


Original Article

Performance of length-based data-limited methods in a multifleet context: application to small tunas, mackerels, and bonitos in the Atlantic Ocean

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Large scombrids, commercial tuna species, are regularly assessed and managed. However, most of the small scombrids, many mackerels and bonitos, lack accurate catch data to implement traditional stock assessments despite their economic importance in many small-scale fisheries. In this study, we analysed different approaches using length composition data from multiple fleets with different gear selectivity to assess small scombrids in the Atlantic Ocean. Using simulated populations, we compared two length-based methods (length-based spawning potential ratio and length-based integrated mixed effects), under different length data grouping scenarios. We found that using length data from the fleet targeting the broadest range of sizes resulted in the lowest bias in spawning potential ratio of all options tested. Based on these results, we used biological and length data to estimate a quantitative proxy of current stock status for ten small scombrid stocks in the Atlantic Ocean. We found that some stocks are likely to be overfished, such as little tunny (*Euthynnus alletteratus*) in the Southeast Atlantic and wahoo (*Acanthocybium solandri*) in the Northwest Atlantic. This is a starting point in the estimation of stock status for these species, but should not be thought of as a replacement for other more data-intensive assessments.

Keywords: length-based assessments, management, scombrids, spawning potential ratio.

Introduction

For the “principal market tunas,” like Southern (*Thunnus maccoyii*), Pacific (*T. orientalis*), and Atlantic bluefin (*T. thynnus*), bigeye (*T. obesus*), yellowfin (*T. albacares*), albacore (*T. alalunga*), and skipjack (*Katsuwonus pelamis*), stock assessments are performed regularly, and a variety of management procedures are in place to protect these stocks from overfishing (Pons *et al.*, 2017). However, there are also other scombrid species, commonly referred to as “small tunas, mackerels, Spanish mackerels and bonitos” (from now on “small scombrids”), that account for a notable proportion of the total tuna and tuna-like species catch

and that are mostly unassessed and unmanaged (Juan-Jordá *et al.*, 2015; Pons *et al.*, 2018). Small scombrids are generally coastal and associated with continental shelves and islands (Collette and Nauen, 1983). Although their economic value is lower than that of the principal market tunas (Collette *et al.*, 2011), they sustain important regional commercial fisheries in many coastal communities throughout their distributions (Majkowski, 2007). Juan-Jordá *et al.* (2011) showed that within the Scombridae family, the fastest declines in biomass are exhibited not only for the largest, longest-lived, most valuable tunas, but also for a few smaller, short-lived mackerels. Also, some small

Scombridae stocks in the Atlantic Ocean were assigned as “moderate to high risk” of being overfished or subject to overfishing in a recent qualitative risk assessment, even if they have not been formally assessed in recent years (Lucena-Frédou, Kell, *et al.*, 2017).

Total catch is one of the main data sources required for most classical stock assessment methods, particularly when estimating absolute estimates of spawning or total biomass. Stock assessment methods used for principal market tunas use catch data, but obtaining accurate landings and discards for small scombrids is generally challenging (Pitcher *et al.*, 2002). Small scombrids are targeted by multiple fleets, particularly medium- and small-scale fisheries, and caught as bycatch in many industrial fisheries targeting commercial tuna species. Available catch data usually consist of incomplete catch time-series from tuna regional fisheries management organizations statistics and from catch time-series that might be highly aggregated by species from the Food and Agriculture Organization database (FAO, 2016). While quantifying total catch is difficult, there is a wide-ranging toolbox of qualitative and quantitative assessment approaches for data-limited fisheries to infer the exploitation status of the stocks (Chrysafi and Kuparinen, 2016; Dowling *et al.*, 2016). In 2017, Lucena-Frédou, Frédéric, *et al.* (2017) performed a qualitative risk assessment for small scombrids in the Atlantic Ocean. They identified 5 of 13 species as priority for evaluation and implementation of future management actions: the low productivity and susceptible *Euthynnus alletteratus* (little tunny), *Acanthocybium solandri* (wahoo), and *Scomberomorus cavalla* (king mackerel), and the highly targeted *Sarda sarda* (bonito) and *Auxis thazard* (frigate tuna). This study served to identify priority species, but does not estimate population processes, productivity, or stock status that would be required for more specific management advice. In addition, qualitative risk assessment methods have been questioned recently since their performance is poor under a wide range of conditions (Hordyk and Carruthers, 2018).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) suggested that length composition of the catch available in the ICCAT database should be used to quantitatively assess the status of these species and inform management advice (ICCAT, 2017). In fisheries without total catch data or information on relative or absolute abundance, stock assessments typically use the spawning potential ratio (SPR) as an alternative reference point to the biomass at maximum sustainable yield (B_{MSY}). SPR can be expressed in terms of spawning stock biomass per recruit (SSBR), which is often defined as the expected lifetime reproductive potential of an average recruit. SPR then is the ratio of the fished SSBR to the unfished SSBR under equilibrium conditions (Goodyear, 1993). SPR has been recommended for data-limited assessment because it can be estimated using only biological information and length data (Brooks *et al.*, 2010).

There are several methods that use life history information and length composition from the catch to estimate fishing intensity and derive values of SPR that can be used as a proxy for stock status. One of them is length-based spawning potential ratio (LBSPR, Hordyk *et al.*, 2015). This method uses the Beverton–Holt life history ratios in an equilibrium-based population model applying the shape of the length composition data compared to the expected unfished length structure to estimate the ratio of fishing mortality and natural mortality (F/M) and derive SPR. Another new method is the length-based integrated mixed effects model (LIME, Rudd and Thorson, 2018), that also requires

biological information and length composition data to derive SPR, but relaxes the equilibrium conditions by treating recruitment as a random effect over time and estimating annual F as fixed effects (Rudd and Thorson, 2018). Both methods can be implemented in R (Hordyk, 2017; R Core Team, 2017; Rudd, 2018).

Data-limited, length-based stock assessment methods typically assume selectivity is asymptotic by default (Hordyk *et al.*, 2015; Rudd and Thorson, 2018). If large fish are absent from the catch, logistic selectivity models assume that they do not exist in the population (as opposed to being present in the population, but evading the fishing gear). The logistic selectivity assumption is usually violated in highly size-selective fisheries (i.e. gillnets), and it could be problematic in multifleet fisheries where stocks are caught in different proportions by multiple gears with different selectivity patterns. As an example, the majority of the catch of the North Atlantic albacore stock comes from pole and line fisheries which have dome-shaped selectivity, catching mainly juvenile albacores. In addition, a smaller proportion of the catch comes from longline fisheries targeting larger individuals, but with different selectivity patterns depending on the fishery (ICCAT, 2014). These different selectivity patterns, catches, and indices of abundance are included in complex assessment models that allow for multiple fleet interactions in the formal assessment performed regularly by ICCAT. When fitting only to the length composition of a proportion of the catch, assumptions regarding fishery dynamics, particularly the shape of the selectivity curve, need to be carefully analysed.

The main objective of this study is to determine the current stock status of small scombrids in the Atlantic Ocean. However, the only data available to evaluate these populations are limited biological information and length composition of the catch coming from different fleets with different selectivity patterns. Therefore, before applying any length-based assessment, we need to determine how to combine these length data to obtain an unbiased estimate of fishing intensity. Developing best practices for combining length data across multiple fleets for length-based assessments of small scombrids in the Atlantic Ocean thus becomes a critical challenge to face to estimate stock status. To address this challenge and meet the main objective, we used simulation testing to evaluate the performance of LBSPR and LIME by combining length composition data of the catch from multiple fleets with different selectivity patterns. Using conclusions from the simulation, we applied both length-based approaches to estimate a proxy of stock status for the priority small scombrid species determined by ICCAT (2018).

Methods

First, we compared the performance of two length-based methods using a simulation study based on North Atlantic albacore. Then, based on the insight about the robustness of the methods, we estimated stock status for the small scombrid stocks.

