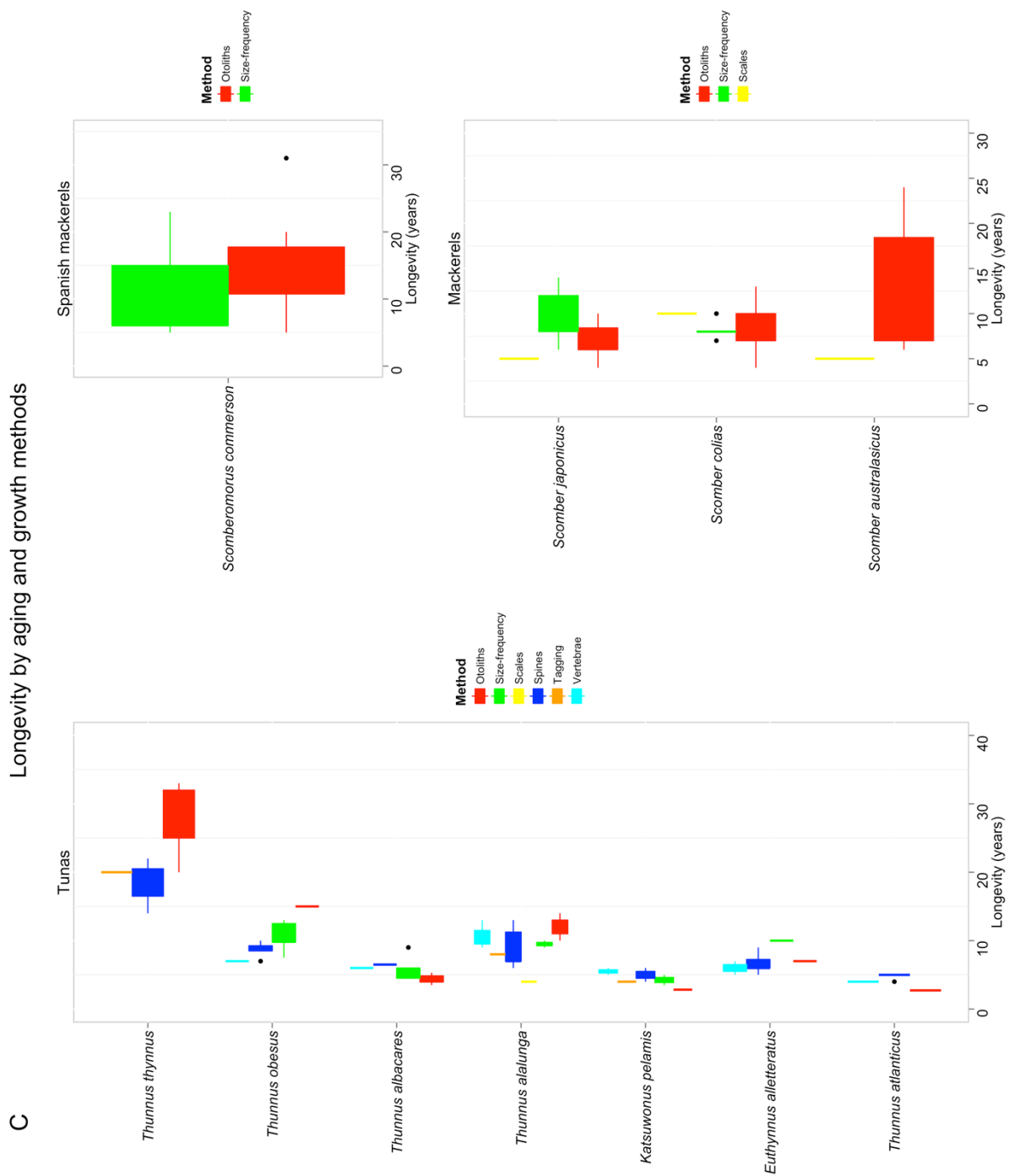
Figure 3.S2   Illustration of the effect of different aging and growth techniques on the estimation of life history parameters.

(A) Growth performance index, **(B)** Von Bertalanffy growth parameter K and **(C)** longevity. Only species having more than 15 Von Bertalanffy growth curves are shown.

Supplementary Tables

Table 3.S1 ***List of scombrid species with a brief description of their fisheries. (*) Commonly known as principal market tunas***

Latin name	Geographical distribution	Fisheries
*Thunnus alalunga	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea	Supports important commercial fisheries globally ranging from large-scale industrial fisheries to small-scale artisanal fisheries throughout their distributions. Traded in the international markets for canning and sashimi. Also caught by recreational fisheries worldwide [1-3].
*Thunnus albacares	Atlantic, Pacific and Indian oceans	
*Thunnus maccoyii	Southern waters of the Atlantic, Pacific and Indian oceans	
*Thunnus obesus	Atlantic, Pacific and Indian oceans	
*Thunnus thynnus	Atlantic Ocean	
*Thunnus orientalis	Pacific Ocean	
*Katsuwonus pelamis	Atlantic, Pacific and Indian oceans	
Thunnus atlanticus	Western Atlantic Ocean	Caught by commercial fisheries throughout its range, mainly in Venezuela, Martinique, Guadeloupe, Cuba and Dominican Republic [4,5]. Also important to the local economy in northeastern Brazil [6]. Caught by recreational fisheries in Florida and Bahamas [7].
Thunnus tonggol	Northern Indian Ocean, Indo-Pacific region, Western Pacific Ocean	Caught by small-scale commercial fisheries throughout its range such as in countries bordering the north Arabian Sea and the southeast Asian region [8-10]. Caught by recreational fisheries in Australia [11,12].
Euthynnus affinis	Indian Ocean, Indo-Pacific region	Caught by small-scale commercial fisheries throughout its range [11,13-16]. The largest catches are reported in the southeast Asian region of Thailand and Malaysia [11]. Also caught by recreational fisheries [3].
Euthynnus alleteratus	Atlantic Ocean, including the Mediterranean and Black seas	Caught by small-scale commercial fisheries throughout its range, in the Mediterranean Sea in countries such as Spain and Turkey [17] and in the Caribbean Sea in countries such as Venezuela [18]. Also caught by recreational fisheries [3].
Euthynnus lineatus	Eastern Pacific Ocean	Caught by small-scale commercial fisheries and as by-catch from other tuna fisheries [19]. Also caught by recreational fisheries [3].
Auxis rochei	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea	Caught by small-scale commercial fisheries throughout its range. Some regions report the catches of *Auxis sp.* mixed, reflecting the confusion surrounding the identification of these species worldwide. It is believed that Atlantic catches are predominantly bullet tuna (*Auxis rochei*) with the highest catches occurring in the Mediterranean Sea and off the northwest African coast where they are commercially exploited by seasonal coastal fisheries [20]. Also caught by recreational fisheries [3].
Auxis thazard	Atlantic, Pacific and Indian oceans	Caught by small-scale commercial fisheries throughout its range. Some regions report the catches of *Auxis sp.* mixed, reflecting the confusion surrounding the identification of these species worldwide. In the Pacific and Indian Ocean the main commercial fisheries exist in Japan, the Philippines, India and the Maldives where most of the catches reported are predominantly frigate tuna (*Auxis thazard*) [21-23]. Also caught by recreational fisheries [3].
Allothunnus fallai	Southern waters of the Atlantic, Pacific and Indian oceans	There are no developed commercial fisheries for this species. It has no commercial value and it is caught incidentally as by-catch in the longline tuna fisheries in oceanic waters [24].

Species	Distribution	Fisheries
Cybiosarda elegans	Western Pacific Ocean restricted to the southern coast of Papua Guinea and northern Australia	Caught by commercial fisheries in Australia and used as bait [25,26].
Gymnosarda unicolor	Disjoint distribution in the Indian Ocean and Indo-Pacific region	Caught by small-scale commercial and recreational fisheries throughout the Indian Ocean and Indo-West Pacific region [27,28]. Also caught by recreational fisheries [3].
Orcynopsis unicolor	Eastern Atlantic Ocean including Mediterranean Sea	Caught by small-scale commercial fisheries throughout its range in countries such as Tunisia [20,29].
Sarda australis	Southwest Pacific Ocean in south western Australia and northern New Zealand	Caught by small commercial fisheries and used as bait in Australia [25]. Also caught by recreational fisheries [3].
Sarda chiliensis	Eastern Pacific Ocean	Caught by small-scale commercial fisheries and as by-catch species in tuna purse seine fisheries in the eastern Pacific. The catches reported by IATTC combines the two species of bonito, *S. chiliensis* and *S. orientalis* [19]. Also caught by recreational fisheries [3].
Sarda orientalis	Indian and Pacific Oceans	Caught by small-scale commercial fisheries and as by-catch species in tuna purse seine fisheries in the eastern Pacific. The catches reported by IATTC combines the two species of bonito, *S. chiliensis* and *S. orientalis* [19]. Small commercial fisheries also exist in India [30] and Australia [25]. Also caught by recreational fisheries [3].
Sarda sarda	Atlantic Ocean including Mediterranean Sea	Caught by small-scale commercial fisheries throughout its range and an important commercial species in the Mediterranean and Black Seas [20]. Also caught by recreational fisheries [3].
Acanthocybium solandri	Atlantic, Pacific and Indian oceans, including the Mediterranean Sea	Caught by small-scale commercial fisheries throughout its range. In the Atlantic Ocean the most important known fisheries are found in the east coast of the USA, through the Gulf of Mexico, Caribbean Sea and northern South America [31]. In the Pacific Ocean, the most important fisheries are found in Fiji, Samoa and Cook Islands [32]. In the Indian Ocean, it is caught by commercial fisheries in India together with *S. commerson*, *S. lineonatus* and *S. guttatus* [33,34]. Also caught by recreational fisheries [3].
Scomberomorus brasiliensis	Western Atlantic Ocean	Caught by small-scale commercial fisheries in the western central Atlantic waters such as in Trinidad [35] and also off the northwestern coast of Brazil [36].
Scomberomorus cavalla	Western Atlantic Ocean	Sustains one of the most important commercial and recreational fisheries of *Scomberomorus* species in the Atlantic ocean, principally in the southeastern coast of the United States [37], Gulf of Mexico [38] and Brazil [39].
Scomberomorus commerson	Indian Ocean and Western Pacific Ocean. Recently found in the Mediterranean Sea along the northern African countries.	The most important commercial species of *Scomberomorus* in the Indian Ocean and the Indo-West Pacific region. It is taken throughout its range by small-scale commercial fisheries, sustaining important fisheries in the Arabian Sea [40], India [41] and Australia [42]. Also caught by recreational fisheries [3].
Scomberomorus concolor	Eastern Central Pacific Ocean. Current distribution is restricted to the northern part of the Gulf of California.	Caught together with *Scomberomorus sierra* by small-scale commercial fisheries in the Gulf of California [43].
Scomberomorus guttatus	Northern Indian Ocean and Indo-Pacific region	Caught by small-scale commercial fisheries throughout its range. Particularly, it sustains an important commercial fishery in India together with *S. commerson*, *S. lineonatus* and *Acanthocybium solandri* [33,34].

Species	Distribution	Fisheries
Scomberomorus koreanus	Northern Indian Ocean and northwestern Pacific Ocean	Caught by small-scale commercial fisheries throughout its range. Particularly, it is caught by small commercial fisheries in India, together with *S. commerson, guttatus* and *lineolatus*, but it forms a negligible portion of the fishery [44] and in China, Korea and Japan together with *S. niphonius* [45]
Scomberomorus lineolatus	Northern Indian Ocean and Indo-Pacific region	Caught by small-scale fisheries throughout its range. Particularly, it sustains an important commercial fishery in India together with *S. commerson, S. guttatus* and *Acanthocybium solandri* [33,34].
Scomberomorus maculatus	Northwestern Atlantic Ocean	Sustains one of the most important commercial and recreational fisheries of *Scomberomorus* species in the Atlantic ocean, principally in the Southeastern Coast of the United States and the Gulf of Mexico [46,47].
Scomberomorus multiradiatus	Restricted to the Gulf of Papua and Timor Sea in the Indo-Pacific	Caught by small-scale fisheries, particularly as by-catch within its range [48].
Scomberomorus munroi	Indo-Pacific region restricted to northern Australia and Papua New Guinea	Caught by commercial and recreational fisheries in Australia together with *S.commerson, S. queenslandicus* and *S. semifasciatus* [49].
Scomberomorus niphonius	Northwest Pacific Ocean	Caught by commercial fisheries throughout its range, in particular in Japan, South Korea and China [45,50,51]. Also caught by recreational fisheries [3].
Scomberomorus plurilineatus	Western Indian Ocean along the Eastern African Coast	Caught by small-scale commercial fisheries throughout its range although the magnitude of the catches is uncertain [52]. It is an important component of the catches by the recreational fisheries in South Africa [53].
Scomberomorus queenslandicus	Indo-Pacific region restricted to northern Australia and Papua New Guinea	Caught by commercial and recreational fisheries in Australia together with *S.commerson, S. munroi* and *S. semifasciatus [49]*.
Scomberomorus regalis	Western Atlantic Ocean	Caught by small-scale commercial and recreational fisheries throughout its range in particular in the Caribbean countries such as Jamaica [54] and Puerto Rico [55].
Scomberomorus semifasciatus	Indo-Pacific region restricted to northern Australia and Papua New Guinea	Caught by commercial and recreational fisheries in northern Australia [56].
Scomberomorus sierra	Eastern Pacific Ocean	Caught by small-scale commercial fisheries throughout its range. Particularly it has a well developed commercial fishery in Mexico [57]. Also caught by recreational fisheries [3].
Scomberomorus sinensis	Northwestern Pacific Ocean	Caught by small-scale commercial fisheries throughout its range in particular in Japan, South Korea and China but catch statistics are commonly mixed with other *Scomberomorus* species [45,58]. Caught by artisanal fleets in the Mekong River of Cambodia [48]. Also caught by recreational fisheries [3].
Scomberomorus tritor	Eastern Atlantic Ocean including the Mediterranean Sea	Caught by small-scale fisheries throughout the eastern Atlantic in particular Senegal and Gambia [59] and caught as bay-catch in the Mediterranean Sea [20].
Grammatorcynus bicarinatus	Southwestern Pacific restricted to the northern coast of Australia	Caught by minor small-scale commercial fisheries but catch statistics data do not exist [7]. Only one known direct fishery for bait exists in Queensland, Australia[60]. Also caught by recreational fisheries [3].
Grammatorcynus bilineatus	Northern Indian Ocean and Indo-Pacific region with a disjoint distribution	Caught by minor small-scale commercial fisheries at least in some parts of its range, for example in Fiji and Andaman Islands but catch statistics data do not exist [7]. Also caught by recreational fisheries [3].
Rastrelliger brachysoma	Indo-Pacific region	Caught by small-scale commercial fisheries throughout its range such as in Malaysia [61,62] and Philippines [63]. In many parts of its range landings are primarily reported in combination with mixed *Rastrelliger* spp.

Species	Distribution	Fisheries
Rastrelliger faughni	Indo-Pacific region	Caught by minor small-scale commercial fisheries throughout its range and it is the least abundant among the *Rastrelliger* sp. In many parts of its range landings are primarily reported in combination with mixed *Rastrelliger* spp [64].
Rastrelliger kanagurta	Indian Ocean, Indo-Pacific region and Western Pacific Ocean	Caught by small-scale commercial fisheries throughout its range such as in India [62,65], Philippines [63] and Egypt [66]. In many parts of its range landings are primarily reported in combination with mixed *Rastrelliger* spp.
Scomber australasicus	Western Pacific Ocean and northwestern Indian Ocean	Caught by commercial fisheries throughout its range such as in New Zealand [67], Australia [68], Taiwan [69], Japan[70] and Gulf of Suez [71].
Scomber japonicus	Northwest Pacific Ocean and Eastern Pacific Ocean	Caught by commercial fisheries throughout its range in particular in China [72], Japan [73], Chile [74]and California [75].
Scomber scombrus	Northwest Atlantic Ocean and Northeast Atlantic Ocean including the Mediterranean Sea	Caught by commercial fisheries throughout its range, particularly in northwestern Europe [76], Canada and USA [77].
Scomber colias	Eastern Atlantic Ocean including Mediterranean Sea	Caught by commercial fisheries throughout its range such as in Spain [78] and the Hellenic Seas [79].
Gasterochisma melampus	Southern waters of the Atlantic, Pacific and Indian oceans	There are no developed commercial fisheries for this species. It has no commercial value and it is caught incidentally as by-catch in the longline tuna fisheries in oceanic waters [24].

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Table 3.S2   Criteria to construct the Venn Diagram of life history research priorities in scombrid species.

We differentiated between life history data-poor and data-rich species (see definition in main text), between species targeted and not-targeted by commercial fisheries (see Table 3.S1), and between species listed as Threatened, Near Threatened and Data Deficient from those listed as Least Concern in the IUCN Red List [10]. IUCN Red List categories: CR - Critically Endangered, EN - Endangered, VU - Vulnerable, NT - Near Threatened, LC - Least Concern and DD - Data Deficient.

Taxonomic group	Latin name	Life history research	Fisheries	IUCN Status
Tunas	*Allothunnus fallai*	Data-poor	Not-targeted	LC
	Auxis rochei	Data-rich	Targeted	LC
	Auxis thazard	Data-poor	Targeted	LC
	Euthynnus affinis	Data-rich	Targeted	LC
	Euthynnus alletteratus	Data-poor	Targeted	LC
	Euthynnus lineatus	Data-rich	Targeted	LC
	Katsuwonus pelamis	Data-rich	Targeted	LC
	Thunnus alalunga	Data-rich	Targeted	NT
	Thunnus albacares	Data-rich	Targeted	NT
	Thunnus atlanticus	Data-poor	Targeted	LC
	Thunnus maccoyii	Data-rich	Targeted	CR
	Thunnus obesus	Data-rich	Targeted	VU
	Thunnus orientalis	Data-poor	Targeted	LC
	Thunnus thynnus	Data-rich	Targeted	EN
	Thunnus tonggol	Data-poor	Targeted	DD
Bonitos	*Cybiosarda elegans*	Data-poor	Targeted	LC
	Gymnosarda unicolor	Data-poor	Targeted	LC
	Orcynopsis unicolor	Data-poor	Targeted	LC
	Sarda australis	Data-poor	Targeted	LC
	Sarda chiliensis	Data-poor	Targeted	LC
	Sarda orientalis	Data-poor	Targeted	LC
	Sarda sarda	Data-rich	Targeted	LC
Spanish mackerels	*Acanthocybium solandri*	Data-rich	Targeted	LC
	Grammatorcynus bicarinatus	Data-poor	Targeted	LC
	Grammatorcynus bilineatus	Data-poor	Targeted	LC
	Scomberomorus brasiliensis	Data-poor	Targeted	LC
	Scomberomorus cavalla	Data-rich	Targeted	LC
	Scomberomorus commerson	Data-rich	Targeted	NT
	Scomberomorus concolor	Data-poor	Targeted	VU
	Scomberomorus guttatus	Data-poor	Targeted	DD
	Scomberomorus koreanus	Data-poor	Targeted	LC
	Scomberomorus lineolatus	Data-poor	Targeted	LC
	Scomberomorus maculatus	Data-rich	Targeted	LC
	Scomberomorus multiradiatus	Data-poor	Targeted	LC
	Scomberomorus munroi	Data-poor	Targeted	VU
	Scomberomorus niphonius	Data-poor	Targeted	DD
	Scomberomorus plurilineatus	Data-poor	Targeted	DD
	Scomberomorus queenslandicus	Data-poor	Targeted	LC
	Scomberomorus regalis	Data-poor	Targeted	LC
	Scomberomorus semifasciatus	Data-poor	Targeted	LC
	Scomberomorus sierra	Data-poor	Targeted	LC
	Scomberomorus sinensis	Data-poor	Targeted	DD
	Scomberomorus tritor	Data-poor	Targeted	LC
Mackerels	*Rastrelliger brachysoma*	Data-poor	Targeted	DD
	Rastrelliger faughni	Data-poor	Targeted	DD
	Rastrelliger kanagurta	Data-poor	Targeted	DD
	Scomber australasicus	Data-rich	Targeted	LC
	Scomber colias	Data-poor	Targeted	LC
	Scomber japonicus	Data-rich	Targeted	LC
	Scomber scombrus	Data-rich	Targeted	LC
Gasterochisma	*Gasterochisma melampus*	Data-poor	Not-targeted	LC

Chapter 4

Chapter 4.

Life in 3-D: Life history strategies in tunas, mackerels and bonitos[1]

Abstract

The scombrids (tunas, bonitos, Spanish mackerels and mackerels) sustain some of the most important fisheries in the world and their sustainable management depends on better understanding of their life history strategies. Here, we assemble life history information on maximum size, growth, longevity, maturity, fecundity and spawning duration and interval for all scombrid species and we characterize their life history patterns and trait co-variation and evaluate how many principal axes of trait variation underlie scombrid life history strategies. Most of their life history variation can be explained along three axes or dimensions: size, speed, and reproductive schedule. Body size governs the first axis ranking species along a small-large continuum. The second axis was mostly influenced by time-related traits, such as longevity, growth rates, spawning duration, time between spawning events, ranking species along a slow-fast continuum of life histories. Scombrid species with the slowest life histories such as Atlantic bluefin tuna *Thunnus thynnus* and Atlantic mackerel *Scomber scombrus* tend to inhabit more temperate waters while species with faster life histories such as yellowfin tuna *Thunnus albacares* and short mackerel *Rastrelliger brachysoma* are typically found in more tropical waters. The third axis comprises the negative relationship between number of eggs produced at length of maturity and rate in gain of fecundity with size describing the schedule of reproductive allocation which reflects a fundamental trade-off between reproduction and growth. Finally, in addition we show that the life history strategies of scombrids conform more closely to the Periodic and Opportunistic strategists within the triangular model of fish life histories.

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Introduction

Information on the life history traits of species, such as patterns of growth and reproduction, has many uses in biology, theoretical ecology and applied resource management (Beverton 1992, Molles 2000). The life history attributes of species and their life history strategies are fundamental to our understanding of how species respond to human exploitation (Beverton and Holt 1959, Jennings et al. 1998), habitat degradation (Ockinger et al. 2010), invasions (Olden et al. 2008), and climate change (Dalgleish et al. 2010). In addition, the life history attributes are major determinants of the population dynamics of fishes and underpin the sustainable exploitation and management of species through selectivity, effort and allowable catch controls (Beverton and Holt 1959, Dulvy et al. 2004), or spatial management (Claudet et al. 2010). Here, we compile life history information for the 51 species in the family Scombridae (Table 4.1) with the aim of characterizing their life history strategies and promote the use of life history information to enhance the management of exploited species of scombrids, particularly species for which biological knowledge is limited. In an era where one of the major impediments for ecosystem assessments and management is the lack of information on the status for the majority of the species exploited, the knowledge of life history parameters can provide a starting framework in support of management (King and McFarlane 2003).

The scombrid species (tunas, bonitos, Spanish mackerels and mackerels) are major components of the pelagic ecosystems being epipelagic and epi-mesopelagic predators with their life cycles confined to marine open waters although some species are associated to coral reefs and use estuarine and riverine habitats (Collette and Nauen 1983). They are widely distributed either in coastal or oceanic waters throughout the tropical, subtropical and temperate waters of the world oceans. Most species are migratory, particularly the three species of bluefin tuna (*Thunnus thynnus, T. orientalis and T. maccoyii*) which can tolerate a wide thermal range from feeding grounds in cold temperate waters to spawning grounds in warmer waters (Boyce et al. 2008). Scombrids are also among the most advanced groups of pelagic fishes. The tunas are endothermic having evolved a countercurrent heat exchanger system with the function of retaining metabolic heat that increases their body temperature above the surrounding water (Block and Finnerty 1994). Tunas have also evolved the highest swimming speeds among fish and a high efficient oxygen uptake system to fuel their high metabolic rates (Graham and Dickson 2004). In addition to their biological and ecological importance, scombrid species support important fisheries worldwide from large-scale industrial to small-scale fisheries

Table 4.1 List of species in the family Scombridae with their taxonomic information, oceanic environments and geographic distributions.

The current accepted classification of the family Scombridae is based on morphological studies (Collette et al. 2001). (*) Commonly known as principal market tuna species.

Subfamily and tribe	Code	Latin name	Common name	Oceanic environments	Geographical distribution
Subfamily Scombrinae	ALB	Thunnus alalunga*	Albacore tuna	Subtropical	Cosmopolitan
	YFT	Thunnus albacares*	Yellowfin tuna	Tropical	Cosmopolitan
	SBF	Thunnus maccoyii*	Southern bluefin tuna	Temperate	Southern Oceans
	BET	Thunnus obesus*	Bigeye tuna	Subtropical	Cosmopolitan
Tribe Thunnini (tunas)	BFT	Thunnus thynnus*	Atlantic bluefin tuna	Temperate	Atlantic Ocean
	PBF	Thunnus orientalis*	Pacific bluefin tuna	Temperate	Pacific Ocean
	SKJ	Katsuwonus pelamis*	Skipjack tuna	Tropical	Cosmopolitan
	BLF	Thunnus atlanticus	Blackfin tuna	Tropical	Western Atlantic Ocean
	LOT	Thunnus tonggol	Longtail tuna	Tropical	Indian Ocean, Indo-Pacific region, Western Pacific Ocean
	KAW	Euthynnus affinis	Kawakawa	Tropical	Indian Ocean, Indo-Pacific region
	LTA	Euthynnus alletteratus	Little tunny	Tropical	Atlantic Ocean, including the Mediterranean and Black sea
	BKJ	Euthynnus lineatus	Black skipjack	Tropical	Eastern Pacific Ocean
	BLT	Auxis rochei	Bullet tuna	Tropical	Cosmopolitan
	FRI	Auxis thazard	Frigate tuna	Tropical	Cosmopolitan
	SLT	Allothunnus fallai	Slender tuna	Subtropical	Southern Oceans
Subfamily Scombrinae	LEB	Cybiosarda elegans	Leaping bonito	Tropical	Indo-Pacific region
	DOT	Gymnosarda unicolor	Dogtooth tuna	Tropical	Indian Ocean, Indo-Pacific region. Disjoint distribution, found primarily around reefs.
Tribe Sardini (bonitos)	BOP	Orcynopsis unicolor	Plain bonito	Subtropical	Eastern Atlantic Ocean including the Mediterranean Sea
	BAU	Sarda australis	Australian bonito	Subtropical	Indian and Pacific Oceans
	BEP	Sarda chiliensis	Eastern Pacific bonito	Subtropical	Eastern Pacific Ocean
	BIP	Sarda orientalis	Indo-Pacific bonito	Subtropical	Indian and Pacific Oceans
	BON	Sarda sarda	Atlantic bonito	Subtropical	Atlantic Ocean including the Mediterranean Sea
Subfamily Scombrinae	WAH	Acanthocybium solandri	Wahoo	Tropical	Cosmopolitan
	BRS	Scomberomorus brasiliensis	Serra Spanish mackerel	Tropical	Western Atlantic Ocean
	KGM	Scomberomorus cavalla	King mackerel	Tropical	Western Atlantic Ocean
Tribe Scomberomorini (Spanish mackerels)	COM	Scomberomorus commerson	Narrow-barred king mackerel	Tropical	Indian Ocean and Western Pacific Ocean. Recently found in the Mediterranean Sea along the northern African countries.
	MOS	Scomberomorus concolor	Monterey Spanish mackerel	Subtropical	Eastern central Pacific Ocean. The current distribution is restricted to the upper two-thirds of the Gulf of California.
	GUT	Scomberomorus guttatus	Indo-Pacific king mackerel	Tropical	Indian Ocean and Western Pacific Ocean
	KOS	Scomberomorus koreanus	Korean seerfish	Tropical	Indian Ocean and Western Pacific Ocean
	STS	Scomberomorus lineolatus	Streaked seerfish	Tropical	Indian Ocean and Indo-Pacific region
	SSM	Scomberomorus maculatus	Atlantic Spanish mackerel	Subtropical	Western Atlantic Ocean
	PAP	Scomberomorus multiradiatus	Papuan seerfish	Tropical	Restricted to the Gulf of Papua and the Timor Sea in the Indo-Pacific
	ASM	Scomberomorus munroi	Australian spotted mackerel	Tropical	Indo-Pacific region restricted to northern Australia and Papua New Guinea
	NPH	Scomberomorus niphonius	Japanese Spanish mackerel	Temperate	Northwest Pacific
	KAK	Scomberomorus plurilineatus	Kanadi kingfish	Subtropical	Western Indian Ocean along the eastern African Coast
	QUM	Scomberomorus queenslandicus	Queensland school mackerel	Tropical	Indo-Pacific region restricted to northern Australia and Papua New Guinea

SCE	*Scomberomorus regalis*	Cero	Tropical	Western Atlantic Ocean
BBM	*Scomberomorus semifasciatus*	Broad-barred king mackerel	Tropical	Indo-Pacific region restricted to northern Australia and Papua New Guinea
SIE	*Scomberomorus sierra*	Pacific sierra	Tropical	Eastern Pacific Ocean
CHY	*Scomberomorus sinensis*	Chinese seerfish	Subtropical	Western Pacific Ocean
STR	*Scomberomorus tritor*	West African Spanish mackerel	Tropical	Eastern Atlantic Ocean including the Mediterranean Sea
SHM	*Grammatorcynus bicarinatus*	Shark mackerel	Subtropical	Indo-Pacific region
DBM	*Grammatorcynus bilineatus*	Double-lined mackerel	Subtropical	Indian Ocean and Indo-Pacific region. It is not clear if the distribution is continuous, at least around the Indian Ocean.
Subfamily Scombrinae Tribe Scombrini (mackerels)				
RAB	*Rastrelliger brachysoma*	Short mackerel	Tropical	Indo-Pacific region
RAF	*Rastrelliger faughni*	Island mackerel	Tropical	Indo-Pacific region
RAG	*Rastrelliger kanagurta*	Indian mackerel	Tropical	Indian Ocean and Western Pacific Ocean
MAA	*Scomber australasicus*	Spotted chub mackerel	Subtropical	Indo-West Pacific region
MAS	*Scomber japonicus*	Chub mackerel	Subtropical	Indian and Pacific Oceans
MAC	*Scomber scombrus*	Atlantic mackerel	Temperate	North Atlantic Ocean
MASA	*Scomber colias*	Atlantic chub mackerel	Subtropical	Atlantic Ocean including the Mediterranean Sea
Subfamily Gasterochismatinae				
BUK	*Gasterochisma melampus*	Butterfly kingfish	Subtropical	Southern Oceans

(Majkowski 2007, Juan-Jordá et al. 2011). Their commercial importance and economic value have also led to numerous life history studies in the last 50 years, although the degree of life history research varies across species (Juan-Jorda et al, in review). This family of fish represents an opportunity to study life history variation and life history strategies given their wide ranging geographic extent in their distributions and migrations, and their fascinating adaptations to the pelagic environment, including species with a wide breath of life history attributes differing greatly in ecology.

The scombrid species (tunas, bonitos, Spanish mackerels and mackerels) are major components of the pelagic ecosystems being epipelagic and epi-mesopelagic predators with their life cycles confined to marine open waters although some species are associated to coral reefs and use estuarine and riverine habitats (Collette and Nauen 1983). They are widely distributed either in coastal or oceanic waters throughout the tropical, subtropical and temperate waters of the world oceans. Most species are migratory, particularly the three species of bluefin tuna (*Thunnus thynnus, T. orientalis and T. maccoyii*) which can tolerate a wide thermal range from feeding grounds in cold temperate waters to spawning grounds in warmer waters (Boyce et al. 2008). Scombrids are also among the most advanced groups of pelagic fishes. The tunas are endothermic having evolved a countercurrent heat exchanger system with the function of retaining metabolic heat that increases their body temperature above the surrounding water (Block and Finnerty 1994). Tunas have also evolved the highest swimming speeds among fish and a high efficient oxygen uptake system to fuel their high metabolic rates (Graham and Dickson 2004). In addition to their biological and ecological importance, scombrid species support important fisheries worldwide from large-scale industrial to small-scale fisheries (Majkowski 2007, Juan-Jordá et al. 2011). Their commercial importance and economic value have also led to numerous life history studies in the last 50 years, although the degree of life history research varies across species (Juan-Jorda et al, in review). This family of fish represents an opportunity to study life history variation and life history strategies given their wide ranging geographic extent in their distributions and migrations, and their fascinating adaptations to the pelagic environment, including species with a wide breath of life history attributes differing greatly in ecology.

There have been several theories developed to predict the evolution of specific sets of life history traits and life history strategies of species in response to environmental conditions (MacArthur and Wilson 1967, Murphy 1968, Pianka 1972, Stearns 1976, Grime and Pierce 2012). The *r-K* selection theory was one of the first, predicting a one-dimensional continuum of life histories with extreme *r-* and *K*-selected species at each end. This theory

now is seen as incomplete and has been challenged by theoretical and empirical work (Stearns 1977, Reznick et al. 2002). Alternatively, there is now evidence that three-way adaptive trade-off exists in all organisms including bacteria, plants and animals, recognizing that multiple trade-offs occur and not simple single dimensions (r-K) are involved in the evolution of primary adaptive life history strategies in organisms (Grime 1977, Southwood 1977, Winemiller and Rose 1992, Golovlev 2001, Grime and Pierce 2012). One of the first theories predicting three-way trade-offs, and now the most mature and empirically-supported theory, is the CSR plant theory of primary adaptive strategies (Grime 1974, 1977, 2001). The CSR theory predicts that the strategies of plant species are an adaptive response to a three-way trade-offs in the investment of resources between the control of resource acquisition in productive habitats (Competition or C strategy), the persistence of individuals in unproductive habitats (Stress tolerant or S strategy), or regeneration of species in response to disturbance or lethal events (Ruderal or R strategy). Although originally proposed for plants, there is growing evidence that identical three way trade-offs between resource acquisition, maintenance and regeneration constraints adaptive strategies exists in a wide phylogenetic range of organisms as diverse as bacteria, fungi and animals (Grime and Pierce 2012).

One of the key lines of evidence for three primary adaptive strategies in fishes comes from comparative life history studies (Winemiller 1989, Winemiller and Rose 1992 , Vila-Gispert et al. 2002, King and McFarlane 2003, Grime and Pierce 2012). Using life history information from 216 North American marine and freshwater fishes Winemiller and Rose 1992 identified three primary life history strategies in fishes arising from trade-offs between survival, fecundity and generation length. At one end, the Opportunistic strategists, such as sardines, are small, short-lived species with early maturation, intermediate fecundity, but high annual reproductive effort, which produce small offspring. They argued that this combination of traits maximizes the colonization ability of species across environments with frequent and intense disturbances (similar to R-selected strategists in plants). The Periodic strategists, such as rockfishes, are intermediate to large sized, long-lived species with a late maturation; short reproductive seasons and large clutches of small eggs. This strategy is advantageous in variable but predictable environments because producing a large number of offspring over long period of time allows bet-hedging and success during the infrequent periods of conditions favoring successful reproduction (similar to C-selected strategists in plants). The Equilibrium strategists, such as spiny dogfish, vary in body size (from small to large) and have moderate to late age at maturation, small clutches of large eggs, high juvenile survivorship

and well developed parental care, which are associated in habitats with low environmental variation (similar to S-selected strategist in plans). The scombrids appear to be intermediate strategists within the Opportunistic-Periodic-Equilibrium life history triangle, but this was based on two species of scombrids, albacore tuna *Thunnus alalunga* and chub mackerel *Scomber japonicus* (Winemiller and Rose 1992, King and McFarlane 2003). While, three-way trade-offs explains universal patterns of adaptive life history strategies of fishes and all organisms across the tree of life, it may not capture all of the detail. It is not expected that all the life history traits of organisms to be associated with the axes of the CSR model of plants life histories or Opportunistic-Periodic-Equilibrium model of fish life histories. Many of the life history traits can vary independently and influence the finer dimensions of life history variation in species and populations (Grime and Pierce 2012). In addition, not all taxonomic groups of fishes will have traits occupying the full space of the Opportunistic-Periodic-Equilibrium life history triangle since phylogenetic constrains restrict the range of adaptive strategies possible. For example, chondrichthyan species with life histories characterized by slow growth and high investment in the survival of adults and young conform more closely to the Equilibrium strategists (King and McFarlane 2003, Dulvy and Forrest 2009).

A comparative life history study of ten Atlantic scombrid and billfish species revealed one major dominant life history axis shaped by the environment (Fromentin and Fonteneau 2001). Tropical species such as yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* have short-medium body sizes, early age at maturity, fast growth and extended spawning seasons whereas temperate species, such as Atlantic bluefin tuna, had the opposite set of traits. Although in such study the life histories of tropical tuna species were closely associated with the *r*-selected species and temperate tuna species were closely associated with *K*-selected species of the *r-k* selection model, it was also acknowledged that the *r-k* selection model was insufficient to explain the full spectrum of life histories and population dynamics of tunas and billfishes. The *r-K* theory predicts *r*-selected species in variable environments while tropical tunas spend their whole life cycle in tropical warm waters which are commonly perceived as more stable environments than temperate waters (Fromentin and Fonteneau 2001). In addition, the high fecundities in bet-hedging strategies observed in tunas and billfishes do not correspond to the expectations of the *r-k* selection theory either (Rochet et al. 2000, Longhurst 2002). It is evident that the one-dimensional *r-k* theory is unable to explain the richness of scombrid life history strategies. In addition, the small number scombrid species included in previous comparative analysis of life histories leaves unanswered whether there is a single

dominant life history strategy within the Scombridae family or if instead there is a wide range of variation in adaptive strategies.

The main objective of this study is to characterize the scombrid life history strategies. First, we compile life history information (maximum size, growth, longevity, maturity, fecundity and spawning duration and interval) for all scombrid species on a global scale. Second, we examine the main patterns in the life history traits across scombrid species and use multivariate analyses to examine the co-variation among traits and evaluate how many principal axes of trait variation underlie scombrid life history strategies. Finally, we tested for sexual dimorphism in the following life history traits: maximum size, longevity, length of maturity and growth rates.

Methodology

Data collection, data sources and data standardization

We assembled life-history data for the 51 species of scombrids on a global scale from a wide range of published literature including: scientific journals, grey literature and theses published in English, Spanish, French, Portuguese, Italian and any other language that provided an English summary. We reviewed and included only the original studies; excluding review articles. By reviewing only original information, we avoided propagating widely-used but poorly-supported or erroneous parameter estimates. From each life history study, we extracted the trait estimates reported for females, males, and both sexes combined along with the sample sizes and the method used to estimate each of the life history parameters. In our life history analysis we preferentially used the female estimates whenever the traits were reported separately for sexes. We report length-based estimates as fork lengths throughout. We transformed standard lengths or total lengths into fork lengths using published length conversion equations.

Life history traits

For each species we collected the following life history parameters:

Maximum length: We extracted the maximum length (L_{max}, cm) of the fish observed from each life history study.

Growth: We extracted the three parameters (L_∞, k and t_o) of the von Bertalanffy growth function, $L_t = L_\infty (1-e^{-k(t-to)})$, from each growth study. L_t is the length at age t in years. L_∞ is asymptotic length in cm - the mean size the individuals in the population would reach if they were to grow indefinitely. The growth coefficient k (year^{-1}) expresses the rate at which the asymptotic length is approached and t_o is defined as the hypothetical age in years that fish would have at zero length. We compared the maximum observed length (L_{max}) and the theoretical maximum length or asymptotic length estimates (L_∞) of species to evaluate their interchangeability.

Longevity or maximum age: We extracted the maximum observed age (T_{max}, *years*), here referred as empirical longevity, from all growth studies where age was estimated. Many growth studies did not report longevity. Consequently, theoretical longevities (T_∞, years) are commonly estimated using Taylor's relationship based on the von Bertalanffy growth rate parameter k as $T_\infty = 3/k$ (Taylor 1958). The Taylor's longevity estimate is the age that a fish population would reach at L_∞. Therefore, we also extracted theoretical longevities from the studies or we estimated them using Taylor's relationship. We compared the empirical (T_{max}) and theoretical (T_∞) longevity estimates to evaluate their interchangeability.

Length and age at maturity: We extracted both the length (L_m, cm) and age (T_m, years) at first maturity (the length and age at which maturity is first reached by an individual in a sample) and length (L_{m50}) and age (T_{m50}, years) at 50% maturity (length and age at which 50% of the sampled individuals have matured) from maturity studies. However, some studies only estimated length and age at first maturity. In the majority of the studies, age at maturity was estimated by converting length at maturity to age using a Von Bertalanffy growth equation.

