Life in 3-D: life history strategies in tunas, mackerels and bonitos

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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 first assemble life history information on maximum size, growth, longevity, maturity, fecundity and spawning duration and interval for all scombrid species. Second 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 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 (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 (Collette et al. 2011). 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

Table 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)

Subfamily and tribe	Code	Latin name	Common name	Oceanic environments	Geographical distribution
Subfamily Scombrinae					
Tribe Thunnini (tunas)	ALB	*Thunnus alalunga*[a]	Albacore tuna	Subtropical	Cosmopolitan
	YFT	*Thunnus albacares*[a]	Yellowfin tuna	Tropical	Cosmopolitan
	SBF	*Thunnus maccoyii*[a]	Southern bluefin tuna	Temperate	Southern Oceans
	BET	*Thunnus obesus*[a]	Bigeye tuna	Subtropical	Cosmopolitan
	BFT	*Thunnus thynnus*[a]	Atlantic bluefin tuna	Temperate	Atlantic Ocean
	PBF	*Thunnus orientalis*[a]	Pacific bluefin tuna	Temperate	Pacific Ocean
	SKJ	*Katsuwonus pelamis*[a]	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
Tribe Sardini (bonitos)	DOT	*Gymnosarda unicolor*	Dogtooth tuna	Tropical	Indian Ocean, Indo-Pacific region. Disjoint distribution, found primarily around reefs
	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

Table 1 continued

Subfamily and tribe	Code	Latin name	Common name	Oceanic environments	Geographical distribution
Subfamily Scombrinae					
Tribe Scomberomorini (Spanish mackerels)					
	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
	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

Table 1 continued

Subfamily and tribe	Code	Latin name	Common name	Oceanic environments	Geographical distribution
	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	RAB	*Rastrelliger brachysoma*	Short mackerel	Tropical	Indo-Pacific region
Tribe Scombrini (mackerels)	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

[a] Commonly known as principal market tuna species

(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 strategists in plants). 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 *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 ($L_{m50, cm}$) 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* $= a \times$ *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 within each species. 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 662 articles (Appendix 1 in Electronic Supplementary Material) 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, 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 maximum lengths were significantly larger than the maximum observed lengths of each study (Fig. S1a in Electronic Supplementary Material), after aggregating the data for each species, the species maximum observed lengths were significantly larger than their averaged theoretical maximum lengths (Fig. 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 (Fig. S1c) and across all species (Fig. 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 relationship. 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 (Fig. 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 S1 in Electronic Supplementary Material). The relatively high interspecific variation (compared with intraspecific variation) in traits allows us to estimate and use average species traits for our analysis (Table S2 in Electronic Supplementary Material).

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 2010), 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 2