Simulation study

We chose the North Atlantic albacore stock on which to develop an operating model (OM) to simulate resource dynamics to evaluate the performance of the different assessment methods. ICCAT, in the 2017 report of the small tunas species group inter-session meeting (ICCAT, 2017), suggested the North Atlantic

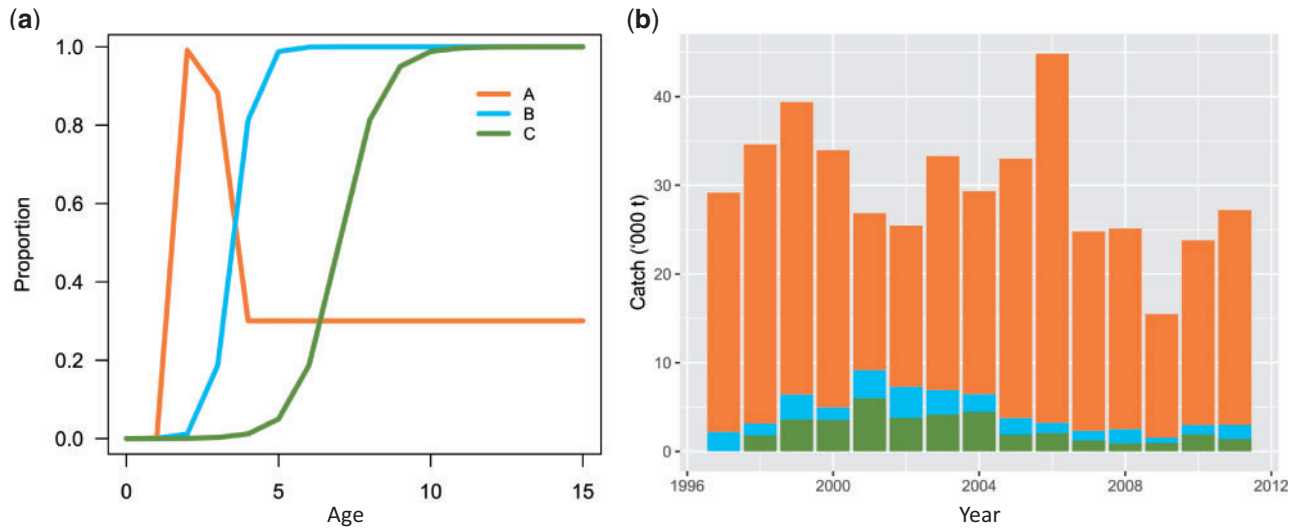


Figure 1. (a) Selectivity patterns include in the OM for each fleet. (b) Catch time-series included in the OM by fleet in the last 15 years (1997–2011) taken from the North Atlantic albacore assessment (ICCAT, 2014). Fleets A, B, and C are combination of fleets described in the main text.

albacore stock as a good example of a multifleet fishery to use for simulation purposes, where the selectivity patterns are considered well estimated for 12 different fleets (ICCAT, 2014). This stock is targeted by pole and line, troll, longline, and other surface gears in the Atlantic Ocean.

In the following sections, we describe the data and specifications used in the OM, the estimation models (EMs), namely LBSPR and LIME, and how we measured their performance under different scenarios.

Operating models

Input data

We extracted the catch time-series (Supplementary Figure S1), selectivity patterns from 12 different fleets (Supplementary Figure S2), and the biological parameters (Table 1) from the formal assessment performed by ICCAT in 2013 for North Atlantic albacore (ICCAT, 2014) to use for the OM. For simplicity and based on similarity of selectivity patterns (Supplementary Figure S2), we combined some fleets using an average age-specific selectivity: (A) fleets 1 and 2 (bait boat and troll fisheries) which target small individuals and have a dome-shaped selectivity curve; (B) fleets 4 and 12 which are other surface gears targeting a broader range of sizes; and (C) fleets 10 and 11 which are longline fisheries targeting mainly adults with an asymptotic selectivity curve (Supplementary Figure S2). During the last 15 years only, the three fleet combinations mentioned earlier were still operating plus fleet 7, which is a longline fleet that captures less than 1% of the total catch and was left out of the analysis. Eighty-seven per cent of the total catch corresponds to the fleets’ bait boat and troll fisheries (A), 6% longline (C) and 7% other surface gears with same selectivity (B) (Figure 1).

Model specifications

We simulated an age-structured population using stock synthesis (SS) version 3.30.12 (Methot and Wetzel, 2013; Methot et al., 2018). We specified a final depletion fitting to an artificial abundance survey index equal to 1 at the beginning of the time-series

Table 1. OM biological inputs parameters for North Atlantic albacore (ICCAT, 2014).

Biological information	Symbol	Value
Maximum age (years)	T_{max}	15
Length where 50% of the fish are mature (cm)	L_{50}	90
Length where 95% of the fish are mature (cm)	L_{95}	100
Length–weight scaling parameter (g)	a	1.34×10^{-5}
Length–weight allometric parameter (g)	b	3.107
von Bertalanffy Brody growth coefficient	k	0.209
von Bertalanffy asymptotic length (cm)	L_{∞}	122
Theoretical age at length 0	t_0	−1.3
Variability of length at age	CVL_{∞}	0.1
Recruitment deviations	σ_R	0.4
Steepness	h	0.9

(1930) and 0.4 B_0 in the last year (2011). The depletion value was arbitrarily selected to mimic the current depletion of the North Atlantic albacore population. All parameters were fixed, except the average recruitment in the unfisher state (R_0). We assumed a Beverton–Holt spawner-recruit function (Beverton and Holt, 1957; Methot and Wetzel, 2013). We simulated two populations, one with and one without recruitment deviations to verify if the outputs were different between the estimations models since LIME specifically estimates recruitment.

Fishing intensity in SS was estimated to match the observed North Atlantic albacore catch. SS assumes that the absolute level of catch is known, using the catch time-series to calculate the level of fishing intensity needed to obtain that level of catch, conditioned on the model’s current estimate of age-specific population abundance and age-specific selectivity (Methot and Wetzel, 2013). Single estimates of fishing mortality rates (F) were calculated for all gears combined in SS. LBSPR and LIME (see the Estimation models section) assume a single gear, so the F estimates represent the F as covered by the stock sampled. SS calculates the SPR as the equilibrium level of spawning biomass per recruit that would occur with the current year’s level of fishing

intensity relative to the unfished level of spawning biomass per recruit (Goodyear, 1993).

After running SS to generate the OM, we extracted the expected catch at age by year and fleet from the SS report. We converted this catch at age in biomass into catch at age in numbers using the mean weight at age. We used the age-length transition matrix output from SS to assign a distribution of length at each age (Supplementary Table S1). Summing across each length bin by gear gave us the length distribution of the catch. We used a 2-cm length bin, which corresponds to the bin structure applied in the formal ICCAT assessment (ICCAT, 2014). To analyse different length sampling scenarios, we sampled 100 individuals from the catch by year and fleet with a multinomial distribution using the probability of being harvested at each length bin for each year. We repeated this process of simulating a population and generating data for 100 replicates for each scenario. We chose to sample only 100 individuals because no big differences in the results were found when using a larger sample size (i.e. 1000 and 10 000 individuals), just a small reduction in variance (see Pons, 2018).