Batch fecundity, spawning season and spawning interval: Scombrids batch spawn repeatedly over the spawning season. We collected information on absolute batch fecundity (average number of oocytes in a batch), fecundity-length relationships (*Fecundity* = a × *Length* ^{b}) and relative batch fecundities (F_{rel}, number of oocytes per gram). We used the fecundity-length equation to estimate the absolute batch fecundity at the length of 50% maturity (F_{Lm50}) interpreted as the number of oocytes of mature females at the length of 50% maturity in a single spawning. We also extracted the exponent of the fecundity-length relationship (or slope of the log-log fecundity-length regression), which describes the increase of fecundity with size (F_{slope}). Finally, we also collected information

on the spawning intervals (Spw_{int}, the average number of days between spawning events in the population) and duration of the spawning season (Spw_{season}, months).

Data screening and aggregation of data at the species level

We screened our data set using established criteria to remove poor estimates, errors, and outliers. We focused mostly on the von Bertalanffy growth parameters since they showed the largest variation among all the life history parameters. We evaluated the reliability of the von Bertalanffy growth curves of each of the species using two criteria. First, we estimated the variability in the ratio between the maximum observed length (L_{max}) and asymptotic length (L_∞) for each study and across all the studies and species pooled. We eliminated those studies with ratios more than three standard deviations away from the mean ratio across all studies. Second, we examined the variability of the phi-prime parameter ($\Phi' = \log_{10}k + 2* \log_{10}L_\infty$) calculated from each study across all studies and species pooled, where k and L_∞ are parameters of the von Bertalanffy growth function. The Φ' values for a given species or taxonomically related group of species should be normally distributed around the mean Φ of the taxonomic unit, and values further away from the mean of the distribution must be interpreted with increasing caution (Pauly and Munro 1984). We standardized the Φ' values of each study by dividing each by the mean of Φ' within each species. Second, we removed the outlying growth equations in which the standardized Φ' value was bigger than three standard deviations away from the mean standardized Φ' values across all the studies and species. We arbitrarily choose a value of three standard deviations away from the mean based on the histograms of the ratios (all data pooled) which highlighted those studies away from the pooled mean. The life history data set contains 684 articles (Appendix C) and is available upon request from the corresponding author.

In order to aggregate the life history parameters from multiple studies at the species level we selected data for analysis based on the following rules. (1) We chose the maximum value for those traits at the extreme of the life cycle (maximum length and empirical longevity). (2) We calculated a sample-size weighted average for those reproductive traits within the lifecycle (maturity, fecundity and spawning interval). (3) For the growth traits derived from model estimates (growth coefficient, the asymptotic length coefficient and theoretical longevity), we calculated a simple arithmetic mean (giving equal weight to all the studies), because these parameters are more difficult to combine across studies due to the differing methodologies used to estimate age and growth among studies. For example, the precision and sample size of otoliths measurements and length interval

analyses are not comparable. In our analysis we used the maximum length ever observed across all the studies for each species instead of their theoretical maximum lengths. While at the study level the theoretical estimated lengths were significantly larger than the maximum observed lengths of each study (Figure 4.S1A), after aggregating the data for each species, the species maximum observed lengths were significantly larger than their averaged theoretical maximum lengths (Figure 4.S1B). This is expected given that the theoretical maximum length is the mean size the individuals in a population would reach if they were to grow indefinitely. In addition, the maximum observed lengths were available for the 51 species of scombrids while theoretical maximum lengths were available for 41 species. Moreover, the relationship between empirical longevities (maximum estimated age) and theoretical longevities (estimated with Taylor's relationship) was more variable and noisy. We found a high scatter between the empirical longevities and theoretical longevities across all the studies (Figure 4.S1C) and across all species (Figure 4.S1D) and the relationships were increasingly noisier for species with the lager longevities. This suggests that theoretical longevities are not a good proxy for empirical longevities in scombrids particularly for longer-lived species. Therefore, for our analysis, we used the maximum value of all empirical longevities across all the studies for each species over the theoretical longevities estimated with Taylor's relationships. However, for those species with no empirical longevity estimates, we used an average of the theoretical longevities available. We recommend caution in the use of these longevity estimates and on the interpretations of longevities in our analysis. Empirical longevities are dependent on the sample size of the studies and aging methods and theoretical longevities are weakly correlated with empirical longevities across scombrid species (Figure 4.S1).

We used analysis of variance (ANOVA) to quantify the relative magnitude of the variability between species compared to the variability between studies within species in each life history trait in order to assess the implications of trait averaging across multiple studies at the biological unit of species. We also calculated the Relative Intraspecific Variation (RIC) ratio for each trait as the variance among studies within species (intraspecific variation) divided by the total variance (sum of the intraspecific and interspecific variation) (Blanck and Lamouroux 2007). A small ratio indicates that traits vary more among species and a big ratio indicates that traits vary more among studies. All life history traits differed significantly among scombrid species (Table 4.S1). The relatively high interspecific variation (compared with intraspecific variation) in traits allows us to estimate and use average species traits for our analysis (Table 4.S2).

Analysis of life history patterns and sexual dimorphism

We used Pearson's correlations to examine the bivariate relationships among all the life history traits across all 51 species of scombrids. We also performed a principal component analysis (PCA) on the life history data to explore patterns of linear relationships among the life history traits and identify the number of major axes of life history variation. We interpreted the principal components as major axes of life history variation. The PCA included ten life history traits resulting in an ordination of seven scombrid species, which had complete life history information, spanning a wide range of values in their life history attributes. We log-transformed (natural logarithm) all the life history traits prior to the analysis, except the slope from the fecundity-length relationship which was already estimated from log-transformed data. We performed all the PCAs on the correlation matrix to standardize for the influence of unequal variances among life history traits.

We also tested for sexual dimorphism in the following life history traits (maximum size, longevity, length of maturity and growth rate) within each taxonomic group. We regressed the female life history traits on the male life history traits using reduced major axis regression (Warton et al. 2006). The regression slopes significantly different from one indicates sexual dimorphisms in the traits.

All data management, analysis and figures were done using the R statistical software v.2.14.2 (R Development Core Team 2012) , including the R packages "*ggplot2*" (Wickham 2009), "*smatr*" (Warton et al. 2006) and "*vegan*"(Philip 2003).

Results

Bivariate and multivariate life history patterns across scombrid species

The life history traits across the 51 species of scombrids display a wide range of variation (Table 4.2 and S2). Maximum observed length (L_{max}) varies over one order of magnitude of length from 31 cm in the island mackerel (*Rastrelliger faughni*) to 372 cm in the Atlantic bluefin tuna. Body size strongly influences many demographic rates and biological processes (Peters 1983), hence we also observe large variation in the all the growth and reproductive life history traits across the scombrid species (Table 4.2). Age and growth related traits are highly correlated with maximum body size, such that large scombrid species tend to live longer and complete their growth at a lower rate than species with

smaller maximum sizes. Maximum body size is positively correlated with longevity (r = 0.68, Figure 4.1A) and negatively correlated with growth rate (r = -0.62, Figure 4.1B). In addition, longer-lived species also tend to reach their maximum body sizes at a lower rate than the shorter-lived species. There is a significant negative correlation between growth rate and empirical longevity (r = -0.80, Figure 4.1C).

Several reproductive life history traits also vary with maximum body size. Maximum size is positively correlated with both length- and age-at-maturity (r = 0.92 and r= 0.49, respectively, Figure 4.1D-E). Scombrids mature at around half of their maximum length; the length at maturity is typically 45.7% of the maximum length. Scombrids mature at around one quarter of the way through their life; the age at maturity is reached about 25.4% of the maximum age across all the species. Larger scombrids are more fecund than smaller species, as shown by the positive correlation between the absolute fecundity at length of maturity and maximum length (r = 0.81, Figure 4.1F). However, smaller scombrids have higher mass-specific fecundities, spawning a greater number of oocytes per gram of body mass (r = -0.55), and have greater spawning intervals between spawning events (r = -0.7) than scombrids attaining larger maximum sizes (Figure 4.1G-H). Moreover, small scombrids have a greater gain in fecundity with size. Although the negative correlation between maximum length and the slope of the fecundity-length relationship was weak (r = -0.13); the correlation becomes significant after removing the outlying data point of the Southern bluefin tuna, indicating that smaller species appear to have a steeper gain in fecundity with increasing body size (r = 0.42, Figure 4.1I). We also find a negative correlation between the absolute fecundity at length of maturity and the slope of the fecundity length relationship (r = -0.12 including the Southern bluefin tuna and r = -0.51, excluding it, Figure 4.1J), indicating that smaller species have lower fecundities at maturity with their fecundities increasing steeply with body size, while bigger species invest more in fecundity at maturity but their fecundities increase less steeply with body size. Finally, the duration of the spawning season is the only reproductive trait that is not correlated with maximum body size or any other life history trait (Figure 4.1K). Instead, the spawning duration seems to be associated with the type of environment species inhabit. Although there are some exceptions, generally tropical species have longer spawning seasons (an average of 6 months), than their subtropical (5 months) and temperate (4 months) relatives (Figure 4.1L). Tropical species also have the largest variation in spawning duration ranging from one to twelve months. Additional correlations between life history traits are presented in Table 4.3.

Table 4.2 *Summary statistics for ten life history traits, with mean values, standard deviations (SD), sample sizes (n), minimum and maximum values and coefficient of variation (CV).*

Life history traits	Mean	SD	n	Min	Max	CV
Maximum length L_{max} (cm)	125.7	73.9	51	30.9	372.0	58.8
Growth coefficient k (1/years)	0.5	0.4	41	0.1	2.3	85.1
Empirical longevity T_{max} (years)	10.9	8.6	42	1.0	41.0	78.9
Length at 50% maturity L_{m50} (cm)	55.1	32.9	37	16.8	158.9	59.7
Age at 50% maturity T_{m50} (years)	2.4	1.6	31	0.7	9.9	65.4
Fecundity at maturity F_{Lm50} (number of oocytes in thousands)	510.1	607.3	24	13.1	2250.6	119
Slope of fecundity-length relationship F_{slope}	4.3	1.5	17	2.4	7.8	34
Relative fecundity F_{rel} (number of oocytes per gram)	182.7	203.0	18	41.5	825.2	111.1
Spawning interval Spw_{int} (days)	5.3	7.1	16	1.1	30.0	132.8
Spawning duration Spw_{season} (months)	5.5	2.3	42	1.0	12.0	42.5

Figure 4.1   Bivariate relationships between various pairs of life history traits (A-K) and duration of spawning season by oceanic environment (L) for scombrid species.

See Table 4.1 for the name of the species and Table 4.3 for the correlations among life history traits.
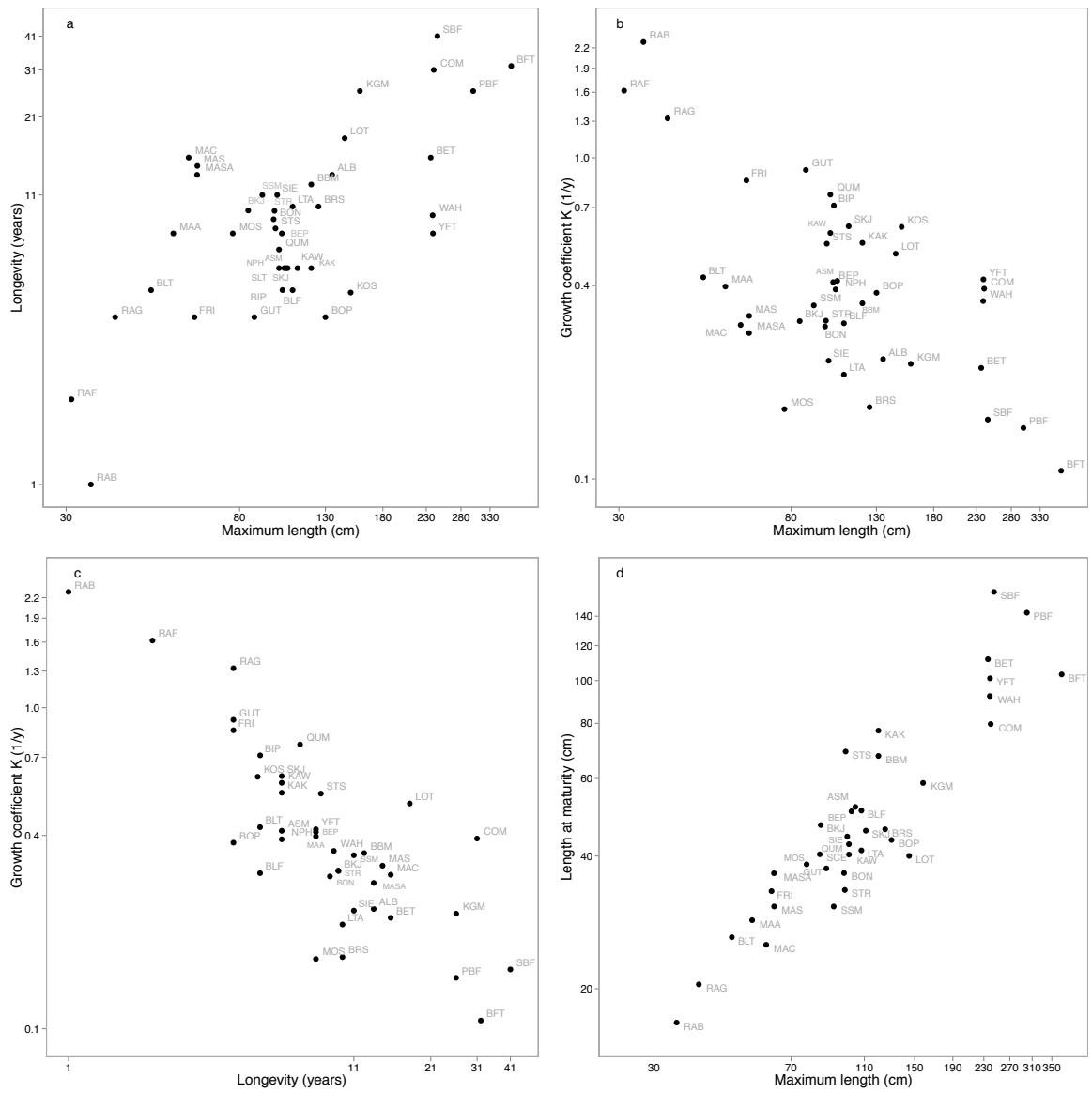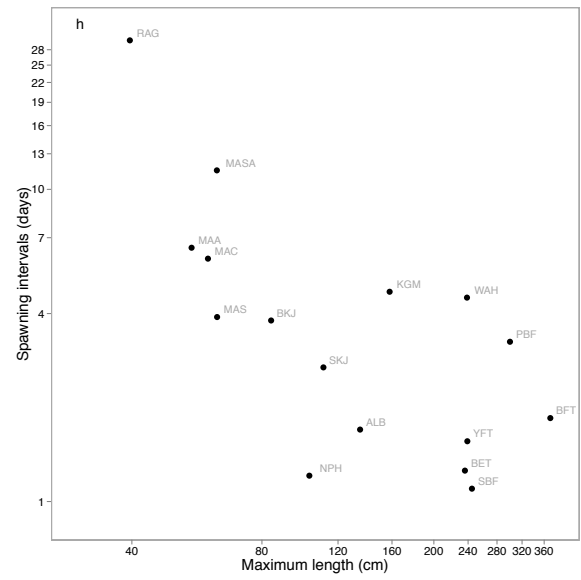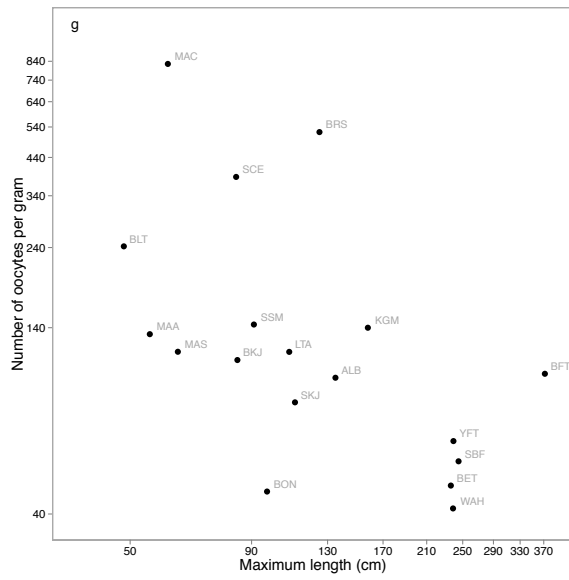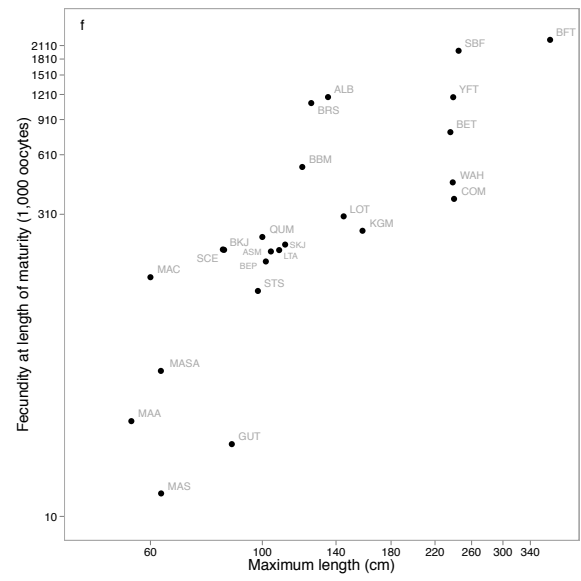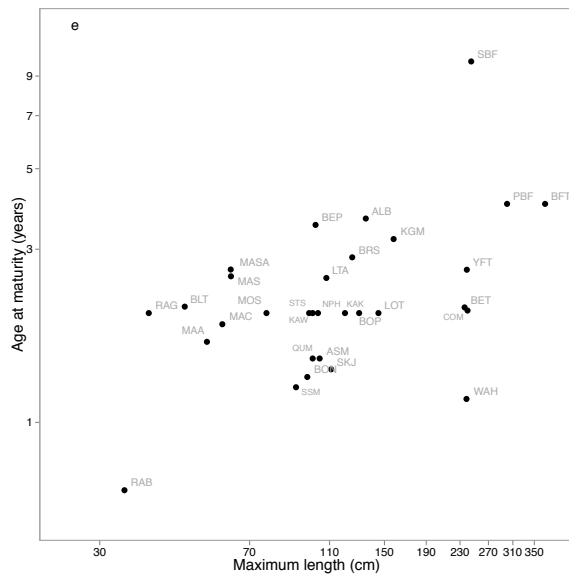
Table 4.3 **Pearson's correlations matrix of life history traits of scombrid species with p-values (lower diagonal) and sample sizes (upper diagonal).**

Correlations are based on all available data for scombrid species.

Life history traits	L_{max}	L_{m50}	T_{m50}	F_{Lm50}	F_{slope}	F_{rel}	Spw_{int}	Spw_{season}	k	T_{max}
Maximum length L_{max} (cm)		37	31	24	17	18	16	42	42	41
Length at 50% maturity L_{m50} (cm)	0.92***		29	23	16	17	14	35	36	36
Age at 50% maturity T_{m50} (years)	0.49**	0.59***		20	17	16	15	30	31	31
Fecundity at maturity F_{Lm50} (# of oocytes in '000)	0.81***	0.77***	0.43		15	15	13	24	23	23
Slope of fecundity-length relationship (F_{slope})	-0.13	0.23	0.4	-0.12		11	8	17	17	17
Relative fecundity F_{rel} (# of oocytes per gram)	-0.55*	-0.6*	-0.01	-0.23	-0.14		12	18	17	17
Spawning interval Spw_{int} (days)	-0.7**	-0.8***	-0.38	-0.78**	-0.14	0.58*		16	16	16
Spawning season Spw_{season} (months)	-0.18	-0.14	-0.12	0.07	-0.18	-0.16	0.15		39	38
Growth coefficient k (1/years)	0.68***	0.62***	0.7***	0.46*	0.07	-0.09	-0.38	0.01		41
Longevity T_{max} & T_{inf} (years)	-0.62***	-0.55***	-0.67***	-0.55**	-0.07	-0.05	0.57*	0.07	-0.8***	

*** = P <0.001; ** = P<0.01; * = P = <0.05

The principal component analysis (PCA) of all 10 life history traits for seven scombrid species resulted in a first component with endpoints contrasting species with large body size, long-lived, late maturing, slow growing, having high absolute fecundities at length of maturity and small spawning intervals between spawning events against those species with the opposite suite of traits (Table 4.4, Figure 4.2A). The first component explained 59% of the variance, and consisted mainly of size-related traits. The second PCA component ordinated species along a slow-fast continuum of time-related life history traits. This axis separated longer-lived, slow growing species with shorter spawning seasons, also having higher relative fecundities, and spawning higher number of oocytes per gram from species with the opposite suite of traits. This second component explained 23% of the variance. The ordination of species along the two main gradients of variation revealed two pairs groups of species with distinct life history strategies (large size versus small size) separated by environment (slow life histories in temperate waters versus fast life histories in tropical waters):

> (1a.) Large, slow temperate. Larger-size, longer-lived, and slower growing Atlantic bluefin and Southern bluefin tunas.

> (1b.) Large, fast tropical. Larger-size but shorter-lived, and faster growing bigeye tuna *Thunnus obesus* and yellowfin tuna.

> (2a.) Small, slow temperate. Smaller-size, longer-lived, and slow-growing Atlantic mackerel *Scomber scombrus* and spotted chub mackerel *S. australasicus*.

> (2b) Small, fast tropical. Smaller-size but shorter-lived, and fast-growing skipjack tuna.

The third component explained 13% of the total variance and captured trade-offs in reproductive allocation and correlated positively with the slope of the fecundity-length relationship, and negatively with maximum size and the absolute fecundity at length of maturity (Table 4.4, Figure 4.2B). The third component mainly distinguished species with high fecundity at maturity but with a slow increase of fecundity with body size from species with low fecundity at the length of maturity with a steeper increase of fecundity with body size. The second and third component together ordinated the species along a slow-fast continuum and at the same time separated the Atlantic bluefin tuna with a slow increase of fecundity with size, from the Southern bluefin and yellowfin tunas, which appear to have a steeper increase in fecundity with size. Together the first three axes combined explained 95% of the total variation in the data.

Table 4.4 **PCA statistics for seven scombrid species based on ten life history traits.**

Life history traits	PC1	PC2	PC3
Maximum length L_{max} (cm)	-0.38	0.13	-0.30
Growth coefficient k (1/years)	0.32	0.37	0.12
Empirical longevity T_{max} (years)	-0.32	-0.39	0.11
Length at 50% maturity L_{m50} (cm)	-0.40	0.18	-0.02
Age at 50% maturity T_{m50} (years)	-0.36	-0.20	0.29
Fecundity at maturity F_{Lm50} (# of oocytes in '000)	-0.38	0.06	-0.21
Slope of fecundity-length relationship ($F_{slope)}$	-0.13	-0.08	0.82
Relative fecundity F_{rel} (# of oocytes per gram)	0.25	-0.44	-0.05
Spawning interval Spw_{int} (days)	0.37	-0.28	0.02
Spawning duration Spw_{season} (months)	0.06	0.58	0.28
% Variance explained	59	23	13
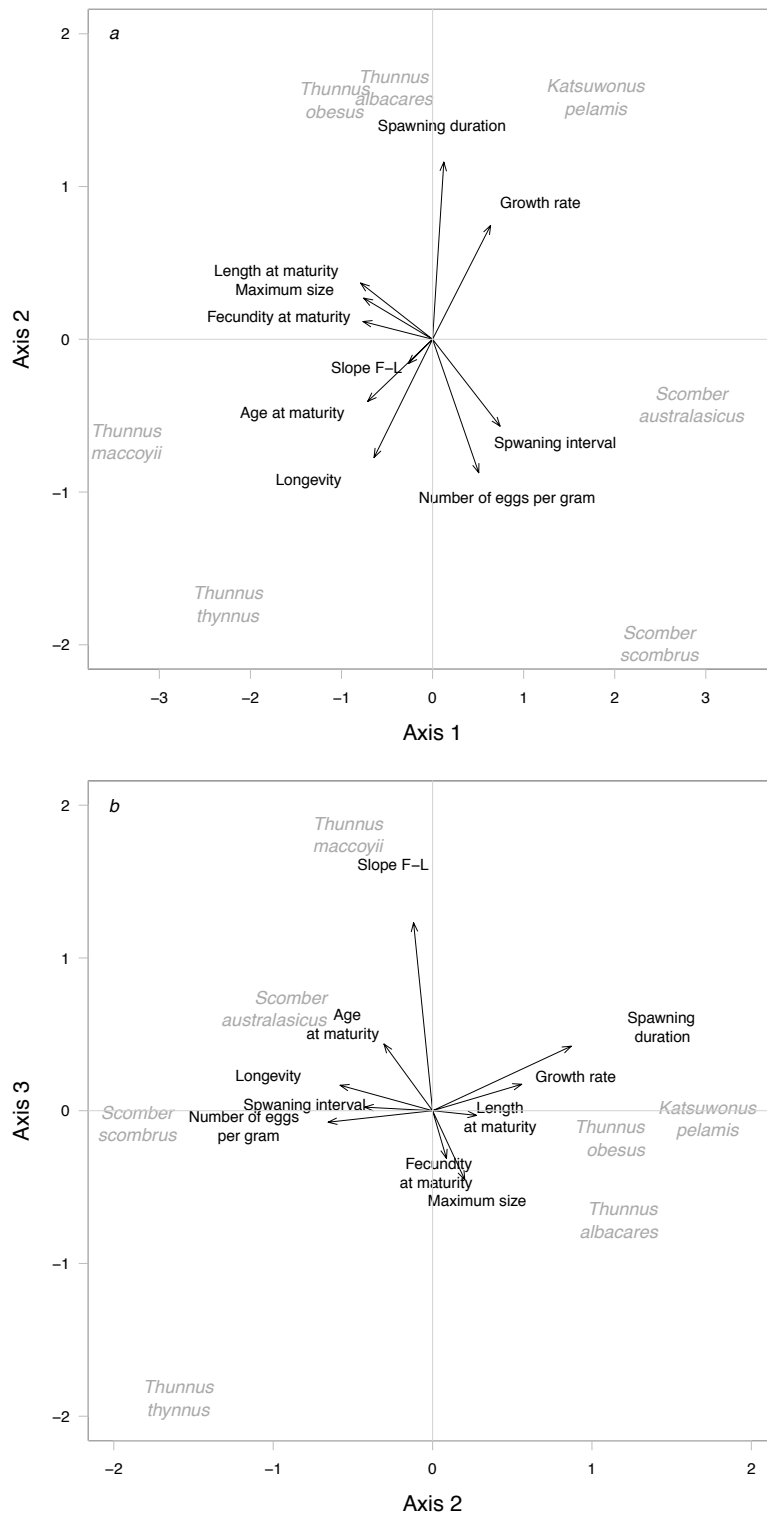
Figure 4.2   ***Principal component analysis (PCA) results of 10 life history traits and 7 species of scombrids including the species scores and vector plots of the trait scores.***

See Table 4.4 for the factor loadings of the PCA.

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Here we extend and generalize the first two dimensions of tuna life histories revealed by the PCA upon the seven scombrid species which had complete life history information. We placed the life history variation of forty-two species of scombrids along the first two major axis of variation, ranking species both along a small-large continuum and along a slow-fast continuum (Figure 4.3). We size-corrected the time-related traits of longevity and growth by calculating the residuals from linear regressions of each life history trait on maximum length. While we observe a positive relationship between the maximum lengths and longevities of the species reflecting that larger species appear to be longer-lived, we also observed that for any given maximum body size of the species there is a wide range of longevities (Figure 4.3A). For example, for species with maximum lengths larger than 2 meters, the tropical yellowfin tuna has a maximum length of 239 cm and can live up to 8 years, compared to the similar-sized temperate Southern bluefin tuna with a maximum length of 245 cm can live up to 41 years. For the smallest scombrid species with maximum lengths smaller than a meter, tropical frigate tuna *Auxis thazard* (62 cm) has a longevity of 4 years while temperate Atlantic mackerel (60 cm) has a longevity of 15 years. Finally, for species with intermediate body sizes, we also find a wide range of longevities for a given body size, for example Korean seerfish *Scomberomorus koreanus* (maximum length of 150 cm) has a longevity of 4.9 year and narrow-barred Spanish mackerel *Scomberomorus commerson* (240 cm) has a longevity of 31 years. However, all the medium size species in this case inhabited the tropics or the subtropical oceans. Using the size-corrected traits of growth and longevity we ranked the species according to their speed of life (irrespective of their body sizes) (Figure 4.3B). Temperate species tended to have the slowest life histories while tropical and subtropical species spread along most of the slow-fast continuum of life histories. We find that the tropical island mackerel and yellowfin tuna have the fastest life histories while temperate Atlantic mackerel and Southern bluefin tuna have the slowest life histories among all the scombrid species.

Sexual dimorphisms in life history traits in scombrid species

The patterns of sexual dimorphism differed among taxonomic groups. In Spanish mackerels, the females attain larger body sizes and mature at a larger body size than males, and also appear to live longer (Figure 4.4A,B and C). Females grow at a slower rate than males (Figure 4.4C). In contrast, tunas only showed significant sexual dimorphism in maximum size with males reaching larger maximum sizes than females (Figure 4.4A) and there was no significant evidence for sex differences in size of maturity,
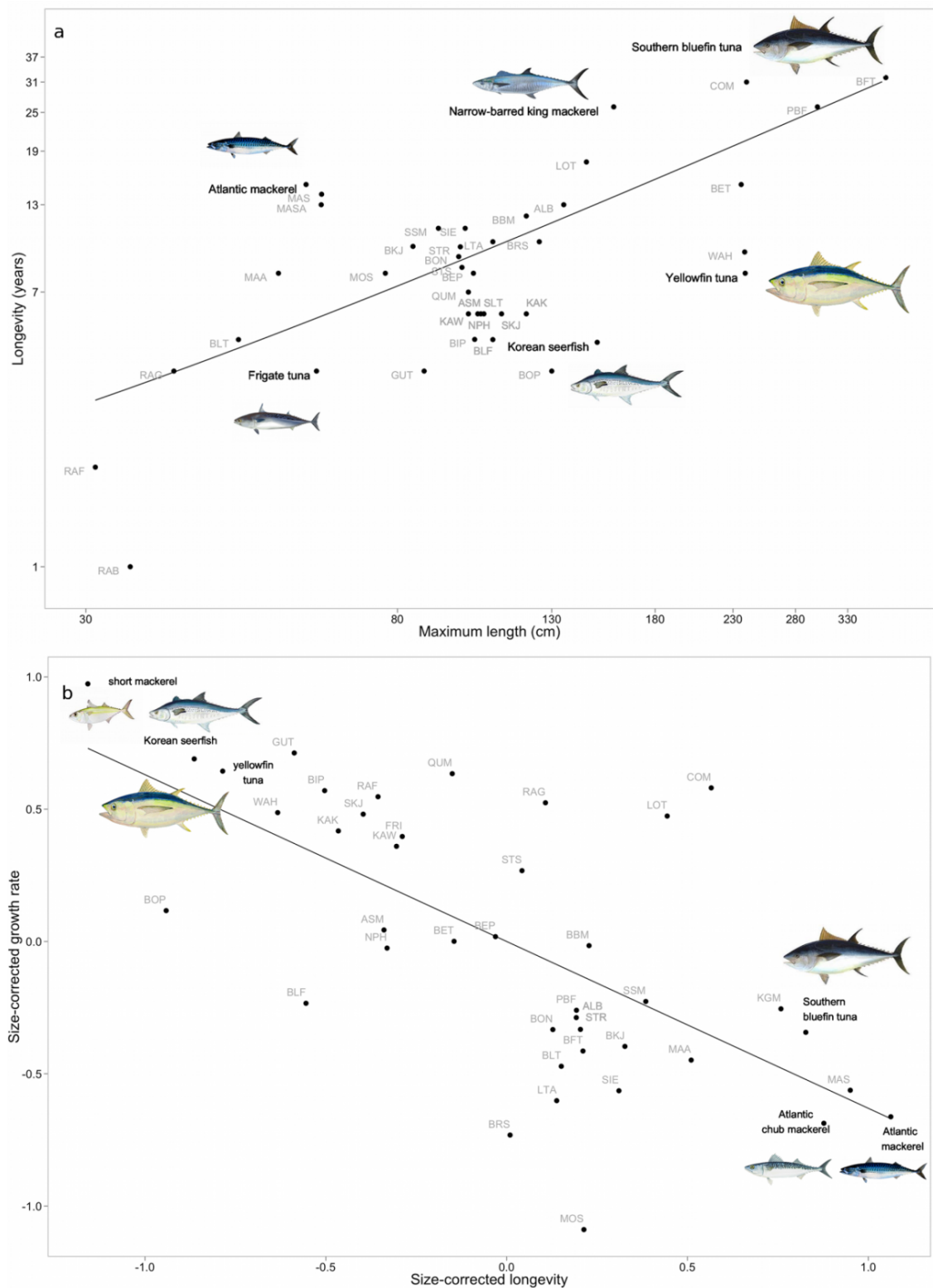
Figure 4.3   Life history variation of forty-two species of scombrids along the small-large continuum and along the slow-fast continuum.

(A) Relationship between maximum length and longevity across scombrid species (B) Relationship between size-corrected longevity and size-corrected growth rate across scombrid species. Regression line (black solid line).
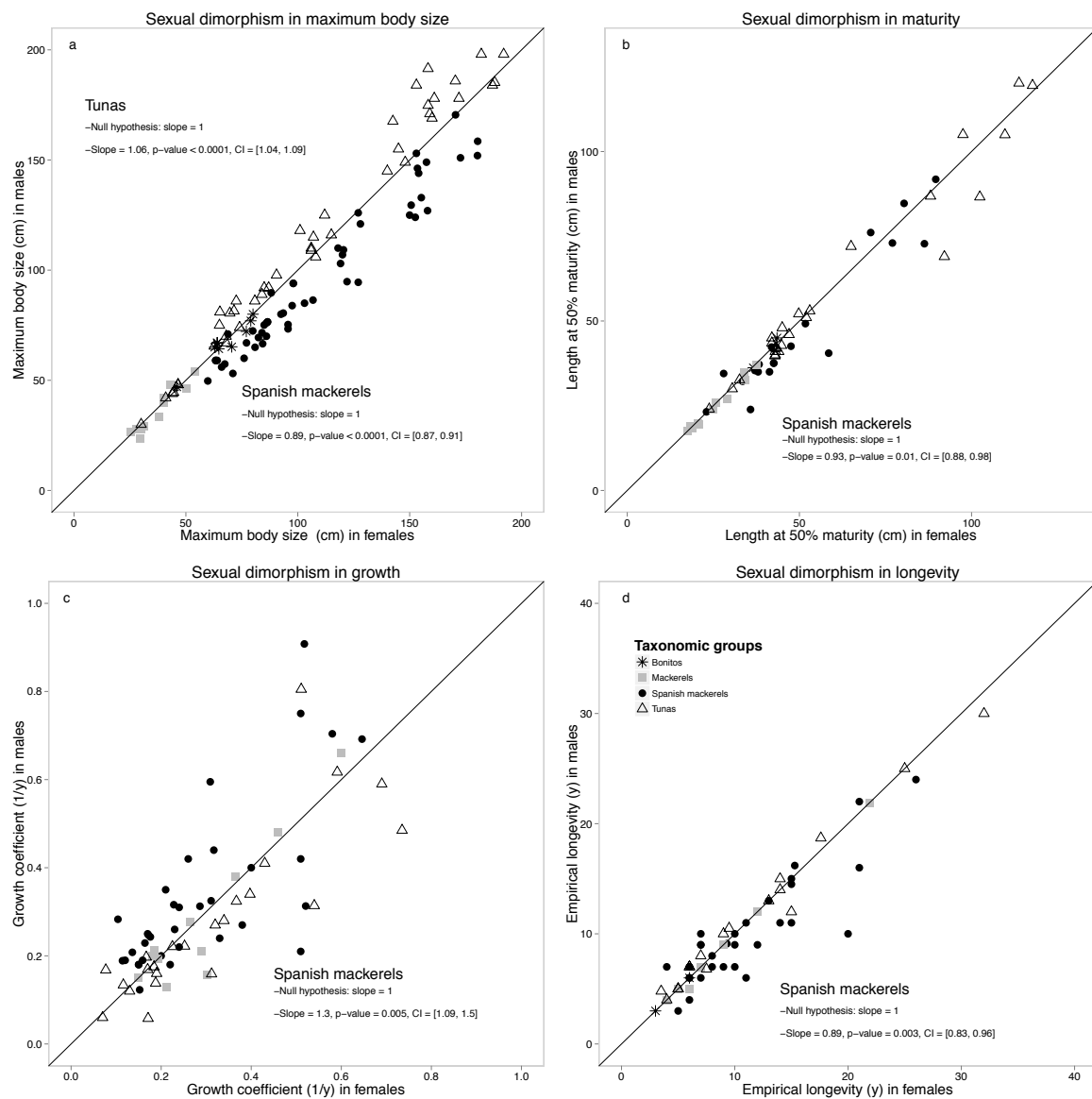
Figure 4.4   Patterns in sexual dimorphism

In (A) maximum observed length, (B) length of maturity, (C) growth and (D) longevity within the major taxonomic groups of scombrids; bonitos, mackerels, Spanish mackerels and tunas. See Table 4.1 for full list of species within each taxonomic group. 1:1 line (black solid ablines).

growth or longevity (Figure 4.4B-D). Mackerels did not show sexual dimorphisms in any life history trait and there was not enough data to explore sexual dimorphisms in the bonito species.

Discussion

Patterns of covariation among life history traits of scombrids revealed that most of the variation in the traits can be explained along three gradients: size, speed and reproductive schedule. We first explore these three dimensions further, then suggest the implications of such a narrowly bounded range of life histories for fisheries assessment and management, finally placing the scombrids within the larger envelop of fish life histories. Last we discuss what factors are likely to shape sexual differences in the life history traits of scombrid species.

The first gradient of variation is mostly influenced by maximum size and highlights that all traits, except spawning duration, are correlated with size. Size governs the first gradient of life history variation in scombrids primarily ranking species along a small-large continuum as it is commonly viewed as a fundamental determinant of and constraint upon species life history evolution (Sibly and Brown 2007). Current views explaining the variations in body size suggest that competition and predation are the driving forces of adaptation leading to the evolution of species to attain optimum sizes to fill specific niches in nature (Brown and Sibly 2006). The second gradient of life history variation is mostly influenced by time-related traits (longevity, age at maturity, growth rates, spawning duration, time between spawning events) and highlights the trade-off between longevity and growth, ranking species from the slowest to the fastest life histories (irrespective of their body size) and ordinating them along the slow-fast continuum of life histories. This pattern is consistent with the discovery of the importance of a similar slow-fast continuum in mammals, birds, and reptiles (Gaillard et al. 1989, Saether et al. 2002, Bielby et al. 2007).

Scombrid species with the slowest life histories tend to inhabit more temperate environments and these species were characterized by having relatively longer life spans, slower growth rates, short spawning seasons and produce several batches of large number of eggs per gram with a lower frequency (large intervals between spawning events). While scombrid species with faster life histories are typically found in more tropical environments, and their life histories were characterized by shorter life spans, faster growth rates, long spawning season where species spawn multiple batches of small

number of eggs per gram at a higher frequency (small time intervals between spawning events). Current knowledge suggests that variations in the speed of life of species along the slow-fast continuum are adaptations to temperature-driven extrinsic rates of mortality imposed by the environment (Promislow and Harvey 1990, Brown et al. 2004, Dobson 2007). Individuals experiencing high mortality rates due to the metabolic forcing at high temperatures evolve fast life histories in order to reproduce before dying, shifting the whole life cycle towards a faster end of the continuum. While species facing low mortality rates and reaching longer life expectancies have larger sizes at maturity, and invest more heavily in reproduction after maturing, thus shifting their whole life cycle towards the slow end of the continuum.