Table 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
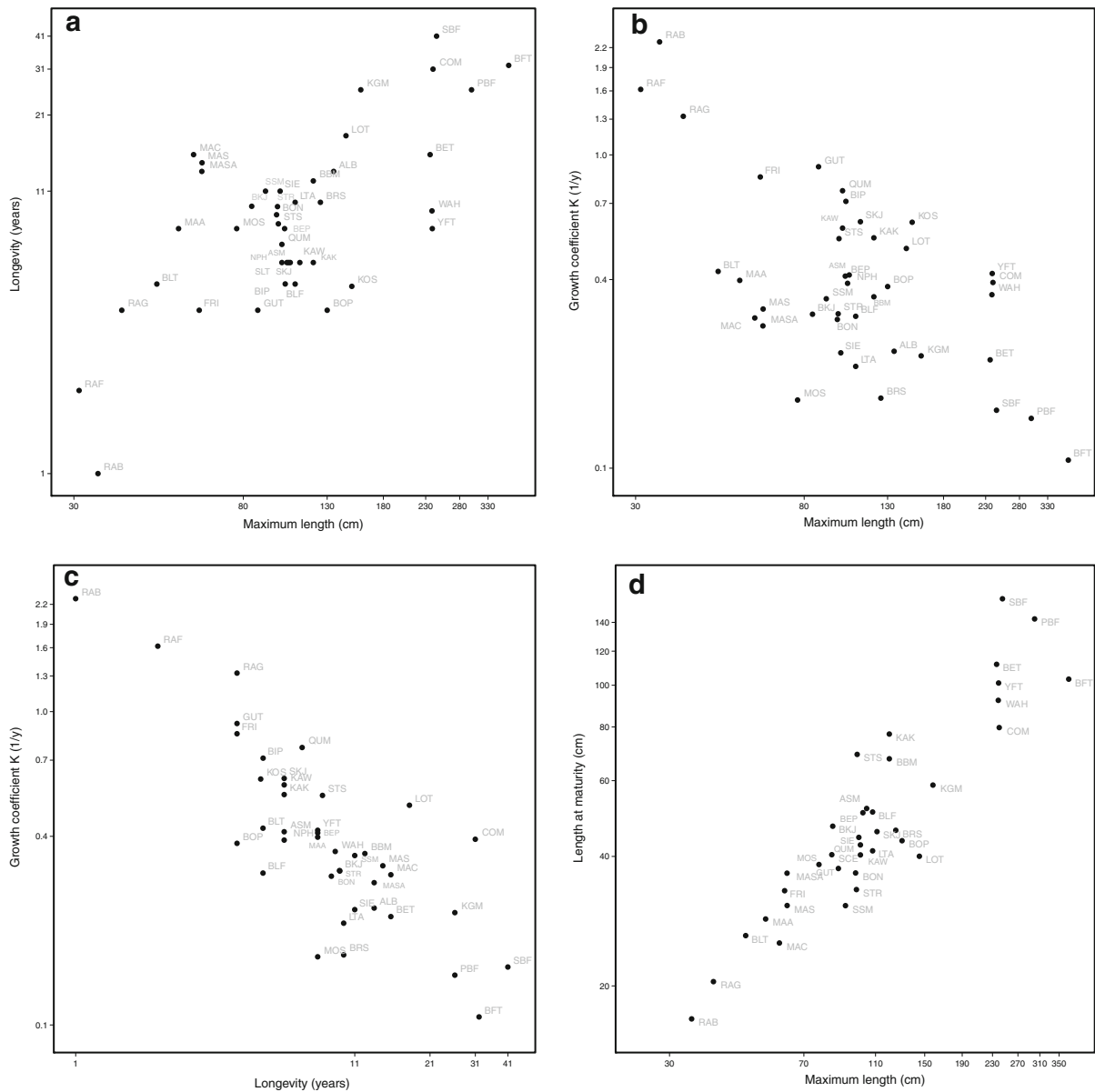
Fig. 1 Bivariate relationships between various pairs of life history traits (**a–k**) and duration of spawning season by oceanic environment (**l**) for scombrid species. See Table 1 for the name of the species and Table 3 for the correlations among life history traits