Scenarios

A common question that arises with length data from multifleet fisheries with different selectivity patterns is which fleets to use and how to combine data when applying length-based, data-limited methods that only estimate selectivity and fishing mortality for one fishing gear. We explored the performance of each estimation method under different approaches combining length data into one common “fleet.” The single fleet could actually be one selected fleet or multiple fleets combined in some way. In all scenarios, the selectivity for this one fleet was estimated and starting values were the same for each model run. We explored five possible scenarios:

- Scenario 1: Length composition sampled proportional to the catch of each fleet (Figure 1). This means that fish measured from the fleet with the highest catch would be more represented in the length composition data than other fleets.
- Scenario 2: Length composition sampled with equal weight from each fleet. This means that the same number of individuals were measured from each fleet and combined in one length-sample. All fleets are equally represented in the length composition data.
- Scenario 3: Only use length data from the fleet that targets small individuals (fleet A). Fleet A has a dome-shaped selectivity (Figure 1a) where the true S_{50} is 57 cm (\sim age 1.5) and S_{95} is 61 cm (\sim age 2). It was modeled in SS with a double normal distribution with six parameters. This fishery catches mainly juveniles and it is the main fishery for North Atlantic albacore in terms of catch (Figure 1b).
- Scenario 4: Only use length data from the fleet that targets a broad range of lengths (fleet B). Fleet B has an asymptotic selectivity harvesting both juveniles and adults, with a true S_{50} of 78 cm (\sim age 3.5) and S_{95} of 90 cm (\sim age 5, Figure 1a). In terms of catch, this fleet represents a small proportion of the total (Figure 1b).
- Scenario 5: Only use length data from the fleets that target adults (fleet C). Fleet C also catches a small fraction of the total catch (Figure 1b), but is a longline fishery that targets mainly

adults with a true S_{50} of 100 cm (\sim age 7) and a S_{95} of 108 cm (\sim age 9) (Figure 1a).

Estimation models

In LBSPR, SPR in an exploited population is a function of the ratio of fishing mortality to natural mortality (F/M), selectivity and the two life history ratios M/k and L_m/L_∞ ; k is the von Bertalanffy growth coefficient, L_m is the size of maturity, and L_∞ is asymptotic size (Hordyk *et al.*, 2015). The inputs to the LBSPR are: M/k , L_∞ , the variability of length-at-age (CVL_∞), which was set as 10% in the OMs; and size of maturity specified in terms of L_{50} and L_{95} , the size at which 50 and 95% of a population matures (Table 1). Given the assumed values for the M/k and L_∞ parameters and length composition data from an exploited stock, the LBSPR model uses maximum likelihood methods to estimate the selectivity ogive, which is assumed to be a logistic curve defined by the selectivity-at-length parameters S_{50} and S_{95} and the relative fishing mortality (F/M), which are then used to calculate the SPR (Hordyk *et al.*, 2015). LBSPR estimates a selectivity curve for each length sample. Estimates of SPR are primarily determined by the length of the fish in a sample, relative to the maturity and L_∞ . For example, if a reasonable proportion of fish in a sample attain lengths approaching L_∞ , estimates of F/M will be relatively low leading to a high estimate of SPR. However, the proportion of length samples near L_∞ will vary with the life history parameters such as fecundity-at-age/length and selectivity. LBSPR is an equilibrium-based method with some underlying assumptions including: (i) asymptotic selectivity, (ii) growth adequately described by the von Bertalanffy equation, (iii) a single growth curve can be used to describe both sexes which have equal catchability, (iv) length-at-age is normally distributed, (v) rates of natural mortality are constant across adult age classes, (vi) growth rates remain constant across the cohorts within a stock, and (vii) constant recruitment (Hordyk *et al.*, 2015). In this study, we used LBSPR package version 0.1.2 in R (Hordyk, 2017). The LBSPR package uses the Rauch–Tung–Striebel smoother function to smooth out the multiyear estimates of SPR (Hordyk, 2017), and these smoothed values were used for comparisons to the OM.

LIME is an integrated, age-structured model which requires, as input, biological information such as growth, natural mortality, and maturity, and, at minimum, 1 year of length composition data. LIME estimates, as fixed effects, annual fishing mortality rates F , S_{50} , and S_{95} , the recruitment standard deviation, and a Dirichlet-multinomial parameter governing the relationship between the nominal and effective sample size of length measurements. LIME has most of the same assumptions as LBSPR, but LIME does not assume equilibrium conditions when recruitments can be estimated (i.e. more than 1 year of length data). LIME extends length-based methods by deriving time-varying recruitment deviations (Rudd and Thorson, 2018) using automatic differentiation and Laplace approximations (TMB) (Kristensen *et al.*, 2015) to calculate the marginal likelihood for the random effect on recruitment. Using the assumed biological information, recruitment deviates, estimated F , and estimated selectivity, LIME calculates the predicted abundance-at-age over time. To predict length composition of the catch, LIME calculates the predicted probability of being captured at age over time, the probability of being in a length bin given age, and then the probability of being captured in each length bin. LIME fits the predicted length composition to the observed length composition using the

Dirichlet-multinomial likelihood function. In addition to the length composition marginal likelihood, the joint negative log likelihood also includes a penalty on the fishing mortality rate to avoid varying unrealistically between years and the likelihood of the random effect of annual recruitment deviations. LIME can also accommodate catch and/or abundance data if available (Rudd and Thorson, 2018), although this feature was not used in this study. We used the LIME package version 1.0.5 (Rudd, 2018).

Performance measures

The performance of the EMs under different scenarios was compared to the simulated “truth” from the OM using relative error (RE) calculated as $(estimated - true) / true$, where *estimated* comes from the EM and *true* from the OM. This is a measure of uncertainty, in both bias and precision, of the EM under each scenario, and it is commonly used as a standardized metric of model performance. We used SPR as the performance measure for all scenarios estimated by both LIME and LBSPR. We presented the RE of the last year of the time-series of SPR in all cases for the 100 simulation replicates for each scenario.

Assessment of small scombrids in the Atlantic Ocean

Little tunny, bonito, wahoo, king mackerel, and frigate tuna have been identified as priority to be evaluated by ICCAT in 2017 (ICCAT, 2017). In this study, the only species that we did not evaluate was king mackerel. In the Southwest Atlantic, there is no good information on length data to evaluate this stock; in the Northwest Atlantic, it is regularly assessed by the United States as two independent stocks: one in the Gulf of Mexico and the other off the southeast coast of the United States (SEDAR, 2014a, b). According to these reports, neither stock of king mackerel in the Northwest Atlantic is currently overfished nor undergoing overfishing.

None of the other four species of small scombrids has studies defining stocks boundaries in the Atlantic Ocean. So, for management purposes, ICCAT uses five sampling or statistical areas for small scombrids: Northwest Atlantic, Southwest Atlantic, Northeast Atlantic, Southeast Atlantic, and Mediterranean Sea (Supplementary Figure S3). Hence, we decided to use these areas as proxies for stock boundaries to assess these putative “stocks.”

The ICCAT database (<http://iccat.es/en/accessingdb.htm>) has length data from 1975 to 2016 for the four priority species assessed in this study. The length composition data available for each stock come from different regions and different gear types. To estimate current stock status, we used only data from 2010 to the present where there is a better representation of the length composition of the catch by year and gear (Supplementary Figure S4). We used the length data reported in 1- and 2-cm bins and pooled them into 2-cm length bins for the analysis. The number of fish measured by year for the priority species varies between 17 429 individuals measured in 2016 and 98 173 in 2014, all species combined (Supplementary Figure S4). We presented the stock status for the year 2014 where there are more length data and are consistent among species and representative of different gears.

For some stocks, the length data available were limited, so we removed samples numbering fewer than 100 fish per year and gear combination (Supplementary Figure S4). Some stocks, such as wahoo in the Southwest Atlantic, were excluded from the analysis because they are targeted by multiple fleets, but length

data are available only for one gear (gillnets) and would bias the results. This filtering process reduced the number of stocks with enough information to run the length-based models. We did not run these models for bonito in the Southeast, Northwest, and Southwest, little tunny in the Southwest, wahoo in the Mediterranean, Southeast, and Southwest (stock not present in the Mediterranean), and frigate tuna in the Mediterranean, Southwest, and Southeast, resulting in ten stocks with representative information of length composition data of catch by gear (Supplementary Figure S5 and Table S2).