The third gradient found in scombrid life histories highlights the negative correlation between number of eggs produced at length of maturity and the slope of the fecundity-length relationship. Although the third gradient of variation identified in our analysis was weak in part because there were only seven species of scombrids with full reproductive and fecundity life history information, we also observed a negative correlation between fecundity at length of maturity and the rate at which fecundity increases with size across a larger number scombrid species which hints that the pattern may be more general (Figure 4.1J). This pattern has been interpreted in fishes as a gradient describing a schedule of reproductive effort reflecting the fundamental trade-off between reproduction and somatic growth (Rochet et al. 2000). Small scombrid species (irrespective of their climate) such us spotted chub mackerel and Atlantic mackerel first allocate more energy to growth and as soon as they mature, spawn fewer eggs (due to their small body cavity size) but then increase their fecundity steeply with size, investing more energy into reproduction, thus having less resources for growth at their disposal (Charnov 2008). In contrast, larger scombrid species such as Atlantic bluefin tuna and yellowfin tuna initially invest relatively more in fecundity at maturity, but their fecundity increases less steeply with size leaving more resources for somatic growth. As an aside we note that the steep rate of increase of fecundity with size observed in Southern bluefin tuna does not follow the general pattern across scombrid species. We wonder whether the steep rate of increase in fecundity with size in southern bluefin tuna is a response of the species to the high rates of fishing mortality experienced during the last half century (CCSBT 2009). Other studies have reported an increase in fecundity at maturity and higher rates of increase of fecundity with size in species with high rates of fishing exploitation. Increasing fishing pressure results in an increase in the reproductive investment of species during their individual lifetime (Rochet et al. 2000). Although a gradient of slow and fast life histories, after accounting for

the effect of size, has been observed in previous comparative studies of life histories, and is well supported in fishes as well other vertebrate groups such as birds, reptiles and mammals (Gaillard et al. 1989, Saether et al. 2002, Bielby et al. 2007) a further third axis of life history variation is less well supported and its interpretation varies among groups (Rochet et al. 2000, Dobson 2007).

By ranking the forty-one species of scombrids along a small-large continuum and a slow-fast continuum, we could identify what species have similar and dissimilar life history strategies. Although we acknowledge that the life history strategies of species vary along a continuum, we highlight the importance of identifying similarities among species and identify groups of species with similar life histories since life history groupings can be used as the basis to construct a conceptual framework of management options for data-poor species (King and McFarlane 2003). Conceptual management frameworks to provide advice for those exploited species lacking information on their exploitation status, but based on their life history strategies, have already been put forward, as life histories of species are fundamental to understanding how species respond to fisheries exploitation and ocean changes (King and McFarlane 2003). The exploitation status for the majority of scombrid species and populations is unknown or uncertain (Juan-Jorda et al., 2012), therefore management scenarios using simple life history driven models such us the ones provided here, could be used as the basis for the assessment and management of data-poor scombrid species.

So how do scombrids fit within the Opportunistic-Periodic-Equilibrium triangular model of life histories? Earlier comparative analysis of a broad range of fish life histories examined only two scombrid species (chub mackerel and albacore tuna) and classified them as intermediate within the triangular model of life histories (Winemiller and Rose 1992, King and McFarlane 2003). As we have shown here, scombrid fishes have a wide range of life history attributes exhibiting variation in longevities, growth rates, maturity and fecundity schedules, sizes and habitat preferences, but lacking investment in the survival of young. Along the small-large and slow-fast gradients of life history variation in scombrids identified in this study, we can discern a continuum of life history patterns, and the strategies at the two extremes typify the Opportunistic and Periodic strategists identified by Winemiller (1989) and Winemiller and Rose (1992). On one extreme, the three bluefin tuna species (*Thunnus thynnus, T. maccoyii* and *T. orientalis*) which are the largest (245-372 cm) and longest-lived (26-41 y) species of scombrids and are characterized by slow growth rates (0.11-0.15 y^{-1}), late maturation (103-159 cm and 4-9 y), high fecundities (average batch fecundities of two million eggs at length of maturity) and short spawning

seasons (2-5 months) correspond well with the Periodic fish strategists (Winemiller and Rose 1992, King and McFarlane 2003). On the other extreme, three mackerels species (*Rastrelliger brachysoma, R. faughni* and *R. kanagurta)* which are the smallest (31-39 cm) and shortest-lived (1-4 y) species of scombrids and are characterized by early maturation (17-20 cm and 0.6-2 y), fast growth (1.3-2.9 y^{-1}), presumably lower average batch fecundities at maturity (no data available) and extended spawning seasons (5-6 months), correspond well to fish species with Opportunistic strategists (Winemiller and Rose 1992, King and McFarlane 2003).

Therefore, in this study we show that the life histories of scombrid species displayed a broad range of intermediate strategies along the gradient between the Opportunistic and Periodic strategists, with tropical mackerel species being the best example in the group of an Opportunistic strategist, and temperate bluefin tuna species providing good examples of Periodic strategists. Temperate tuna species spent most of their annual cycle in colder higher latitudes and perform large-scale migrations to exploit the relatively predictable seasonal environmental cycles to reproduce in very specific time and well-defined warmer habitats during spring time (Block et al. 2003). Migrating to favorable habitats to reproduce within a small environmental window is a strategy favorable for growth and survival of larvae that reduces uncertainty and minimize large scale temporal and spatial environmental variability, a common strategy among many Periodic strategist (Winemiller and Rose 1992). It has also been observed that long-lived marine teleosts, which are typically temperate or deep-water species, tend to have larger recruitment variability, an indicator of poor years in recruitment success, than shorter-lived species which are typically tropical species (Longhurst 2002). At first glance, the high recruitment variability generally observed in temperate scombrids species would not correspond very well with the typical environment characteristic in Periodic strategies (predictable large scale temporal and spatial environmental variation). However, it has been hypothesized that longevity, a characteristic of Periodic strategists, is crucial factor to sustain a safe level of successful recruitment over the long term when autocorrelated environmental variability across a series of years might produce poor recruitment (Murphy 1968, Longhurst 2002). Tropical mackerels and tunas with life history characteristics more typical of Opportunistic strategists appear to have adopted the strategy of maturing earlier, spawning more frequently and expanding their spawning seasons which provide a larger number of reproductive opportunities to maximize the probability of successful recruitment within the relatively low seasonality of many low latitude oceanographic regions (Longhurst and Pauly 1987, Winemiller and Rose 1992). Therefore the life history variation observed in

scombrids corroborates the triangular model of fish life histories proposed by Winemiller and Rose (1992) as this model explains well the life history variation observed in scombrids.

The life history patterns and strategies described in this study were mostly based on female life history traits that we preferentially used over male traits. However, we also showed that sexual dimorphism in some life history traits exist in the tunas and Spanish mackerels, but not in the mackerels. Past studies have also reported significant sexual dimorphisms in size, weight, growth and longevity in several species of Spanish mackerels (McPherson 1992, Claereboudt et al. 2005, McIlwain et al. 2005). It has been hypothesized that the observed sexual dimorphisms in size and growth in Spanish mackerels could be related to the different amount of investment in gametogenesis by the two sexes (McIlwain et al. 2005). Sexual dimorphism in size has also been reported in many species of tunas, while dimorphism in growth has only been reported in temperate tuna species such as Atlantic bluefin tuna and Southern bluefin tuna and appears to be non-existent in tropical tuna species of bigeye and yellowfin (Schaefer 2001, Gunn et al. 2008). It has been suggested that higher natural mortality rates in females than in males could explain the predominance of males within the larger size classes of tunas rather than sex differences in growth or vulnerability to capture (Schaefer 1998).

Acknowledgements

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Supplementary Figures
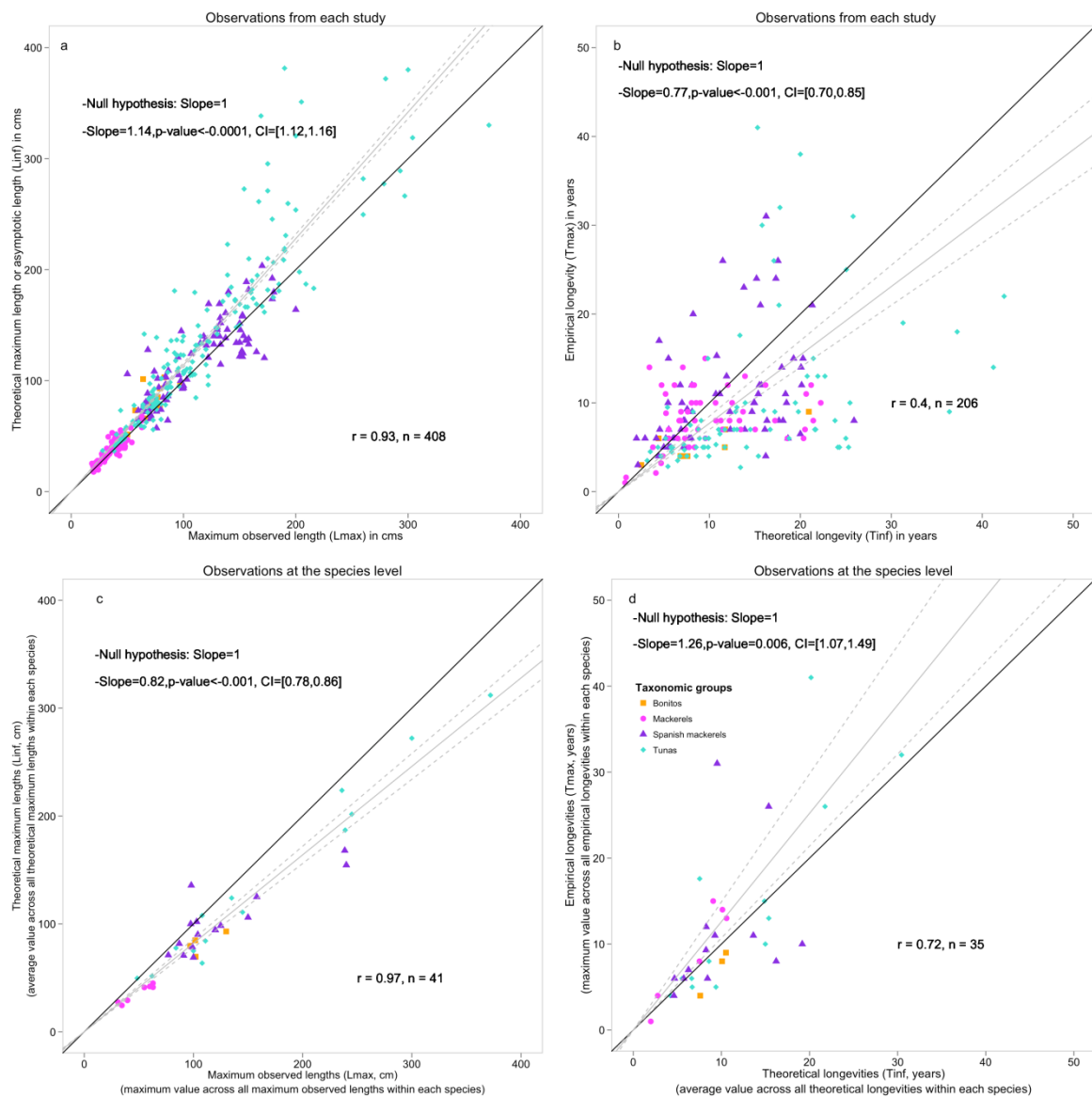
Figure 4.S1   Relationships between observed and empirical data.

Relationship between maximum observed length (L_{max}) and the theoretical maximum length (L_∞) (A-B) and the relationship between empirical longevities (T_{max}) and theoretical longevities (T_∞) across scombrid species (C-D). Fitted lines (grey solid ablines) with 95% confidence intervals (grey dashed ablines) were estimated using a reduced major axis regression model. 1:1 line (black solid ablines). Each point of panel A and C is an observation extracted from life history studies. Each point of panel B and D represents a species average.

Supplementary Tables

Table 4.S1   *Analysis of variance (ANOVA) and Relative Intraspecific Variation (RIV) ratio in each life history trait.*

Life history traits	RIV(%)	ANOVA statistics
Growth coefficient k (1/years)	69.7	$F(36,508)=32; p < 0.001$
Length at 50% maturity L_{m50} (cm)	6.8	$F(29,506)=97.65; p < 0.001$
Age at 50% maturity T_{m50} (years)	41.4	$F(23,137)=8.4; p < 0.001$
Fecundity at maturity F_{Lm50} (# of oocytes in '000)	13.4	$F(14,41)=18.9; p < 0.001$
Slope of fecundity-length relationship (F_{slope})	31.6	$F(8,22)=5.93; p < 0.001$
Relative fecundity F_{rel} (# of oocytes per gram)	29.4	$F(11,23)=5.01; p < 0.001$
Spawning interval Spw_{int} (days)	33.1	$F(9,20)=4.4; p = 0.002$
Spawning duration Spw_{season} (months)	67.9	$F(35,277)=3.7; p < 0.001$

Table 4.S2   Data matrix of life history traits for scombrid species.

Each life history trait estimate is a species average across multiple studies. See Section 2.3 for methods to aggregate data at the species level.

Species names	Code	L_{max}	k	T_{max}	L_{m50}	T_{m50}	F_{Lm50}	F_{slope}	F_{rel}	Spw_{int}	Spw_{season}
Allothunnus fallai	SLT	105		6							3
Auxis rochei	BLT	48.5	0.4	5	26.2	2.1			242		5.4
Auxis thazard	FRI	62	0.9	4	33.3						5.6
Euthynnus affinis	KAW	100	0.6	6	40.3	2		2.4			5.7
Euthynnus alletteratus	LTA	108	0.2	10	41.2	2.5	206.4	2.9	119		5.7
Euthynnus lineatus	BKJ	84	0.3		47		206.9		112.6	3.8	7.3
Katsuwonus pelamis	SKJ	111	0.6	6	45.7	1.4	219.8	4.1	84.8	2.7	10.4
Thunnus alalunga	ALB	135	0.2	13		3.6	1174.6	2.9	100	1.7	5
Thunnus albacares	YFT	239	0.4	8	101.2	2.6	1172.9	3.5	65.3	1.6	6.9
Thunnus atlanticus	BLF	108	0.3	5	50.7						5.8
Thunnus maccoyii	SBF	245	0.2	41	158.9	9.9	1988.4	7.8	57	1.1	5.5
Thunnus obesus	BET	236	0.2	15	111.8	2.1	788.9	4.3	48.4	1.3	9.8
Thunnus orientalis	PBF	300	0.1	26	142.6	4				3.3	3
Thunnus thynnus	BFT	372	0.1	32	103.3	4	2250.6	3	102.7	1.9	2.2
Thunnus tonggol	LOT	145	0.5	17.6	40	2	302.8	3.5			5.3
Cybiosarda elegans	LEB	45									
Gymnosarda unicolor	DOT	248									3
Orcynopsis unicolor	BOP	130	0.4	4	43.5	2					4.7
Sarda australis	BAU	180									
Sarda chiliensis	BEP	101.6	0.4	8	50.5	3.5	181.3	7			5.8
Sarda orientalis	BIP	102	0.7								4
Sarda sarda	BON	97	0.3	9	36.6	1.3		4.6	46.5		3.1
Acanthocybium solandri	WAH	238.6	0.4	9.3	92.2	1.2	445.7		41.5	4.5	6.7
Grammatorcynus bicarinatus	SHM	122									
Grammatorcynus bilineatus	DBM	100									4.5
Scomberomorus brasiliensis	BRS	125	0.2	10	46	2.9	1097	4.3	521.7		10.3
Scomberomorus cavalla	KGM	158	0.2	26	58.6	3.2	257.1		140	4.7	9.7
Scomberomorus commerson	COM	240	0.4	31	79.7	2	369.3	2.9			4.6
Scomberomorus concolor	MOS	77	0.2	8	38.3	2					7.5
Scomberomorus guttatus	GUT	87	0.9	4	37.5		22.8				6
Scomberomorus koreanus	KOS	150	0.6								1
Scomberomorus lineolatus	STS	98	0.5		69.1	2	129.7	5.4			5
Scomberomorus maculatus	SSM	91	0.3	11	30.7	1.3			143		4.1
Scomberomorus multiradiatus	PAP	35									
Scomberomorus munroi	ASM	104	0.4	6	51.7	1.5	203	4.9			3.1
Scomberomorus niphonius	PH	103	0.4	6		2				1.2	3.3
Scomberomorus plurilineatus	KAK	120	0.5	6	77	2					
Scomberomorus queenslandicus	QUM	100	0.8	7	42.6	1.5	239.4				4
Scomberomorus regalis	SCE	83.5			40.4		207.7		386		12
Scomberomorus semifasciatus	BBM	120	0.4	12	67.5		531				5
Scomberomorus sierra	SIE	99	0.2	11	44.3						
Scomberomorus sinensis	CHY	218									
Scomberomorus tritor	STR	97.5	0.3		33.5						6.8
Rastrelliger brachysoma	RAB	34.5	2.3	1	16.8	0.7					4.7
Rastrelliger faughni	RAF	30.9	1.6								
Rastrelliger kanagurta	RAG	39.6	1.3	4	20.5	2				30	6.3
Scomber australasicus	MAA	55	0.4	8	28.6	1.7	29.5	4.9	134	6.5	4.3
Scomber colias	MASA	62.9	0.3	13	36.6	2.6	52.3			11.5	4.3
Scomber japonicus	MAS	63	0.3	14	30.7	2.5	13		119.1	3.9	5.1
Scomber scombrus	MAC	60	0.3	15	25.2	1.9	151.6	4.3	825.2	6	4.3
Gasterochisma melampus	BUK	195									

Chapter 5
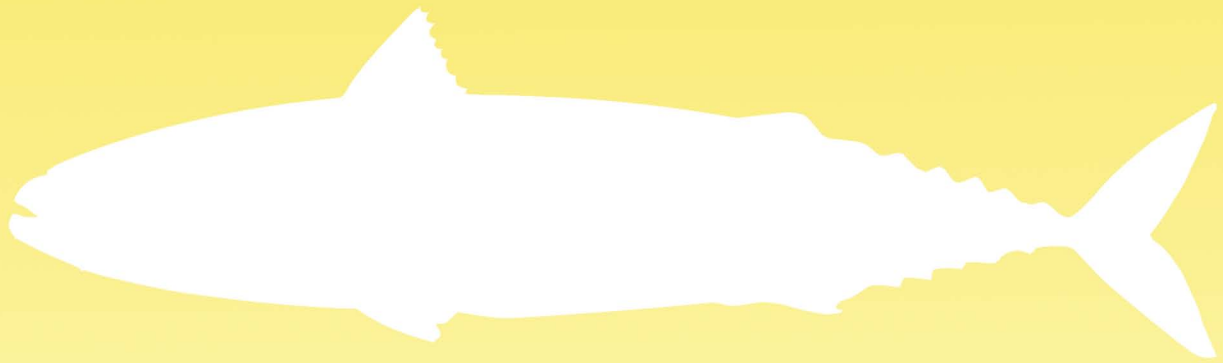
Chapter 5.

The speed of life and the decline of tunas and their relatives[1]

Abstract

Fishing has been identified as the primary threat in marine ecosystems, yet less than 1% of marine fish species are properly assessed. Understanding what species might be most at risk and developing methods to identify *a priori* what species might be most vulnerable to fishing exploitation remains a major challenge. The vulnerability of a species is a combination of its degree of exposure to extrinsic threats, such as fishing, and its intrinsic sensitivity to the threatening process. While there is increasing evidence for the idea that life histories and demography relate to measures of vulnerability including, threat status, and population trends, our literature review of comparative studies of vulnerability in marine fishes suggest that the efficacy of different life history traits to predict vulnerability varies greatly. Here, we examine the role of life histories and fishing in determining the population trajectories and current exploitation status of scombrids. What populations of scombrids are most vulnerable to fishing exploitation, and what life history correlates are best predictors of their trajectories and current exploitation status? After controlling for fishing mortality rates, scombrid populations with slow life histories, which are mostly found in temperate climates, are more likely to have experienced faster and larger declines and have a higher probability of being overfished, suggesting temperate scombrids such as the Atlantic bluefin tuna (*Thunnus thynnus*) and chub mackerel (*Scomber japonicus*) are more sensitive to fisheries exploitation. We stress differences in life history strategies need to be taken more into account in current fisheries management. Moreover, our analyses also suggests that growth rate and longevity are the best predictors of scombrid declines and current exploitation status, therefore, we recommend to use them to identify and rank species sensitivities to fishing exploitation in order to plan effective conservation strategies in data-poor situations.

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[1] Juan-Jordá, M.J., Mosqueira, I., Freire, J. & Dulvy, N.K. (2013) The speed of life and the decline of tunas and their relatives. *(in preparation for publicacion).*

Introduction

Fishing has been identified as the primary threat in marine ecosystems, leading to population declines, overexploitation and local and global extinctions of marine species (Reynolds et al. 2005, Sala and Knowlton 2006, Jackson 2008, McClenachan et al. 2012). Over the last century, industrial fisheries have sequentially expanded from coastal areas to the high seas and now fisheries cover the majority of the world's oceans (Swartz et al. 2010). Concomitantly, the intensity of fishing effort has also increased for all the countries by an average of 10-fold since the 1950s (Watson et al. 2012). Despite the expansion and increase in fishing effort in the last two decades, the global catch of marine fish species started to stagnate in the mid-1980s and since then has been slowly declining, indicating that a limit in the world's fish catches has been reached (Pauly et al. 2005, Chassot et al. 2010). While there is a good understanding of how fishing effort and intensity has expanded and where it concentrates now in the world's oceans (Watson et al. 2012), the biological status for the immense majority of marine fish species that are impacted directly or indirectly by fisheries are not known (Worm et al. 2009, Costello et al. 2012, Ricard et al. 2012). Globally there are more than 15,000 marine fish species; however landing data are only available for 925 species (Sea Around Us database) and the number of species formally assessed with stock assessments is even lower (295 fish populations of 147 species are available in the RAM Legacy Stock Assessment Database). Therefore, less than 1% of the fish species are properly assessed, largely because assessments are data intensive and costly (Dulvy et al. 2004, Costello et al. 2012, Pardo et al. 2012). Currently, it is not known how many species are potentially overexploited and ultimately threatened with extinction (Polidoro et al. 2008). Therefore, understanding what species might be most at risk and the development of methods to identify *a priori* what species are most vulnerable to fishing exploitation can be very useful for guiding the management and planning effective conservation strategies (Cheung et al. 2005, Reynolds et al. 2005, Pinsky et al. 2011). However, understanding what species might be most vulnerable to fishing exploitation remains a pressing challenge.

One way to approach this challenge has been to identify which intrinsic biological characteristics of the species make them more sensitive to known threats such as fishing or habitat destruction (Jennings et al. 1998, Dulvy et al. 2004, Reynolds et al. 2005, Pardo et al. 2012). The vulnerability of a species is a combination of its degree of exposure to extrinsic threats, such as fishing, and its intrinsic sensitivity to the threatening process (Dulvy et al. 2004, Reynolds et al. 2005, Patrick et al. 2010). The sensitivity of a species to

external threats is determined by its intrinsic characteristics, such as life history, which underlie the productivity of the species and their capacity to cope with and recover from known threats (Hutchings et al. 2012b). Theoretical analysis suggest that species with life history strategies characterized by high rates of growth and natural mortality, early age-at-maturity and short lifespan are generally able to sustain higher fishing mortality rates, while species characterized by slow growth, late maturity and long life spans are more sensitive to fishing and may only sustain lower rates of fishing mortality (Adams 1980, Roff 1984). There may be a real opportunity to rank species vulnerabilities, by using intrinsic traits combined with a measure of possible exposure to a threatening process and this is the basis for ecological risk assessment frameworks (Hobday et al. 2011).

The need to prioritize management and efforts to protect the most threatened species has led to numerous comparative studies of species vulnerability and extinction risk in many taxonomic groups, and fish are not an exception (Cardillo and Meijaard 2011). It is only recently that sufficient comparative population trends and life history data in fishes have become available to allow empirical testing (Reynolds et al. 2005). We have reviewed the findings of 23 empirical studies with the objective of summarizing what life history correlates have been identified to date as most useful in marine fishes to predict their vulnerability to fishing (Figure 5.1, Table 5.S1). Our review focused on examining the usefulness of life history correlates to determine species vulnerability, however ecological and behavioral correlates can also be important predictors of vulnerability to fishing (Reynolds and Jennings 2000, Cheung et al. 2005, Reynolds et al. 2005, Hutchings et al. 2012a). We find that empirical testing for life history correlates has proceeded on two fronts: (1) linking life histories to demography and (2) linking life histories to population status.

The first research front has focused on quantifying potential correlations between the maximum per capita population growth rate (r_{max}) of species, which is a standard measurement of population productivity, and their life history traits in order to use the more easily available life history information to identify species that has low r_{max}. Species with low r_{max} are more sensitive to external threats and might face higher risk of extinction (Hutchings et al. 2012b). Our literature review reveals that up to eight life history traits have been tested to quantify their relative importance as reliable predictors of r_{max} and we find that age-at-maturity has been consistently identified as the most reliable predictor of species r_{max} (Figure 5.1A, Table 5.S1A).

Life history correlates of maximum population growth rate

Life history correlates of population status

Figure 5.1   Empirical comparative analyses of life history correlates of vulnerability in fishes.

Literature review of empirical studies that have examined the links between (A) life history correlates and population growth rate, and (B-D) life history correlates and population status in marine fishes. (A) Potential life history correlates of demography, usually measured as maximum per capita population growth rates (r_{max}). Potential life history correlates of population status, (B) usually measured as IUCN threat status categories, (C) population trajectories (including declines and recoveries), and (D) population trajectories while controlling for exposure to fishing. Colors illustrate the strength of the relationship between life history traits and the metrics of demography and population status. Strength of support (based on p-values or AIC) is represented by the following colors: strong - dark green, weak - light green, and none - dark red.

The second research front has focused on linking the life histories of populations and species to their population status, usually measured as trends in population trajectories, threat status, extinction risk or probability of collapse while accounting for their exposure to fishing (Figure 5.1B-D, Table 5.S1B). Population biomass trajectories including declines, recoveries and collapses as well as the Red List threat status are commonly used as proxies to evaluate the species vulnerability to fishing exploitation. Our literature review reveals that maximum body size has been most frequently identified as a reliable life history correlate of species threat status (Figure 5.1B), of population trajectories including declines and recoveries (Figure 5.1C) and these findings hold true especially when analyses control for the different exposure of the species and populations to fishing (Figure 5.1D, Table 5.S1B). While the other eight life history traits have also been tested as predictors of species vulnerability, surprisingly we find mixed evidence for their usefulness. Moreover, this review underscores that fecundity has never been identified as a useful life history correlate of vulnerability in marine fishes (specifically marine teleosts, Figure 5.1, Table 5.S1). This confirms that the production of large number of eggs does not protect teleost fishes from extinction risk (Jennings et al. 1998, Jennings et al. 1999c, Denney et al. 2002, Reynolds et al. 2005, Hutchings et al. 2012b). Understanding the interactions between fishing and the intrinsic biological characteristics among related species, and which biological characteristics make species more vulnerable is critical to predict how species respond to exploitation and identify what species are more at risk (Jennings et al. 1999a, Jennings et al. 1999b). Thus, these studies provide the quantitative basis to develop tools for predicting species responses to fishing, their threat status and probability of extinction in data-poor situations (Jennings et al. 1998, Anderson et al. 2011, Pardo et al. 2012).

While there is broadening support for the idea that life histories and demography relate to measures of vulnerability including, threat status, extinction risk, population trends including declines and recoveries, and population collapses, we find that the efficacy of different traits to predict vulnerability varies greatly among empirical studies (Figure 5.1), and may limit their general applicability as predictors (Anderson et al. 2011). Consequently, comparative analysis of vulnerability in fishes and other vertebrate groups are failing in transmitting a clear message into conservation practice by conveying inconsistent results with a large amount of uncertainty (Cardillo and Meijaard 2011). Several reasons have been proposed that might be causing these inconsistencies confounding the role of life histories in comparative analyses of vulnerability: (1) the aggregation of large datasets from diverse taxonomic groups where the type and

magnitude of threats are different; (2) the use of different methodologies to identify life history correlates of vulnerability and to control for the effects of threats such as fishing; (3) the different spatial scale of analyses that might vary from regional to global scales; and (4) the reduced number of life history and ecological traits tested in the analyses, which are chosen mainly by its easy availability rather than their known *a priori* biological relevance (Sadovy 2001, Reynolds 2003, Anderson et al. 2011, Cardillo and Meijaard 2011). Moreover, several recommendations have also been put forward in order to advance this field further, and transform the outcomes of comparative analysis into more conservation practice. Comparative studies should distinguish between the form of vulnerability (e.g. population declines, reduction in range size, or probability of extinction) and their causes (e.g. overfishing, habitat destruction, pollution) when pooling diverse data sets (Reynolds 2003). Comparative studies should be also developed focusing on testing *a priori* hypotheses and attempt to include a range of life history, ecological and behavioral traits chosen based on biological relevance. Finally, it has also been suggested that by concentrating on smaller taxonomic groups of species, it might help in focusing outcomes and testing of *a priori* hypotheses (Sadovy 2001, Cardillo and Meijaard 2011).

In this study we focus on the taxonomic group of scombrids with the aim of investigating the role of life histories in determining their responses to fishing and identify those species and population most vulnerable to fishing. Scombrids, commonly known as tunas, Spanish mackerels, bonitos and mackerels (Family Scombridae), sustain some of the most important fisheries in the world (Majkowski 2007, Collette et al. 2011). Their economic importance has led to a relatively large number of biological studies and fisheries assessments, providing one of the longest, large-scale fisheries data sets for testing the role of life histories in predicting species responses to fishing while accounting for their exposure to fishing mortality rates. A recent study has provided the most accurate picture of the global biomass trajectories of scombrid assessed populations within the last half century and summarized their current exploitation status (Juan-Jordá et al. 2011). Moreover, the life history patterns in scombrid species and how traits covary within this family have also been evaluated recently (Juan-Jordá et al. 2012); this study reveals the life history variation in scombrid species can be explained at least along two axes or dimensions. Maximum body size, together with other size-related traits such as length-at-maturity, maximum weight or fecundity at length of maturity governs the first trait axis of life history variation, ranking species along a small-large continuum. Time-related traits such as longevity, age-at-maturity and growth rate underlie the second trait axis, ranking species along a slow-fast continuum of life histories. This second axis separates species

which are longer lived and have slower growth rates given their maximum size, from species with are shorter lived and have faster growth rates given their maximum body size. Fecundity-related traits such as fecundity at length of maturity and the rate of change of fecundity with size underlies the third trait axis, describing the schedule of reproductive allocation in fishes (Rochet et al. 2000, Juan-Jordá et al. 2012). The first two axes of life history variation are well supported in fishes as well other vertebrate groups such as birds, reptiles and mammals (Gaillard et al. 1989, Saether et al. 2002, Bielby et al. 2007), while a further third axis of life history variation is less well supported and its interpretation varies among groups (Rochet et al. 2000, Dobson 2007).

Using the population and life history data sets provided in these two recent studies (Juan-Jordá et al. 2011, Juan-Jordá et al. 2012), we examine here the role of life histories and fishing exploitation in determining the population trajectories and current exploitation status of scombrids. We investigated whether differences between population long-term trends and current status can be explained by differences in life histories and fishing mortality rates. Ultimately, we aim to identify those species and population of scombrids most vulnerable to fishing and what life history correlates are best predictors of populations' responses to fishing.

Based on existing knowledge, we developed and tested the following three *a priori* hypotheses (Table 5.1). First, we test whether the fishing mortality rates experienced by scombrid populations within their exploitation period is the main factor determining their rate and extent of decline in adult biomass and their current exploitation status. Then, we examine whether the fishing mortality rates in combination with the life histories of scombrids determine their population decline and their current exploitation status. Specifically, we test whether the small-large life history trait axis of scombrids determine their rate and extent of decline and current exploitation status, after accounting for the different fishing mortality rates experienced by populations. Third, we tested whether the slow-fast trait axis determine their rate and extent of decline and current exploitation status, after accounting for the different fishing mortality rates experienced by populations.

Table 5.1   *Suite of biological relevant models developed a priori to examine the role of life histories and fishing in determining the population trajectories and current exploitation status of scombrids.*

Hypothesis:

The relative fishing mortality rate experienced by scombrid populations within their exploitation period is the main factor determining their trajectories in adult biomass (measured as rates of decline and extent of decline) and their current exploitation status (whether they are overfished or not).

Hypothesis 1: Populations that have experienced greater relative fishing mortality rates ($F_{average}/F_{MSY}$), on average, within their periods of exploitation have suffered faster (rate of change) and larger population declines (extent of decline) in adult biomass and have a higher probability of being overfished.

Model 1: Vulnerability metric ~ relative fishing mortality ($F_{average}/F_{MSY}$)

The relative fishing mortality rates experienced by scombrid populations within their exploitation period in combination with their life histories determines their trajectories in adult biomass (measured as rates of decline and extent of decline) and their current exploitation status.

Hypothesis 2 : After accounting for the different relative fishing mortality rates experienced by populations, populations with larger maximum body sizes (using maximum body size as a proxy to described the first axis –the small-large axis- of life history variation in scombrid species) have experienced faster (rate of change) and larger population declines (extent of decline) and have a higher probability of being overfished.

Model 2: Vulnerability metric ~ relative fishing mortality ($F_{average}/F_{MSY}$) + maximum body size (L_{max})

Hypothesis 3 : After accounting for the different relative fishing mortality rates experienced by populations, populations with slower growth rates (using growth rate as a proxy to described the second axis –the slow-fast axis- of life history variation in scombrid species) have experienced faster (rate of change) and larger population declines (extent of decline) and have a higher probability of being overfished.

Model 3: Vulnerability metric ~ relative fishing mortality ($F_{average}/F_{MSY}$) + growth rate (k)

Methods

Data

Population decline data and metrics of vulnerability

We extracted time series of adult biomass, fishing mortality rates and standard fisheries reference points, $B_{current}/B_{MSY}$ and $F_{current}/F_{MSY}$, for 26 populations of 11 species of scombrids from age-structured stock assessments (Juan-Jordá et al. 2011). See Juan-Jordá et al 2011 for a detailed description of the stock assessment data set. The populations included 17 principal market tunas (7 species), five mackerels (2 species), and four Spanish mackerels (2 species) (Table 5.2, Table 5.S2, Figure 5.S1).

We used three metrics as proxies to evaluate the intrinsic sensitivity of scombrid populations to fishing exploitation. Two metrics described the population trajectories of scombrids: (1) the average annual rate of change in adult biomass (Figure 5.S2A); (2) the total extent of change in adult biomass (Figure 5.S2B); and one metric described their current exploitation status: (3) whether a population is currently overfished or not, designated by the fisheries reference point, $B_{current}/B_{MSY}$ (Figure 5.S2). $B_{current}/B_{MSY}$ is the ratio of the current adult biomass relative to the adult biomass that would provide the maximum sustainable yield (MSY).

To calculate the first metric, the average annual rate of change in adult biomass, we first converted the raw time series of adult biomass of each population to annual rates of change (r_i), $r_i = \ln(AB_{i+1}/AB_i)$, where AB_i is the adult biomass in year *i*. Most of the time series of adult biomass showed non-linearity and temporal autocorrelation, and differencing or taking the ratios in log-space is a common method of removing temporal autocorrelation from a time series (Shumway and Stoffer 2006a). We then estimated the average of the annual rates of change in adult biomass across all the years for each population using a generalized least-squares model of the form $r_i = b_o + e_i$. r_i is the dependent variable, interpreted as the annual (*i*) rate of change in adult biomass; b_o, the intercept, is interpreted as the average annual rate of change in adult biomass across all the years; and e_i is the residual error. We used maximum likelihood to fit all the generalized least-squares models, and we examined the residuals of all model fits and

Table 5.2   **List of scombrid populations including their type of climate.**

Taxonomic group	Latin name	Population common name	Population code	Climate
Tunas	*Katsuwonus pelamis*	Skipjack tuna, West Pacific	SKJwp	Tropical
Tunas	*Thunnus alalunga*	Albacore tuna, North Atlantic	ALBna	Subtropical
Tunas	*Thunnus alalunga*	Albacore tuna, South Atlantic	ALBsa	Subtropical
Tunas	*Thunnus alalunga*	Albacore tuna, North Pacific	ALBnp	Subtropical
Tunas	*Thunnus alalunga*	Albacore tuna, South Pacific	ALBsp	Subtropical
Tunas	*Thunnus albacares*	Yellowfin tuna, Atlantic	YFTa	Tropical
Tunas	*Thunnus albacares*	Yellowfin tuna, Indian	YFTi	Tropical
Tunas	*Thunnus albacares*	Yellowfin tuna, East Pacific	YFTep	Tropical
Tunas	*Thunnus albacares*	Yellowfin tuna, West Pacific	YFTwp	Tropical
Tunas	*Thunnus maccoyii*	Southern bluefin tuna	SBF	Temperate
Tunas	*Thunnus obesus*	Bigeye tuna, Atlantic	BETa	Subtropical
Tunas	*Thunnus obesus*	Bigeye tuna, Indian	BETi	Subtropical
Tunas	*Thunnus obesus*	Bigeye tuna, East Pacific	BETep	Subtropical
Tunas	*Thunnus obesus*	Bigeye tuna, West Pacific	BETwp	Subtropical
Tunas	*Thunnus orientalis*	Pacific bluefin tuna	PBF	Temperate
Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, East	BFTea	Temperate
Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, West	BFTwa	Temperate
Mackerels	*Scomber japonicus*	Chub mackerel, Chilean	MASch	Subtropical
Mackerels	*Scomber japonicus*	Chub mackerel, Japanese	MASj	Subtropical
Mackerels	*Scomber japonicus*	Chub mackerel, North East Pacific	MASnep	Subtropical
Mackerels	*Scomber japonicus*	Chub mackerel, Tsushima Current Pacific	MAStcj	Subtropical
Mackerels	*Scomber scombrus*	Atlantic mackerel, North east	MACnea	Temperate
Spanish mackerels	*Scomberomorus cavalla*	King mackerel, Gulf of Mexico	KGMgm	Tropical
Spanish mackerels	*Scomberomorus cavalla*	King mackerel, U.S. Atlantic	KGMwa	Tropical
Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, Gulf of Mexico	SSMgm	Subtropical
Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, U.S. Atlantic	SSMwa	Subtropical

further corrected for temporal autocorrelation with AR1 and AR2 processes when necessary (Figure 5.S2A). In order to calculate the second metric, the total extent of change in adult biomass over the entire time period of exploitation for each population, we estimated as follows: $(1 - \exp(b_o \cdot n)) \cdot 100$, where b_o is the model estimated average annual rate of change for each individual population and n is the length of the time series of each individual population (Figure 5.S2B). Finally, for the third metric we simply used the fisheries reference point, $B_{current}/B_{MSY,}$ to describes whether a population is currently overfished ($B/B_{MSY} < 1$) or not overfished ($B/B_{MSY} > 1$) (Figure 5.S2).

The majority of scombrid populations have experienced declines in biomass in the last half century (Figure 5.S1). In this study, we aim to identify useful life history correlates of population declines, and therefore, we excluded from the statistical analyses the four populations of Spanish mackerels. These four populations were severely overfished in the 1970s and 1980s and, after a successful recovery plan, their biomasses have increased to healthy levels and now they are considered fully rebuilt.

Life history data

We collated information on life history traits from the scombrid life history data set compiled and described by Juan-Jordá et al. (2013). We extracted the following life-history traits for the 26 populations of scombrids: maximum body size (L_{max}, cm), length and age-at-maturity (L_m, cm and T_m, years), longevity (T_{max}, years), growth rates described with the von Bertalanffy growth coefficient k (1/year), batch fecundity (absolute and relative fecundity) and spawning interval (Spw_{int}, days) and duration (Spw_{season}, months). In order to describe fecundity in scombrids, which spawn repeatedly over the spawning season, we used three measures: (1) the average absolute batch fecundity (F_{abs}); (2) the exponent b of the batch fecundity–length relationship (Fecundity = a $\cdot$ Length^b), which describes the increase of fecundity with size (F_{slope}); and (3) the relative batch fecundity (F_{rel}, number of oocytes per gram), which describe reproductive effort.

For each life history trait, we calculated a population level estimate (Table 5.S3). We selected and aggregated the life history information from multiple life history studies based on the following rules: (1) we chose the maximum value across all the studies for those traits at the extreme of the life cycle (maximum length and empirical longevity); (2) we calculated a sample-size weighted average across studies for those reproductive traits within the lifecycle (maturity, fecundity and spawning interval); and (3) for the von Bertalanffy growth coefficient k we calculated a simple arithmetic mean (giving equal

weight to all the studies), as this parameter is more difficult to combine across studies, due to the differing methodologies used to estimate age and growth. We preferentially used the female estimates whenever the traits were reported separately for sexes.