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 all the growth and reproductive life history traits across the scombrid species (Table 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, Fig. 1a) and negatively correlated with growth rate (r = −0.62, Fig. 1b). In addition, longer-lived species also tend to reach their maximum body
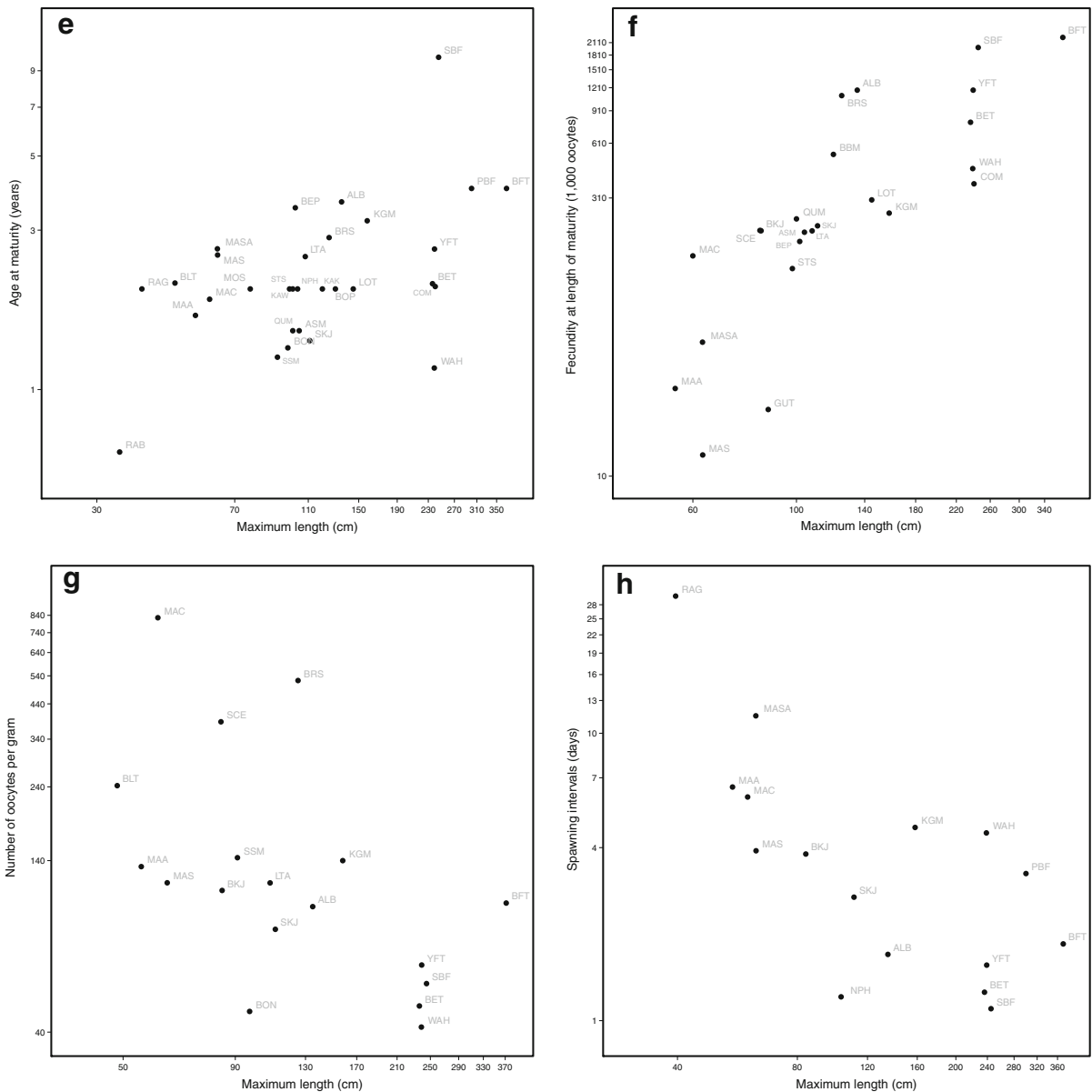
Fig. 1 continued