Both LBSPR and LIME require life history information on growth, maturity, and length–weight relationships as input parameters. These methods are very sensitive to these parameters (Hordyk et al., 2015; Rudd and Thorson, 2018). In 2018, the ICCAT small tunas working group met, and a set of life history parameters were agreed among scientists from each region in the Atlantic Ocean for each stock to run data-limited methods (ICCAT, 2018, Supplementary Table S2). There are many gaps in the life history information available for these species. In cases where there was missing information, we borrowed information from the nearest stock of that species (i.e. when missing information existed for the Southeast Atlantic, we borrowed the information from the Northeast Atlantic) to run the length-based models.

Table 2 shows the final parameters used for each stock to run LBSPR and LIME. Natural mortality (M) was calculated using a suite of empirical life history-based methods (Cope, 2017, see http://barefooteologist.com.au/shiny_m). We used nine empirical methods that used growth parameters (L_{∞} , k , t_0 , and maximum age). Four of these methods are described in Then et al. (2015), two in Jensen (1996), and the other three in Alverson and Carney (1975), Chen and Watanabe (1989), and Jensen (1997), respectively. Table 2 shows the median and first and third quantile of the distribution of M estimated for each stock. LBSPR and LIME were run with these three M values to test their sensitivity to these parameter estimations.

Reference points for small scombrids

We used SPR as a biological reference point. In general, it is used as a proxy for B_{MSY} when information on the scale population size is not available. A harvest strategy that targets a fishing mortality rate that is expected to result in 40% of the unfished spawning output ($SPR_{40\%}$) is considered a reasonable proxy even for stocks with very low resiliency (Clark, 2002). Moreover, 30% SPR is sometimes considered a threshold beyond when the stock is overfished (Clark, 2002; Nadon et al., 2015; Rudd and Thorson, 2018). In addition, we presented the estimated ratio F/M for each stock.

Results

Simulation testing: length data in multifleet fisheries

Based on the observed catch data for North Atlantic albacore used in the OM, the true SPR value in the terminal year was 0.55 for the OM without recruitment deviations; for the OM that includes random recruitment deviations, the median was 0.66, with a range 0.50–0.74 (Supplementary Figure S6). LBSPR was least biased when using length data from the fleet with asymptotic selectivity catching a broad range of lengths from juveniles to adults (Scenario 4; Figure 2). LIME was least biased with length data from the fleet that targets only adults when considering

Table 2. Life history parameters used as inputs to assess stock status of small scombrids in the Atlantic Ocean using length-based data-limited methods.

Species	Parameter	Northeast	Southeast	Mediterranean	Northwest	Southwest	
<i>Sarda sarda</i> (BON)	L_{∞} (cm)	73 (Baibbat <i>et al.</i> , 2016)		70 (Kahraman <i>et al.</i> , 2014)			
	k (years ⁻¹)	0.31 (Baibbat <i>et al.</i> , 2016)		0.44 (Kahraman <i>et al.</i> , 2014)			
	t_0 (years)	-2.45 (Baibbat <i>et al.</i> , 2016)		-1.33 (Kahraman <i>et al.</i> , 2014)			
	T_{max} (years)	5 (Baibbat <i>et al.</i> , 2016)		5 (Cayré <i>et al.</i> , 1993)			
	L_{50} (cm)	42.6 (Baibbat <i>et al.</i> , 2016)		39.9 (Saber <i>et al.</i> , 2017)			
	M^* (years ⁻¹)	0.43; 0.78; 1.11		0.60; 0.83; 1.09			
	WL_a (g)	5.0×10^{-5} (Baibbat <i>et al.</i> , 2016)		6.3×10^{-6} (Saber <i>et al.</i> , 2017)			
	WL_b	2.79 (Baibbat <i>et al.</i> , 2016)		3.21 (Saber <i>et al.</i> , 2017)			
	<i>Euthynnus alletteratus</i> (LTA)	L_{∞} (cm)	86 (Cabrera <i>et al.</i> , 2005) ^a	86 (Cabrera <i>et al.</i> , 2005) ^a	117 (Hattour, 2009)	86 (Cabrera <i>et al.</i> , 2005)	
		k (years ⁻¹)	0.26 (Cabrera <i>et al.</i> , 2005) ^a	0.26 (Cabrera <i>et al.</i> , 2005) ^a	0.19 (Hattour, 2009)	0.26 (Cabrera <i>et al.</i> , 2005)	
t_0 (years)		-0.32 (Cabrera <i>et al.</i> , 2005) ^a	-0.32 (Cabrera <i>et al.</i> , 2005) ^a	-1.13 (Hattour, 2009)	-0.32 (Cabrera <i>et al.</i> , 2005)		
T_{max} (years)		8 (Cayré and Diouf, 1980)	8 (Cayré and Diouf, 1980) ^b	10 (Hattour, 2009)	8 (Cayré and Diouf, 1980) ^b		
L_{50} (cm)		42.0 (Diouf, 1980)	42.0 (Diouf, 1980) ^b	51.1 (Hajje <i>et al.</i> , 2012)	39.7 (Ramírez-Arredondo, 1993)		
M^* (years ⁻¹)		0.4; 0.53; 0.68	0.4; 0.53; 0.68	0.29; 0.43; 0.54	0.4; 0.53; 0.68		
WL_a (g)		1.4×10^{-5} (Diouf, 1980)	1.4×10^{-5} (Diouf, 1980) ^b	1.2×10^{-5} (Saber <i>et al.</i> , 2017)	2.1×10^{-5} (Ramírez-Arredondo <i>et al.</i> , 1996)		
WL_b		3.04 (Diouf, 1980)	3.04 (Diouf, 1980) ^b	3.06 (Saber <i>et al.</i> , 2017)	2.96 (Ramírez-Arredondo <i>et al.</i> , 1996)		
<i>Acanthocybium solandri</i> (WAH)		L_{∞} (cm)	179.7 (Viana <i>et al.</i> , 2013) ^a		179.7 (Viana <i>et al.</i> , 2013)		
		k (years ⁻¹)	0.32 (McBride <i>et al.</i> , 2008) ^a		0.32 (McBride <i>et al.</i> , 2008)		
	t_0 (years)	-1.91 (McBride <i>et al.</i> , 2008) ^a		-1.91 (McBride <i>et al.</i> , 2008)			
	T_{max} (years)	9 (McBride <i>et al.</i> , 2008) ^a		9 (McBride <i>et al.</i> , 2008)			
	L_{50} (cm)	92.5 (Jenkins and McBride, 2009) ^a		92.5 (Jenkins and McBride, 2009)			
	M^* (years ⁻¹)	0.43; 0.49; 0.60		0.43; 0.49; 0.60			
	WL_a (g)	2.8×10^{-4} (Santana <i>et al.</i> , 1993)		2.0×10^{-6} (Beerkircher, 2005)			
	WL_b	2.72 (Santana <i>et al.</i> , 1993)		3.24 (Beerkircher, 2005)			
	<i>Axius thazard</i> (FRI)	L_{∞} (cm)	52 (Grudtsev and Korolevich, 1986) ^c	52 (Grudtsev and Korolevich, 1986)	Stock not defined		
		k (years ⁻¹)	0.32 (Grudtsev and Korolevich, 1986) ^c	0.32 (Grudtsev and Korolevich, 1986)			
t_0 (years)		-0.83 (Grudtsev and Korolevich, 1986) ^c	-0.83 (Grudtsev and Korolevich, 1986)				
T_{max} (years)		4 (Grudtsev and Korolevich, 1986) ^c	4 (Grudtsev and Korolevich, 1986)				
L_{50} (cm)		30 (Cayré <i>et al.</i> , 1993) ^c	30 (Cayré <i>et al.</i> , 1993)				
M^* (years ⁻¹)		0.48; 1.01; 1.37	0.48; 1.01; 1.37				
WL_a (g)		8.9×10^{-6} (Frota <i>et al.</i> , 2004) ^d	8.9×10^{-6} (Frota <i>et al.</i> , 2004) ^d				
WL_b		3.17 (Frota <i>et al.</i> , 2004) ^d	3.17 (Frota <i>et al.</i> , 2004) ^d				
				Insufficient length data	Insufficient length data	Insufficient length data	

*M was estimated empirically through different methods. The first quantile, median, and third quantile are presented. For the same species:

^aInformation borrowed from the Northwest stock.