Fishing mortality data

We extracted time series of fishing mortality from the age-structured stock assessments to control in our analysis for the different fishing mortality rates experienced by each population over their history of exploitation. For each population, we calculated the average fishing mortality across all ages and years and divided it by the fishing mortality predicted to produce maximum sustainable yield (F_{MSY}), which we refer to as relative fishing mortality rate ($F_{average}/F_{MSY}$, Figure 5.S3). The standard fishing reference points ($B_{current}/B_{MSY}$, $F_{current}/F_{MSY}$) or the fishing mortality predicted to produce maximum sustainable yield (F_{MSY}) were not available for three populations of scombrids, Pacific bluefin tuna (*Thunnus orientalis*), North Pacific albacore tuna (*T. alalunga*) and Japanese chub mackerel (*Scomber japonicus*) (Table 5.S2). Therefore we could not include these populations in the statistical analyses.

Statistical analyses

Bivariate relationships and correlation analyses

We used bivariate plots and Pearson's correlation coefficients (r) to conduct exploratory analyses of our three measures of vulnerability against each of the predictor variables (the life history traits and the relative fishing mortality rates). We also examined the correlation between several life history traits and several fishery reference points.

Constructing a priori hypotheses and models

The life history trait variation in scombrid species can be mainly explained along three axes or dimensions (size, speed, and reproductive schedule) (Juan-Jordá et al. 2012). Using this existing knowledge, we constructed a plausible set of *a priori* biologically relevant hypotheses and models (Table 5.1), with the aim of examining the role of life histories and fishing as reliable predictors of three measures of vulnerability describing population declines and the current exploitation status in scombrids. These hypotheses focused on testing for the importance of the first two axes of life history variation in scombrids in determining their declines and current status. The first axis of life history variation, governed by size-related traits, ranks species along a small-large body size continuum of life histories, and the second axis, governed by time-related traits, ranks

species along a slow-fast continuum of life histories. These two axes have been well identified in other taxonomic groups (e.g. birds, mammals) and they support the current paradigm surrounding the evolution of life histories in all organisms (Dobson 2007). We could not test whether the reproductive allocation of species, describing the third axis of life history variation in scombrids, might be an important life history correlate of vulnerability, because fecundity traits and specifically fecundity-length relationships were lacking for the majority of scombrid populations and species (Table 5.S3). Although our analysis only includes 26 populations of 11 species of scombrids (out of 51 species in the family Scombridae), in this small set of population and species there is enough life history variation, and we find the two first axes of life history variation (small-large trait axis and slow-fast trait axis) are present (see section 2.2.3).

We grouped the life history traits into small-large and slow-fast sets: (1) small-large traits [maximum size (L_{max}), length-at-maturity (L_m), absolute average batch fecundity (F_{abs}) and relative batch fecundity (F_{rel})], and (2) slow-fast traits [longevity (T_{max}), age-at-maturity (T_m), growth rate (k)]. Within each set of variables, the traits were highly correlated and we could use any of them alone to describe the first and second axis of life history variation. We tested whether the traits were biologically exchangeable within each set of traits and find that our results were robust when using any of the traits in each set (see results section). Therefore, we used maximum body size as a proxy to described the first small-large life history trait axis, and used growth rate to describe the second slow-fast life history trait axis, which form the basis of our hypotheses (Table 5.1). We did not test for any of the fecundity related traits in the analyses given that empirical analyses have shown numerous times that fecundity is not a biological predictor of vulnerability and extinction risk in teleost fishes (Figure 5.1, Table 5.S1). We also did not include spawning duration in our analyses because it has never been identified as a potential predictor of vulnerability, and in scombrids, this trait is spatially highly variable since most tuna species spawn in waters where the surface temperature are greater than 25°C (Schaefer 2001).

To test our hypotheses we fitted generalized linear models to 19 populations of scombrids. The first two metrics, the average annual rate of decline and extent of decline in adult biomass, are two continuous variables, therefore we fitted linear regression with normally distributed errors, including life history traits and relative fishing mortality as predictor variables. The linear model can be expressed as: $Y_i = B_o + B_1 X_{1,i} + \ldots + B_k X_{k,1}$, where Y_i, the response variable, is either of the metrics of vulnerability for a given population i, B_o is the intercept, and B_1 through B_k are the coefficients of the predictor variables $X_{1,i}$ through $X_{k,1}$. For the third metric, we coded the current exploitation status, whether the population

is overfished or not, as a binomial response variable and fitted a logistic regression to the data, including the life history traits and relative fishing mortality as predictor variables, assigning a binomial error distribution and a logit link function. The binomial model can be expressed as: $\text{logit}(p_i) = \log(p_i/1-p_i) = B_o + B_1 X_{1,i} + \ldots + B_k X_{k,1}$, where p_i is the estimated probability of being overfished for a given population i, B_o is the intercept, and B_1 through B_k are the coefficients of the predictor variables $X_{1,i}$ through $X_{k,1}$.

We used an information-theoretic approach with Akaike's Information Criterion corrected for small sample sizes (AICc) to evaluate all the candidate models and assign them relative strengths of evidence (Burnham and Anderson 2002). Given a set of carefully constructed *a priori* candidate models (hypotheses), information theoretic methods provide a quantitative assessment of the "strength of evidence" in the data regarding the plausibility of each model relative to the entire set of models (Burnham and Anderson 2002, Anderson 2008). We determined the maximized log-likelihood for each candidate model (*i*) and calculated the values for AIC_c, $\mathbf{\Delta A}ICc$ ($\Delta AIC_c = AIC_{ci}$ - min AIC_c, where AIC_{ci} is the AIC_c for model *i*, and min AIC_c is the smallest AIC_c value in the set of models), and the Akaike weight (w_i). The Akaike weights expresses the relative support of candidate models relative to the model set, with the weight of any particular model varying from 0 (no support) to 1 (complete support) (Burnham and Anderson 2002). We selected the best models (with largest Akaike weights) and calculated the standard error and the 95% confidence intervals for each covariate to assess the effect size, and those variables whose confidence intervals excluded zero were deemed to have a strong effect on the predictor variables (Mazerolle 2006).

We examined model diagnostics for heteroscedasticity, normality and independence of residuals (Zuur et al. 2009). Due to issues of non-normality and non-constancy of variance (observed within the residual analysis), all the models were linearized by taking the natural logarithms of the response variables and all the predictor variables including the life history traits and relative fishing mortality. All data management, analyses and figures were done using the R statistical software v.2.14.2 (R Development Core Team 2012), including the R packages "MuMIn" (Bartón 2009) and "ggplot2" (Wickham 2009).

Double-checking the foundations of our a priori hypotheses -principal component analysis of life history traits

We used principal component analysis to examine the trait co-variation among the 26 populations of scombrids and assess whether at least the first two axes of life history variation identified in Juan-Jordá et al. 2012 are present in this subset of 26 populations

and 11 species of scombrids, which forms the basis of the hypotheses in this study. In order to maximize the number of populations included in the analyses, we filled the missing life history information following these criteria: first, we combined all available studies in the scombrid life history dataset (Juan-Jordá et al. 2012) and calculated a species average for each life history trait (this combined information from all populations within each species distribution); and (2) we substituted the population's missing traits using the species average value of each trait (Table 5.S3). Notice that after all the substitutions, some life history traits were still missing in those populations for which life history data was not even available at the species level. Given that some life history traits are missing in some scombrid populations, we conducted two principal component analyses (Figure 5.S4, Table 5.S4). The first principal component analysis attempted to maximize the number of life history traits, at the cost of including smaller number of populations (8 traits, and 22 populations), and the second principal component analysis attempted to maximize the number of populations at the cost of including a smaller number of life history traits (26 populations and 4 life history traits).

Both principal component analyses confirmed the existence of the first two main axes of life history variation in scombrids. As expected, the first axis was driven by length-related traits raking species along a size continuum and the second axis was driven by time-related traits raking species along a slow-fast continuum (Figure 5.S4 and Table 5.S4). The first axis differentiates between populations with large body size, late maturing, having high absolute fecundities that are also relatively long-lived and slow growing against those species with the opposite suite of traits. The second axis ordinates populations along a slow-fast continuum differentiating populations which are longer lived and have slower growth rates given their maximum size, from populations which are shorter lived and have faster growth rates given their maximum body size. The first axis explained 76% of the variation and the first and second axes together explained 90% of the life history variation. We could not interpret the third principal component, which we expected to describe the reproduction allocation of species, in part because, the trait describing the increase of fecundity with size (the exponent b of the fecundity–length relationship was not available for the majority of scombrid population) and the small amount of remaining variation to explain.

Finally, we carried out an additional complementary analysis and tested for the usefulness of the principal component one (PC1) and two (PC2) derived from the PCA analysis, as predictors of scombrids population trajectories and current exploitation status. We used the population scores of the first and second principal components (PC1 and PC2,

respectively) extracted from the principal component analysis (Figure 5.S4B and Table 5.S4B) and included them as predictor variables in the generalized linear models. PC1 summarizes all the size-related traits (L_{max} and L_m) into one variable, ranking populations along the small-large continuum of life histories. Populations with a larger-maximum body, and large size at maturation have positive and higher scores than populations with smaller-maximum body sizes and smaller size at maturation. While the PC2 reduces the time-related traits (T_{max} and k) into one variable, ranking populations along the slow-fast continuum of life histories (Figure 5.S4B and Table 5.4SB). Longer-lived and slower growing species given their maximum body size, have positive and higher scores along PC2 than shorter-lived and faster-growing populations given their maximum body size. Yet, we find advantageous to use the trait maximum size as a proxy for PC1 and the trait growth rate as a proxy of PC2 in our main analyses, instead of using just the PC1 and PC2 population scores, as they can be easily interpreted and can be easily used to identify and rank species according to their sensitivities to fishing exploitation.

Results

Bivariate relationships among the three measures of vulnerability, life history traits and fishing mortality

Scombrid populations with slower growth rates, greater longevities and later age-at-maturity appear to have declined in adult biomass more rapidly (measured by the annual rate of declines) and to a greater extent (measured by total extent of declines) (Figure 5.2 G,H,J,K,M,N). We find that growth rate, longevity and age-at-maturity are moderately correlated with the rate and extent of decline in adult biomass in scombrid populations (absolute value of the Pearson's correlation coefficient [r] ranging from 0.41 to 0.55). Maximum body size and length-at-maturity are uncorrelated and are poor predictors of the rate and extent of decline in adult biomass in scombrid populations (Figure 5.2A,B,D,E, absolute value of r ranging from =0.05-0.25). Moreover, scombrid populations that are currently overfished tend to be longer-lived, mature later and have slower growth rates than populations that are not currently overfished (Figure 5.2I,L,O). While there are not clear patterns between the exploitation status of the populations and their maximum body size and length-at-maturity (Figure 5.2C,F). Moreover, we also find that scombrid populations that are overfished tend to have been exposed to higher relative fishing mortality rates, on average, during their period of exploitation than populations that are not currently overfished (Figure2R). The relative fishing mortality rate in scombrid populations

is weakly positively correlated with rate and extent of decline in biomass (r=0.28-0.35), such that populations that have been exposed to higher relative fishing mortality rates, on average, have tended to decline in adult biomass faster and to a greater extent (Figure 5.2P-Q).

Bivariate relationships between life history traits and fishing mortality rates

Fisheries have not disproportionally targeted scombrids populations with specific life history traits such as the large and the slowest scombrid populations (Figure 5.3A-B). The relative fishing mortality rate ($F_{average}$/F_{MSY}) is weakly correlated with growth rate (r=-0.29, Figure, 3B) and uncorrelated with maximum body size (r=0.11, Figure3A). Instead, we find scombrid species irrespective of their maximum body size and growth rates have been exposed to a range of average relative fishing mortality rates values within their period of exploitation, which allow us to test our *a priori* hypotheses. Is it just fishing mortality determining the rate and extent of decline and current exploitation of scombrid populations? Or is it life histories in combination with fishing rates determining their rate and extent of decline and their current exploitation status? And what aspects of their life histories are most useful to predict their trajectories and current status? When examining the role of life histories in determining population trajectories and status, it is critical we control for the different fishing mortality rates experienced by each population; and we controlled for it using the metric of relative fishing mortality ($F_{average}$/F_{MSY}), instead of just the average fishing mortality rates ($F_{average}$). This is because the fishing mortality rates a species can cope with and therefore their F_{MSY} (the fishing mortality rate that will result in a population size of B_{MSY}) is determined by their life histories. We find that F_{MSY} is highly correlated with the time-related trait of growth rate (r=0.71, Figure 5.3D) and moderately correlated with the length-related trait of maximum body size (r=-0.53, Figure 5.3C).
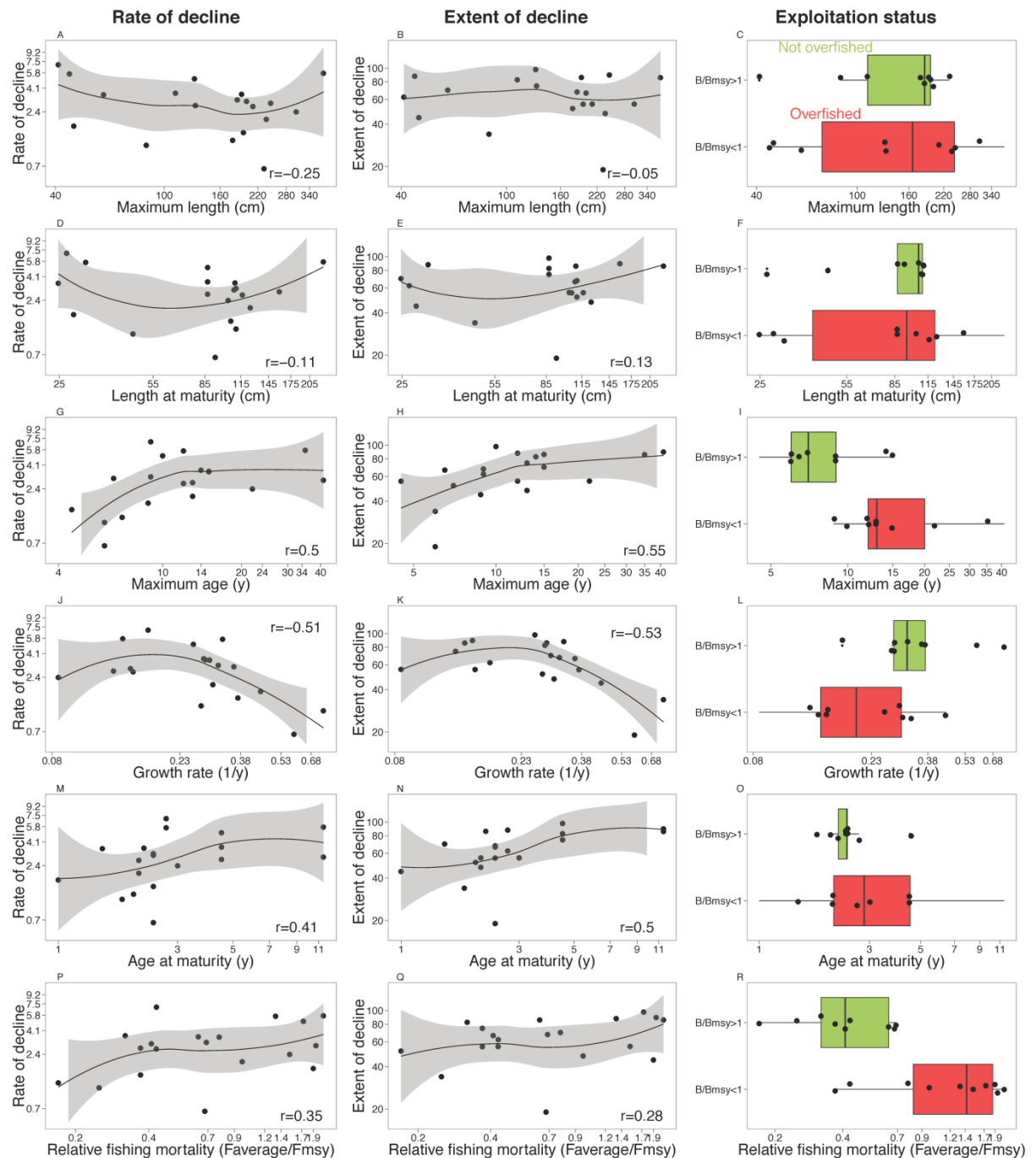
Figure 5.2 Relationships between three measures of vulnerability (columns) and each of the predictor variables (rows) in scombrid populations.

The three measures of vulnerability are: average annual rate of decline in adult biomass over time (% decline per year), total extent of decline in adult biomass within the whole period of exploitation (total % decline), and current exploitation status of the populations (whether the populations are overfished [B/B_{MSY} <1] or not [B/B_{MSY} >1]). The predictor variables include five life history traits and the relative fishing mortality rate. Pearson's correlation coefficients (r) and lowess smooth lines with 95% confidence intervals are shown to highlight the main patterns.
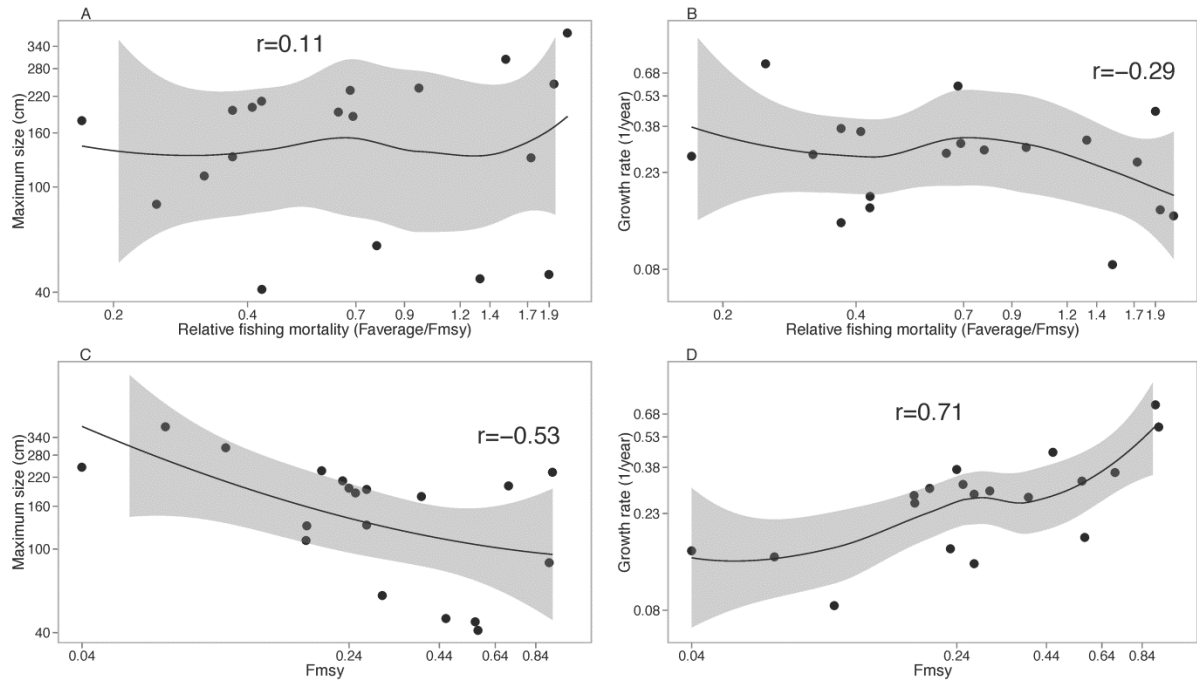
Figure 5.3 *Relationships between life history traits and relative fishing mortality rates ($F_{average}/F_{MSY}$) and F_{MSY} in scombrid populations.*

(A-B) Correlations between maximum size and somatic growth rate and the fishing mortality predicted to supply maximum sustainable yield (F_{MSY}). (C-D) Correlations between maximum body size and somatic growth rate and the relative fishing mortality ($F_{average}/F_{MSY}$), which is calculated as the ratio between the average fishing mortality rate experienced by each population within their period of exploitation and the fishing mortality predicted to provide the maximum sustainable yield. Pearson's correlation coefficients (r) and lowess smooth lines with 95% confidence intervals are shown to highlight the main patterns.
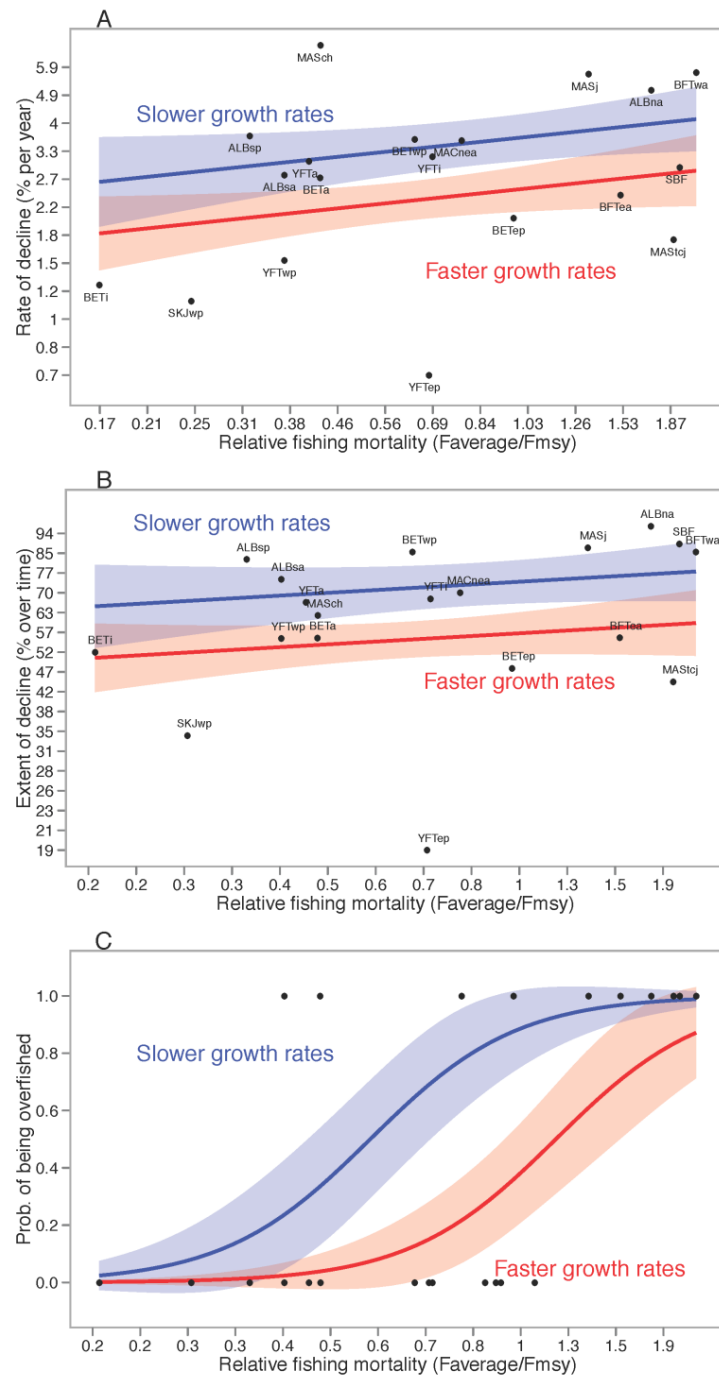
Figure 5.4 *Vulnerability to fishing depends on somatic growth rates for 19 scombrid populations.*

(A) Predicted average annual rates of decline in adult biomass with separate lines set for two values of growth rates corresponding to the first (blue line, slow growth k=0.16) and third (red line, fast growth k=3.4) quartile values. (B) Predicted total extent of decline in adult biomass with separate lines set for two values of growth rates corresponding to the first (blue line) and third (red line) quartile values, k=0.16 and k=3.4, respectively. (C) Predicted probability of being overfished (B/B$_{MSY}$<1). Panels show regression lines and 95% confidence intervals derived from (A-B) linear models and (C) logistic regression models. Table S5 summarizes the statistical detail from each of the single predictor generalized linear models. Predictions with 95% confidence values correspond to the best models (the models with the largest Akaike weights, see Table 5.4). Population codes are found in Table 5.2.

Testing our a priori hypotheses

There is broad agreement between the three different measures of vulnerability and the predictive life history correlates, once the relative fishing mortality experienced by the populations is controlled for (Table 5.3). The combination of life histories and relative fishing pressure best explained the rate and extent of declines in adult biomass and the current exploitation status of scombrid populations. The pace of life (growth) was a better predictor of decline and current exploitation status than the large-small life history dimension (maximum body size). We found greatest support for the models (largest Akaike weights, w_i, and lowest AIC_c) including growth rate and the relative fishing mortality rate as predictor variables given the set of candidate models (w_i ranging from 0.56 to 0.75, Table 5.3A-C). There was weaker support (w_i =0.19-0.29) for the models which only included the relative fishing mortality rates as predictor variable. We found weakest support (w_i =0.05-0.13) for the models including maximum body size and the relative fishing mortality rate as predictor variables (Table 5.3).

After controlling for the different fishing mortality rates experienced by each population, those populations with slower growth rates, rather than population with larger body size, are 4 times more likely to have experienced faster populations declines (evidence ratio = 0.56/0.13), are 12 times more likely to have experienced larger extents of population declines (evidence ratio=0.69/0.05), and are 14.5 times more likely to be currently overfished (evidence ratio=0.75/0.5; Table 5.3, Figure 5.4). Indeed, we find strong evidence for an effect of growth rate, as the 0 is excluded from the 95% confidence intervals, on all three measures of vulnerability (Table 5.4). We also find evidence that, both growth rate and relative fishing mortality in combination, have a strong effect on the probability of populations being overfished as 0 was excluded from their 95% confidence intervals (Table 5.4).

We also observe those scombrid populations with the slowest growth rates that have experienced the fastest and greatest declines in adult biomass and are currently overfished, are populations of temperate and subtropical scombrid species (Figure 5.4, Table 5.2). Populations of the temperate and subtropical species of scombrids such as chub mackerel (*Scomber japonicus*), Atlantic mackerel (*Scomber scombrus*), albacore tuna (*Thunnus alalunga*) and Atlantic and Southern bluefin tuna (*T. thynnus* and *T. maccoyii*) have suffered the fastest and greatest decline in adult biomass and have a higher probability of being overfished (Figure 5.4).

Table 5.3   *Summary of the regression models sorted by AIC$_c$, evaluating the effects of relative fishing mortality ($F_{average}/F_{MSY}$) and life histories on three measures of vulnerability in scombrids.*

(A) The rates of decline in adult biomass, (B) the extents of decline in adult biomass and (C) current exploitation status (probability of being overfished) in scombrid populations. (A-B) Linear regression with normally distributed errors and (C) logistic regression with binomial distributed errors. AICc, Akaike's information criterion with a correction for small sample sizes; df, number of parameters; l (θ), the value of the maximizes log-likelihood function; ΔAICc =AICci - min AIC, where AICci is the AICc for model i, and min AICc is the smallest AICc value in the set of models; wi , the Akaike weights, expresses the relative likelihoods of candidate models, with the weigh of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set; R2, coefficient of determination.

A - Rate of decline in adult biomass

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i	R^2
Relative fishing mortality + growth rate	4	-13.48	37.82	0	0.57	0.31
Relative fishing mortality	3	-15.76	39.11	1.29	0.3	0.12
Relative fishing mortality + maximum body size	4	-14.88	40.62	2.81	0.14	0.20

B - Extent of decline in adult biomass

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i	R^2
Relative fishing mortality + growth rate	4	-5.49	21.80	0.00	0.69	0.30
Relative fishing mortality	3	-8.09	23.80	1.93	0.26	0.08
Relative fishing mortality + maximum body size	4	-8.04	26.90	5.08	0.05	0.08

C - Probability of being overfished

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i
Relative fishing mortality + growth rate	4	-8.88	25.00	0.00	0.75
Relative fishing mortality	3	-11.56	27.70	2.69	0.20
Relative fishing mortality + maximum body size	4	-11.54	30.30	5.33	0.05

Table 5.4 *Vulnerability to fishing depends on somatic growth rates for 19 scombrid populations.*

Panels show selected best models (models with the largest Akaike weights from Table 3) for each measure of vulnerability. (A) The rates of decline in adult biomass, (B) the extents of decline in adult biomass and (C) current exploitation status (probability of being overfished) in scombrid populations. (A-B) Linear regression with normally distributed errors and (C) logistic regression with binomial distributed errors. The summary of the models includes the estimated coefficients, standard errors (SE) and the 95% confidence intervals (CI) for each covariate. (*)Parameter deemed significant as confidence interval excludes 0.

A - Rate of decline in adult biomass

Parameter	Estimate	SE	Lower CI	Upper CI
Relative fishing mortality	0.18	0.17	-0.16	0.52
Growth rate	-0.51	0.24	-0.99	-0.03

B - Extent of decline in adult biomass

Parameter	Estimate	SE	Lower CI	Upper CI
Relative fishing mortality	0.07	0.11	-0.15	0.29
Growth rate	-0.36	0.16	-0.68	-0.05

C - Probability of being overfished

Parameter	Estimate	SE	Lower CI	Upper CI	Odds ratio Exp (Est.)	Inverse odd ratio 1/exp (Est.)
Relative fishing mortality	3.25	1.72	0.79	7.99	25.70	
Growth rate	-3.96	2.35	-10.36	-0.48		52.35

Our results were robust to the choice of the variable used as a proxy for the small-large and slow-fast life history dimensions (Table 5.S5). The analyses revealed the greatest support for the models including time-related traits (growth rate, longevity and age-at-maturity) and showed the weakest support for the models including the length-related traits (maximum size and length-at-maturity) (Table 5.S5). Moreover, among the time-related traits growth rate tended to be the most consistently important predictor of the rate of decline in adult biomass and probability of being overfished. In the case of extent of decline, the strength of support for those models including either longevity or growth rate as predictors of extent of decline was very similar, suggesting these traits are highly biologically exchangeable.

Finally, our results were also robust to our choice of using the first two principal components -PC1 and PC2 (which describe the first two axis of life history variation in scombrids) as predictor variables of our three metrics of vulnerability (Table 5.S6). Our analyses revealed the greatest support for the models including both, PC2 and relative fishing mortality, as the predictor variables. The predictor variable PC2, which ranks scombrid species along the slow-fast continuum of life histories, was the most important predictor of rate of decline and exploitation status (and to lesser extent a predictor of extent of decline) once relative fishing mortality has been controlled for, suggesting that longer-lived, slower growing and late maturing species given their maximum body size have decreased faster in adult biomass and have a higher probability of being overfished.

Consequently, our analysis revealed higher support for the hypothesis than after accounting for the different relative fishing mortality rates experienced by populations, scombrid populations at the slow-side of the slow-fast continuum of life histories, those longer-lived, late maturing and with slower growth rates given their maximum body size, have experienced faster and larger population declines and have a higher probability of being overfished (Figure 5.4).

Discussion

The combination of life histories and relative fishing pressure best explained the rate and extent of declines in adult biomass and the current exploitation status of scombrid populations. After controlling for the different fishing mortality rates experienced by each population, those populations with a slower pace of life (slower growth rates and longer-lived), rather than populations with larger body size, are more likely to have experienced

faster and larger populations declines and have a higher probability of being overfished. Among all scombrid species, we find that populations of temperate and subtropical species, such as chub mackerel (*Scomber japonicus*), Atlantic mackerel (*S. scombrus*), albacore tuna (*Thunnus alalunga*) and Atlantic and Southern bluefin tuna (*T. thynnus* and *T. maccoyii*), which have the slowest growth rates and greatest longevities, have suffered the fastest and greatest declines in adult biomass and have a higher probability of being overfished even after fishing pressure has been controlled for. Whereas the majority of tropical populations of scombrid species, such as skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*T. albacares*) and bigeye tuna (*T. obesus*), which are among the fastest growers and shortest-lived species of scombrids, have suffered the slowest, and less severe population declines in adult biomass, and have a lower probability of being overfished. Therefore, this study suggests scombrids species with slow life histories, which are mostly found in temperate climates, appear to be the most sensitive to fishing exploitation. Our findings concur with a simulation study that modeled the responses of two tuna species with contrasting life histories, the tropical skipjack tuna (*Katsuwonus pelamis*) and temperate Atlantic bluefin tuna (*Thunnus thynnus*), to different levels of exploitation (Fromentin and Fonteneau 2001). This study revealed that given the same levels of fishing mortality (starting at the age of 1), the adult biomass of Atlantic bluefin tuna decreased faster and to a larger extent in the same period of time than in skipjack tuna, concluding that Atlantic bluefin tuna is more vulnerable to recruitment overfishing and collapse, and less productive than skipjack tuna. Moreover, our analyses also suggest that we could use the time-related life history traits of growth and longevity, rather than maximum body size, as best surrogates of vulnerability to fishing. Yet, maximum body has been identified more often as the best surrogate of vulnerability in marine fishes suggesting that it might be sufficient to predict what species are more vulnerable to fishing exploitation (Figure 5.1). Next, we first discuss why a successful precautionary management of scombrid species may require better consideration of their life history strategies. Second, we discuss why large body size might be most frequently identified as the best predictor of vulnerability to fishing exploitation in marine fish vulnerability, and its implications to guide management in data poor situations. Finally, we highlight some of the caveats and limitations in our study and suggest future directions.

The life history strategies of temperate scombrids differ from their tropical counterparts in many aspects, which ultimately have consequences on how tropical and temperate scombrid species should be managed. Perhaps this may be generalized for all tropical and temperate fish species (Ursin 1984, Longhurst 1998a). Because of the higher

temperatures found in lower latitudes, tropical fish species tend to have higher metabolic rates, growth rates and consumption rates, requiring a higher oxygen supply (which is limited by the surface area of their gills). Other things being equal, tropical species will tend to reach the size where oxygen is limiting faster, therefore attaining smaller maximum body sizes and shorter live spans (Pauly 2010). Tropical scombrids such as skipjack tuna (*Kastuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*), and Indian mackerels (*Rastrelliger* spp.) have fast life histories, having faster growth rates and shorter life spans given their maximum size (Juan-Jordá et al. 2012). The tropical yellowfin tuna (*Thunnus albacares*) which have a relatively large size for being a tropical species have evolved disproportionally large gills surface areas relative to its body weight allowing high rates of the oxygen acquisition to maintain its high rates of growth performance resulting in a larger maximum body size (Wegner et al. 2010), yet their life span is relatively short given their maximum body size, reflecting a fast life history strategy. On the other hand, species in colder water environments have lower metabolic rates, having a lower oxygen demand. Therefore, fish need less oxygen for maintenance, thus, devoting more oxygen for growth resulting in larger maximum sizes, which comes with reaching longer life spans (Pauly 2010). An example of temperate scombrids are the bluefin tuna species (*T. thunnus, T. orientalis* and *T. maccoyii*) and Atlantic mackerel (*Scomber scombrus*) which have slow growth rates and longer life spans for their maximum body size spans, reflecting a slow life history strategy (Juan-Jordá et al. 2012).

The oceanographic conditions between tropical and temperate seas are also fundamentally different, resulting in fish reproductive strategies that are adapted to the environmental conditions to ensure survival of their larvae and successful years of recruitment (Ursin 1984, Longhurst 1998a). Tropical scombrids with fast life histories such as yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) have evolved a reproductive strategy that is well-matched for tropical environments. At lower latitudes, there is little seasonal variation in primary production; therefore, primary production and zooplankton biomass remain relatively stable through the year, resulting in a remarkably predictable food supply for fish larvae (Ursin 1984, Longhurst 1998a, 2002). Tropical scombrids have longer spawning seasons, for example yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) spawn uninterruptedly during the whole year in their core habitats (water temperature above 25° C), which result remarkably in constant recruitment (Schaefer 2001, Longhurst 2002). In contrast, the high seasonality and high intra- and inter-annual variability in ocean conditions characteristic of the temperate oceans, results in peaks of primary production that are highly variable in time

(Longhurst 1998b). This variability translates into unpredictable food supply for fish larvae, leading to unpredictable random good and bad recruitment years, where bad recruitment conditions can last for several years and even decades (Longhurst 2002, Beamish et al. 2006). Temperate scombrid species have a shorter spawning season, increasing the probability of a miss-match between the production peaks of plankton and the time larvae starts feeding. Thus, the large longevities and well-evolved age structures characteristic of temperate scombrid species might become essential to endure long periods of poor recruitment during unfavorable environmental conditions (Longhurst 1998a, Fromentin and Fonteneau 2001).

While the life history strategies of temperate and tropical scombrid species are well adapted to their environments, traditional fisheries management is not well suited to maintain and protect the naturally evolved aspects of their life histories, particularly for longer-lived species. The immediate effects of a fishing management strategy does not only results in adult biomass reductions; fisheries management usually aims to reduce biomass levels to the point where the biomass left provides the maximum sustainable yield. Fishing also truncates the age structure of populations and reduces their age diversity by targeting preferentially the large and older fish individuals (Berkeley et al. 2004). There is increasing evidence that the age-structure of longer-lived species has an effect on the productivity and stability of populations by increasing their buffering capacity to sustain long periods of unsuccessful recruitment (Beamish et al. 2006, Rouyer et al. 2011) and increasing their reproductive potential (Marshall 2009). Therefore maintaining natural age-structures is essential for the successful management of fish populations (Longhurst 2002, Berkeley et al. 2004, Brunel 2010). In the case of scombrid species, globally it has been quantified that the adult biomass of 26 scombrid populations have been reduced, on average, by 60% in the last half century (Juan-Jordá et al. 2011) and there is evidence that concomitant with these decreases in biomass the natural age structure of some scombrid populations have also being altered by fishing (Figure 5.5). However, it is not known to what extent (and if any) it might be impairing their buffering capacity to sustain poor periods of recruitment or affecting their reproductive potential. The present study suggests that scombrid species with slow life histories which are associated with subtropical and temperate climates appear to be the most vulnerable to fishing and therefore, we stress the importance of taking into account their different life history strategies into fisheries management. The current management strategy for assessed scombrid populations (in tropical and temperate species) mainly focuses in maintaining biomass levels at or above B_{MSY} levels and maintaining fishing mortality rates

at or below F_{MSY} levels (Juan-Jordá et al. 2011). This management strategy can also be generalized to many of the world-assessed fisheries (Worm et al. 2009). A management strategy that only protects biomass in the long-lived species, when long-lived species rely in a diverse age structure as a natural evolved mechanism to survive long periods of poor recruitment, is not precautionary management.

Previous empirical studies linking life histories with population and species trajectories under fishing pressure suggest maximum size is the best predictor of vulnerability in marine fish species. These studies show large bodied species have declined more and faster in abundance once fishing mortality is controlled for (Jennings et al. 1998, Jennings et al. 1999a, Jennings et al. 1999b). Similarly, studies linking life histories with species Red List threat status also show large bodied species are threatened with a relatively higher risk of extinction (Olden et al. 2007, Field et al. 2009). Thus, these empirical studies suggest that maximum size might be sufficient to predict what species and populations are more sensitive to fishing exploitation and instructive about the likelihood of decline under a scenario of fishing pressure. In contrast, our study suggests that maximum size is not necessarily the best predictor of scombrid population declines and exploitation status. Instead, time-related traits, such as longevity and growth rates, were better predictors of rate and extent of decline, and exploitation status in scombrid populations. How do we reconcile these results?

Here we present four suggestions why maximum body size is most frequently the best predictor of marine fish vulnerability. First, it is the most commonly available trait and often the only life history trait tested (Figure 5.1B-D) (Reynolds 2003, Reynolds et al. 2005). By comparison, growth and longevity have been less frequently tested, presumably because they are harder to estimate than maximum body size (Figure 5.1B-D). Second, large bodied fishes tend to be preferentially targeted over the smaller species because they are often more economically important and valuable (Reynolds 2003, Sethi et al. 2010), and yet we find some studies did not control for the different fishing mortalities experienced by the species (Table 5.S1). This makes it difficult to disentangle the individual effect of fishing and life histories (Dulvy and Reynolds 2002, Olden et al. 2007, Field et al. 2009). Third, it is well known that maximum body size is the first element explaining the diversity of life histories across all organisms and it governs the first axis of life history variation (Dobson 2007). Given that other life history traits also scale with size such as that large species will tend to mature later and be longer-lived, maximum size tends to approximate other aspects of species life histories (e.g. length-at-maturity, longevity), their ecology

Figure 5.5   Trajectories of the adult mean age (in years) over time for 19 populations of scombrids (9 species) grouped by climate (temperate, subtropical and tropical).

We calculated the mean age of spawners using the matrix of abundance at age over time extracted from stock assessments and averaging the age of adults (spawners) weighting it by the number of individuals in each age class. For sources of stock assessments see Table 5.S2.