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, Fig. 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, Fig. 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, Fig. 1f). However, smaller scombrids have higher mass-
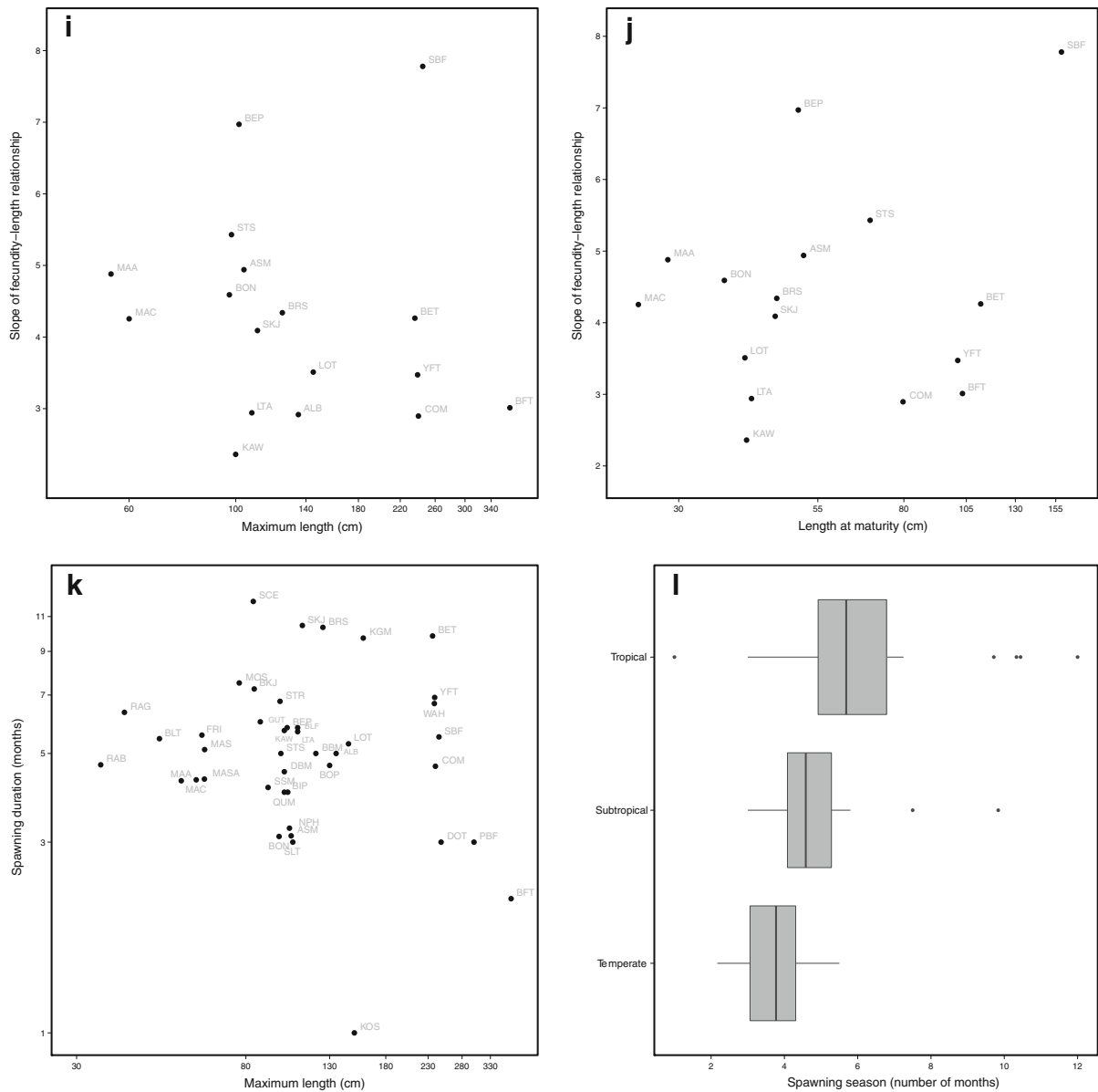
Fig. 1 continued

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 (Fig. 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 ($r = 0.42$, Fig. 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, Fig. 1j), indicating that smaller species have lower fecundities at maturity with their fecundities increasing steeply with body size, while bigger species invest more in

Table 3 Pearson's correlations matrix of life history traits of scombrid species with p values (lower diagonal) and sample sizes (upper diagonal)

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***	

Correlations are based on all available data for scombrid species

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

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 (Fig. 1k and Table 3). 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 (Fig. 1l). Additional correlations between life history traits are presented in Table 3.

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, Fig. 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.

Table 4 PCA statistics for seven scombrid species based on ten life history traits