^bInformation borrowed from the Northeast stock.

^cInformation borrowed from the Southeast stock, and

^dInformation borrowed from the Southwest stock.

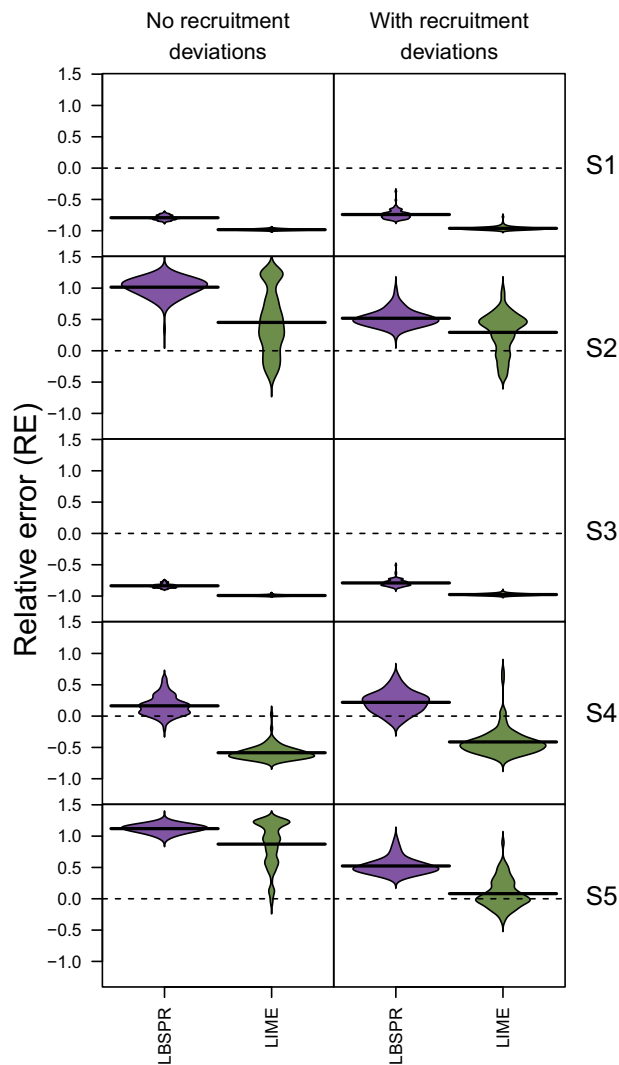


Figure 2. RE for the five scenarios tested (S1–S5) for LIME and LBSPR compared to the OMs with (right column) and without (left column) recruitment deviations.

recruitment variability (Scenario 5; Figure 2). In the Supplementary, we presented potential biases in the EMs compared to our OMs under perfect equilibrium conditions. It seems that a persistent bias exists for both assessment methods compared to the OM, except for LBSPR when fish are selected before reaching the length at maturity. In general, LIME underestimates SPR for this species (North Atlantic albacore), particularly when individuals are selected by the fishery before maturing. LIME also overestimates selectivity most of the time, but is less biased when adults are present in the samples. LBSPR is slightly positively biased only when the sampled individuals are above the size at maturity (Supplementary Table S3).

In Scenario 1, length composition data was weighted by the fleet's proportional catch, meaning that more weight was given to the fleet with dome-shaped selectivity. In this scenario, both LBSPR and LIME underestimated SPR on average in both recruitment scenarios (Figure 2). Under an asymptotic selectivity assumption, if large individuals are absent from the catch, both assessment methods estimate F to be higher than the truth and

SPR lower than the truth. LIME estimated SPR to be almost zero. Results from Scenario 3 were similar to Scenario 1 since both scenarios put higher weight on length compositions consisting of mainly juveniles or smaller individuals than the full span of vulnerable fish.

Under Scenario 2, sampling the same number of individuals by gear type, LBSPR and LIME estimated SPR higher than the truth, particularly when the OM did not consider recruitment variability. When considering recruitment variability, LBSPR was positively biased, although LIME was less biased, but less precise. Under these scenarios, the proportion of large individuals in the catch was over-represented, leading to the EMs estimating higher SPR values than expected. The same overestimation of SPR occurred in Scenario 5 using the fleet that targets adults when no recruitment variability was included in the OM due to the proportions of large individuals in the catch. However, as was shown under perfect equilibrium conditions (Supplementary Table S3), LIME tends to be less biased when large individuals are in the samples.

LBSPR was less biased in Scenario 4 when considering only the fleet with an asymptotic selectivity that captures a broad range of sizes (from juveniles to adults), while LIME was less biased under the scenarios with recruitment variability when considering the fleets with gears that selected mainly adults in Scenario 5 (Figure 2). We observed that, in many cases, even under equilibrium conditions (Supplementary Table S3), LIME estimated higher selectivity parameter values, S_{50} and S_{95} , and lower SPR values than LBSPR. This is probably the reason why LIME performs better when using fleets that target large fish and why LIME SPR estimates are lower than LBSPR SPR estimates when using the same data.

Assessments of small scombrids in the Atlantic Ocean

Based on simulation testing, none of the scenarios produced the best performance for both EMs (LIME and LBSPR) simultaneously. LBSPR performed best in Scenario 4, which used the length data coming from the fleet with an asymptotic selectivity targeting a broad range of lengths. LIME, however, performed better in Scenarios 5, where mainly adults were represented in the catch. So, based on these results, we decided to apply both LIME and LBSPR using the length composition data from small scombrids from the fleet that has a broader range of sizes including adults, but not restricted to the adult portion of the catch. The gears used then varied among small tuna stocks (Figure 3).

The length composition data for each stock by gear, filtered by year–gear combinations with at least 100 length measurements, varies among areas. These differences likely stem from variable fleets operations in each region. Length composition data for little tunny are available for two gears in the Northwest Atlantic, but rod and reel has more representative sampling by year and length range compared to traps (Supplementary Figure S5). In this case, we used length data only from rod and reel to assess this stock (Figure 3). For little tunny in the Northeast Atlantic, we selected the length data coming from traps since they cover a broader range of ages including adults, despite the fact that there are no data in 2011. For little tunny in the Mediterranean, we used length data from longlines; for the Southeast Atlantic, we used data from gillnets (Supplementary Figure S5 and Figure 3). For wahoo in the Northeast, we used the length composition from handlines since it was the only information available; we used rod