(e.g. trophic level) and their behavior (e.g. migrations and home range size) (Reynolds 2003). Therefore, when life history traits other than maximum size are unavailable and therefore not tested in the comparative analyses, it is not surprising that maximum size is identified as an important predictor of vulnerability and therefore proposed to be used as a rule of thumb to rank vulnerability of species. After all, there are two main axes surrounding the evolution of life histories and size governs the first axis. When the influence of size on other traits is held constant, a second new axis emerges where a new continuum of slow and faster life histories emerges which are a reflection of the different life styles of species (Dobson 2007, Juan-Jordá et al. 2012). Fourth, we also observe that the majority of previous empirical studies identifying life history correlates of vulnerability in marine fishes are regional studies focusing on an assemblage of species, for example, temperate benthic fish communities in the North Sea (Jennings et al. 1999b) and UK shelf seas (Jennings et al. 1998) or Fijian coral reef fish assemblages (Jennings et al. 1999a). Within a regional context of populations and species within relatively similar habitats, we might expect maximum size to be a better proxy of distinct life history strategies and thus, appear more often as a correlate of vulnerability to fishing, than at larger geographical scales across multiple habitats.

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identified as an important predictor of vulnerability and therefore proposed to be used as a rule of thumb to rank vulnerability of species. After all, there are two main axes surrounding the evolution of life histories and size governs the first axis. When the influence of size on other traits is held constant, a second new axis emerges where a new continuum of slow and faster life histories emerges which are a reflection of the different life styles of species (Dobson 2007, Juan-Jordá et al. 2012). Fourth, we also observe that the majority of previous empirical studies identifying life history correlates of vulnerability in marine fishes are regional studies focusing on an assemblage of species, for example, temperate benthic fish communities in the North Sea (Jennings et al. 1999b) and UK shelf seas (Jennings et al. 1998) or Fijian coral reef fish assemblages (Jennings et al. 1999a). Within a regional context of populations and species within relatively similar habitats, we might expect maximum size to be a better proxy of distinct life history strategies and thus, appear more often as a correlate of vulnerability to fishing, than at larger geographical scales across multiple habitats.

To the best of our knowledge, there has been only one global analysis where multiple life history traits have been used to test which are strong predictors of population collapses in marine fishes (Pinsky et al. 2011). This study tested which species-level life history traits best explained the proportion of collapsed populations within a species. When estimates of collapses were based on abundance data extracted from fishery stock assessments, they found that small, short-lived species, commonly assumed to be less vulnerable to fisheries, have collapsed as often as large, higher trophic-level species, even after controlling for the fishing mortality rates experienced by each species (Pinsky et al. 2011). We agree on the main message of this study that the vulnerability of a species is the combination of their life histories and the magnitude of the fishing impacts, and therefore any population or species regardless of their life histories can be driven to collapse by fisheries if fished hard enough. However, based on life history theory and the evidence from multiple empirical analyses, we would expect the life histories of fishes to be a useful predictor of collapses after controlling for fishing mortality rates. We suggest several reasons why life history traits where not strong predictors of species collapses (after fishing mortality was controlled for) in this study. First, in contrast to all other studies (which focus on a single taxonomic level -- population or species) this study mixed taxonomic scales by explaining population trajectories with species-level traits. This study modeled proportion of collapse populations within a species, therefore the probability of a population collapsing within each species against multiple species-level life history traits. Presumably driven by data availability, life history traits (extracted from FishBase), and

metrics of fishing mortality and collapses (which were available at the population level) were averaged across all populations within species, perhaps losing some critical information reducing the power to test hypotheses that are well-supported in better controlled regional-scale studies. Second, statistically it is a challenge to control for the different fishing mortality rates experienced by populations to test whether fishing characteristics have an effect on the prevalence of collapse. In the Pinsky study, the relative fishing mortality rates ($F_{average}/F_{MSY}$) were not included as a main covariate in the models; instead it was analyzed using regression of residuals. This is not a recommended statistical practice (Freckleton 2002). Our study shows that population declines can be best explained be the combination of life history traits and relative fishing mortality, especially time-based traits. Fishing is a rate-based process of the number killed per unit time and hence it makes sense that life history rates that capture the rate of renewal of numbers and biomass are most closely related to population trajectories.

One of the original motivations of our study was to test the usefulness of several life history traits to predict scombrids vulnerability to fishing, with the aim of advancing methods based on the life history of the species to identify the most sensitive species and prioritize resources for those species most at threat in data-poor situations. In a data-poor context with pressing conservation needs where proactive management is more needed, we are most in need of simple methods (or simple rules-of-thumb) to use the data that already exists to make proactive decisions (Beddington and Kirkwood 2005, Reynolds et al. 2005, Cardillo and Meijaard 2011). So we wonder, what aspects of the life history of the species should we used as the best surrogate of species sensitivity to fishing in data-poor situations? We agree with previous studies that when only maximum size of the species is known, it is probably the best surrogate of species vulnerability to fishing (Jennings et al. 1998, Jennings et al. 1999c, Reynolds 2003, Reynolds et al. 2005). Maximum size is commonly available for the large majority of the species, and may be sufficient to predict and rank the relative sensitivity of species to fishing exploitation, particularly within a regional context with a restricted geographic scope and taxonomic group of species. Yet, we show in this study how yellowfin tuna is a clear example of why maximum size is not always a surrogate of vulnerability to fishing. Therefore, when more life history data are available, time-related traits such growth and longevity in addition to maximum body size should be used to characterize the life history strategies of the species and identify their potential intrinsic sensitivities to external threats such as fishing, particularly within a context where the geographic and taxonomic scope of the analysis is large. After all, there are two main axes surrounding the evolution of life histories. Size

governs the first axis, and when the influence of size on other traits is held constant, a second new axis emerges where time related traits become important (Dobson 2007, Juan-Jordá et al. 2012).

Finally, we would like to highlight three caveats of this study and suggest future directions. First, in our study we presented three *a priori* hypotheses to test for the importance of life histories and fishing in determining the population declines and current exploitation status for 19 populations of scombrids. We caution that the sample size of this study is moderate, if not small, given that generally it is recommended seven to ten observations for each predictor variable estimated in a model (Anderson 2008). We encourage re-evaluation of our hypotheses as new data becomes available. Second, we find that relative fishing mortality rates, expressed as $F_{average}/F_{MSY}$, experienced by each population throughout its history of exploitation was not a strong correlate (by itself) of either rate of decline or extent of decline in scombrid populations, although it was statistically significant predictor of the current exploitation status of populations. These findings are counterintuitive, given than prolonged levels of high fishing mortality rates have been associated with higher and faster rates of decline, and fishing pressure has been identified as the most important threat in marine species (Hutchings and Reynolds 2004a, Reynolds et al. 2005). As previously mentioned, it is a challenge to statistically test whether fishing patterns have an effect on the vulnerability of species. Perhaps, by averaging fishing mortality rates across all age classes (juveniles and adults) and across time over the entire history of exploitation of each population, we are loosing the finer temporal details of how fishing rates directly affect abundance levels over time. Consequently, it may be difficult to reduce the history of exploitation into a single metric of average fishing mortality rate. Third, our study together with previous comparative analyses of species vulnerability to fishing, focuses in testing the importance of life history traits, while it gives less focus to the role of behavior (e.g. migrations, strength of school aggregations) and ecology of the species and how all these factors interact with human activities in determining species vulnerabilities and ultimately risk of extinction (Reynolds and Jennings 2000). We therefore encourage future studies to explore the interactions between biological, behavior and ecological factors in determining vulnerability in marine fishes, which are lagging behind studies of extinction risk when compared with terrestrial species (Dulvy et al. 2003, Reynolds 2003, Reynolds et al. 2005).

Conclusions

Certainly both small and large, and short-lived and long-lived species are vulnerable to overexploitation, collapse and ultimately to extinction if fished above the fishing mortality rates they can cope with. However, as life history theory predicts, this empirical study shows evidence for the role of life histories of scombrid populations and species in determining their responses to fishing. Once fishing is controlled for, scombrids populations and species with slow life histories, which are mostly found in temperate climates, are more likely to have experienced faster and larger declines in adult biomass and have a higher probability of being overfished and therefore, appear to be the most sensitive to fishing exploitation. Because the life history strategies of temperate scombrid fish species differ from their tropical counterparts in many aspects, we stress these differences in life history strategies need to be taken more into account in current fisheries management. Identifying and quantifying the relative importance of biological, behavioral and ecological factors and how all these factors interact with human activities in determining species vulnerabilities and ultimately risk of extinction in marine fishes continues to be a challenge and is poorly understood. A better understanding of these factors and their interactions is crucial to build tools to predict species responses to fishing and their risk of depletion and extinction particularly in data-poor situations where conservation needs are pressing. These methods are critical to bring one step closer a realistic precautionary ecosystem-based approach to fisheries management. Finally, we emphasize that global datasets of fisheries data (such as the RAM Legacy Stock Assessment Database) and life history data (such as FishBase), although with their limitations, have only recently started to become available which opens new opportunities to test global hypothesis and advance our understanding of which marine species are most at risk and vulnerable to overexploitation.

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Supplementary Figures
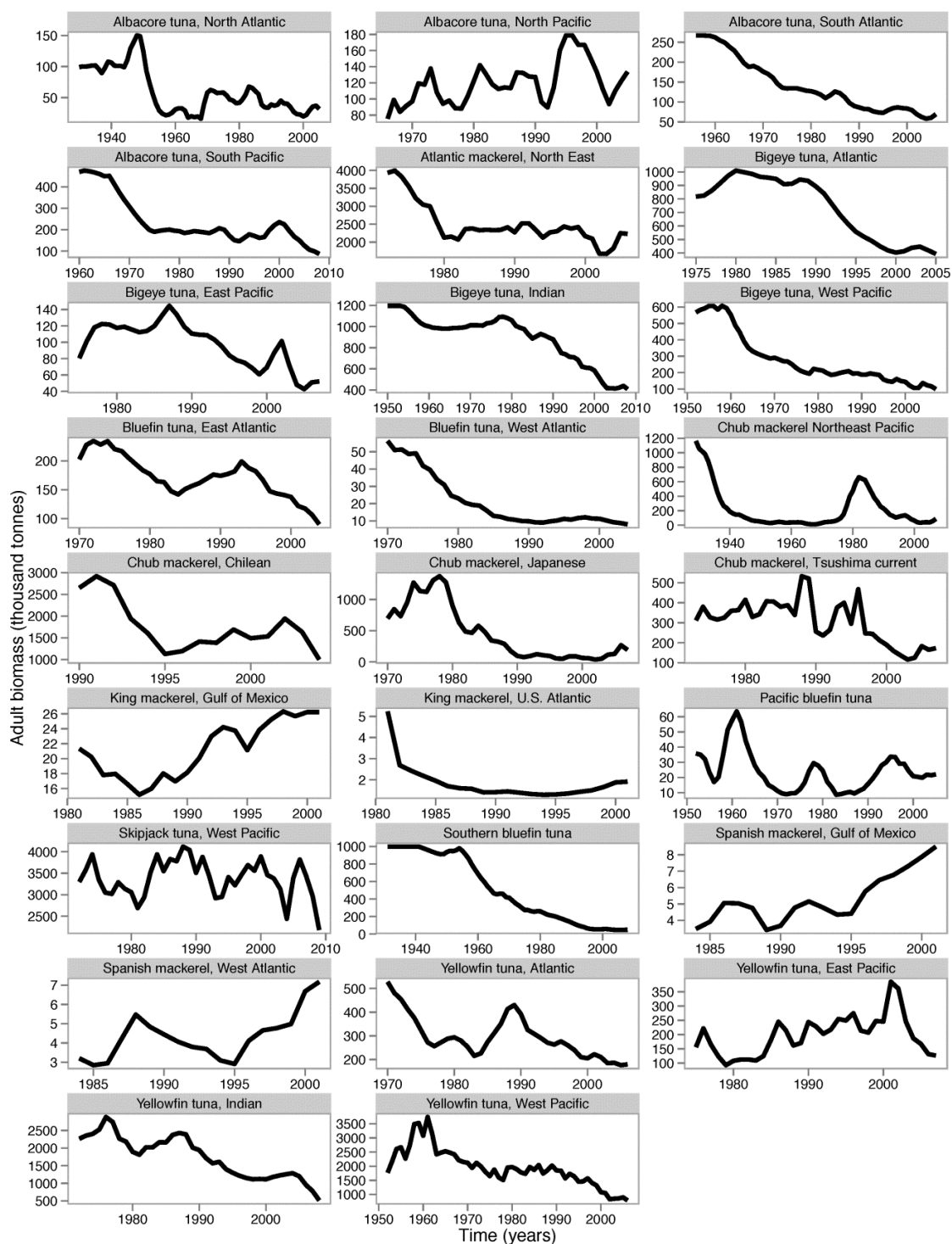
Figure 5.S1   Trajectories of adult biomass (1,000 tonnes) for 26 populations of scombrids (11 species).

For sources of stock assessments see Table 5.S2.
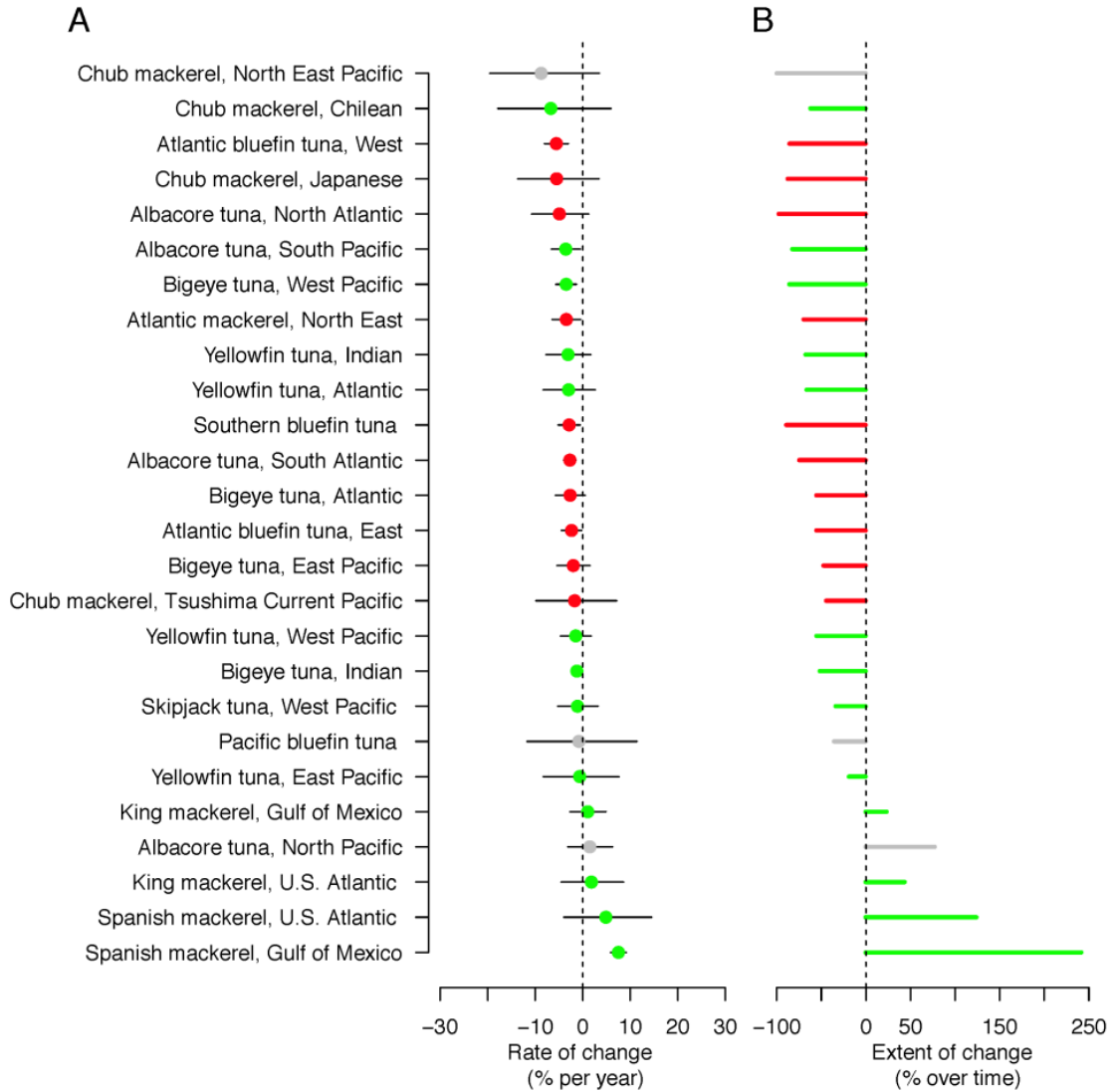
Figure 5.S2   Vulnerability metrics for the 26 populations of scombrids (11 species).

(A) Average annual rate of change in adult biomass (mean ± 95% CIs) for each population across the entire period of available data. (B) Overall extent of decline or recovery in adult biomass for each population from the first year to the last year of available data. Population are colored according to their exploitation status according to the fisheries reference point, $B_{current}/B_{MSY}$. Red populations are overfished ($B < B_{MSY}$) and green populations are not overfished ($B > B_{MSY}$). Populations for which reference points were unavailable are shown in grey.
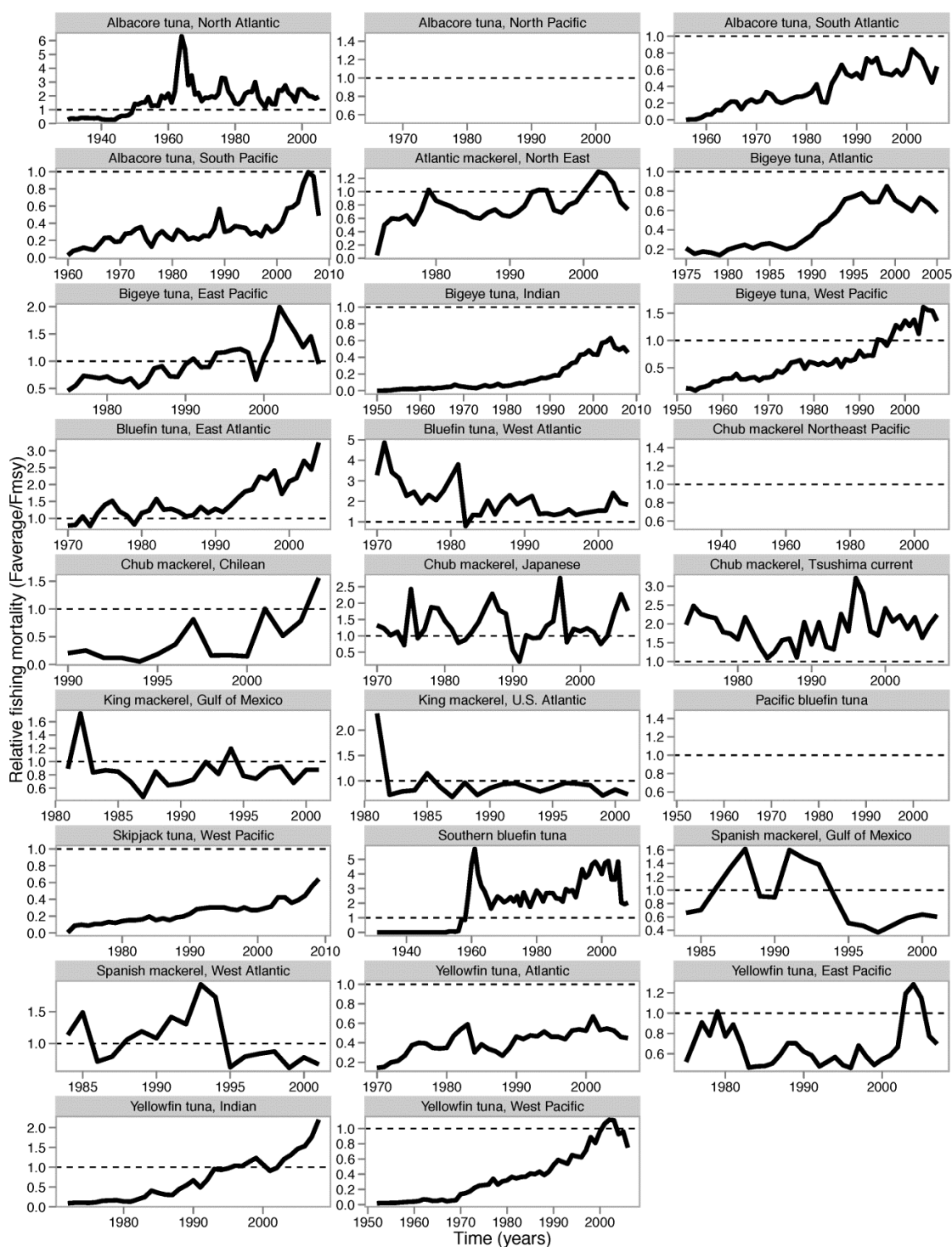
Figure 5.S3 ***Trajectories of relative fishing mortality rates for 26 populations of scombrids (11 species).***

The metric of relative fishing mortality was calculated as the ratio between the average fishing mortality rate across all ages and years and the fishing mortality predicted to produce maximum sustainable yield ($F_{average}/F_{MSY}$). Broken horizontal line shows when $F_{average}/F_{MSY}$ is one. For sources of stock assessments see Table S2.
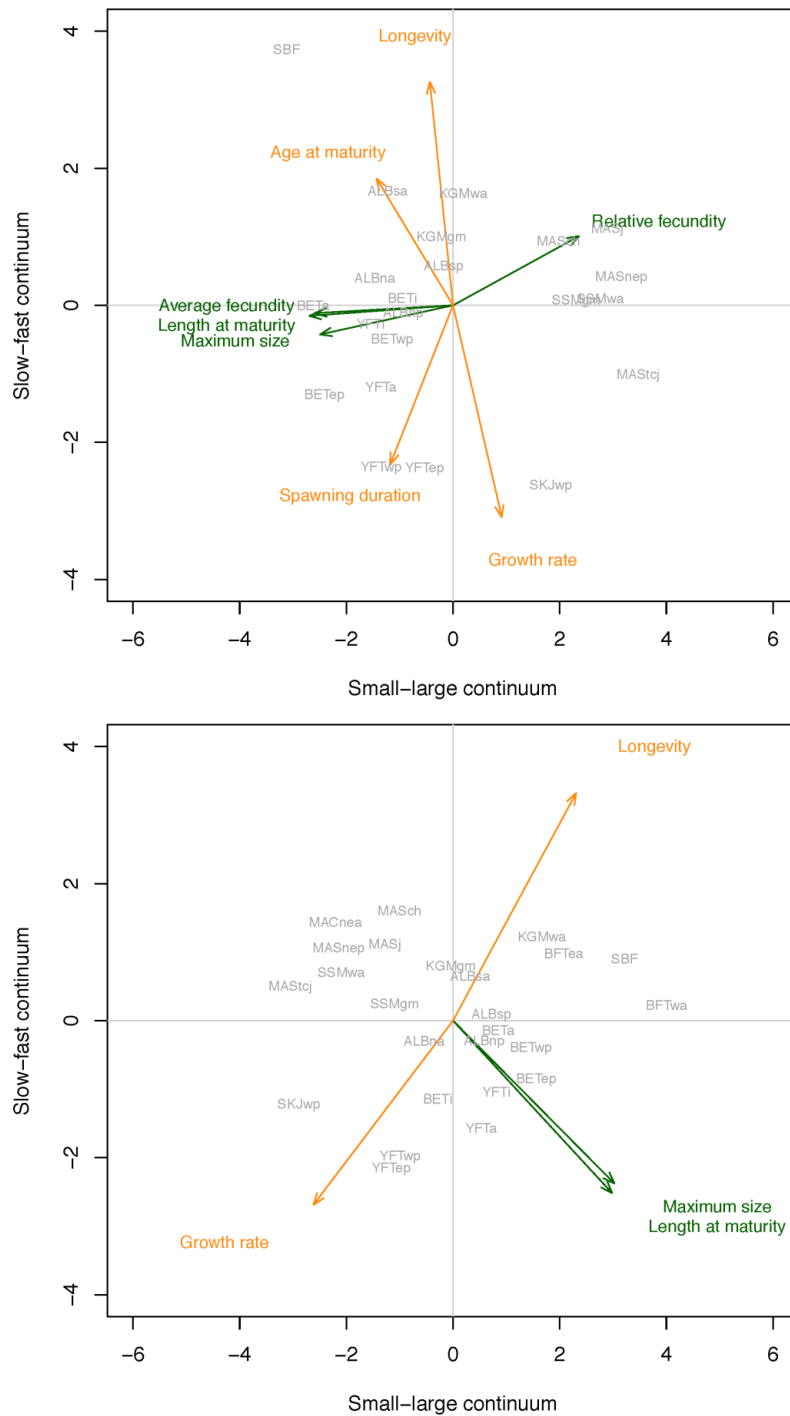
Figure 5.S4   Results from the Principal Component Analysis (PCA) examining the trait co-variation among populations of scombrids.

(A) This PCA maximizes the number of life history traits including eight life history traits and only 22 populations of scombrids. (B) This PCA maximizes the number of populations including all 26 populations and only 4 life history traits. Both PCA confirm the existence of the first two main axes of life history variation in scombrids. The first axis is driven by length-related traits (green color) raking species along a size continuum and the second axis is driven by time-related traits (orange color) raking species along the slow-fast continuum of life histories. See PCA results in Table 5.S4.

Supplementary Tables

Table 5.S1 ***Literature review of empirical studies examining the links between life histories and demography and population status in marine fishes.***

(A) Potential life history correlates of demography, usually measured as maximum per capita population growth rates (r_{max}).

Geographic location	Taxonomy	# of sp. or pop.	Sensitivity metrics	Potential life history correlates	Life history correlates of species sensitivity	References
Global	Chondrichthyan fishes (sharks)	41 populations	Annual population growth rates (lambda)	Body size, age-at-maturity, generation time	Late age-at-maturity and large generation time	(Cortés 2002)
Northeast Atlantic Ocean	Teleost fishes	63 populations	Maximum rates of recruits at low population size (index of r_{max})	Body size, age-at-maturity, growth and fecundity	Large size, late age-at-maturity, slow growth and large fecundities (this is because fecundity is correlated with size). After removing the size effect on fecundity, fecundity was not associated.	(Denney et al. 2002)
Northeast Atlantic Ocean	Teleost fishes	63 populations	Adult production per adult at low population sizes (index of r_{max})	Body size, age-at-maturity, growth and fecundity	Large size and slow growth	(Denney et al. 2002)
Global	Chondrichthyan fishes (sharks and skates)	33 populations	Potential rate of population increase (index of r_{max})	Body size, age-at-maturity and growth	Large body size and late age-at-maturity	(Frisk et al. 2001)
Global	Chondrichthyan fishes (sharks, rays and chimaeras)	127 populations, 105 species	Extinction risk ($F_{extinct}$)	Body size, length-at-maturity, age-at-maturity, longevity, growth, litter size, interbirth interval, reproductive mode	Deep water habitat species (slower growth, later age-at-maturity and higher longevity). Reproductive mode (matrotrophically viviparous)	(Garcia et al. 2008)
Global	Teleost fishes	38 species	Maximum generational growth rate for the population (r_{max})	Body mass	No associated with body mass	(Ginzburg et al. 2010)
Global	Teleost fishes	47 species, 19 families and 8 orders	Maximum per capita population growth rate (r_{max})	Fecundity, body mass, and age-at-maturity	Late age-at-maturity	(Hutchings et al. 2012b)
Global	Chondrichthyan fishes	82 species, 23 families and 12 orders	Maximum per capita population growth rate (r_{max})	Fecundity, body mass, and age-at-maturity	Large size and late age-at-maturity	(Hutchings et al. 2012b)
Atlantic	Teleost fishes (Atlantic cod)	20 populations	Maximum per capita population growth rate (r_{max})	Age-at-maturity	Late age-at-maturity	(Myers and Fowlow 1997)
Pacific	Chondrichthyan fishes (sharks)	20 species	Rebound potential at MSY	Body size, age-at-maturity, maximum age	Late age-at-maturity, large maximum age	(Smith et al. 1998)

(B) Potential life history correlates of population status, usually measured as IUCN threat status categories, population trajectories including declines, recoveries and collapses, and population trajectories while controlling for exposure to fishing.

Geographic location	Taxonomic groups	# of sp. or pop.	Vulnerability metrics	Tested and accounted for fishing?	Potential life history correlates	Life history correlates of species vulnerability	Potential ecological and biogeographical correlates	Ecological and biogeographical correlates of species vulnerability	References
Global	Chondrichthyan fishes	227 sp.	IUCN Red List Categories	No	Body size	Large size	Habitat, range, environmental temperature	Small range size	(Field et al. 2009)
Global	Teleost fishes	386 sp.	IUCN Red List Categories	No	Body size	Large size	Habitat, range, environmental temperature	Small range, environmental temperature (deep-water sp.) and habitat (reef sp.)	(Field et al. 2009)
Global	Teleost and chondrichthyan fishes	12477 sp.	IUCN Red List Categories	No	Body size	Large size			(Olden et al. 2007)
Canada	Teleost and chondrichthyan fishes	34 sp.	IUCN Red List Categories	No	Body size, age-at-maturity	Late age-at-maturity and large body size	Latitude midpoint, depth point, fishing intensity	Deeper waters	(Anderson et al. 2011)
Global	Teleost and chondrichthyan fishes	353 sp.	IUCN Red List Categories	No	Interval between spawning events in years (which is correlated with degree of spawning migrations and parental care)	High interval between spawning events (in years), long-spawning migrations and parental care			(Jager et al. 2008)
Global	Teleost and chondrichthyan fishes	40 species	IUCN Red List Categories	No	Body size and Cheung's intrinsic vulnerability index	Greater intrinsic vulnerability			(Cheung et al. 2005)
Global	Chondrichthyan fishes	230 sp.	Locally extinct	No	Body size	Large size	Latitudinal range and depth range	None	(Dulvy and Reynolds 2002)
Global	Teleost fishes	223 pop., 120 sp.	Collapses (based on abundance data)	No	Longevity, age-at-maturity, maximum weight, maximum size, growth rate, fecundity, egg size	Fast growth rates	Trophic level	None	(Pinsky et al. 2011)
Global	Teleost fishes	223 pop., 120 sp.	Collapses (based on abundance data)	Yes	Longevity, age-at-maturity, maximum weight, maximum size, growth rate, fecundity, egg size	Fast growth rates and short lived	Trophic level	None	(Pinsky et al. 2011)
Global	Teleost fishes	458 sp.	Collapses (based on landing data)	No	Longevity, age-at-maturity, maximum weight, maximum size, growth rate, fecundity, egg size	Long-lived, late age-at-maturity, large body size and slow growth	Trophic level	None	(Pinsky et al. 2011)

Location	Taxa	Number	Trend	Life-history effect?	Traits/Method	Finding	Reference
Global	Teleost fishes	90 pop.	Population trends (declines and recoveries)	No	Several taxonomic groups with different life histories (Demersal vs pelagic clupeids vs other pelagics)	Demersal benthic species appear more vulnerable to fishing exploitation. Pelagics such as clupeids appear more resilient and have better recovery rates than the rest of the species or families.	(Hutchings 2000)
Irish Sea, and Bristol Channel, Western UK	Chondrichthyan fishes	7 sp.	Population trends (declines and increases)	Yes	Body size, growth rate and length-at-maturity	Large size	(Dulvy et al. 2000)
Northeast Atlantic Ocean	Teleost fishes	9 sp., 18 pop.	Population trends (declines and increases)	Yes	Body size, age-at-maturity, growth rate, fecundity at length of maturity and potential rate of population increase	Large size, late age-at-maturity and low potential rate of population increase	(Jennings et al. 1998)
Philippines	Teleost fishes	Various families	Population trends (declines and increases)	Yes	Three semi-quantitative codes were assigned to each species based on their life history trait [Body size, longevity, rates of natural mortality, growth rate, recruitment]. Codes were mainly by maximum size.	Large size	(Russ and Alcala 1998)
North Sea	Teleost and chondrichthyan fishes	23 sp.	Population trends (declines and increases)	Yes	Body size, length and age-at-maturity, growth, average annual fecundity, potential rate of population increase	Large size, large size and late age-at-maturity, slow grow rate, low potential rates of population increase	(Jennings et al. 1999b)
Fiji	Teleost fishes	33 sp.	Population trends (declines and increases)	Yes	Body size	Large size	(Jennings et al. 1999c)
Global	Teleost and chondrichthyan fishes (all marine fishes vs seamount fishes)	14924 non seamount fishes, 821 seamount fishes	Simulated population trends	Yes	Cheung's intrinsic vulnerability index	Greater intrinsic vulnerability which was correlated with a longer life span, later sexual maturation, slower growth and lower natural mortality	(Morato et al. 2006)

Northern South China Sea	Teleost and chondrichthyan fishes	17 sp. groups	Population trends (declines)	No	Cheung's intrinsic vulnerability index	Greater intrinsic vulnerability	(Cheung and Pitcher 2008)
North Sea	Teleost and chondrichthyan fishes	23 sp.	Population trends (declines and increases)	Yes	Body size, age-at-maturity and Cheung's intrinsic vulnerability index	Greater intrinsic vulnerability, larger size, later age-at-maturity	(Cheung et al. 2005)
Fiji	Teleost fishes	13 sp.	Population trends (declines and increases)	Yes	Body size and Cheung's intrinsic vulnerability index	Greater intrinsic vulnerability, larger size	(Cheung et al. 2005)

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Table 5.S2 *List of scombrid populations including fisheries management reference points and sources of stock assessments.*

Species Latin name	Population common name	$B_{current}/B_{MSY}$	$F_{current}/F_{MSY}$	F_{MSY}	Current year	Sources of the stock assessments
Scomber scombrus	Atlantic mackerel, North East	0.98	0.73	0.3	2006	(ICES 2007)
Scomberomorus cavalla	King mackerel, Gulf of Mexico	0.95	0.8	0.18	2002	(Ortiz 2004)
Scomberomorus cavalla	King mackerel, U.S. Atlantic	0.98	0.72	0.25	2002	(NMFS 2003)
Scomberomorus maculatus	Spanish mackerel, Gulf of Mexico	1.07	0.6	0.4	2002	(NMFS 2003)
Scomberomorus maculatus	Spanish mackerel, U.S. Atlantic	1.44	0.65	0.32	2002	(NMFS 2003)
Thunnus alalunga	Albacore tuna, North Atlantic	0.81	1.49	0.12	2005	(ICCAT 2008a)
Thunnus alalunga	Albacore tuna, South Atlantic	0.8	0.71	0.27	2005	(ICCAT 2008a)
Thunnus thynnus	Atlantic bluefin tuna, East	0.245	3.23	0.105	2007	(ICCAT 2007)
Thunnus thynnus	Atlantic bluefin tuna, West	0.41	1.725	0.07	2004	(ICCAT 2007)
Thunnus obesus	Bigeye tuna, Atlantic	0.992	0.91	0.23	2005	(ICCAT 2008b)
Thunnus albacares	Yellowfin tuna, Atlantic	1.09	0.84	0.7	2006	(ICCAT 2008c)
Thunnus obesus	Bigeye tuna, Indian	1.17	0.89	0.39	2008	(IOTC 2009)
Thunnus maccoyii	Southern bluefin tuna	0.17	1.91	0.04	2008	(CCSBT 2009)
Thunnus albacares	Yellowfin tuna, Indian	1	1.4	0.2	2007	(IOTC 2009)
Scomber japonicus	Chub mackerel, Chilean	2.78	2.07	0.57	2004	(Canales 2006)
Scomber japonicus	Chub mackerel, Japanese	<1	-	-	2005-2007	(Watanabe et al. 2008)
Scomber japonicus	Chub mackerel, North East Pacific	-	-	-	-	(Dorval et al. 2007)
Scomber japonicus	Chub mackerel, Tsushima Current Pacific	<1	-	0.46	2008	(Yukami et al. 2008)
Thunnus alalunga	Albacore tuna, North Pacific	-	-	-	-	(ISC 2007)
Thunnus alalunga	Albacore tuna, South Pacific	2.99	0.44	0.18	2004-2006	(Hoyle et al. 2008)
Thunnus obesus	Bigeye tuna, East Pacific	0.9	1.2	0.2	2005-2007	(Aires-da-Silva and Maunder 2008)
Thunnus obesus	Bigeye tuna, West Pacific	1.19	1.44	0.27	2003-2006	(Langley et al. 2008)
Thunnus orientalis	Pacific bluefin tuna	-	-	-	-	(ISC 2008)
Katsuwonus pelamis	Skipjack tuna, West Pacific	2.67	0.34	0.92	2005-2008	(Hoyle et al. 2010)
Thunnus albacares	Yellowfin tuna, East Pacific	1.05	0.8	0.94	2005-2007	(Maunder and Aires-Da-Silva 2008)
Thunnus albacares	Yellowfin tuna, West Pacific	1.11	0.95	0.24	2002-2005	(Langley et al. 2007)

Sources of the Stock Assessments of Table 5.S2

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Table 5.S3 Life history traits for 26 populations of scombrids.

In order to maximize the number of populations included in the analyses, we estimated missing life history information (estimates values are shown with *) following a set of rules (see methods).

Population name	Code	L_{max} (cm)	L_{m50} (cm)	F_{abs} (# eggs)	F_{rel} (eggs/g)	F_{slope}	T_{max} (years)	k (1/years)	T_{m50} (years)	Spw_{dur} (months)	Spw_{int} (days)
Skipjack tuna, West Pacific	SKJwp	86	46.4	341292	79.8	4.09	6	0.75	1.8*	9.0	3.1
Chub mackerel, Chilean	MASch	41	26.6	53168	117.0		9	0.18	2.7*	4.0	3.5*
Chub mackerel, Japanese	MASj	45	31.2	89200	158.0		12	0.33	2.7	4.0	5.7
Chub mackerel, North East Pacific	MASnep	63	30.6*	68400	168.0		14	0.33	2.7*	6.3	1.3
Chub mackerel, Tsushima Current Pacific	MAStcj	47	28.2	63018*	135.0*		8.83	0.45	1.0	3.3	3.5*
Atlantic mackerel, North east	MACnea	60	24.8		53.0		15	0.29	1.5	4.8	
King mackerel, Gulf of Mexico	KGMgm	158	61.7	1501462	140.0	3.05*	24	0.25	1.1	5.0	5.7
King mackerel, U.S. Atlantic	KGMwa	152	60.9	1139500	140.0	3.05*	26	0.18	2.0	4.5	3.7
Spanish mackerel, Gulf of Mexico	SSMgm	80	29.2*	74077*	143.0*		9	0.40	1.5*	3.0	
Spanish mackerel, U. S. Atlantic	SSMwa	79	29.2	74077	143.0		11	0.32	1.5*	3.3	
Albacore tuna, North Atlantic	ALBna	129	87.0*	1134946*	61.3*		10	0.26	4.5*	6.0	
Albacore tuna, North Pacific	ALBnp	120	87.0*	915000	50.8		10	0.27	4.5*	6.0	1.7
Albacore tuna, South Atlantic	ALBsa	130	87.0*	1134946*	61.3*		13	0.13	4.5*	5.4	1.5*
Albacore tuna, South Pacific	ALBsp	110	87.0	1200000	64.4		14	0.28	4.5	5.0	1.3
Yellowfin tuna, Atlantic	YFTa	200	108.6	2100000	54.2		6.5	0.36	2.4*	5.7	3.4
Yellowfin tuna, East Pacific	YFTep	232	92.7	2470736	67.3	3.23	6	0.59	2.4*	12.0	1.2
Yellowfin tuna, Indian	YFTi	185	110.4	2546062*	65.2*	3.49*	9	0.32	2.4*	5.0	1.9*
Yellowfin tuna, West Pacific	YFTwp	195	105.6	2705027	61.3	4.05	4.5	0.37	2.4	8.4	1.8
Southern bluefin tuna	SBF	245	158.9	6000000	57.0	7.53	41	0.15	11.5	3.5	1.1
Bigeye tuna, Atlantic	BETa	211	116.5	2462874*	48.4*	4.27*	12	0.16	2.1*	9.6	1.2*
Bigeye tuna, East Pacific	BETep	236	124.5	1451459	23.7	4.27*	13	0.30	2.1*	10.5	1.3
Bigeye tuna, Indian	BETi	178	110.4	2462874*	48.4*	4.27*	7	0.27	2.0	3.0	1.2*
Bigeye tuna, West Pacific	BETwp	192	109.4	2498098	49.3	4.27	15	0.28	2.2	12.0	1.1
Pacific bluefin tuna	PBF	300		16000000			26	0.14	4.0	3.0	3.3
Atlantic bluefin tuna, East	BFTea	304	103.3		92.8		22	0.08	3.0	1.8	1.2
Atlantic bluefin tuna, West	BFTwa	382	230.0		92.8*		35	0.14	11.5	3.0	1.2*

Table 5.S4 **Results from the Principal Component Analysis (PCA) examining the trait co-variation among populations of scombrids.**

(A) This PCA maximizes the number of life history traits including eight life history traits and only 22 populations of scombrids. (B) This PCA maximizes the number of populations including all 26 populations and only 4 life history traits. Both PCA confirmed the existence of the first two main axes of life history variation in scombrids. The first axis was driven by length-related traits raking species along a size continuum and the second axis was driven by time-related traits raking species along the slow-fast continuum of life histories. See PCA results in Figure S4.