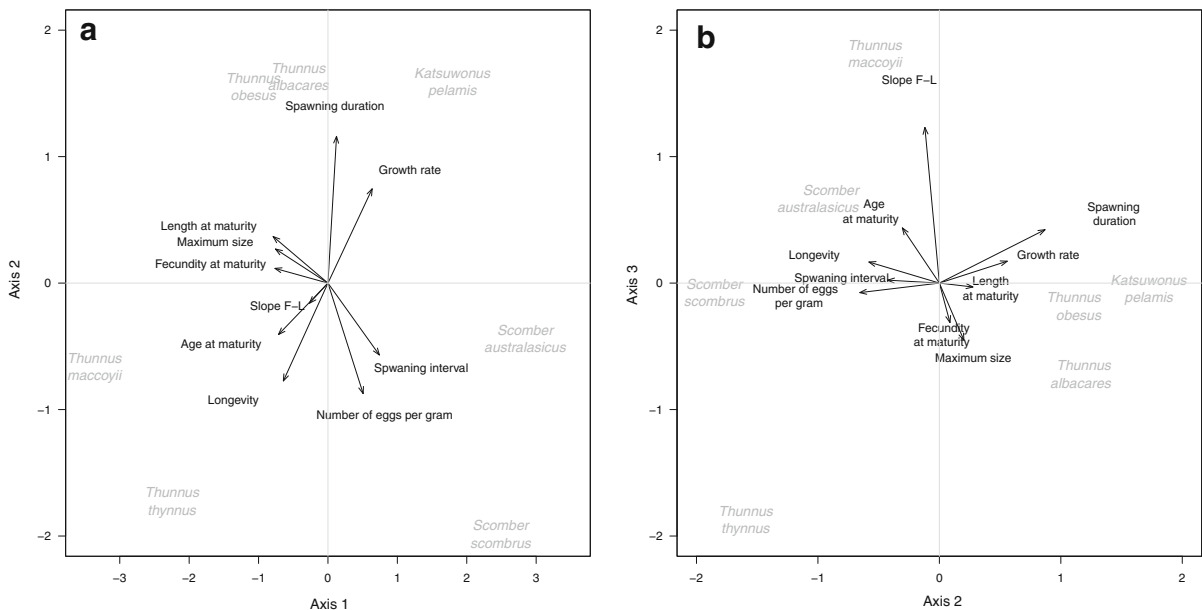| Life history traits	PC1	PC2	PC3
Maximum length L_{max} (cm)	−0.38	0.13	−0.30
Growth coefficient k (1/years)	0.32	0.37	0.12
Empirical longevity T_{max} (years)	−0.32	−0.39	0.11
Length at 50 % maturity L_{m50} (cm)	−0.40	0.18	−0.02
Age at 50 % maturity T_{m50} (years)	−0.36	−0.20	0.29
Fecundity at maturity 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

Fig. 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 for the factor loadings of the PCA

(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, Fig. 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.