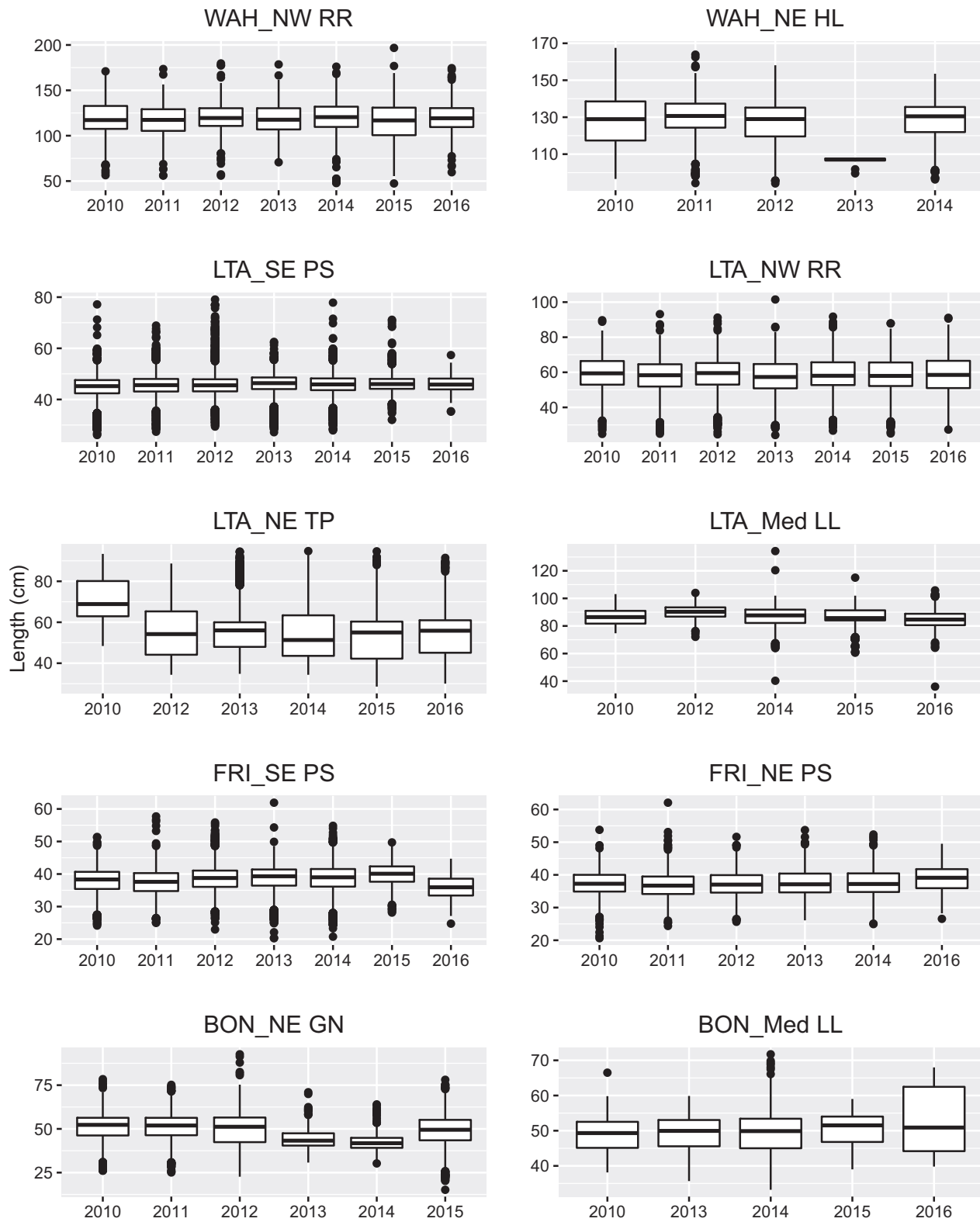


Figure 3. Length distribution (in cm) included in LBSPR and LIME models by stock. Species codes: LTA, little tunny; WAH, wahoo; BON, bonito; FRI, frigate tuna. Stock area codes: NE, Northeast; SE, Southeast; NW, Northwest; Med, Mediterranean Sea. Gears code: RR, rod and reel; HL, handline; PS, purse-seine; TP, trap; LL, longline; GN, gillnet.

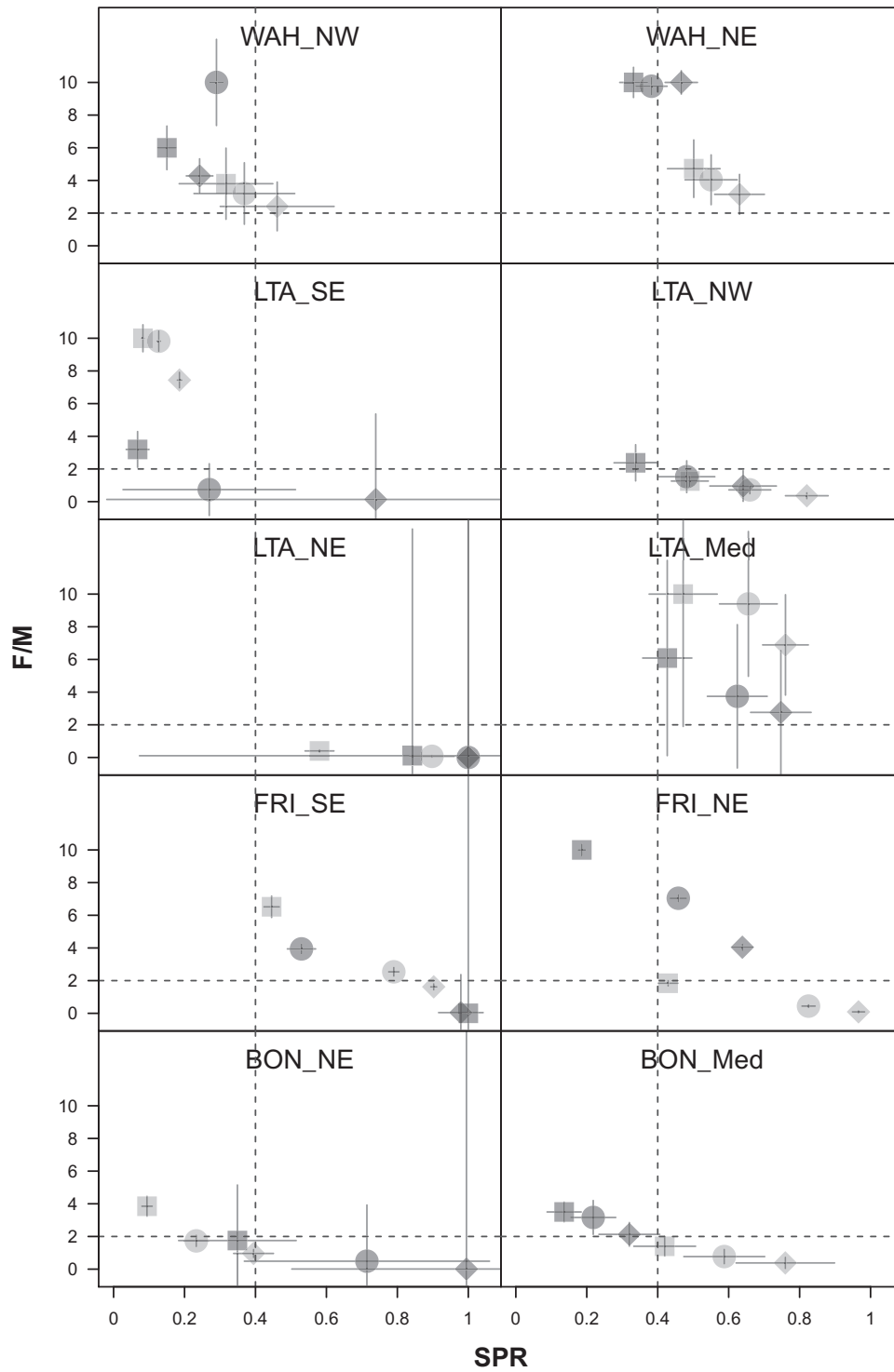


Figure 4. Proxy of stock status for priority small scombrid species. Vertical dashed line represents where $SPR = 40\%$ and horizontal line represents $F/M = 2$. Results from LIME are in dark grey, and results from LBSPR are in light grey for the three values of M considered. Circles are median M , squares are M at the first quartile, and diamonds M at the third quartile. Grey lines are the confidence intervals of the estimated SPR and F/M . Species codes: LTA, little tunny; WAH, wahoo; BON, bonito; FRI, frigate tuna. Stock areas code: NE, Northeast; SE, Southeast; NW, Northwest; Med, Mediterranean Sea.

Table 3. Summary of stock status for small scombrids in the Atlantic Ocean.