A – PCA results including eight life history traits and 22 populations of scombrids

	Life history traits	PC1	PC2	PC3
Length-related traits	Maximum length L_{max} (cm)	**-0.454**	-0.077	0.396
	Length at 50% maturity L_{m50} (cm)	**-0.490**	-0.028	0.093
	Average batch fecundity F_b (# of oocytes)	**-0.471**	-0.021	0.260
	Relative fecundity F_{rel} (# of oocytes per gram)	**0.429**	0.183	0.189
Time-related traits	Empirical longevity T_{max} (years)	-0.079	**0.593**	0.240
	Growth coefficient k (1/years)	0.166	**-0.562**	0.098
	Age-at-maturity T_{m50} (years)	-0.260	**0.336**	-0.722
	Spawning duration (months)	-0.214	**-0.423**	-0.378
	% Variance explained	0.51	0.25	0.09

B - PCA results including three life history traits and 26 populations of scombrids

	Life history traits	PC1	PC2	PC3
Length-related traits	Maximum length L_{max} (cm)	**0.550**	-0.432	0.128
	Length at 50% maturity L_{m50} (cm)	**0.542**	-0.458	-0.011
Time-related traits	Empirical longevity T_{max} (years)	0.420	**0.604**	0.673
	Growth coefficient k (1/years)	-0.476	**-0.489**	0.729
	% Variance explained	0.61	0.29	0.08

Table 5.S5 **_Summary of the generalized regression models including all length-related and time-related life history traits sorted by AICc._**

Models evaluate the effects of fishing mortality and life histories on (A) the rates of decline in adult biomass, (B) the extents of decline in adult biomass and (C) current exploitation status of scombrids. Length-related traits include maximum size (Lmax) and length-at-maturity (Lm). Time-related traits include longevity (Tmax), age-at-maturity (Tm), growth rate (k). AICc, Akaike's information criterion with a correction for small sample sizes. df, number of parameters. l (θ), the value of the maximizes log-likelihood function; ΔAICc =AICci - min AIC, where AICci is the AICc for model i, and min AICc is the smallest AICc value in the set of models). wi , the Akaike weights,expresses the relative likelihoods of candidate models, with the weigh of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. R2, coefficient of determination.

A - Rate of decline in adult biomass

Models	df	l (θ)	AIC_c	ΔAIC_c	w_i	R^2
Relative fishing mortality + growth rate	23	4	-13.48	37.82	0	0.37
Relative fishing mortality	2	3	-15.76	39.11	1.29	0.2
Relative fishing mortality + longevity	24	4	-14.22	39.3	1.49	0.18
Relative fishing mortality + age-at-maturity	26	4	-14.65	40.15	2.33	0.12
Relative fishing mortality + maximum body size	12	4	-14.88	40.62	2.81	0.09
Relative fishing mortality + length-at-maturity	25	4	-15.57	41.99	4.17	0.05

B - Extent of decline in adult biomass

Models	df	l (θ)	AIC_c	ΔAIC_c	w_i	R^2
Relative fishing mortality +longevity	4	-5.38	21.62	0	0.34	0.30
Relative fishing mortality + growth rate	4	-5.49	21.85	0.22	0.3	0.29
Relative fishing mortality + age-at-maturity	4	-5.9	22.65	1.03	0.2	0.27
Relative fishing mortality	3	-8.09	23.77	2.15	0.11	0.08
Relative fishing mortality + length-at-maturity	4	-7.96	26.77	5.15	0.03	0.09
Relative fishing mortality + maximum body size	4	-8.03	26.93	5.3	0.02	0.08

C - Probability of being overfished

Models	df	l (θ)	AIC_c	ΔAIC_c	w_i
Relative fishing mortality + growth rate	3	-8.88	25.02	0	0.54
Relative fishing mortality + age-at-maturity	3	-10.02	27.3	2.28	0.17
Relative fishing mortality	2	-11.55	27.71	2.69	0.14
Relative fishing mortality + length-at-maturity	3	-11.19	29.64	4.62	0.05
Relative fishing mortality + longevity	3	-11.3	29.86	4.84	0.05
Relative fishing mortality + maximum body size	3	-11.54	30.34	5.33	0.04

Table 5.S6 *Summary of the generalized regression models including as predictor variables the first and second principal components (PC1 and PC2, respectively) and fishing mortality rates, sorted by AICc.*

Models evaluate the effects of fishing mortality and life histories on (A) the rates of decline in adult biomass, (B) the extents of decline in adult biomass and (C) current exploitation status of scombrid species. PC1 summarizes all the length related traits (L_{max} and L_m) into one variable, ranking populations along the size-continuum. Populations with a larger-maximum body, and large size at maturation have positive and higher scores than populations with smaller-maximum body size and smaller size at maturation. PC2 reduces the time related traits (T_{max}, k and T_m) into one variable ranking populations along slow-fast continuum. Longer-lived and slower growing species given their maximum body size, have positive and higher scores along PC2 than shorter-lived and faster-growing populations given their maximum body size. AICc, Akaike's information criterion with a correction for small sample sizes. df, number of parameters. l (θ), the value of the maximizes log-likelihood function; $\Delta AIC_c = AIC_{ci}$ - min AIC, where AIC_{ci} is the AIC_c for model i, and min AIC_c is the smallest AIC_c value in the set of models). w_i, the Akaike weights, expresses the relative likelihoods of candidate models, with the weight of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. R^2, coefficient of determination.

A - Rate of decline in adult biomass

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i	R^2
Relative fishing mortality + PC2	4	55.484	-100.1	0	0.872	0.3844
Relative fishing mortality	3	51.75	-95.9	4.21	0.106	0.0879
Relative fishing mortality + PC1	4	51.776	-92.7	7.42	0.021	0.0904

B – Extent of decline in adult biomass

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i	R^2
Relative fishing mortality	3	-82.692	173	0	0.428	0.1331
Relative fishing mortality + PC2	4	-81.102	173.1	0.08	0.412	0.2667
Relative fishing mortality + PC1	4	-82.051	175	1.97	0.16	0.1897

C – Probability of being overfished

Hypothesis	df	l (θ)	AIC$_c$	ΔAIC$_c$	w_i
Relative fishing mortality + PC2	3	-5.45	18.5	0	**0.435**
Relative fishing mortality	2	-7.01	18.8	0.27	0.38
Relative fishing mortality + PC1	3	-6.304	20.2	1.71	0.185

Chapter 6

Chapter 6.

General discussion and concluding remarks

Two global challenges hinder the implementation of successful ecosystem-based management in the world's fisheries. The first challenge reflects our limited and fragmentary understanding of the scale and extent of the impacts of fishing on marine species and marine ecosystems (Sala and Knowlton 2006, Crowder et al. 2008, Blanchard et al. 2010). The second challenge reflects our limited knowledge on the biological status for the immense majority of marine fish species (Reynolds et al. 2001, Dulvy et al. 2004, Costello et al. 2012). In this thesis I focus on the 51 scombrid species to provide new insights and some answers to these challenges using meta-analysis and comparative techniques. Specifically, I first quantify the impacts of fishing on this group of species within the last century and summarize their current exploitation status (Chapter 2). Second I prioritize life history research needs, and characterize the diversity of life history strategies in scombrid species, which is fundamental to our understanding of how species respond to human exploitation (Chapter 3 and 4), and third, I examine what aspects of their life histories makes scombrid species to be most vulnerable to fishing with the aim of advancing our abilities to diagnose what species might be most threatened in data-poor situations (Chapter 5). Next, I briefly summarize the main findings of each chapter and discuss their implications in the management and conservation of scombrids species. Then, I contextualize the main findings towards advancing the implementation of ecosystem considerations in the management of world's fisheries with a focus on scombrid fisheries, and discuss the many challenges ahead, and potential avenues for future work.

General summary

Tunas and their relatives dominate the world's largest ecosystems and sustain some of the most valuable fisheries. The impacts of fishing on these species have been debated intensively over the past decade, giving rise to divergent views on the scale and extent of the impacts of fisheries on pelagic ecosystems. In Chapter 2, I carry out a meta-analysis of biomass and fishing mortality trends across 26 populations of scombrids and provide the most accurate picture of the global population trajectories of tunas and mackerels within the last 50 years and summarize their current exploitation status. This study

resolves a decade long debate on the trajectory of tunas and the health of tuna populations globally from a fisheries management point of view. Overall, populations have declined, on average, by 60% over the past half century, but the decline in the total adult biomass is lower (52%), driven by a few abundant populations. Hence, this study reveals that tuna population declines are not as bad as previously thought. However, the meta-analysis of biomass trends raises the alarm for temperate tuna and mackerel populations, which have experience the steepest and largest declines in biomass in the last half century, and are mostly currently overexploited and under recovery management plans. The study also reveals that the fisheries management objectives of achieving maximum sustainable yield have been largely met for the majority of tuna populations. Thus, the majority of scombrid populations are fully exploited, which means that in the near short term there are few opportunities to expand catches in these fisheries without jeopardizing the long-term sustainability of these fisheries. There are some notable exceptions, the majority of mackerel and bluefin tuna populations are currently overfished and experiencing overfishing.

Chapter 2 also highlights three issues that need to be tackled with urgency: (1) tuna productivity is declining, as the Maximum Sustainable Yield (MSY) levels are lower than in the past (Allen 2010); (2) the current demand for tunas and mackerels and fishing capacity is increasing globally in a context where already there is overcapitalization and a sustainable increase of catches is limited (Chapter 2, Aranda et al. 2010, De Bruyn et al. 2013); and (3) the impacts of tuna fisheries on other less productive species such as sharks need to be better understood (Dulvy et al. 2008, Baum and Worm 2009, Gerrodette et al. 2012, Hunsicker 2012). Additionally, the study also proposes two solution that could alleviate some of the issues jeopardizing the long-term sustainability of scombrid fisheries: (1) the effective implementation of precautionary reference points by the tuna Regional Fisheries Management Organization (RFMOs) for those species under their mandates, a long standing recommendation of several United Nations Food and Agricultural Organization agreements and guidelines over the last 15 years; and (2) the development of stringent rebuilding plans and enforcement of current on-going recovery plans for those overexploited populations. The implementation of precautionary reference points and recovery plans can be enabled by other activities such as a reduction in the global fishing effort and a strict and efficient monitoring system in place. There are many benefits at stake. Ensuring that the fully exploited scombrid populations remain well managed and recovering exploited populations to healthy levels, will not only secure the

economic and social benefits that scombrid fisheries already produce worldwide, but also it could make fisheries more profitable in the long term (Sumaila et al. 2012).

Accurate life history information is vital for the development of quantitative fisheries stock assessments and in the fishery data-poor situations for the identification of vulnerable species. The global compilation and synthesis of life history data for the 51 species of scombrids in Chapter 3 identifies major biological gaps in life history research hindering the effective management and conservation of scombrid species, and prioritizes research needs for this group of species. Priorities in life history research are based on the combination of (1) biological gaps in knowledge, (2) the importance of their fisheries, and (3) IUCN Red List status. This synthesis reveals that the growth and reproductive biology of tunas and mackerel species have been more extensively studied than for Spanish mackerels and bonitos, although there are notable exceptions in all groups. It also shows that the reproductive biology of species, particularly fecundity, is the least studied biological aspect in scombrids. This synthesis raises the urgent need for more research on the life histories of the smaller coastal scombrid species, which although they have lower economic values in the global markets, they support diverse fisheries throughout their ranges and are an important source of wealth and food security to the local fishing communities of many countries. Scombrid fisheries are likely to continue to grow in the foreseeable future in a context where the economic resources to carry out life history research for all scombrids species are limited, therefore, this synthesis highlights the important gaps in biological knowledge and provides a priority setting for life history research in scombrid species. Thus, this study sets the life history research agenda for the next decades, provides guidance for management and conservation, and serves as a guide for biologists and resource managers interested in the biology, ecology, and management of scombrid species.

The 51 species of scombrids, which are widely distributed throughout the tropical, subtropical and temperate waters of the world's oceans, display diverse life history characteristics. Can the diversity of scombrid life histories be narrowed to a handful of strategies or dimensions? In Chapter 4, I analyze the life history patterns across scombrid species and how traits co-vary within this family and reveal that most of their life history variation can be explained along three main axes or dimensions: size, speed and reproductive schedule, which underlie scombrid life history strategies. Maximum body size, together with other size-related traits such as length at maturity, maximum weight or fecundity at length of maturity, governs the first axis of life history variation ranking species along a *small-large* continuum of life histories. Maximum size in scombrid species varies

over an order of magnitude in length from 31 cm in the Island mackerel (*Rastrelliger faughni*) to 372 cm in the Atlantic bluefin tuna (*Thunnus thynnus*). Time-related traits such as longevity, age at maturity and growth rates underlie the second axis of a *slow-fast* continuum depicting species which are longer lived and have slower growth rates given their maximum size, from species which are shorter lived and have faster growth rates given their maximum body size. Tropical species of scombrids, irrespective of their maximum size, such as the island mackerel (*Rastrelliger faughni*) and yellowfin tuna (*Thunnus albacares*) have the fastest life histories, while temperate species, irrespective of their sizes, such as Atlantic mackerel (*Scomber scombrus*) and Southern bluefin tuna (*Thunnus maccoyii*) have the slowest life histories among all the scombrid species. Fecundity-related traits, such as fecundity at length of maturity and the rate of change of fecundity with size, underlies the third axis describing the schedule of reproductive allocation in fishes. Although the first two axes of life history variation are well supported in fishes as well other vertebrate groups such as birds, reptiles and mammals (Gaillard et al. 1989, Saether et al. 2002, Bielby et al. 2007), a further third axis of life history variation is less well supported and its interpretation varies among groups (Rochet et al. 2000, Dobson 2007). Moreover, within the larger envelop of fish life histories strategies – the Opportunistic- Periodic-Equilibrium triangular model of fish life histories of Winemiller and Rose 1992 – scombrids display life history characteristics between the Opportunistic and Periodic strategists, with tropical mackerel species being the best example of an Opportunistic strategists, and temperate bluefin tuna species providing good examples of Periodic strategists. The life history attributes of species are major determinants of their population dynamics and underpin their sustainable exploitation and management. In data-poor situation where species are subject to intense fisheries and their current exploitation status is unknown and uncertain, the knowledge of their life histories and life history strategies, particularly when presented in a comparative framework, become very valuable, since they can provide a starting framework in support of management (King and McFarlane 2003).

What life history traits best diagnose those species most likely to decline and be overfished? What scombrid species are most vulnerable to fishing? In Chapter 5, I examine the role of life histories and fishing in determining the population trajectories and current exploitation status of scombrids. My research reveals that the life history traits of growth and longevity are the best predictors of both rates and extent of decline in adult biomass and the current exploitation status of scombrid populations. After controlling for fishing mortality rates, scombrid populations with slow life histories (slow growth rates and

large longevities given their maximum body size), which are mostly found in temperate climates, are more likely to have experienced faster and larger declines and have a higher probability of being overfished. This study suggests temperate scombrids such as the Atlantic bluefin tuna (*Thunnus thynnus*) and chub mackerel (*Scomber japonicus*) are more sensitive to fisheries exploitation. Because the life history strategies of temperate scombrid fish species differ from their tropical counterparts in many aspects, these differences need to be taken into account for fisheries management. Temperate scombrids tend to be longer-lived, and thus, have well-evolved age structures which are essential to endure long periods of poor recruitment during unfavorable environmental conditions (Beamish et al. 2006, Rouyer et al. 2011). However, traditional fisheries management is not yet well suited to maintain and protect the naturally evolved aspects of their life histories, particularly for longer-lived species(Longhurst 2002). Moreover, the original motivation of this study was to advance our understanding of the links between species life history and their vulnerability to fishing to build methods and create simple "rules-of-thumb" based on the life histories of the species to identify the most sensitive species to fishing and focus resources in data-poor situations. I agree with previous studies that when only maximum size of the species is known, it is probably the best surrogate of species sensitivity to fishing (Jennings et al. 1998, Jennings et al. 1999c, Reynolds 2003, Reynolds et al. 2005). However, when more life history data are available, time-related traits such growth and longevity in addition to maximum size, should be the preferred source of information to rank species sensitivities to fishing exploitation and to plan effective conservation strategies in data-poor situations.

Implications for management and conservation, challenges ahead and future work

This thesis provides the most accurate picture of the global population trajectories of tunas and mackerels within the last 50 years and documents widespread declines in the adult biomass of scombrid species in all the world's oceans (Chapter 2). Moreover, there is also compelling evidence that other predatory fishes such as billfishes and sharks have experienced widespread declines in abundances globally due to fisheries exploitation (Myers and Worm 2005b, Sibert et al. 2006, Hutchings et al. 2010). While there is an increasing understanding of the impacts of global fisheries on single species, at least for the commercially important species, the most pressing question now is to understand and forecast the ecological consequences of such declines in abundance in oceanic marine

food webs (Heithaus et al. 2008, Bundy et al. 2012). Successful ecosystem-based fisheries management requires both, first to understand the impacts of fishing on single species, and second to understand the ecological effects of fishing on the structure and functioning of the marine food webs and ecosystems, which is proven challenging (Pikitch et al. 2004, Beddington et al. 2007, Garcia 2010). Large removals of top predators such as large scombrid species can reduce species richness, cause trophic cascades and declines in structural diversity in marine ecosystems, as we have learned from coastal systems such as kelp forest, rocky shores and freshwater systems (Knowlton 1992, Menge 1995, Pinnegar et al. 2000, Scheffer et al. 2005). However, in oceanic habitats, the empirical evidence of the ecological effects of fishing is more scarce, fragmentary and has been little studied, fueling different views about the strength of top-down control of oceanic predators (Cury et al. 2003, Kitchell et al. 2006, Essington 2007, Baum and Worm 2009, Coll and Libralato 2011). Empirical studies and ecosystem models are slowly providing new insights about the roles of scombrid, billfish and shark species as apex predators and mesopredators in oceanic ecosystems, and quantifying the strength of the species interactions and how these communities are affected by fishing (Kitchell et al. 1999, Cox et al. 2002, Kitchell et al. 2006, Essington 2007, Ferretti et al. 2010, Hunsicker 2012). Given the difficulty of carrying out large scale experimental studies in marine habitats, ecosystem models (e.g.Ecopath and Ecosim) have become a popular and valuable tool to simulate the ecological consequences of fishing on marine ecosystems and provide guidelines for management. However, these types of models have not been widely applied to simulate the ecological consequences of fishing in oceanic habitats, with the exception of the Pacific Ocean (Kitchell et al. 1999, Cox et al. 2002, Allain 2005, Essington 2007). Despite positive management stories and signs of species recovery to healthy management levels in some regions of the word (Worm et al. 2009), fishing pressure is likely to continue increasing, driving further declines in species abundances and biodiversity (Swartz et al. 2010, Anticamara et al. 2011, Watson et al. 2012). Long-term monitoring programs in combination with simulation ecosystem models are urgently needed in order to identify the functional roles of species in the open-ocean communities, identify predatory-prey interactions and identify which species have the stronger roles in those communities, so early symptoms of changes in ocean communities are identified in advance to develop policy guidelines where ecosystem considerations are taken into account in the management of fisheries (Kitchell et al. 2006, Essington 2007, Baum and Worm 2009). In my opinion, this area of research is urgently needed in the Atlantic and Indian oceans where fishing induced reductions of large predatory fishes from the oceanic food webs are least understood.

Marine fish species with slow life histories (late maturing, slow growing and long-lived), may warrant greater conservation concern given the current traditional fisheries management strategies (Chapter 5) (Longhurst 1998a, 2002). My research suggests scombrids species with slow life histories, mostly temperate tuna and mackerel populations, have experienced the fastest and greatest decline in adult biomass and have a higher probability of being overfished, after fishing mortality rates have been controlled for. These findings concur with emerging demands to develop more precautionary fishing management strategies; species with slow life histories may require a management strategy that maintains their age structures and protects age diversity (King and McFarlane 2003, Beamish et al. 2006, Garcia et al. 2012, Law et al. 2012). However, fisheries management traditionally has focused on maintaining minimum biomass levels, which in part, is a reflection of the lack of biological realisms in the traditional stock assessment models (Kuparinen et al. 2012). One way to move forward is to improve the biological realisms of stock assessments and management decision made by more effectively incorporating the information from other fields such as life history and ecological theory as well as borrowing information from comparable species (Ulltang 1996, Mangel and Levin 2005, Kuparinen et al. 2012). Moreover, my research also suggests that time-related life history traits such as growth and longevity, describing the slow-fast continuum of life histories in scombrids, are the best proxies to rank scombrid species according to their sensitivities to fishing exploitation. These findings have implications for future development and application of risk-assessment methods in data-poor contexts, which requires identifying what aspects of the species biology makes them most vulnerable to fishing exploitation. In data-poor situations, simple methods that are pragmatic and generalist can ease the implementation of ecosystem based fisheries management in many regions of the world where lack of data and finite capacity of resources impedes the assessments of species and populations with low economic value.

Understanding the biology of vulnerability and the biology of extinction in marine fishes is in its infancy (Sadovy 2001, Dulvy et al. 2003, Cheung et al. 2005). In this thesis, I examined the role of life histories and fishing in determining the population trajectories of scombrids and their current exploitation status. These analyses used as a proxy of vulnerability the following three measures: rates of declines in biomass, extent of decline in biomass, and the current exploitation status of populations (Chapter 5). It is not yet known how or to what extent these proxies reflect vulnerability in marine species and ultimately extinction risk, in part because the biology of vulnerability and the biology of extinction is still poorly known (Cheung et al. 2005, Reynolds et al. 2005, Briggs 2010).

However, in the last decade there have been several advances in this field. Some myths have been reversed: (1) empirical studies have now repeatedly shown that high fecundities do not confer teleost fishes with higher recovery potential and lower risk of extinction, as often assumed (Sadovy 2001, Denney et al. 2002, Hutchings et al. 2012b) (2) the recovery potential of teleost fishes is not lower than in terrestrial mammals, as often claimed (Hutchings et al. 2012b). Moreover, there is also an increasing recognition that age diversity and longevity might be key considerations to protect in exploited populations, which might be a factor impeding the recovery of some populations from low population biomasses (Longhurst 1998a, Hutchings and Reynolds 2004b, Hutchings et al. 2012a). Despite some advances in the field, there are many questions to be answered. The population dynamics of species at low population sizes and how frequent and perverse are allee effects in marine fishes is poorly understood (Stephens and Sutherland 1999, Dulvy et al. 2004, Hutchings et al. 2012a, Keith and Hutchings 2012). Another key topic of research, in which marine species are lagging behind terrestrial species, is the calculations of extinction thresholds for which minimum population size is commonly used. The minimum viable population size is the size that would ensure the persistence of populations within a time frame (Dulvy et al. 2004, Traill et al. 2007, Flather et al. 2011). Further advances in these areas of research show great promise and potentially will improve the biology of vulnerability and extinction in marine fishes as well as encourage the development of methods to provide shortcuts in implementing ecosystem management in fisheries management.

My research has also shown that there are substantial gaps in biological knowledge hindering the management and conservation of many scombrid species that need to be addressed. The global meta-analysis of biomass trends revealed that the large majority of small tunnies, Spanish mackerels and mackerel species are in need of up-to-date age-structured fishery stock assessments (Chapter 2). Similarly, the global synthesis of life history data across the 51 species of scombrids also revealed relevant gaps in life history research for many of the small tunnies, Spanish mackerels and mackerel species (Chapter 3). Globally, the majority of the life history research and formal fishery evaluations has focused, and still is focusing, on the seven principal market tuna species and a few temperate mackerel species (although there are some exceptions), with less priority given to the life history research and management for the rest of scombrid species. Although I encourage more field and life history studies as well as the improvement of existing fishery stock assessments for the data-rich species of scombrids, and particularly those efforts that aim to increase the use of the available biological knowledge to increase

the biological realisms in stock assessment (Kuparinen et al. 2012); I also hope this thesis has raised the urgent need to focus more effort and resources for the smaller coastal scombrid species. I encourage future life history research as well as fishery evaluations to focus on scombrid species that need it the most and are potentially under the most threat. In terms of future life history research, a strategy would be to focus on scombrid species with large life history-data gaps that are currently targeted by commercial fisheries throughout their distributions and are listed in the Threatened or Data Deficient categories of the IUCN Red List (Chapter 3). Regarding future opportunities for fishery evaluations, I would focus resources on populations and species that are currently targeted by fisheries but never been evaluated formally or have stock assessments that are outdated (Chapter 2) and last and most important, focus on species with life histories towards the slow side of the slow-fast continuum of life histories, which are species that are slow-growing and potentially long-lived and therefore most sensitive to fishing exploitation (Chapter 4). The fisheries of small and coastal species of scombrid are still growing and the widespread perception that these fisheries are irrelevant in terms of catches or revenues has now been reversed in many regions of the world (Gillett et al. 2001, Pillai et al. 2002, Di Natale et al. 2009, Collette et al. 2011).

But who is ultimately in charge of the management and conservation of scombrid species? And who is in charge of evaluating and mitigating the wider ecosystem considerations in the management of single species fisheries? Many coastal species of scombrids, together with the principal market tuna species, are under the mandates of the tuna Regional Fisheries Management Organizations (RFMOs) because of their highly migratory nature and widespread coastal and oceanic distributions. Since their creation, the five tuna RFMOs have mostly focused their efforts, resources, and personnel into managing the principal market tuna species (Chapter 2). Even through the mandates of all the tuna RFMOS, except the CCSBT which only manages the southern bluefin tuna, include in their basis the responsibility of ensuring the management and conservation of the principal market tuna species as well as other tuna-like species (term that includes the billfishes and some of the smaller scombrid species) within their jurisdiction. Given the small number of fishery evaluations I found for non-principal market tuna species, it appears the current structure of tunas RFMOs might not be appropriate or might be lacking in capacity to provide quantitative scientific advice for the many of the small tunas, bonitos and Spanish mackerels, as well as other species interacting with tuna fisheries such as sharks under their jurisdictions. Moreover, although all the tuna RFMOs recognize the importance of incorporating ecological considerations and the Precautionary Approach into fisheries

management, these important points are not being implemented widely by the tuna RFMOs (Lodge et al. 2007, Mooney-Seus and Rosenberg 2007, Cullis-Suzuki and Pauly 2010). Nonetheless, the five tuna RFMOs have recently developed several initiatives to reverse this trend with the aim of incorporating and making more effective the Precautionary Approach as well as incorporating ecosystem considerations in their fisheries management (Lodge et al. 2007, De Bruyn et al. 2013). I would highlight the following three recent initiatives: (1) the creation of specialized working groups on small scombrid species and other tuna-like species, as well as the creation of working groups on ecosystems considerations; (2) the on-going progress to develop strategies to implement the FAO International Plan of Actions which addresses ecosystem consideration, and promotes the sustainability of marine resources; and (3) the creation of programs to collect more data on ecosystems, the environment, social and economic statistics, as well as monitoring plans for bycatch species. However, the on-going progress and implementation of these initiatives vary greatly among the tuna RFMOs, in part due to historical reasons and in part due to the lack of capabilities to implement them and lack of quality data which generally paralyze any attempt to carry out stock assessment evaluations for the non principal market tuna species (Lodge et al. 2007, Aranda et al. 2010, De Bruyn et al. 2013). Currently, it is imperative an effective cooperation among the five tuna RFMOs as well as the collaboration between the tuna RFMOs and others (e.g. GFCM) in order to reduce their different level of achievements as well as to standardize goals and expectations, share resources and knowledge, decrease duplicities and potentially increase their efficiency to manage tuna and tuna-like species under their jurisdictions. During the last few years, there have been several joint meetings between the tuna RFMOs (Kobe meetings) which have established the basis for their cooperation and joint commitments (Anonymous 2011). Although these initiatives are significantly shaping the path towards a more efficient way of combining resources, efforts and knowledge among the five tuna RFMOs, there is still much to be accomplished to ensure that these commitments are put in place and are translated into action and to secure the long term sustainability of all tuna and tuna like species and ensure that ecosystem considerations are taken into account in fisheries management.

Finally, I would like to emphasize that two main products of this thesis are two data sets - a compilation of 26 age-structured fishery stock assessments and a life history data set including 684 life history studies for the 51 species of scombrids. These data sets have already been used in several research projects and will continue to support new research projects in the future. In the past, these data sets supported the first IUCN Red List

assessment of scombrid species. I had the great opportunity to participate in the species evaluations as a member of the IUCN Tuna and Billfish Specialist group. These data sets were used in several tasks, as for example, to estimate the generation length of scombrid species, which is a key parameter used to apply the IUCN criteria and determine the Red List Status of species. This work resulted in the publication of the first global evaluation of the conservation status of all scombrid species using the International Union for Conservation of Nature (IUCN) Red List criteria (see Appendix B). Currently, these data sets are also supporting several research projects. I am carrying out a meta-analysis of trends in the age structure of scombrid species to quantify the magnitude of the changes in their age structures and determine whether these changes might be impairing their recruitment success and therefore their buffering capacity to sustain poor periods of recruitment or affecting their reproductive potential. Moreover, I am also collaborating on a project to develop a time-calibrated molecular phylogeny tree for the scombrids (family Scombridae). This molecular phylogeny in combination with the life history and ecological information assembled in this thesis will be used to examine the effect of phylogeny in the evolution of life histories in scombrids. These are two examples of ongoing projects, however I expect to continue working and exploiting these two data sets to support the management and conservation of scombrid species as well to increase our understanding on the direct and indirect ecological impacts of fishing on scombrid species and marine ecosystems. It is important these data sets continue to be updated, become publicly available, and become part of the larger existing fishery and life history data sets to promote further meta-analysis and comparative analyses in multiple topics in marine ecology and fisheries. In the last few decades, there has been an increasing impetus to develop global life history, fishery and extinction threat data sets; for example, (1) the Fishbase data sets compiles life history and ecological information for over 32,500 species of fish (Froese and Pauly 2013); (2) the FAO landings data set further completed but the Sea Around Us Project includes time series of catches for over 900 species (FAO 2008); (3) the RAM Legacy Stock Assessment Database includes fishery stock assessment derived-data (e.g. time series of biomass, fishing mortality rates as well as fisheries reference points) for over 300 fish stocks (Ricard et al. 2012); and (4) the IUCN Red List assessments provide a global data set including the species-specific global distributions, population status, habitat, ecology, major threats and conservation measures, which is used to assess the relative risk of extinction of species. The Global Marine Species Assessment, a joint initiative of IUCN and Conservation International, is currently under the task of completing the Red List assessments for approximately 20,000 marine species (Abdul Malak et al. 2011). All these data sets have their trade-offs, advantages and

limitations, but it is undisputable that they are being instrumental and valuable to test global hypothesis and to advance our understanding on the functioning and structure of marine ecosystems and the resilience of marine biodiversity and marine ecosystems to human perturbations and impacts. However, challenges lie ahead. On challenge is how to keep these data sets up to date, particularly the stock assessment database. Stock assessments are conducted regularly as new fisheries and biological data becomes available and the compilation and extraction of data from the stock assessments is laborious. Another challenge is how to efficiently integrate and connect the information from all these data sets (FishBase, FAO and the Sea Around Project, IUCN Red List assessments, and RAM Legacy Stock Assessment database). The integration or easily link among these data sets would foster more detailed analysis about the global status of the world's fisheries as well as engage more analyses to examine the role of life histories in determining species vulnerability to fishing, species recovery from overfishing and species risk of extinction, which potentially can assist in the management of data poor species in many regions of the world.

Concluding remarks

Our society is faced with the trade-off of exploiting marine fish species, which are a source of protein, employment and security, and at the same time, it is our responsibility to conserve and sustainably manage them for the benefit of humanity. Incorporating ecosystem considerations into fisheries management facilitates and balances this trade-off. This requires that informed choices and decisions must be made, based on the best scientific information, in order to achieve the best possible results. This thesis focus on scombrid species and provides new insights upon the global impacts of fishing on their population trajectories within the last 50 years. I reveal that total biomass of scombrids has been halved globally over the past half century and that most populations are currently fully exploited. This means that there are few opportunities to expand catches in these fisheries in the short term. I also identify major biological gaps in life history research and establish priorities in research needs for this group of species, raising the urgent need to focus more research on the life histories of the coastal scombrid species. Then, I turn my focus to examine the diversity of life histories in scombrid species and find that most of the life history variation can be simplified to three dimensions (governed by size, speed of life, and reproductive schedule), which underlie their life history strategies. Finally, this thesis provides insights about the biology of vulnerability in scombrid species

with the aim of advancing our ability to identify, *a priori*, the characteristics of species that render them most vulnerable to overfishing. I show that those scombrid populations with slowest life histories, mostly temperate tuna and mackerel populations, have experienced the fastest and greatest decline in adult biomass and have a higher probability of being overfished, after fishing mortality rates have been controlled for. The speed of life traits - growth rate and longevity - rather than maximum size as often suggested, are the best life history indicators of vulnerability to fishing in scombrids. Therefore, we recommend using them to identify and rank species sensitivies to fishing exploitation in order to plan effective conservation strategies in data-poor situations. My thesis can be considered as a case-study in the importance of accounting for the varying life history strategies of species when planning conservation and management strategies and highlights species with slow life histories may warrant greater conservation concern given the current traditional fisheries management strategies.

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Appendices

Appendix A.

Spanish summary of thesis

Esta tesis forma parte de un proyecto europeo titulado METAOCEANS "*Elucidating the structure and functioning of marine ecosystems through synthesis and comparative analysis*" (Metaoceans 2006). La motivación principal del proyecto METAOCEANS es capacitar a una nueva generación de científicos para utilizar técnicas nuevas y novedosas, como el meta-análisis y análisis comparativos, para sintetizar y explotar la gran cantidad de información sobre el mar generada por cientos de proyectos locales de investigación, con el fin de extraer una perspectiva global de la estructura y funcionamiento de los ecosistemas marinos. Siguiendo la visión del proyecto METAOCEANS, esta tesis aspira a aportar nuevos conocimientos sobre los efectos globales de la pesca en las especies de peces y ecosistemas marinos, y avanzar nuestra capacidad de predicción para identificar qué especies son más vulnerables a la pesca.

Hace casi dos décadas que surgió el movimiento para gestionar los recursos pesqueros con un enfoque ecosistémico. Este enfoque consiste en incorporar las consideraciones relativas al ecosistema a la gestión pesquera, y así evitar que el foco principal de la gestión se centre exclusivamente en maximizar las capturas de las especies objetivo. Este enfoque más holístico para la gestión de las pesquerías pretende garantizar un equilibrio entre la explotación de los recursos marinos y el mantenimiento de unos ecosistemas saludables (FAO 2003, Pikitch et al. 2004, Garcia 2010, Jennings and Rice 2011). Dos obstáculos globales están frenando nuestros avances en la implementación de una gestión basada en los ecosistemas en las pesquerías del mundo. El primer obstáculo refleja nuestro desconocimiento sobre la escala y el alcance de los impactos de la pesca sobre las especies y los ecosistemas marinos, ya que es limitado, fragmentario e incierto (Sala and Knowlton 2006, Crowder et al. 2008, Shin et al. 2010). El segundo obstáculo refleja nuestra ignorancia sobre la situación biológica para la inmensa mayoría de especies que están siendo directa o indirectamente afectadas por la pesca. Menos del 1% de especies de peces marinos han sido evaluados adecuadamente a nivel global (Dulvy et al. 2004, Costello et al. 2012, Ricard et al. 2012).

Esta tesis aborda estos dos desafíos globales empleando las especies de escómbridos como caso de estudio. Los escómbridos incluyen 51 especies de atunes, petos, bonitos y caballas (familia Scombridae), son peces depredadores y epipelágicos distribuidos por

todos los océanos del mundo en aguas tropicales y templadas (Collette and Nauen 1983). Sus ciclos de vida se limitan al uso de aguas marinas en el océano abierto, aunque algunas especies están asociadas con los arrecifes de coral y estuarios (Collette and Nauen 1983). Además de su papel ecológico clave como depredadores en los ecosistemas marinos, estas especies sostienen una de las pesquerías más importantes del mundo desde el punto de vista económico y social (Collette 2002, Pillai et al. 2002, Majkowski 2007, Di Natale et al. 2009, Miyake et al. 2010). Las pesquerías de escómbridos son una importante fuente de riqueza, empleo y seguridad alimentaria en muchas comunidades pesqueras en todo el mundo.

Hay dos razones principales por las cuales esta tesis se centra en las especies de escómbridos. En primer lugar, los efectos de la pesca sobre especies de peces pelágicos, en particular los grandes atunes, ha sido objeto en el pasado de intensos debates, dando lugar a distintas opiniones sobre cuál es el impacto de la pesca sobre las especies de atunes (Myers and Worm 2003, Hampton et al. 2005, Myers and Worm 2005a, Sibert et al. 2006). Dada la importancia económica, ecológica y social de las pesquerías de escómbridos en el mundo, uno esperaría conocer la escala y el alcance de los impactos de la pesca en este grupo de especies a nivel global, sin embargo la magnitud de los impactos son sorprendentemente inciertos. En 2003, una de las primeras síntesis de los impactos globales de la pesca en las poblaciones de peces concluyó que la biomasa de los grandes peces pelágicos, entre ellos los grandes atunes, había disminuido un 90% en los últimos 50 años a nivel global (Myers and Worm 2003). Este trabajo fue muy criticado por la comunidad científica porque utilizó como índice de abundancia las series temporales de capturas y esfuerzo de las flotas de los palangreros japoneses, lo que resultó en una sobreestimación de las disminuciones en abundancia (Walters 2003, Hampton et al. 2005, Polacheck 2006). Para la mayoría de las poblaciones de escómbridos existen en estos momentos evaluaciones de stock de buena calidad, que proporcionan datos fiables de la abundancia y la mortalidad por pesca en estas poblaciones durante los últimos 50 años. Las evaluaciones de stock deberían ser la fuente preferida de información para evaluar los efectos de la pesca sobre las poblaciones de peces y los ecosistemas (Polacheck 2006, Sibert et al. 2006, Worm et al. 2009). Dada la creciente disponibilidad de evaluaciones de stock para las poblaciones de escómbridos, parece oportuno evaluar los impactos globales de la pesca sobre este grupo de especies y evaluar el desarrollo de sus trayectorias y la sostenibilidad de sus pesquerías. En segundo lugar, la creciente importancia económica de los escómbridos durante los últimos 50 años ha dado lugar a un número relativamente elevado de estudios

biológicos y evaluaciones de stocks en estas especies. Esta fuente de información biológica y de pesquerías ofrece la oportunidad de estudiar la diversidad en historias de vida en esta familia de peces (familia Scombridae), información fundamental para comprender su distinta respuesta a la explotación humana y diagnosticar qué especies son más vulnerables a la pesca (Jennings et al. 1998, Jennings et al. 1999b). Potencialmente, un análisis comparativo de historias de vida entre múltiples especies con distintas estrategias de vida e historias de explotación pesquera, puede aportar información valiosa sobre qué características biológicas hacen que unas especies sean más vulnerables a la pesca que otras, y así apoyar la creación de planes de evaluación y conservación para gestionar pesquerías con escasez de datos (Jennings et al. 1998, Jennings et al. 1999b, Anderson et al. 2011).

Objetivos

El objetivo general de esta tesis es proporcionar las herramientas necesarias para gestionar de forma sostenible las pesquerías de escómbridos. Para ello, esta tesis trata de evaluar a escala global las trayectorias de biomasa de los escómbridos y su estado de explotación actual, proporcionando una imagen más precisa de los impactos globales de la pesca en este grupo de especies. Asimismo, otro objetivo primordial es evaluar la influencia de las distintas historias de vida de los escómbridos en sus trayectorias globales, con el fin de progresar en nuestra capacidad predictiva para identificar *a priori* qué especies son más vulnerables a la pesca.