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 (Fig. 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 (Fig. 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 tropical 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) (Fig. 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 (Fig. 4a,b and d). Females grow at a slower rate than males (Fig. 4c). In contrast, tunas only showed significant sexual dimorphism in maximum size with males reaching larger maximum sizes than females (Fig. 4a) and there was no significant evidence for sex differences in size of maturity, growth or longevity (Fig. 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
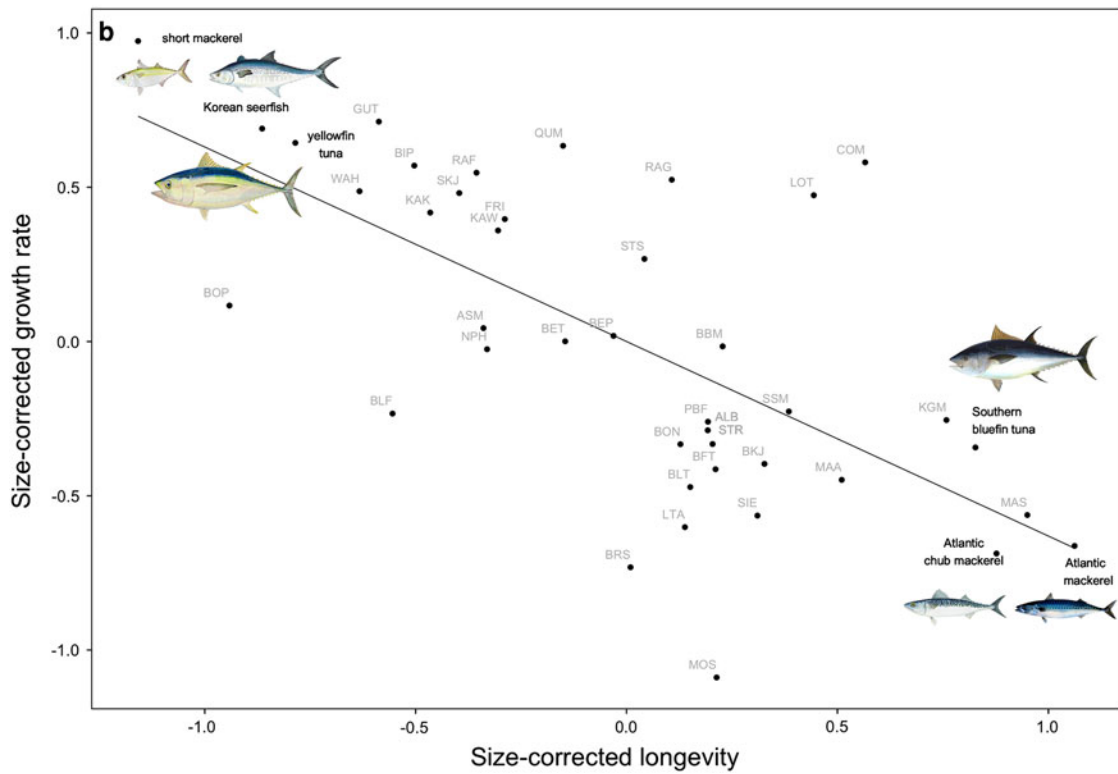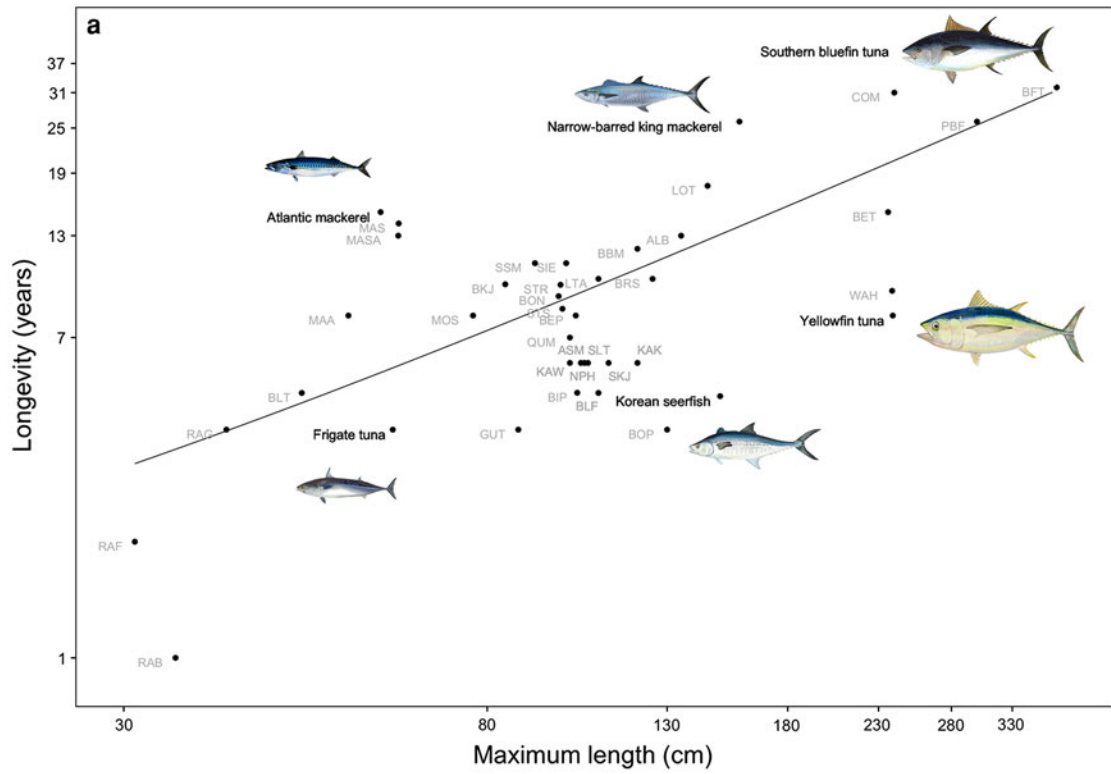
◄ Fig. 3 Life history variation of forty-two species of scombrids along the small-large continuum and along the slow-fast continuum. **a** Relationship between maximum length and longevity across scombrid species. **b** Relationship between size-corrected longevity and size-corrected growth rate across scombrid species. Regression line (*black solid line*)