Species	Stock	LBSPR			LIME		
		SPR	CI_low	CI_up	SPR	CI_low	CI_up
Little tunny	Southeast	0.13	0.12	0.13	0.27	0.03	0.51
Bonito	Northeast	0.23	0.20	0.27	0.71	0.37	1.06
Wahoo	Northwest	0.37	0.23	0.51	0.29	0.27	0.31
Wahoo	Northeast	0.55	0.48	0.62	0.38	0.34	0.43
Bonito	Mediterranean	0.59	0.47	0.70	0.22	0.15	0.28
Little tunny	Mediterranean	0.66	0.57	0.74	0.62	0.54	0.71
Little tunny	Northwest	0.66	0.60	0.72	0.48	0.40	0.56
Frigate tuna	Southeast	0.79	0.78	0.80	0.53	0.49	0.57
Frigate tuna	Northeast	0.83	0.81	0.84	0.46	0.44	0.48
Little tunny	Northeast	0.90	0.83	0.96	1.00	1.00	1.00

SPR is shown for both models, LBSPR and LIME, with the lower (CI_low) and upper (CI_up) confidence interval for the base model (median M).

and reel data for the Northwest. For bonito in the Mediterranean, we used length data coming from longlines, such as for little tunny in the same area. Finally, for frigate tuna in the Northeast and Southeast, we selected the length data coming from purse-seine fisheries (Supplementary Figure S5 and Figure 3).

For some small scombrid stocks, the SPR estimates were below the target of 40%, but the results varied between assumptions about M and the estimation method considered (Figure 4). LBSPR and LIME predicted different values of SPR; the estimated values were sometimes far apart, such as for bonito in the Mediterranean and in the Northeast (e.g. 0.2 with LIME and 0.6 with LBSPR). LIME estimated a higher F and lower SPR than LBSPR (Supplementary Figure S7). In contrast, for bonito in the Northeast, LIME estimated a higher selectivity ogive, lower F , and higher SPR than LBSPR. For 2014, LIME estimated high recruitment; the small individuals in the catch were attributed to the recruitment spike, as opposed to LBSPR, which interpreted the small individuals as a high F (Supplementary Figure S7). As expected, when M was assumed to be lower than in the base case scenario (median M), the SPR estimations were lower (Figure 4).

SPR for little tunny in the Southeast was below 0.40 in all cases, except when LIME assumed a high M , which resulted in a SPR estimate of 0.70 (Figure 4). Assuming the median value of M , LBSPR predicted a very high F and SPR values below 0.20 for the entire time-series. LIME also predicted low SPR values, around 0.30, and a much lower S_{50} than LBSPR (Supplementary Figure S8). The results of LBSPR and LIME were more similar for little tunny in the Northwest, Mediterranean, and Northeast Atlantic (Supplementary Figure S8). SPR for these stocks were above the 40% target reference point. For little tunny in the Mediterranean, the ratio between F/M is high (above 2), even though SPR is above 40%.

SPR estimates for both LBSPR and LIME for wahoo in the Northwest were below 40% (except in the high M scenario with LIME). LIME predicted very high F/M and SPR below 40%, except when assuming a higher M for wahoo in the Northeast. In both the Northwest and Northeast, LIME predicted a higher S_{50} and a lower SPR than LBSPR (Supplementary Figure S9). None of the frigate tuna stock assessments estimated SPR below 40%, except with LIME in the low M scenario where SPR was estimated at ca. 20% for the Northeast and Southeast stocks (Figure 4 and Supplementary Figure S10). Table 3 summarizes the status of the

ten small Scombrids stocks assessed under the base-case scenario, considering the median of the M distribution.

Discussion

Length data in multifleet fisheries

We showed how stock assessment results could be highly biased when using only one gear that is not representative of the length composition of the exploited population, particularly when the assumptions of asymptotic selectivity are violated (e.g. albacore length data coming from bait boat and troll fisheries targeting juveniles with dome-shaped selectivity). In this case, high catches of smaller individuals resulted in an under-representation of the proportion of adults in the population, estimating a lower SPR value than the actual value. Even if the asymptotic selectivity assumption is met (i.e. albacore length data coming from longline fleets targeting adults), SPR was overestimated. Hordyk *et al.* (2015) suggested that when there are multiple fleets targeting the same stock, the LBSPR model should be applied to the data from the fleet that targets the adult portion of the stock. However, we found that SPR estimates were positively biased when fish are caught after reaching the size at maturity L_{50} (Supplementary Table S3). In all the scenarios analysed by Hordyk *et al.* (2015), the S_{50} was lower than the L_{50} , but in our Scenarios 5 and 6, the S_{50} was higher than L_{50} , explaining why they did not find this bias in their results. SPR estimates are primarily determined by the size of the fish in a sample relative to both size at maturity L_{50} and L_{∞} . In our Scenario 4, where the S_{50} was lower than the L_{50} , LBSPR was less biased, as we also showed assuming perfect equilibrium conditions (Supplementary Table S3).

Rudd and Thorson (2018) tested the performance of LIME under LBSPR's own OM (Hordyk *et al.*, 2015), with relative ages based on the M/k ratio. They found that LBSPR performs well across all life history types, but LIME underestimated SPR for the medium- and longer-lived life history types and overestimated SPR for the short-lived life history type. However, in most of the non-equilibrium scenarios, LIME performed better than LBSPR. We also found in most of the scenarios considered that LIME estimated a lower SPR than LBSPR for this medium-lived albacore tuna. Also, we showed how, even under equilibrium conditions, that different OMs structures can show biases in the performance of the EMs (Supplementary Table S3).

Based on our results, we recommend that, when there are multiple fleets with different selectivity patterns targeting one stock, and the length-based estimator assumes asymptotic selectivity, length-based models should be applied to the length data coming from the fleet that targets the broadest range of sizes including adults, but not restricted only to the adult portion of the catch. In particular, it is important to include juveniles because SPR estimates improve when the catch length sample is representative of the length composition of the entire exploited population.

Small scombrids stock status

LBSPR estimates of SPR, selectivity parameters, and the ratio of fishing mortality to natural mortality (F/M) are independently determined each year. However, LIME includes length composition data available for multiple years in the same model to estimate a single selectivity curve for all years, but fishing mortality and recruitment can vary among years. Therefore, assumptions and model structure are different between LIME and LBSPR,

leading, unsurprisingly, to different results on the proxy of the stock status for small scombrids.

We did not find a specific pattern in exploitation status among regions (Figure 4) as regions in the Atlantic Ocean showed comparable stock status. Although some combinations of stock assessment model and natural mortality rate resulted in differing estimates of stock status, the approaches agreed under the base scenario with median M that two stocks out of ten are overfished: the little tunny in the Southeast and wahoo in the Northwest.

Little tunny

The length composition data for little tunny in the Northeast and Northwest Atlantic from purse-seiners were very similar and both assessment methods indicated that these stocks are above stock status targets ($SPR > 0.4$). However, for little tunny in the Southeast, most of the fish caught were below the length at maturity and, in most of the scenarios, this stock was estimated to be overfished. These results agree with a preliminary qualitative risk assessment analysis performed for small scombrids in the Atlantic Ocean considering two populations, north and south. The southern stock was found at high risk, while the northern population was found at moderate risk (Lucena-Frédou, Frédou, et al., 2017). This species has an estimated maximum age between 8 and 10 years (Cayré and Diouf, 1980) and an estimate of L_{∞} between 86 and 117 cm. Adults of this species (>60 cm) in the Southeast are scarce in the length composition leading to low estimates of SPR. Along with bonito and frigate tuna, this species is one of the most captured among all small scombrids in the Atlantic Ocean (ICCAT, 2018).

Bonito

In the base-case scenario, bonito in the Northeast was estimated to have a SPR below target reference points ($SPR < 0.4$) with LBSPR, but not with LIME. The opposite was observed in the Mediterranean, where LIME estimated a lower SPR than LBSPR. Rudd and Thorson (2018) found that LIME generally estimated a higher SPR than the truth for short-lived fish in a yearly time-step. A monthly time-step could be considered in the future for this species to test for sensitivity to this assumption since the life span for this species is 5 years (Baibbat et al., 2016).