Para alcanzar estos objetivos, esta tesis trata de explotar y sacar el mayor rendimiento posible a los datos ya existentes, analizándolos mediante técnicas novedosas, como el meta-análisis y métodos comparativos. Por lo tanto, se recopilaron datos biológicos y datos pesqueros para todas las especies de escómbridos a nivel global, lo que dio lugar a la construcción de dos bases de datos. La primera base de datos consiste en una recopilación de todas las evaluaciones de gestión disponibles, específicamente, evaluaciones de stock realizadas con métodos estructurados por edades. Esta base contiene un total de 26 evaluaciones para 26 poblaciones de 11 especies de escómbridos. La segunda base de datos consiste en una recopilación de caracteres biológicos que describen la historia de vida de las especies, incluyendo el tamaño corporal máximo, crecimiento, longevidad, tamaño y edad de madurez, época de desove y fecundidad de las 51 especies de escómbridos. Esta base de datos incluye información biológica extraída de 684 estudios publicados sobre la biología de las especies.

Para alcanzar el objetivo general de esta tesis, se abordan los siguientes objetivos específicos:

En el Capítulo 2 se evalúan las trayectorias globales de biomasa adulta de 26 poblaciones de escómbridos entre 1954 y 2006, y se cuantifica el impacto de la pesca en este grupo de especies a nivel global mediante modelos mixtos, incluyendo el alcance de los efectos por océano, por grupos taxonómicos y especies con diferentes historias de vida. ¿Ha disminuido la biomasa de los túnidos un 90% globalmente en el último medio siglo? y ¿Cuál es el estado actual de explotación de los escómbridos a nivel mundial? Se examina el estado de explotación actual en las poblaciones de escómbridos y se discute las implicaciones para la sostenibilidad a largo plazo en este grupo de especies.

En el Capítulo 3 se sintetiza toda la información biológica recopilada sobre la historia de vida de los escómbridos y se realiza una evaluación crítica para identificar donde existen carencias y falta de datos biológicos para las 51 especies de escómbridos. ¿Existen carencias críticas en el conocimiento de la biología de las especies que dificultan su gestión y conservación? Se hacen recomendaciones para priorizar esfuerzos y centrar los estudios biológicos para las especies que más lo necesitan.

En el Capítulo 4 se examinan los patrones principales de covarianza en los parámetros biológicos que describen las historias de vida de los escómbridos, con el objetivo de identificar y describir sus estrategias de vida. ¿Podemos simplificar la diversidad en las historias de vida y la variación existente en los parámetros biológicos de los escómbridos a un número reducido de estrategias vitales?

En el Capítulo 5 se utilizan los conocimientos obtenidos en los Capítulos 2, 3 y 4, para desarrollar varias hipótesis y así analizar el efecto de las historias de vida y de la presión pesquera en las trayectorias de biomasa de las poblaciones de escómbridos y su estado actual de explotación. ¿Qué especies de escómbridos son más vulnerables a la sobrepesca? ¿Podemos diagnosticar qué especies son más vulnerables a la sobrepesca basándonos en los parámetros biológicos que describen sus estrategias de vida? En este capítulo se pretende potenciar nuestra capacidad de predicción para identificar *a priori* qué especies son más vulnerables a la pesca.

Capítulo 2: Trayectorias globales de las poblaciones de atunes y especies afines

Las especies de escómbridos sostienen una de las pesquerías más importantes y valiosas del mundo. Durante la última década la magnitud y la escala de los impactos de la pesca sobre estas especies se ha debatido intensamente dando lugar a opiniones divergentes. En este estudio se lleva a cabo un meta-análisis global de las tendencias en biomasa en 26 poblaciones de escómbridos (atunes y caballas). Este análisis proporciona una imagen global de los impactos de la pesca en la biomasa de escómbridos en los últimos 50 años, y resume el estado actual de explotación en este grupo de especies. Así, este estudio resuelve un largo debate de más de una década sobre el estado de explotación de los atunes a nivel mundial desde el punto de vista de gestión pesquera. Globalmente, las poblaciones de escómbridos han disminuido un 60%, en promedio, durante el último medio siglo. La disminución de la biomasa total de adultos es menor (52%), ya que está mitigada por las poblaciones más abundantes y mejor gestionadas. Por lo tanto, este estudio revela que los descensos en biomasa en las poblaciones de atunes a nivel mundial no son tan alarmantes como se pensaba anteriormente. Sin embargo, el estudio muestra que las poblaciones de atunes y caballas de aguas templadas han experimentado los mayores descensos en biomasa en el último medio siglo, y estas poblaciones, en su mayoría, están actualmente sobreexplotadas y bajo planes de recuperación. Además, el estudio también revela que los objetivos de ordenación pesquera para lograr un rendimiento máximo sostenible de los recursos se han cumplido en gran medida para la mayoría de las poblaciones de escómbridos: actualmente la mayoría de las poblaciones están plenamente explotadas a nivel mundial. Esto significa que hay pocas oportunidades para aumentar las capturas en estas pesquerías sin poner en peligro la sostenibilidad a largo plazo de estas especies y sus pesquerías.

Este estudio resalta tres cuestiones que hay que abordar con urgencia: (1) la productividad en las poblaciones de atunes está disminuyendo, ya que el actual rendimiento máximo sostenible de las poblaciones es más bajo que hace unas décadas (Allen 2010); (2) la demanda actual de atún y la capacidad de pesca en las pesquerías de túnidos son cada vez mayores a nivel mundial, en un contexto donde ya existe una flota sobredimensionada y un aumento sostenible en las capturas es muy limitado (Aranda et al. 2010, De Bruyn et al. 2013); y (3) el impacto directo e indirecto de las pesquerías de escómbridos sobre los ecosistemas marinos y otras especies menos productivas, como

son las especies de tiburones, necesitan ser mejor cuantificados (Dulvy et al. 2008, Baum and Worm 2009, Gerrodette et al. 2012, Hunsicker 2012). Además, se proponen dos soluciones que podrían aliviar algunos de los problemas que están poniendo en peligro la sostenibilidad de las pesquerías de escómbridos a largo plazo: (1) la aplicación efectiva de los puntos de referencia biológicos con un enfoque precautorio por las Organizaciones Regionales de Ordenación Pesquera del atún (OROPs); y (2) el desarrollo de planes de recuperación rigurosos y su ejecución para recuperar a las poblaciones sobreexplotadas de escómbridos a niveles de biomasas saludables determinados por los puntos de referencia precautorios. La aplicación de los puntos de referencia precautorios y planes de recuperación requerirían de una reducción en el esfuerzo pesquero a nivel global, y de un sistema más estricto y eficaz de control de pesca. Hay muchos beneficios en juego. Asegurar que las poblaciones de escómbridos que se encuentran actualmente plenamente explotadas permanezcan bien gestionadas, y recuperar las poblaciones sobreexplotadas a niveles saludables, no sólo aseguraría los beneficios económicos y sociales que estas pesquerías ya producen, sino que también se podría aumentar la rentabilidad de estas pesquerías a largo plazo (Sumaila et al. 2012).

Capítulo 3: Determinación de prioridades en estudios biológicos en atunes y especies afines: implicaciones para su gestión y conservación

Para poder desarrollar evaluaciones de gestión y estrategias efectivas de conservación es vital tener un conocimiento preciso de los parámetros biológicos que describen los procesos de crecimiento y reproducción de las especies explotadas. Este estudio sintetiza los datos biológicos disponibles para las 51 especies de escómbridos a nivel global, identifica las principales carencias en información que actualmente están dificultando la gestión y conservación de estas especies, y establece prioridades en investigación. Las prioridades en investigación y futuros estudios biológicos para cada una de las especies de escómbridos se establecen siguiendo el siguiente criterio: (1) las carencias en información biológica específicas de cada especie, (2) la importancia de sus pesquerías, y (3) el estado de conservación establecido por la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza (UICN). Esta síntesis revela que los patrones de crecimiento y la biología reproductiva han sido relativamente bien estudiados en el grupo taxonómico de los atunes y caballas, y poco estudiados en las

especies de petos y bonitos, aunque hay excepciones notables en todos los grupos taxonómicos. El estudio también muestra que la biología reproductiva de las especies, en particular las estimas de fecundidad, es el aspecto biológico menos estudiado en las especies de escómbridos. Esta síntesis urge a centrar esfuerzos, recursos y nuevos estudios biológicos en las especies de escómbridos costeras, especialmente las especies de petos, bonitos y pequeños túnidos. Las especies costeras de escómbridos, a pesar de tener unos valores económicos bajos en los mercados mundiales en comparación con las especies de grandes atunes, sostienen pesquerías muy diversas y son una importante fuente de riqueza y seguridad alimentaria para muchas comunidades pesqueras en muchos países. Es muy probable que las pesquerías de escómbridos y la demanda mundial de estas especies continúe creciendo en el futuro, en un contexto donde los recursos económicos para llevar a cabo estudios biológicos son muy limitados. Por lo tanto, esta síntesis trata de identificar y resaltar donde existen las mayores carencias en conocimiento y establecer prioridades para las especies que más lo necesitan. Este estudio pretende servir como guía para los biólogos y gestores pesqueros interesados en la biología, ecología y gestión de las especies de escómbridos.

Capítulo 4: La vida en 3-D: estrategias de vida en atunes, caballas y bonitos

Las especies de escómbridos muestran características muy diversas en los componentes de sus historias de vida, como son la edad y tamaño de reproducción, fecundidad, crecimiento y longevidad. ¿Podemos simplificar esta diversidad en las historias de vida a un número reducido de estrategias vitales? Una evaluación de los patrones de covarianza entre los componentes de las historias de vida en las especies de escómbridos revela que la mayor parte de la variación en los parámetros biológicos puede ser explicada con tres ejes o dimensiones. El tamaño máximo corporal de las especies, junto con otros parámetros correlacionados con el tamaño máximo, como son el tamaño de madurez o fecundidad, gobiernan el primer eje de historias de vida. Este primer eje ordena a las especies a lo largo de un continuo de tamaños, de la más pequeña a la más grande. El tamaño máximo de los escómbridos varía desde 31 cm en la caballa tropical (*Rastrelliger faughni*) a 372 cm en el atún rojo del Atlántico (*Thunnus thynnus*). Los parámetros biológicos con unidades de medida de tiempo, tales como la longevidad, edad de madurez y las tasas de crecimiento, gobiernan el segundo eje, ordenando a las especies en un continuo lento-rápido. El continuo lento-rápido ordena a las especies desde la

especie con el ciclo de vida más rápido a la especie con el ciclo de vida más lento. Las especies de escómbridos con ciclos de vida lentos son más longevas y tienen tasas de crecimiento más lentas dado su tamaño máximo corporal; y las especies con ciclos de vida rápidos son menos longevas, y tienen tasas de crecimiento más rápido dado su tamaño máximo corporal. Las especies tropicales de escómbridos, con independencia de su tamaño corporal máximo, como caballa tropical (*Rastrelliger faughni*) y el atún aleta amarilla (*Thunnus albacares*), tienen un ciclo de vida rápido, mientras que las especies de clima templado, con independencia de su tamaño, como la caballa del Atlántico (*Scomber scombrus*) y el atún rojo del Sur (*Thunnus maccoyii*), tienen los ciclos de vida más lentos de todas las especies de escómbridos. Los parámetros biológicos relacionados con la fecundidad, tales como la estima de fecundidad en el tamaño de madurez de la especie y la velocidad de cambio de la fecundidad a medida que la especies aumentan en tamaño, gobiernan el tercer eje. Existen estudios en otras especies de peces y otros grupos taxonómicos como las aves, reptiles y mamíferos, que demuestran la existencia de los dos primeros ejes de variación en las historias de vida (Gaillard et al. 1989, Saether et al. 2002, Bielby et al. 2007). Sin embargo, el significado y la existencia del tercer eje varía entre grupos taxonómicos. Esto hace que una interpretación general del tercer eje para todos los organismos sea difícil (Rochet et al. 2000, Dobson 2007).

Por último, estudios comparativos de historias de vida en peces muestran tres tipos de estrategias genéricas en peces (1) Estrategia Oportunista; (2) Estrategia Periódica; y (3) Estrategia en Equilibrio. Estas estrategias describen un modelo triangular de historia de vida en peces (Winemiller and Rose 1992). Los escómbridos muestran rasgos y características biológicas en sus historias de vida típicas de especies entre la estrategia Oportunista y estrategia Periódica. Las caballas tropicales (*Rastrelliger* spp.) son el mejor ejemplo de especies con una estrategia Oportunista, y los atunes rojos de aguas templadas (*Thunnus thunnus, T. maccoyii* y *T. orientalis*) son el mejor ejemplo de especies con una estrategia Periódica. Los componentes de las historias de vida de las especies son los principales determinantes de su dinámica poblacional y de las tasas de explotación que pueden tolerar (Adams 1980). En situaciones donde las especies están sujetas a tasas de explotación pesquera elevadas y se desconoce su estado de explotación, el conocimiento de sus historias de vida y sus estrategias de vida pueden proporcionar una punto de partida a la hora de diseñar y apoyar planes de gestión y conservación efectivos (King and McFarlane 2003).

Capítulo 5: La velocidad de la vida y el declive en atunes y especies afines

¿Podemos diagnosticar qué especies de escómbridos son más vulnerables a la pesca basándonos en sus historias de vida? El Capítulo 5 examina el efecto de las historias de vida y de la presión pesquera en las trayectorias de biomasa de las poblaciones de escómbridos y su estado actual de explotación. Las poblaciones de escómbridos con historias de vida más lentas (con tasas de crecimiento lentas y longevidades altas), principalmente distribuidas en climas templados, han experimentado los mayores descensos en biomasa y tienen una mayor probabilidad de ser objeto de sobrepesca, incluso después de controlar las distintas tasas de mortalidad por pesca experimentadas por cada población durante su historia de explotación. La parámetros biológicos con unidades de medida de tiempo - la tasa de crecimiento y la longevidad - son los mejores indicadores de la vulnerabilidad de las especies de escómbridos a la pesca. Este estudio sugiere que los escómbridos de aguas templadas, como es el atún rojo del Atlántico (*Thunnus thynnus*) y la caballa del Atlántico (*Scomber scombrus*), son más sensibles a la explotación pesquera. La especies tropicales y templadas difieren en sus estrategias de vida en muchos aspectos, por lo tanto, estas diferencias deberían ser tomadas más en cuenta en los actuales planes de gestión de estas especies. Los escómbridos de aguas templadas son más longevos, por lo tanto, han desarrollado estructuras de edad que son esenciales para soportar largos períodos de bajo nivel de reclutamiento durante condiciones ambientales desfavorables (Beamish et al. 2006, Rouyer et al. 2011). Sin embargo, los actuales planes de gestión todavía no están diseñados para proteger las estructuras de edad en las poblaciones, sobre todo en las especies muy longevas (Longhurst 2002). Una de las motivaciones principales en este estudio es avanzar nuestra capacidad para identificar *a priori* las características de las especies que las hacen más vulnerables a la sobrepesca, creando métodos para diagnosticar especies sensibles a la pesca en situaciones con escasez de datos (Jennings et al. 1998, Jennings et al. 1999c, Reynolds 2003, Reynolds et al. 2005). Entre todos los parámetros biológicos estudiados, recomendamos usar los parámetros biológicos de crecimiento y longevidad, y no el tamaño máximo de las especies como se recomienda habitualmente, para clasificar a las especies de acuerdo a su sensibilidad a la pesca y usar esta información para planificar estrategias eficaces de conservación y gestión en situaciones de escasez de datos.

Conclusiones

Nuestra sociedad se enfrenta a la disyuntiva de explotar los recursos marinos, fuente de proteínas, empleo y seguridad, y al mismo tiempo, conservarlos y gestionarlos de manera sostenible. Una gestión pesquera basada en los ecosistemas facilita y equilibra este gran desafío. Sin embargo, esto requiere que la toma de decisiones estén basadas en la mejor información científica para lograr los mejores resultados posibles. Esta tesis aporta nuevos conocimientos sobre los impactos globales de la pesca en las especies de escómbridos, que incluye 51 especies de atunes, petos, bonitos y caballas, y avanza en nuestra capacidad para identificar *a priori* las características de las especies que las hacen más vulnerables a la sobrepesca.

En primer lugar, un meta-análisis global de las tendencias de la biomasa de adultos, muestra que las poblaciones de escómbridos han disminuido, en promedio, un 60% durante el último medio siglo. La disminución de la biomasa total de adultos es menor (52%), ya que está mitigada por las poblaciones más abundantes y mejor gestionadas. También, este estudio muestra que la mayoría de las poblaciones de escómbridos están plenamente explotadas. Esto significa que hay pocas oportunidades a corto plazo para aumentar las capturas de estas pesquerías. En segundo lugar, se identifican carencias y falta de datos biológicos para las 51 especies de escómbridos y se establecen prioridades para dirigir esfuerzos en investigación para las especies que más lo necesitan. Esta síntesis urge a centrar esfuerzos, recursos y nuevos estudios biológicos para las especies de escómbridos con distribuciones costeras, especialmente las especies de petos, bonitos y pequeños túnidos. En tercer lugar, se examina la diversidad de las historias de vida en los escómbridos, y se muestra que la mayor parte de la variación se puede simplificar en tres dimensiones (gobernadas por el tamaño máximo corporal, la velocidad de la vida y el calendario reproductivo). Por último, esta tesis proporciona información acerca de la biología de la vulnerabilidad en especies de escómbridos con el objetivo de avanzar en la identificación *a priori* de especies vulnerables a la pesca. Las poblaciones de escómbridos con historias de vida más lentas (con tasas de crecimiento lentas y longevidades altas), que se encuentran principalmente en climas templados, han experimentado los mayores descensos en biomasa, y tienen una mayor probabilidad de ser objeto de sobrepesca, incluso después de controlar las tasas de mortalidad por pesca experimentadas por cada población durante su historia de explotación. Los parámetros biológicos- la tasa de crecimiento y la longevidad - son los mejores indicadores de la vulnerabilidad de las especies a la pesca. Por lo tanto, se recomienda su utilización para

identificar y clasificar a las especies de acuerdo con su grado de sensibilidad a la explotación pesquera, con el fin de planificar estrategias de conservación eficaces en situaciones de escasez de datos. Esta tesis considera a los escómbridos como un caso de estudio para resaltar la importancia de las distintas estrategias de vida de las especies a la hora de planificar estrategias de conservación y gestión.

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Appendix B.

High value and long life - Double jeopardy for tunas and billfishes

CONSERVATION

High Value and Long Life—Double Jeopardy for Tunas and Billfishes

The first standardized, global assessment of these fishes, using Red List criteria, reveals threatened species needing protection.

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There is growing concern that in spite of the healthy status of several epipelagic (living near the surface) fish stocks (*1*), some scombrid (tunas, bonitos, mackerels, and Spanish mackerels) and billfish (swordfish and marlins) species are heavily overfished and that there is a lack of resolve to protect against overexploitation driven by high prices (*2–5*). Many populations are exploited by multinational fisheries whose regulation, from a political perspective, is exceedingly difficult. Thus, assessment and management is complicated and sometimes ineffective (*4*). Regional Fisheries Management Organizations (RFMOs) were created to manage and conserve scombrids and billfishes because of their transnational distributions and widespread economic importance (*6*). However, species-specific catch data for many scombrids and billfishes are not collected or are aggregated with other species. Even for the larger tunas, for which relatively rich data exist, population assessments and data are complex (*1*) and are difficult to combine across RFMOs, which prompts a need for alternative means of assessment.

We present here the first standardized data on the global distribution, abundance, population trends, and impact of major threats for all known species of scombrids and billfishes [see supporting online material (SOM) for details]. We used International Union for the Conservation of Nature (IUCN) Red List criteria, which focus on global threats to a species but have not previously been used for a commercially important group of marine organisms. This required synthesis of global data from numerous fisheries reports and scientific publications.

Our study is more optimistic than a previous, fundamentally different study using separate population data of 16 of the same species (*2*), as we show only five of those species meet the threshold for a threatened category. However, most of the long-lived, economically valuable species are considered threatened (see the figure). As these large-bodied scombrids and billfishes are at the top of the pelagic food web (*7*), population reduction of these predators may have significant effects on the upper trophic levels of the epipelagic ecosystem (*2*) and lead to cascading effects on lower trophic levels. Hence, there is an urgent need to establish the conservation status of this economically important group of species.

Red List Criteria Reveal Threats

The IUCN Red List Criteria provide a transparent, standardized, peer-reviewed means of global conservation status assessment (*8*). Red List assessments of fisheries species rely heavily on fisheries stock assessments, which provide reliable abundance data, and participation of scientists familiar with fishery management procedures and stock assessments. The IUCN criteria to determine population status are based on a risk-assessment theory that is different from

standard fisheries assessments and include metrics based on the symptoms of population decline such as range size and threats other than fishery pressure (*8*). Red List assessments differ from the objectives of fisheries management in focusing on global threats to a species rather than management of a particular stock of the species.

Of the 61 scombrid and billfish species assessed, 11 (18%) lacked adequate data and were classified as Data Deficient by IUCN criteria, 39 (64%) were Least Concern, four (7%) were Near Threatened, and seven (11%) met the threshold for a threatened category (Critically Endangered, Endangered, or Vulnerable) (*9, 10*). Five of the seven threatened species are tuna and billfishes: southern bluefin (*Thunnus maccoyii*, Critically Endangered, SBF on the chart); Atlantic bluefin (*T. thynnus*, Endangered, ABF); bigeye tuna (*T. obesus*, Vulnerable, BET); blue marlin (*Makaira nigricans*, Vulnerable, BUM); and white marlin (*Kajikia albida*, Vulnerable, WHM). All have relatively long generation lengths (e.g., greater than 4.7 years) and high economic value worldwide (see the chart). Generation length, the average age of reproducing individuals, is a measure of reproductive turnover and is longer for those species that are longer-lived and later to mature. Species with longer generation lengths would be expected to take longer to recover from population declines (*11*). Compared with most IUCN-assessed marine bony fishes, the proportion of threatened species among scombrids and billfishes is high, similar to other valuable and long-lived species such as marine mammals, marine turtles, sharks, and rays (SOM).

All three bluefin tuna species (southern bluefin, *Thunnus maccoyii*; Atlantic bluefin, *T. thynnus*; and Pacific bluefin, *T. orientalis*) are highly valued, long-lived, and large-bodied marine fishes, with geographically restricted spawning sites, as well as relatively short spawning periods of 1 or 2 months, all of which make them susceptible to collapse under continued excessive fishing pressure (*12*). Southern bluefin has already essentially crashed (its current adult biomass is about 5% of its estimated virgin biomass), a trend that is similar to the western Atlantic bluefin, whose popula-

tion was greatly reduced in the 1970s, with little sign that the population is rebuilding. Per kilogram, bluefin species are among the most expensive fresh seafood in the world and can reach extreme values in global markets. Their high value makes them likely to be exploited far beyond the maximum sustainable yield (MSY, the largest catch that can be taken from a species' stock over an indefinite period), and in danger of an anthropogenic Allee effect (low population densities lead to reduction of reproductive success and increased possibility of collapse) (*13*).

The two other threatened species are Spanish mackerels, which in contrast to the threatened tuna and billfish have relatively short generation lengths and low global average market values. Yet Australian spotted mackerel (*Scomberomorus munroi*, Vulnerable) is highly valued locally and is estimated to have rapidly declined over the past 10 to 15 years in waters off eastern Australia (see SOM). Monterey Spanish mackerel (*Scomberomorus concolor*) has disappeared from ~80% of its historical range (Monterey, California, to southern Baja, Mexico) and is considered Vulnerable on the basis of continued fishing pressure within its restricted range in the upper Gulf of California.

Although swordfish (*Xiphias gladius*, SWO on the chart) and Pacific bluefin (*Thunnus orientalis*, PBT) are among the more highly valued species assessed, they are listed as Least Concern. The swordfish is considered well managed in nearly all parts of its range (*14*). However, the only population assessment available for Pacific bluefin is highly uncertain, and decreasing mean age may indicate that the population may not be as healthy as portrayed (*15*).

Successes

There are examples of successful management and recovery of scombrids and bill-
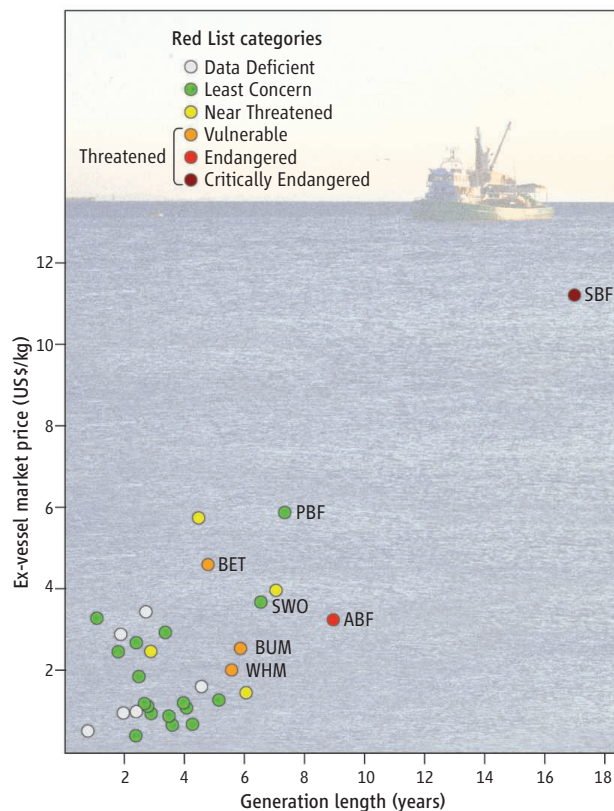
Endangerment of scombrids and billfishes. Generation lengths, average global ex-vessel price (1996–2006), and IUCN Red List categories for scombrids and billfishes. Prices received when landing catch, preprocessing. Both price and generation length data were available for only 32 of 61 species assessed; 29 remaining species, including threatened Australian spotted mackerel and Monterey Spanish mackerel, not shown. Details in SOM.

fishes. Although the highly valued eastern population of Atlantic bluefin was recently exploited at three times the MSY, reduction of the total allowable catch, divided among country-specific quotas, and stricter monitoring and compliance measures have led to recent catch reductions of almost 75% over the past few years (*14*). The North Atlantic swordfish (*14*) and four populations of Spanish mackerels off the southeastern United States have also been rebuilt after years of overfishing.

The future of threatened scombrids and billfishes rests in the ability of RFMOs and fishing nations to properly manage these species. Southern and Atlantic bluefin populations have been so reduced that the most expeditious way to rebuild abundances and avoid collapse with great certainty is to shut down the fishery until stocks are rebuilt to healthy levels. This would cause substantial economic hardship and hinder the ability of RFMOs to control fishing because of the increased incentive for illegal fishing that would be created. Strong deterrents

to illegal fishing are needed, such as controlled international trade through a listing on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), although such a listing would not be a substitute for effective management by the RFMOs (*3*, *16*). Reducing fishing-induced mortality rates to well below MSY, to allow for uncertainties in the stock assessments, should allow recovery to begin. These IUCN Red List assessments, together with lessons learned from past failures and successes, should help RFMOs improve their management of some of the world's most valuable fishery resources.

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Supporting Online Material for

High Value and Long Life—Double Jeopardy for Tunas and Billfishes

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This PDF file includes

Materials and Methods
SOM Text
Figs. S1 to S3
Tables S1 to S4
References

Supporting Online Material

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1. Introduction

1.1 IUCN Tuna and Billfish Specialist Group

Under the IUCN Species Survival Commission (SSC), the Tuna and Billfish Specialist Group (TBSG) was created in 2009 and is currently chaired by Dr. Bruce B. Collette. SSC Specialist Groups are networks of experts on specific taxa who volunteer their time and expertise to produce and disseminate scientific information for the effective delivery of biodiversity conservation. As many of the world's marine fishes are considered to be affected by a number of anthropogenic impacts, including overfishing, destructive fishing practices, pollution, invasive species, and disease (*1*, *2*), one of the first tasks of the newly formed TBSG was to evaluate the population and conservation status of all known species of scombrids, which include the tunas, bonitos, Spanish mackerels and mackerels (Scombridae), and billfishes (Istiophoridae and

Xiphiidae) under the *IUCN Red List Categories and Criteria*. Prior to the formation of the TBSG and the results presented here, IUCN Red List assessments were only available for six scombrid and billfish species, all of which were made in 1996 and were severely outdated and lacked comprehensive data.

1.2 Global Marine Species Assessment

IUCN Red List scombrid and billfish species assessments were conducted under the guidance of the Global Marine Species Assessment (GMSA), a joint initiative of the IUCN Species Survival Commission–Species Programme and Conservation International, based at Old Dominion University, in Norfolk, VA. Created in 2005, the GMSA is tasked with assessing the extinction risk of 20,000 marine species in complete taxonomic groups for inclusion on the *IUCN Red List of Threatened Species* (http://sci.odu.edu/gmsa/). Priority species groups for assessment include all of the world's known marine vertebrates; primary habitat producers such as corals, seagrasses and mangroves; and selected invertebrates of families of crustaceans, echinoderms, and molluscs. The GMSA directly assists IUCN Species Specialist Groups that are focused on marine taxa with the Red Listing process, including the IUCN Tuna and Billfish Specialist Group. Assessments are ongoing, and almost 10,000 species have been assessed under the guidance of the GMSA for the *IUCN Red List of Threatened Species* as of 2010.

1.3 Biology and Physiology of Scombrids and Billfishes

Scombrids and billfishes are distributed throughout the world's oceans, primarily occupying a variety of epipelagic coastal and oceanic tropical and temperate marine habitats. They are highly evolved fishes, with superlative adaptations to the epipelagic environment. The fusiform body shape, anterior corselet, finlets following the dorsal and anal fins, and the keel on the caudal peduncle all help to make scombrids among the fastest swimming fishes. In addition, the higher tunas (tribe Thunnini, Fig. S1) have a counter-current heat-exchanger system that allows the heat of muscular contraction to stay in the body of the fish rather than being dissipated at the gills in oxygen exchange, as happens in almost all other fishes (*3*). Having a warm stomach speeds digestion so that scombrids can process food much faster than other fishes. Billfishes (suborder Xiphioidei) have a rounded bill (marlins and spearfishes, Istiophoridae) or a dorso-ventrally flattened bill (swordfish, Xiphiidae) that may be involved in high-speed swimming but is also used to immobilize their prey. Supreme adaptation to epipelagic predation has consequences, as scombrids and billfishes are also highly desirable to humans as top predators.

Scombrid and billfish species exhibit a great diversity in life history and ecological traits. The largest billfish species, the Blue Marlin (*Makaira nigricans*), and largest scombrid species, the Atlantic Bluefin (*Thunnus thynnus*), can grow to more than 4 meters long. By contrast, the smallest scombrid species, the Indian Mackerel (*Rastrelliger faughni*), only grows to a maximum of 31 cm (*4*). Body size is strongly related to other important biological processes and, therefore, other life history traits, such as the species' length at first maturity, longevity, and growth rate. These traits also vary greatly across species. Among the scombrids, longevity ranges from just 1 year in the Short Mackerel (*Rastrelliger brachysoma)* to about 40 years in the Southern Bluefin (*Thunnus maccoyii*) (*5, 6*). Spawning patterns are also diverse and complex. Some tropical species such as Skipjack (*Katsuwonus pelamis*) spawn continuously all year throughout vast

areas of tropical and subtropical oceans. Some of the more temperate scombrids, such as the Bluefins undertake annual long migrations to spawn in specific areas at only certain times of the year (*7*). The majority of species form large schools, but some species, such as Wahoo (*Acanthocybium solandri*), are frequently solitary or may form small and loose aggregations.

2. Methods

2.1 Summary of IUCN Red List Process

The *IUCN Red List Categories and Criteria* (*8*) were applied to 61 species in the families Scombridae (tunas, bonitos, Spanish mackerels, and mackerels); Istiophoridae (billfishes); and Xiphiidae (swordfish). To conduct the assessments, species-specific data were compiled and reviewed in collaboration with regional and international scientists. Review of data and application of Red List criteria to each species was conducted at three regional workshops, covering the Eastern Pacific, Indo-Pacific and Atlantic populations and species, and at a final synthesis workshop. The resulting assessments were externally reviewed by additional experts, and accurate application of the IUCN Red List criteria was reviewed by IUCN Species Programme Red List Officers. All data, data sources, and complete results will be freely and publically available within each species Red List account on the *IUCN Red List of Threatened Species* (www.iucnredlist.org) when they are officially published on the next website update in November 2011. Until then, draft accounts are available on the GMSA website (http://www.sci.odu.edu/gmsa/).

2.2 Data compilation for IUCN Red List Assessments

Data on each species taxonomy, distribution, population status and trends, habitat, ecology, life history, major threats, and conservation measures were compiled from available literature and stock assessments, and from experts and members of the TBSG. Digital maps of each species distribution were created with GIS.

Direct comparisons of stock assessments with Red List assessments often show a similar degree of accuracy in reflecting predictability of adverse effects of fishing practices (*9*). Evaluation of stock status from fisheries stock assessments typically correspond closely with Red List Assessment Categories (e.g., "Not Known," "Moderately Exploited and Fully Exploited," "Overexploited," and "Depleted" are similar to "Data Deficient," "Least Concern," "Near-Threatened," and "Vulnerable" in Red List categories (*10*). However, Red List assessments were not based on fisheries stock assessment status categories. Instead, species and population specific data—including catch landings, catch-per-unit effort (CPUE) information and when available, estimates of total biomass or adult biomass—were extracted from publically available stock assessments.

2.3 Red List Assessment Process

In collaboration with the TBSG, the GSMA conducted 4 IUCN Red List Workshops to assess the world's scombrid and billfish species: one to assess Eastern Tropical Pacific populations and species held in collaboration with Instituto del Mar del Peru in Lima, Peru, in September 2008; a second to assess Indo-West Pacific populations and species held in collaboration with Academia

Sinica in Taipei, Taiwan, in December 2009; a third to assess Atlantic populations and species held in collaboration with Instituto Chico Mendes de Conservação da Biodiversidade in Brasilia, Brazil, in September 2010; and a fourth to synthesize results for circumglobal species held in collaboration with the International Seafood Sustainability Foundation and the International Fish and Game Association in Fort Lauderdale, Florida, in February 2011.

Together, these IUCN Red List Workshops brought together more than 45 of the world's scombrid and billfish experts, including fisheries scientists, biologists, and taxonomists (Table S1), to review and synthesize regional and global data on each species, to apply the criteria of the *IUCN Red List of Threatened Species*, and to assign each species an IUCN Red List category. Species information and final Red List assessment accounts were then sent to additional experts who were not at the workshops to review the assessments. Technical application of the criteria was checked by IUCN Species Programme Red List staff. This methodology ensures a standardized, transparent, and peer-reviewed process to determine the global population and conservation status of each species.

2.4 IUCN Red List Criteria

The *IUCN Red List Categories and Criteria* are the most widely accepted system for classifying extinction risk at the species level (*11–14*). The IUCN Red List categories comprise eight different levels of extinction risk: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD). A species qualifies for one of the three threatened categories (CR, EN, or VU) by meeting a quantitative threshold for that category in one of the five different available criteria (A to E). A category of Near Threatened is assigned to species that come close to, but do not fully meet all the thresholds or conditions required for a threatened category under criterion A, B, C, D, or E. A category of Least Concern is assigned when there are no known threats to a species, or quantification of known threats for a species does not come close to meeting any of the threatened category thresholds. A category of Data Deficient is assigned when there is insufficient information available to adequately apply the criteria, such as taxonomic uncertainty, lack of key biological information, or inability to adequately quantify the impact of known threats. A species listed as Data Deficient may or may not be threatened when appropriate data becomes available (*15*).

The IUCN criteria (A to E) form the real strength of the IUCN Red List, and are designed to be transparent, reproducible, and conservatively flexible in the handling of uncertainty (*11*). The criteria are a standardized methodology that can be applied consistently to any species from any taxonomic group (*16–19*). Based on extinction risk theory, (*20*), each of the five criteria fall within one of two paradigms of elevated extinction risk: (i) species with small population sizes that are inherently at higher risk of extinction and/or are undergoing decline, and (ii) species with widespread or large populations that are declining faster than they are able to recover.

2.5 Application of Criterion A

Given their widespread distributions, all the scombrids and billfishes for which population data were available were assessed under criterion A (*8*). Criterion A measures extinction risk based

on exceeding a threshold of population decline over a time frame of a minimum of 10 years or three generation lengths (whichever is the longest), a measure of reproductive turnover rate, in the recent past. Taxa specific methodology for application of criterion A to species, relies on first defining an appropriate generation length for the species group and then determining the best proxy or surrogate available to estimate population decline over time (e.g., based on estimates of population size from survey samples or from fishery stock assessments, habitat or range loss). On the basis of IUCN Red List Assessment Guidelines (*15*), if a fishery species is determined to be effectively managed in at least 90% of its range, then subcriterion A1 is used, which has slightly higher thresholds for population decline over three generation lengths to meet the conditions for a threatened category (i.e., 50% for Vulnerable, 70% for Endangered, and 90% for Critically Endangered). If a fishery species is determined to be not effectively managed over more than 10% of its range, then subcriterion A2, A3, or A4 is used, which have lower thresholds for population decline over three generation lengths (i.e., 30% for Vulnerable, 50% for Endangered, and 80% for Critically Endangered). This distinction of an effectively managed fishery is important in order to account for population declines that occur in taxa that are the target of fisheries where the objective is to maximize yields (*15*). Maximum sustainable yield (MSY) is the theoretical maximum catch that can on average be taken over time from a population, and it is commonly used as a target level of catch by many national and international fisheries agencies (*21*).

To be considered effectively managed and therefore qualify under subcriterion A1, a species population (or stock) first needed to have regularly reported catch data, stock assessments conducted, and fishery management measures in place to avoid overfishing. Three factors were then examined to determine whether sustainable management was being achieved for the species, (i) if current biomass estimates were greater or equal to the biomass which would provide the MSY ($B_{current}/B_{msy} \geq 1$), (ii) if current fishing mortality rates were lower or equal to the fishing mortality rate which maintains MSY ($F_{current}/F_{msy} \leq 1$), and (iii) if stock projections based on current management indicate that the population biomass will remain stable or increase. When all three conditions were met in the majority of the species global range (at least in 90% of its range), subcriterion A1 was applied. Those species that did not meet these three conditions were deemed not to be sustainably managed and therefore criterion A2 was applied (Fig. S2).

Only one species, *Scomberomorus concolor* was assessed under criterion A4. Criterion A4 allows for population reduction to be measured over a window of three generation lengths that can include some time in the past and in the near future. *S. concolor* for example, has experienced a more than 80% reduction in range over the past 40 years and is currently restricted to the northern Gulf of California (*22*). With a generation length of just 4 years, the majority of this species' population decline occurred more than three generation lengths ago (i.e., 12 years ago). However, given its current restricted range and ongoing high fishing pressure, this species population is now estimated to decline another 40% over the next 10 years (*23*). Although its current range size and population size are smaller, they are not yet small enough to qualify under a different criterion (e.g. criterion B, C, or D) (*8*). If this species population continues to shrink, it may indeed qualify for a higher threat category under a different criterion in the near future.

2.5.1. Generation Length

Generation length, defined as the average age of the parents of the current cohort (i.e., the newborn individuals in a population) (*15*), can be calculated in a variety of ways for marine species. Generation length is best calculated from a life table with appropriate age- and sex-specific information on survival and fecundity. However, if these data are not available, other methods can be used to estimate generation length, such as determination of the time taken for most (>50%) individuals to reach maximum reproductive output or estimation of the age at which 50% of total reproductive output is achieved. Other approaches require the knowledge of several life history traits to estimate a proxy of generation length. For example, generation length can be estimated as: (i) adult natural mortality + age of first reproduction, or the age of first reproduction + z * length of the reproductive period, where z is usually less than 0.5 depending of the survivorship of the species (*15*). However, it is recognized that there are inherent difficulties for calculating generation length, in particular for very long-lived taxa; taxa with age-related variation in fecundity and mortality; and those with variable reproductive traits under different environmental or population stressors, such as overfishing (*15, 24, 25*).

Age-structured stock assessment models were available for 25 populations (10 species) of scombrids (Table S2). For these populations, generation length was calculated as the average mean age of the adult population using the time series of abundance for each age class and the vector of age of maturity available from stock assessments. In order to create a time series of the average mean age of the adult population, each year's adult age classes were weighted by the number of individuals in each age class. We then used an average of the mean age of the adult population across all years for the generation length of the population. For some species of scombrids, where generation length estimates varied among different populations, declines were calculated for each population based on the generation length of that population.