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 (Fig. 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 such as 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-two 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
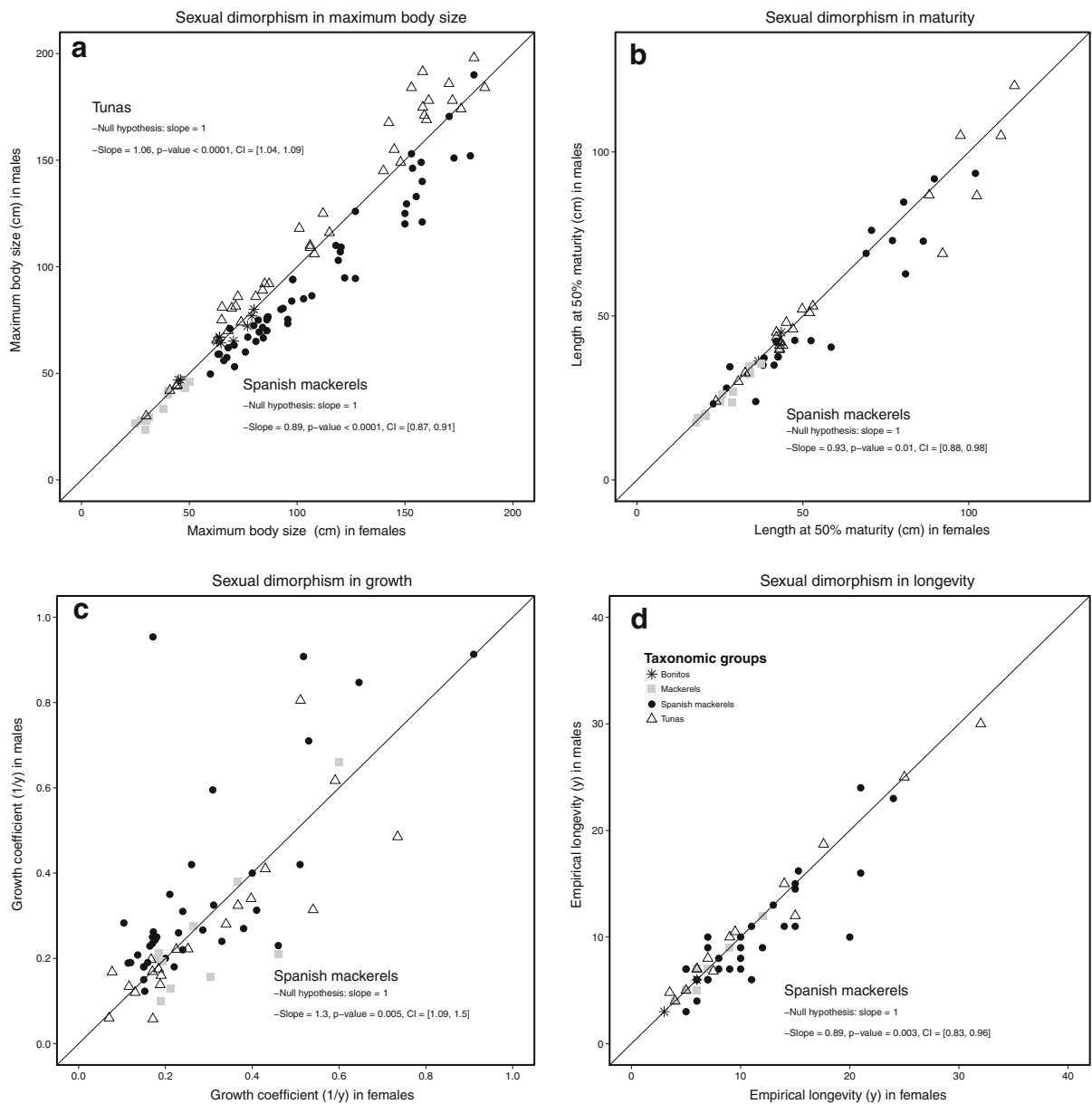
Fig. 4 Patterns in sexual dimorphism in **a** maximum observed length, **b** length of maturity, **c** growth and **d** longevity within the major taxonomic groups of scombrids; bonitos, mackerels, Spanish mackerels and tunas. See Table 1 for full list of species within each taxonomic group. 1:1 line (*black solid ablines*)

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-Jordá et al. 2011), therefore management scenarios using simple life history driven models such as 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 fish 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 years) species of scombrids and are characterized by slow growth rates (0.11–0.15 years^{-1}), late maturation (103–159 cm and 4–9 years), 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 years) species of scombrids and are characterized by early maturation (17–20 cm and 0.6–2 years), fast growth (1.3–2.9 years^{-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).

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