For species and populations for which data on the age structure of the adult population were not available, the generation length was calculated as the average age of maturity +z * (length of the reproductive period). The length of the reproductive period is the difference between the maximum age (T_{max}) and the age of maturity (T_m), with z usually <0.5, depending on survivorship and the relative fecundity of young versus old individuals in the population (*15*). As the z value for scombrid and billfishes is unknown, it was estimated based on the information available for the 25 scombrid populations listed in Table S2. By fitting the equation [GL= $T_m + Z$ * ($T_{max} - T_m$)] to the generation length, maximum age, and age of maturity of the 25 known scombrid populations, z was estimated by solving the equation by using a nonlinear optimization algorithm. The resulting estimate for z was 0.15. Thus, for species for which age-structured data were not available, we estimated generation length by applying the equation [GL= $T_m + Z$ * ($T_{max} - T_m$)] using the z value of 0.15 and the species respective age of maturity and maximum age. For a given species, if several estimates of age of maturity were available, we used an average of all the available estimates, and if several estimates of maximum age were available, we used the maximum value.

Estimation of generation lengths for billfishes was more challenging because they present unique challenges in age determination. In billfishes, otoliths are very small and fragile, which makes them difficult to extract and read; and although spines have proven to be more useful for aging

billfish, they become more difficult to read as the fish ages (*26, 27*). As billfish spines grow in size, the vascular tissue in the center of the spines obscures the early-formed increments. The fish age can be either underestimated, if those early increments are not taken into account, or overestimated, depending on the assumption on how many increments were lost (*28*). Therefore, life-history parameters of billfishes—such as age of maturity, maximum age, size-at-age, and growth rates—are considered to be uncertain as they all rely on accurate methods of age estimation and validation (*29*). For this study, generation length estimates for billfishes relied on the few estimations of maximum age from tagging studies (maximum age was considered as the maximum time of recapture) and on inferred estimates of age of maturity from available life history studies for that species or a similar species. All estimates of age at maturity and longevity for all scombrid and billfish species, along with appropriate references are reported in each species' IUCN Red List account (www.iucnredlist.org or http://sci.odu.edu/gmsa/).

2.5.2. Population Decline

Population decline was quantified using the best available data for each species or subpopulation (e.g., stock) (Fig. S2). Different abundance indices were used depending on data availability and stock assessment methods. Indices of abundance ordered in increasing reliability and preference included catch landings, catch per unit effort (CPUE) data, and total biomass and adult biomass estimates from stock assessment models. In any stock assessment evaluation, it is common to use several models (ranging for example from simple surplus production models to more complex age-structured models, each with alternative cases with varying assumptions) to estimate the status of a populations and to provide estimates of biomass and fishing mortality rates over time and biological reference points. When several stock assessment models and several variations of the models (runs) were available, we used the base-case model specified in the stock assessment report to extract the estimates of biomass over time. In the absence of a specified base case model, usually because all the models had a high degree of uncertainty and poor fits, the standardized CPUE time series used in the assessment as an index of abundance were used to estimate the population decline.

For species with more than one subpopulation (e.g., stock), population parameters such as adult biomass or total biomass were first calculated across the time period of three generation lengths for each individual subpopulation and then summed to estimate the total reduction of biomass over the given timeframe. This method accounts for the contribution of different subpopulation sizes to the global population (*15*). If the decline pattern of the population parameter of interest was either nonlinear or very smooth, with little temporal variability over time, then the first and last data points of the time frame examined were used to estimate the species or subpopulation decline over time. However, if the data series showed linearity and more variability over time, a linear regression was used and then the first and last predicted data points of the regression were used.

If the abundance index was not the same for all subpopulations of the same species (for example, information on abundance for one subpopulation was based on total biomass while for another subpopulation was based on adult biomass or CPUE), percent decline using the available abundance index was calculated for each subpopulation, which was then weighted by the current MSY for that subpopulation to determine the global population decline for the species. In cases

in which MSY was not available for all subpopulations, the maximum historic catch was used to weight the contribution of each subpopulation to the global population. This method allowed for standardization of the different abundance indices to weight the contribution of each subpopulation or stock to the species global population.

2.6 Data Limitations and Data Uncertainty

For some species, there were substantial differences in the estimates of generation lengths among subpopulations. In these cases, plausible and realistic range (interval) of generation length was used, that is, global population declines were estimated using the minimum and maximum value for generation length across all subpopulations, and the declines were calculated for the shortest and longest time frames determined by the range in generation length. For all widely distributed species (with the exception of *Thunnus thynnus* and *Kajikia albida*), the resulting plausible range of decline fell within a single Red List category. However, in the case of *Thunnus thynnus*, global declines were estimated to be between 29% and 50% on the basis of a generation length of between 7 and 13 years. In this case, the longer generation length was chosen, considering that it was likely that this species had a similar generation length over its global range at one point in time, and that the longer, preexploitation generation length should be used (*15*). For *Kajikia albida*, declines ranged from 9 to 37% on the basis of a generation length of between 4.5 and 6.5 years. The higher range of the decline was chosen on the basis of the precautionary principle as this species is well below B_{msy} and is not considered to be effectively managed.

Population declines were calculated over a period of three generation lengths extending backward from the most recent year of data. Given differences in data availability, and timing of stock assessments, the window of time examined was not always the same across subpopulations for a given species (however, usually within only a few years' difference). In other words, declines were calculated by using the generation length appropriate to each stock and by using the most recent data available. Although this method led to comparisons being made for subpopulations over slightly different time periods, it ensured that the most up-to-date information for a given subpopulation was included and that the data used were appropriate for the subpopulation being assessed.

2.7 Avoidance of the "Ski Jump" Effect

It is considered optimal by many fishery biologists for a virgin population to be fished down to MSY or about 40 to 50% of its original adult biomass (*30*). It is acknowledged that these targets can conflict with other criteria for population assessment [e.g., IUCN, Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)] (*8*, *31–33*). Others have also suggested that the biological reference points related to maximum sustainable yield, B_{msy} and F_{msy}, should be treated as limit reference points rather than target reference points for species under Regional Fisheries Management Organization management (*34*, *35*). Regardless, direct comparisons of stock assessments with Red List assessments often show a similar degree of accuracy in reflecting predictability of adverse effects of fishing practices (*9*, *10*). However, if population declines are measured relatively soon after a fishery begins, the resulting ski jump in population trend could lead to an evaluation of Critically Endangered or another threatened category under Red List criteria—when in fact the population may be under a careful management strategy

that may drive down the population to perhaps 50% of virgin biomass (B_0), and therefore, the population might not be under an immediate threat of collapse (*33*). If the same population has been well managed at maximum sustainable yield and has remained relatively stable over time (e.g., three generation lengths) although at much lower levels than the virgin population, it will be assessed as Least Concern.

However, a population that has been heavily overfished for a long time (longer than three generation lengths) and is severely depleted or well below the biomass that would provide B_{msy} would also be assessed as Least Concern because the rate of decline would be too low to qualify for a threatened category under criterion A. The exception would be if the resulting population was so small that it could qualify for a threatened category under a different criterion, such as criterion B, which has thresholds based on a small range size (e.g., <20,000 km^2), or criterion C, which has thresholds based on a small population size (e.g., <10,000 mature individuals) (*8, 15*). In sum, it is important to note that all scombrids and billfishes were assessed several decades after the start of their respective fisheries (generally in the 1950–1970s), and therefore, the ski jump effect of overestimating species risk was not an issue. Rather a discussion on how to more appropriately assess species whose populations have been severely depleted for longer than three generation lengths has been recommended to the Standards and Petitions Committee of the *IUCN Red List of Threatened Species*.

2.8 Ex-Vessel Price, Generation Length, and Red List Category

Both ex-vessel price values or the value of domestic landings before processing (real price corrected for inflation in US$ per ton) and generation length were available for 32 of the 61 species of scombrids and billfishes (Table S3). Average ex-vessel price values between 1996 and 2006 for the 32 scombrid and billfish species were extracted from the global ex-vessel fish price database (*36, 37*). In summary, these data were available for 6 of the 11 Data Deficient species, 18 of the 40 Least Concern species, and all of the threatened and Near Threatened species, except for two Vulnerable species: *Scomberomorus munroi* and *Scomberomorus concolor*.

3. Results

3.1 Final Red List Categories and Criteria for Scombrids and Billfishes

Of the 61 species of scombrids and billfishes, 11% (seven species) are in threatened categories: one species is Critically Endangered (CR), one species is Endangered (EN) and five species are Vulnerable (VU) (Table S4). A total of four species (6%) were listed as Near Threatened (NT), and a relatively high number of species (40 or 67%) were listed as Least Concern (LC). Eleven species (18%) were categorized as Data Deficient (DD) primarily because data were not available to effectively quantify species-specific population trends under IUCN criteria. All species data are available within each species account on the IUCN Red List of Threatened Species. Additionally, population data used for species assessed as Critically Endangered, Endangered, Vulnerable, or Near Threatened are shown by stock in Figure S2.

3.2 Comparison of Red List Categories and Criteria for Scombrids and Billfishes to other Marine Species Groups on the IUCN Red List of Threatened Species

In general, marine taxa that are slower to reproduce and longer-lived are at higher risk of extinction, as populations are slower to recover from repeated impacts that cause significant declines (*15*). Although small, short-lived fishery species that are overfished may be just as vulnerable to collapse as fishery species with slower life histories, collapses among long-lived, later to mature, and slower-growing fishery species are still more likely (*38*) because of their low productivity and consequently high intrinsic vulnerability to overexploitation.

Other groups that comprise species that are valuable and long-lived and have higher proportions of threatened species compared with scombrids and billfish, include marine turtles (*39*), marine mammals (*19*), and sharks and rays (*40*) (Fig. S3). Six of the seven species of marine turtles are in threatened categories. Their life history characteristics, particularly late sexual maturity and long juvenile stage, combined with the many threats from human activities in the sea and on land, contribute to their high risk of extinction. Threats to all sea turtle species occur globally and at all stages of their life cycle (*41*). Marine turtles lay their eggs on beaches, which are subject to threats such as coastal development and sand mining. The eggs and hatchlings are threatened by pollution and predation by introduced predators, such as pigs and dogs, as well as collection by humans for consumption and sale.

With almost one-third of the world's marine mammals in threatened categories, these species are threatened by accidental mortality through entanglement in fishing gear, the effects of noise pollution from military and seismic sonar, or boat strikes (*19, 42*). In many regions, marine mammals are also affected by habitat loss from coastal development, loss of prey or other food sources due to poor fisheries management, and historical or current effects of hunting (*39*). Two marine mammals have already gone extinct in the recent past from relentless hunting and exploitation: Steller's sea cow (*Hydrodamalis gigas*) and the Caribbean monk seal (*Monachus tropicalis*).

About 17% of the worlds 1043 species of sharks and rays are at elevated risk of extinction primarily because of their capture in nets from both targeted and accidental catch. Most shark species grow slowly, mature late, produce few young, and have low rates of population increase, making them highly vulnerable to depletion with a low capacity for recovery from overexploitation (*40, 43, 44*). Shark fisheries have proliferated around the world during recent decades, and millions of sharks are caught each year for their fins which are sold to make the Asian delicacy shark fin soup.

With 10% and 20% of scombrids and billfish in threatened categories, these two groups have relatively higher proportions of threatened species compared with other marine bony fishes assessed to date (Fig. S3). Coastal fishes such as butterflyfishes, angelfishes, wrasses, and parrotfishes all have 5% or less of species in threatened categories. This is partly because most of these colorful reef species are not heavily exploited for food, and those few that are threatened are often heavily exploited and relatively longer-lived (e.g., humphead wrasse) (*45*). With 12% in threatened categories, like scombrids and billfishes, a major threat to groupers is also heavy fishing pressure (*46*). Given their long life span, with some species living up to 40 years or longer (*47*), and late

sexual maturation combined with specializations, such as adult sex change ("protogyny") and aggregation-spawning, groupers are similar to some scombrid species in that they are very vulnerable to fishing pressure and overexploitation (*39, 48*).

Finally, habitat-building primary producers, such as mangroves, seagrasses, and corals, have relatively high levels of species in threat categories (16%, 14%, and 27%, respectively), largely because of significant human impacts in the coastal zone (*16–18*).

References for SOM (a complete list of references is available at the end of this document)

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Table S1. List of participants in IUCN Red List assessment workshops for scombrids and billfishes.

Workshop participant	Affiliation	City, state, country
Acero, Arturo	Universidad Nacional de Colombia	Bogotá, Colombia
Amorim, Alberto	Instituto de Pesca	Santos, SP, Brazil
Boustany, Andre	Duke University	Durham, NC, USA
Canales, Cristian	Instituto de Fomento Pesquero	Valparaíso, Chile
Cardenas, Gladys	Insituto del Mar del Peru	Lima, Peru
Carpenter, Kent	IUCN/Old Dominion University	Norfolk, VA, USA
Chang, Shui-Kai	National Sun Yat-sen Univeristy	Kaohsiung, Taiwan
Chiang, Wei-Chuan	Fisheries Research Institute/Eastern Marine Biology Research Center	Taitung, Taiwan
Chung, Kuo-Nan	National Museum of Marine Biology and Aquarium	Taipei, Taiwan
Collette, Bruce	NOAA National Marine Fisheries Service/Smithsonian Institution	Washington, DC, USA
de Oliveira Leite, Nilamon	Instituto Chico Mendes de Conservação de Biodiversidade	Vitória, ES, Brazil
Di Natale, Antonio	International Commission for the Conservation of Atlantic Tunas (ICCAT)	Genova, Italy
Diaz Acuña, Erich	Instituto del Mar del Peru	Lima, Peru
Die, David	University of Miami	Miami, FL, USA
Elfes, Cristiane	IUCN/Conservation International	Washington, DC, USA
Fox, Bill	World Wildlife Fund	San Diego, CA, USA
Franco, Milagros	Instituto del Mar del Peru	Lima, Peru
Graves, John	Virginia Institute of Marine Science, College of William & Mary	Gloucester Point, VA, USA
Harrison, Lucy	IUCN Species Survival Commission/Simon Fraser University	Burnaby, BC, Canada
Harwell, Heather	IUCN/Old Dominion University	Norfolk, VA, USA
Hazin, Fabio	Universidade Federal Rural de Pernambuco	Recife, PE, Brazil
Hinton, Michael	Inter-American Tropical Tuna Commission (IATTC)	La Jolla, CA, USA
Juan Jorda, Maria Jose	Universidad de A Coruña	A Coruña, Spain
Lessa, Rosangela	Universidade Federal Rural de Pernambuco	Recife, PE, Brazil
Lucena Fredou, Flavia	Universidade Federal Rural de Pernambuco	Recife, PE, Brazil
McManus, Roger	IUCN Species Survival Commission / Perry Institute of Marine Science	Washington, DC, USA
Minte-Vera, Carolina	Universidade Estadual de Maringá	Maringá, PR, Brazil
Miyabe, Naozumi	National Research Institute of Far Seas Fisheries	Tokyo, Japan
Montano, Ramon	Instituto de la Pesca	Quito, Ecuador

Nelson, Russell	Nelson Resources Consulting, Inc./ The Billfish Foundation	Fort Lauderdale, FL, USA
Oxenford, Hazel	CERMES, University of the West Indies	Cave Hill, Barbados
Pellón, Jose	Instituto del Mar del Peru	Lima, Peru
Peres, Monica Brick	Instituto Chico Mendes de Conservação de Biodiversidade	Brasília, DF, Brazil
Polidoro, Beth	IUCN/Old Dominion University	Norfolk, VA, USA
Pollard, David	NSW Fisheries, Australia	Sydney, Australia
Restrepo, Victor	International Seafood Sustainability Foundation	McLean, VA, USA
Schaefer, Kurt	Inter-American Tropical Tuna Commission (IATTC)	La Jolla, CA, USA
Schratwieser, Jason	International Game Fish Association	Dania Beach, FL, USA
Serra, Rodolfo	Instituto de Fomento Pesquero	Valparaiso, Chile
Shao, Kwang-Tsao	Academia Sinica	Taipei, Taiwan
Sun, Chi-Lu	National Taiwan University	Taipei, Taiwan
Uozumi, Yuji	National Research Institute of Far Seas Fisheries	Tokyo, Japan
Wang, Shen-Ping	National Taiwan Ocean University	Keelung, Taiwan
Wu, Ju-Luen	Taiwan Fisheries Research Institute	Keelung, Taiwan
Yanez, Eleuterio	Pontificia Universidad Católica de Valparaíso	Valparaiso, Chile
Yeh, Shien-Ya	National Taiwan University	Taipei, Taiwan

Table S2. Generation length (GL), age of maturity (T_m) and maximum age (T_{max}) for 25 populations of scombrids from age-structured stock assessment models.

Population	GL (years)	T_m (years)	T_{max} (years)	Source of stock assessment data
Thunnus alalunga, N. Atlantic	6.8	5	12	ICCAT (2008) Report of the 2007 ICCAT albacore stock assessment session. Collective Volume of Scientific Papers, ICCAT 62:697-815. (*70*)
Thunnus alalunga, N. Pacific	6.3	5	12	ISC. 2006. Report of the ISC- Albacore Working Group Stock Assessment Workshop. National Research Institute of Far Seas Fisheries (NRIFSF), 5-7-1 Orido, Shimizu-Ku, Shizuoka-Shi, 424-8633 Japan. (*50*)
Thunnus alalunga, S. Atlantic	6.6	5	13	ICCAT (2008) Report of the 2007 ICCAT albacore stock assessment session. Collective Volume of Scientific Papers, ICCAT 62:697-815. (*71*)
Thunnus alalunga, S. Pacific	7.2	6	13	Hoyle S, Langley A, & Hampton J (2008) Stock assessment of albacore tuna in the south Pacific Ocean. Western and Central Pacific Fisheries Commission. Port Moresby, Papua New Guinea. pp. 126. (*57*)
Thunnus obesus, Atlantic	4.8	3	9	ICCAT (2008) Report of the 2007 ICCAT bigeye tuna stock assessment session. Collective Volume of Scientific Papers, ICCAT 62:97-239. (*54*)
Thunnus obesus, E. Pacific	4.4	3.5	5	Aires-da-Silva A & Maunder MN (2008) Status of bigeye tuna in the eastern Pacific Ocean in 2007. Inter-American Tropical Tuna Commission. Inter-American Tropical Tuna Commission. La Jolla, California, United States. (*55*)
Thunnus obesus, Indian	5.0	3	8	IOTC (2009) Report of the Eleventh Session of the IOTC Working Party on Tropical Tunas. IOTC-2009-WPTT-R[E].60 pp. (*56*)
Thunnus obesus, W. Pacific	4.5	4	16	Langley, A., J. Hampton, P. Kleiber and S. Hoyle . 2008. Stock assessment of bigeye tuna in the western and central Pacific Ocean, including an analysis of management options. Western and Central Pacific Fisheries Commission. Port Moresby, Papua New Guinea. (*72*)
Thunnus thynnus, E. Atlantic	7.3	4	22	ICCAT (2007) Report of the 2006 Atlantic bluefin tuna stock assessment session. Collective Volume of Scientific Papers, ICCAT 60:652-880. (*73*)
Thunnus thynnus, W.Atlantic	9.6	8	32	ICCAT (2007) Report of the 2006 Atlantic bluefin tuna stock assessment session. Collective Volume of Scientific Papers, ICCAT 60:652-880. (*74*)
Scomberomorus cavalla, GOM	4.4	2	24	Ortiz, M. 2004. Stock Assessment Analysis on Gulf of Mexico King Mackerel. SEDAR5- 2004 NMFS SEFSC Miami Lab Sustainable Fisheries Division Contribution 2004-004. (*75*)
Scomberomorus cavalla, U.S. Atlantic	4.8	1	26	NMFS. 2003. Stock Assessment Analysis on Spanish and King Mackerel Stocks. Prepared for the 2003 Mackerel Stock Assessment Panel Meeting. Southeast Fisheries Science Center, Miami, Florida, United States (*76*)
Scomber scombrus, N.E.Atlantic	4.4	2	18	ICES (2007) Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy (WGMHSA).

Species				Reference
Scomber japonicus, Japanese	3.0	2	12	Watanabe C, Kawabata A, Suda M, Nishida H, & Honda S (2008) Stock Assessment and evaluation for chub mackerel Pacific stock (fiscal year 2007), in *Marine Fisheries Stock Assessments and Evaluations for Japanese Waters* (fiscal year 2007/2008), Fisheries Agency and Fisheries Research Agency of Japan, 2008), pp. 123–154. (*78*).
Scomber japonicus, N. E. Pacific	3.8	3	14	Dorval E, Hill KT, Lo NCH, & McDaniel JD (2007) Pacific mackerel (*Scomber japonicus*) stock assessment for U.S. Management in the 2007-08 fishing season. Pacific Fishery Management Council, June 2007 Briefing Book, Agenda Item F.2.b, Attachment 1. pp. 253:1-170. (*79*)
Scomber japonicus, Chilean	4.3	3	9	Canales CR (2006) Investigación, evaluación de stock y CTP Caballa 2005-Informe Final. Instituto de Fomento Pesquero, Valparaiso, Chile, pp. 1-40. (*80*)
Scomber japonicus, T.C. Pacific	1.6	1	6	Yukami R, Yoda M, Ooshimo S, & Tanaka H (2008) Stock Assessment and evaluation for chub mackerel Tushima current stock (fiscal year 2007), pp 155-185, in *Marine Fisheries Stock Assessments And Evaluations For Japanese Waters* (fiscal year 2007/2008), Fisheries Agency and Fisheries Research Agency of Japan. (*81*)
Thunnus maccoyii	17.2	10	41	CCSBT (2009) Commission for the Conservation of Southern Bluefin Tuna, Report of the Fourteenth Meeting of the Scientific Committee, Busan, Korea, 5 to 11 September 2009. (*82*)
Katsuwonus pelamis, W. Pacific	0.4	1	6	Langley A & Hampton J (2008) Stock assessment of skipjack tuna in the western and central Pacific Ocean. Western and Central Pacific Fisheries Commission. Port Moresby, Papua New Guinea. pp. 75. (*83*)
Scomberomorus maculatus, GOM	2.9	1.5	9	NMFS. 2003. Stock Assessment Analysis on Spanish and King Mackerel Stocks. Prepared for the 2003 Mackerel Stock Assessment Panel Meeting. Southeast Fisheries Science Center, Miami, Florida, United States (*84*)
Scomberomorus maculatus, U.S. Atlantic	2.8	1.5	11	NMFS. 2003. Stock Assessment Analysis on Spanish and King Mackerel Stocks. Prepared for the 2003 Mackerel Stock Assessment Panel Meeting. Southeast Fisheries Science Center, Miami, Florida, United States (*84*)
Thunnus albacares, Atlantic	3.5	2.5	8	ICCAT (2008) Report of the 2008 ICCAT yellowfin and skipjack stock assessments meeting. Available at www.iccat.int/Documents/Meetings/Docs/2008_TROP_REP_EN.pdf. (*60*)
Thunnus albacares, E. Pacific	2.3	2.5	5	Maunder MN & Aires-Da-Silva A (2008) Status of yellowfin tuna in the eastern Pacific Ocean in 2007 and outlook for the future. Inter-American Tropical Tuna Commission. La Jolla, California, United States. (*61*)
Thunnus albacares, Indian	2.9	2	7	IOTC (2009) Report of the Eleventh Session of the IOTC Working Party on Tropical Tunas. IOTC-2009-WPTT-R[E]. (*56*)
Thunnus albacares, W. Pacific	2.2	2.5	7	Langley A, Hampton J, Kleiber P, & Hoyle S (2007) Stock assessment of yellowfin tuna in the western and central Pacific Ocean, including an analysis of management options. Western and Central Pacific Fisheries Commission. Honolulu, United States. pp. 129. (*85*)

Table S3. Average generation length (GL) and 1996-2006 ex-vessel price for 33 scombrid and billfish species (Fig. 1, manuscript).

Species name	Red List Category	GL (years)	Ex-Vessel Price (US$/ton)
Acanthocybium solandri	LC	2.3	2633
Auxis rochei	LC	2.8	898
Euthynnus affinis	LC	2.6	1126
Euthynnus alletteratus	LC	3.4	836
Istiompax indica	DD	1.8	2817
Istiophorus platypterus	LC	1.7	2414
Kajikia albida (WHM)	VU	5.5	1958
Kajikia audax (STM)	NT	4.4	5713
Katsuwonus pelamis	LC	1.0	3246
Makaira nigricans (BUM)	VU	5.8	2512
Orcynopsis unicolor	LC	2.3	345
Rastrelliger brachysoma	DD	0.7	471
Rastrelliger kanagurta	DD	2.3	961
Sarda chiliensis	LC	3.5	603
Sarda sarda	LC	2.4	1787
Scomber japonicus	LC	3.3	2911
Scomber scombrus	LC	4.2	639
Scomberomorus brasiliensis	LC	3.9	1154
Scomberomorus cavalla	LC	5.1	1220
Scomberomorus commerson (COM)	NT	6.0	1402
Scomberomorus guttatus	DD	1.9	891
Scomberomorus maculatus	LC	2.7	1061
Scomberomorus niphonius	DD	2.6	3396
Scomberomorus sierra	LC	4.0	1025
Thunnus alalunga (ALB)	NT	7.0	3929
Thunnus albacares (YFT)	NT	2.8	2424
Thunnus maccoyii (SBF)	CR	17.0	11218
Thunnus obesus (BET)	VU	4.7	4568
Thunnus orientalis (PBF)	LC	7.3	5836
Thunnus thynnus (ABF)	EN	8.9	3206
Thunnus tonggol	DD	4.5	1561
Xiphias gladius (SWO)	LC	6.5	3624

Table S4. IUCN Red List categories for all scombrid and billfish species. Also shown are criterion applied, generation length (GL) range and total global percent decline over 3 generation lengths for species in threatened and Near Threatened categories.

Family	Species name	Red List category	Criterion applied	GL range (years)	% Decline in 3 GL
Istiophoridae	*Istiompax indica*	DD			
Istiophoridae	*Istiophorus platypterus*	LC			
Istiophoridae	*Kajikia albida*	VU	A2	4.5-6.5	9-37%
Istiophoridae	*Kajikia audax*	NT	A2	5.3	20-25%
Istiophoridae	*Makaira nigricans*	VU	A2	4.5-6	31-38%
Istiophoridae	*Tetrapturus angustirostris*	DD			
Istiophoridae	*Tetrapturus belone*	LC			
Istiophoridae	*Tetrapturus georgii*	DD			
Istiophoridae	*Tetrapturus pfluegeri*	LC			
Scombridae	*Acanthocybium solandri*	LC			
Scombridae	*Allothunnus fallai*	LC			
Scombridae	*Auxis rochei*	LC			
Scombridae	*Auxis thazard*	LC			
Scombridae	*Cybiosarda elegans*	LC			
Scombridae	*Euthynnus affinis*	LC			
Scombridae	*Euthynnus alletteratus*	LC			
Scombridae	*Euthynnus lineatus*	LC			
Scombridae	*Gasterochisma melampus*	LC			
Scombridae	*Grammatorcynus bicarinatus*	LC			
Scombridae	*Grammatorcynus bilineatus*	LC			
Scombridae	*Gymnosarda unicolor*	LC			
Scombridae	*Katsuwonus pelamis*	LC			
Scombridae	*Orcynopsis unicolor*	LC			
Scombridae	*Rastrelliger brachysoma*	DD			
Scombridae	*Rastrelliger faughni*	DD			
Scombridae	*Rastrelliger kanagurta*	DD			
Scombridae	*Sarda australis*	LC			
Scombridae	*Sarda chiliensis*	LC			
Scombridae	*Sarda orientalis*	LC			
Scombridae	*Sarda sarda*	LC			
Scombridae	*Scomber australasicus*	LC			
Scombridae	*Scomber colias*	LC			
Scombridae	*Scomber japonicus*	LC			
Scombridae	*Scomber scombrus*	LC			
Scombridae	*Scomberomorus brasiliensis*	LC			
Scombridae	*Scomberomorus cavalla*	LC			

Scombridae	*Scomberomorus commerson*	NT	A2	8-9	20-30%
Scombridae	*Scomberomorus concolor*	VU	A4	3-4	40%
Scombridae	*Scomberomorus guttatus*	DD			
Scombridae	*Scomberomorus koreanus*	LC			
Scombridae	*Scomberomorus lineolatus*	LC			
Scombridae	*Scomberomorus maculatus*	LC			
Scombridae	*Scomberomorus multiradiatus*	LC			
Scombridae	*Scomberomorus munroi*	VU	A2	3-4	37%
Scombridae	*Scomberomorus niphonius*	DD			
Scombridae	*Scomberomorus plurilineatus*	DD			
Scombridae	*Scomberomorus queenslandicus*	LC			
Scombridae	*Scomberomorus regalis*	LC			
Scombridae	*Scomberomorus semifasciatus*	LC			
Scombridae	*Scomberomorus sierra*	LC			
Scombridae	*Scomberomorus sinensis*	DD			
Scombridae	*Scomberomorus tritor*	LC			
Scombridae	*Thunnus alalunga*	NT	A1	6-7	37%
Scombridae	*Thunnus albacares*	NT	A1	2.2-3.5	33%
Scombridae	*Thunnus atlanticus*	LC			
Scombridae	*Thunnus maccoyii*	CR	A2	12-17	85%
Scombridae	*Thunnus obesus*	VU	A2	4-5	42%
Scombridae	*Thunnus orientalis*	LC			
Scombridae	*Thunnus thynnus*	EN	A2	7-13	29-50%
Scombridae	*Thunnus tonggol*	DD			
Xiphiidae	*Xiphias gladius*	LC			

Figure S1. Phylogeny of the family Scombridae (*3*)
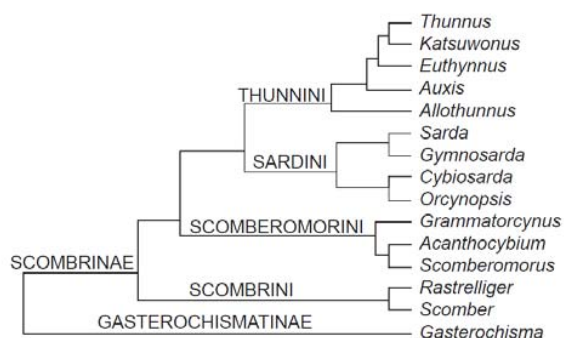
Figure S2. Indices of abundance used to estimate population declines shown by stock for species of (A) tunas, (B) billfishes and (C) Spanish mackerels that were assessed as Critically Endangered, Endangered, Vulnerable and Near Threatened under criterion A1 or A2. Also shown are swordfish and Pacific bluefin, both assessed as Least Concern. Indices of abundance include catch landings in 1000 tonnes, catch per unit effort (CPUE), total biomass in 1000 tonnes, adult biomass in 1000 tonnes, biomass relative to virgin biomass ($B:B_0$), and biomass relative to the biomass that would provide the maximum sustainable yield ($B:B_{msy}$). Projected stock outlook is also indicated by (+) or (–) as this metric was used in combination with the reference points B/B_{msy} and F/F_{msy} when available to evaluate whether criterion A1 or A2 should be used for the global population assessment. Data shown are from the most recent stock assessments (*49–68*).

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Kajikia albida, Atlantic (B:Bmsy, -)

Kajikia audax, Indian Ocean (CPUE from Australia, -)

Kajikia audax, Indian Ocean (CPUE fromSeychelles, -)

Kajikia audax, Northeast Pacific (Adult biomass, +)

Kajikia audax, Northwest Pacific (Adult biomass scenario 1, -)

Kajikia audax, Northwest Pacific (Adult biomass scenario 2, -)

Kajikia audax, Southwest Pacific (Adult biomass, -)

Makaira nigricans, Atlantic (B:Bmsy, -)

Makaira nigricans, East Pacific (Catch, -)

Makaira nigricans, Indian (CPUE from Australia, -)

Makaira nigricans, Indian (CPUE from Seychelles, -)

Xiphias gladius, North Pacific sub area 1 (Biomass, +)

Xiphias gladius, North Pacific sub area 2 (Biomass, +)

Xiphias gladius, Indian (Biomass, +)

Xiphias gladius, Mediterranean (Biomass, -)

Xiphias gladius, North Atlantic (Biomass, +)

Xiphias gladius, South Atlantic (Biomass, +)

Xiphias gladius, Southeast Pacific (Biomass, +)

Xiphias gladius, West Pacific (Biomass, +)

BILLFISHES
- Kajikia albida (White marlin)
- Kajikia audax (Striped marlin)
- Makaira nigricans (Blue marlin)
- Xiphias gladius (Swordfish)

Scomberomorus commerson, Queensland Australia (B:Bo, +)

Scomberomorus commerson, Torres Strait Australia (B:Bo, -)

Scomberomorus munroi, Eastern Australia (B:Bo from model 1, -)

Scomberomorus munroi, Eastern Australia (B:Bo from model 7, -)

SPANISH MACKERELS
- Scomberomorus commerson (Narrow-barred king mackerel)
- Scomberomorus munroi (Spotted mackerel)

22

Figure S3. Red List categories for marine species groups assessed to date (*69*).

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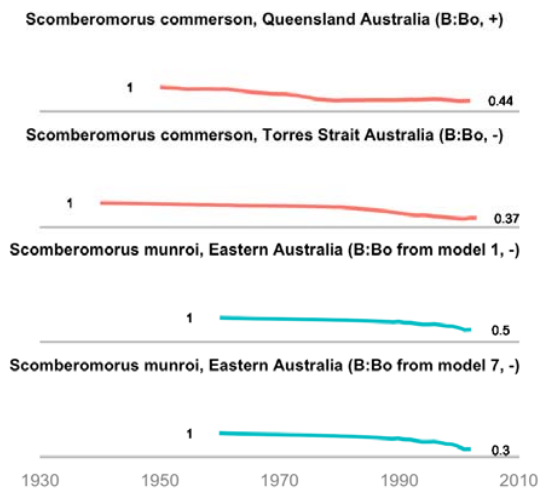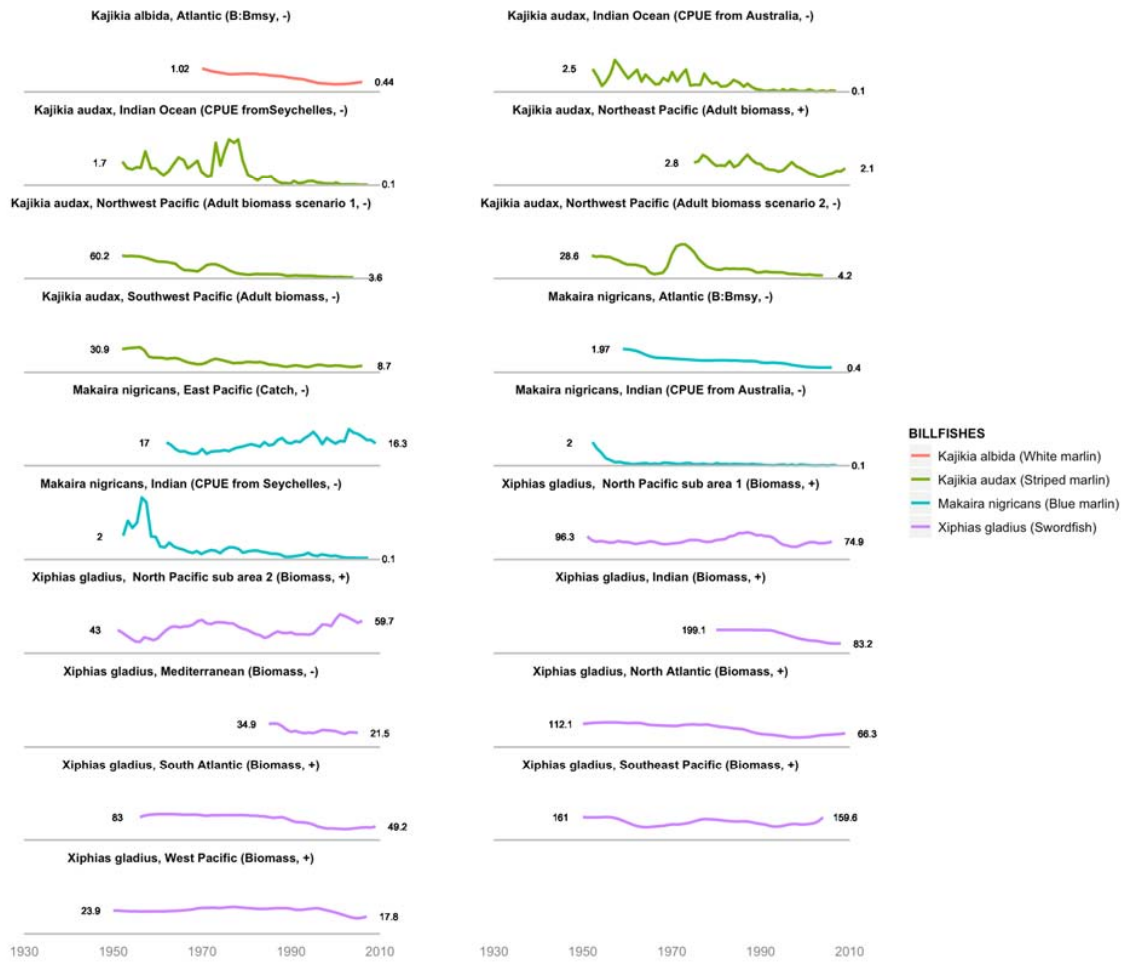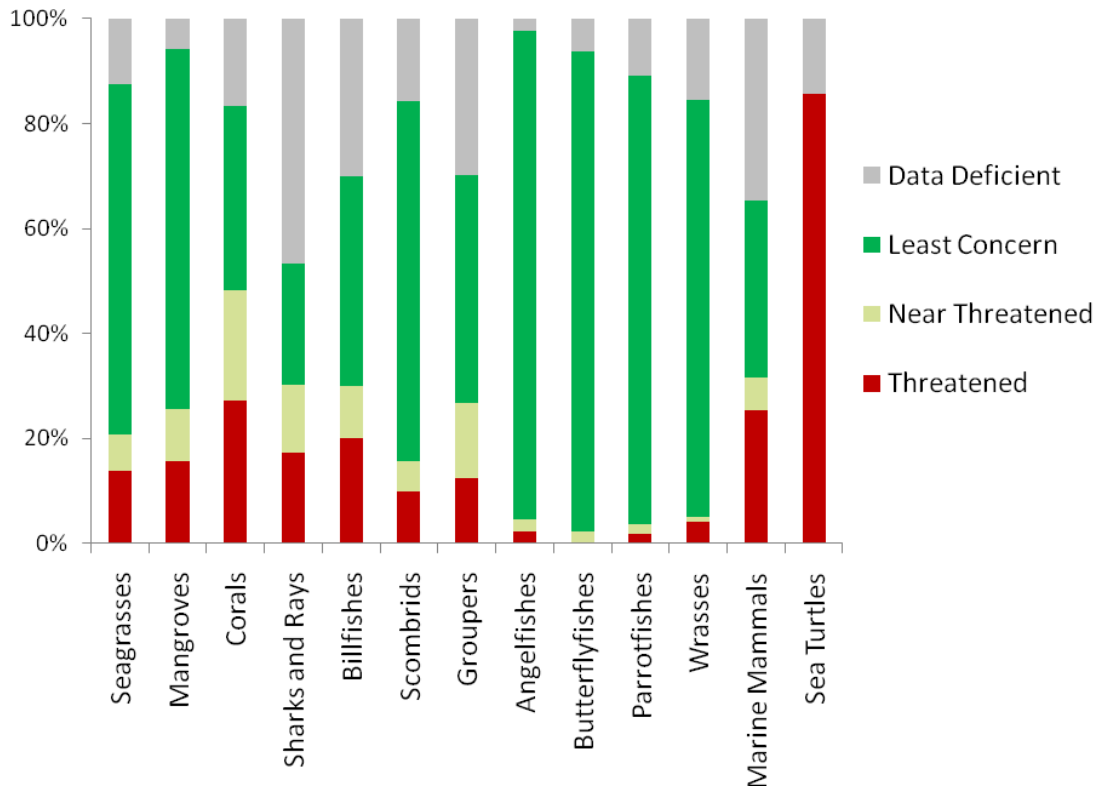
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<foot>9. Data are tabulated in the SOM and also available at the Global Marine Species Assessment (http://sci.odu.edu/gmsa/).</foot>

<foot>10. These data are to be added at IUCN Red List (www.iucnredlist.org) during the semiannual update in November 2011.</foot>

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Appendix C.

Bibliography life history data set

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