Previous data-limited assessment methods were applied for bonito in the Northeast using Morocco landings data between 2012 and 2014. A Powell–Wetherall plot approach was used to explore changes in total mortality based on length samples and catch-curve analysis using lengths converted to age and cohort slicing (Ahmed et al., 2015). Assuming $M = 0.2$, they found that fishing mortality is twice this value and suggested that this stock might be fully exploited. The M values used in this study were >0.2 in all cases, so using such a low value for M could give similar results as in Ahmed et al. (2015). However, for this short-lived species, we assume natural mortality should be >0.2 (as is typical for other short-lived species).

This species is the most captured among all small scombrids (ICCAT, 2018), but the biological information as well as the length composition data available are highly fragmented and variable. Our results should be analysed with caution; as better data becomes available, these stocks should be re-evaluated. This should be a high priority item for ICCAT.

Frigate tuna

In almost all scenarios, the stocks were estimated to be $>40\%$ SPR. However, assessments for the Northeast stock always estimated lower SPR values than for the one in the Southeast. Again, these results matched the preliminary risk assessment for small scombrids in the Atlantic Ocean, where stocks in the south are at lower risk than the ones in the north (Lucena-Frédou, Frédou, et al., 2017). However, both F and SPR estimates in the Southeast should be considered with caution, since some of the results are in the low-right quadrant at F , close to 0 and SPR close to 1 with very high uncertainty. In particular, for LIME, this could indicate an unconverged model (Supplementary Figure S8). If F was estimated to be close to 0, it is likely that the life history information is inaccurate because we know the F is not 0 since fishing is occurring. L_{∞} might be too low, so both models would estimate no fishing if the observed lengths are very close to the asymptotic length. The growth parameters should be discussed again at the next small tuna group meeting to consider different life history values for this stock.

Wahoo

Both LIME and LBSPR estimated low SPR values for the Northwest stock, suggesting that this stock is overfished. In the Northeast, only LIME in the base case and low M scenarios estimated that this stock is overfished, but not LBSPR. In the South Atlantic, wahoo has been categorized as high risk, and no assessments are available for this stock. This species, along with bonito, should be considered as a priority to assess by ICCAT.

Future directions

We estimated for the first time a proxy of current stock status for ten stocks of the small scombrid group of species in the Atlantic Ocean. This is a very important starting point in the estimation of stock status for these species, but the wide uncertainty in estimates combined with differences in results between LBSPR and LIME demonstrate that data-poor methods are not substitutes for more data-intensive assessment techniques. ICCAT still needs to support the collection of improved life history information, length data from all fishing gears, and total removals for these stocks and associated fishing data. While collecting such information in small coastal fisheries is challenging, particularly for catch and effort data, it is important to develop indices of abundance. A full assessment might return estimates with higher precision, although it does not mean that it would be more accurate than the estimates provided here. Data collection should focus on filling gaps and improving existing biological information, particularly for stocks such as little tunny in the Southeast Atlantic, where data were borrowed from the Northwest Atlantic stock. Also, ICCAT should emphasize the importance of obtaining length data across the different gears, particularly those that cover a broad range of sizes. For example, wahoo in the Southwest Atlantic were excluded from the analysis because they are targeted by multiple fleets, but length data are available only for one gear (gillnets) and using only this data could bias the results.

LBSPR and LIME, like all age- or length-based methods, are sensitive to misspecifications of the inputs of life information (Hordyk et al., 2015; Kokkalis et al., 2017; Rudd and Thorson, 2018). Sensitivity tests in these studies demonstrated the impact of the misspecification of biological parameters. Quantification of uncertainty is one of the next steps in the evaluation of these

small scombrid stocks, not only for *M*, but also for other growth and maturity parameters, to provide support for local biological studies of these species. To account for the uncertainty in the biological parameters with the current information available in the Scombridae database (Juan-Jordá *et al.*, 2016), a Monte Carlo algorithm could be applied in specifying prior distributions for life history parameters (Prince *et al.*, 2015) for this group of species.

Small scombrid fisheries in the Atlantic Ocean are medium- to small-scale, data-limited, and generally unassessed, with a lack of management and enforcement, with the exception of some regions in the Northwest Atlantic, such as in the United States. Determining stock status is the first step to protect these stocks from being overfished and to apply management measures to rebuild overfished stocks. Since stock status for these species is highly uncertain, simulation testing is needed to evaluate different management procedures accounting for data and model uncertainty in a management strategy framework. Management strategy evaluation could be used to develop robust management frameworks for such stocks, e.g. using the data-limited methods toolkit (Carruthers and Hordyk, 2018).

Conclusions

This study analysed different approaches using length-based, data-limited assessments when length composition data come from fisheries with multiple gears with different selectivity patterns. An aim of this study was to evaluate how to use length composition data from multifleet fisheries to estimate stock status for small scombrids. We recommend that length-based models should be applied to the length data coming from the fleet that targets the broadest range of sizes, including juveniles and adults when the data are available. Even though the results observed here can be applied to other multifleet fisheries, the results show biases under different selectivity assumptions for the simulated albacore population, so further simulation testing for data-poor, multifleet fisheries with variable life history, selectivity, and exploitation patterns should be explored.

Small tunas are an important social and economic resource for many coastal communities; however, most of these stocks have not been assessed, and their status is unknown. This work is, therefore, an important first step in developing management plans, particularly as the evaluation of uncertainty recognizes where data are needed to identify stock status and reduce risks of overfishing. Little tunny in the Southeast and wahoo in the Northwest are overfished, despite the method and *M* used, which confirms the previous perception of ICCAT. These species have already been assigned priority, given their social-economic importance and also considering that they were two of the top three stocks at risk in the Atlantic Ocean, hence deserving most of the managers' attention (SCRS, 2018). For the Southeast little tunny, life history parameters for the given "stock" are not available, and data used within this study were borrowed from other areas, which may hamper our analysis. This species should be certainly considered as a priority for data collection within the small tuna group within ICCAT. For the Northwest wahoo, although life history parameters are available, length composition is only available for rod and reel, which may not include the majority of size classes. For both species, ICCAT has already developed a research programme to address knowledge gaps regarding size data and biological parameters (from both biological sampling and tagging programmes).

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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References

- Ahmed, B. S., Abid, N., Palma, C., and Kell, L. 2015. A length based assessment for Atlantic bonito (*Sarda sarda*). Collective Volume of Scientific Papers of ICCAT, 72: 2208–2220.
- Alverson, D. L., and Carney, M. J. 1975. A graphic review of the growth and decay of population cohorts. Journal du Conseil International pour l'Exploration de la Mer, 36: 133–143.
- Baibbat, S., Malouli, I., Abid, N., and Benazzouz, B. 2016. Study of the reproduction of Atlantic bonito (*Sarda sarda*) in South Atlantic Ocean of Morocco. Aquaculture, Aquarium, Conservation & Legislation—International Journal of the Bioflux Society, 9: 954–964.
- Beerkircher, L. R. 2005. Length to Weight conversions for Wahoo, *Acanthocybium solandri*, in the Northwest Atlantic. Collective Volume of Scientific Papers of ICCAT, 58: 1616–1619.
- Beverton, R. J. H., and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations (Great Britain, Ministry of Agriculture, Fisheries, and Food), London. 536 pp.
- Brooks, E. N., Powers, J. E., and Cortés, E. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. ICES Journal of Marine Science, 67: 165–175.
- Cabrera, M. A., Defeo, O., Aguilar, F., and Martínez, J. D. D. 2005. La pesquería de bonito (*Euthynnus alletteratus*) del noreste del banco de Campeche, México. Proceedings of the Gulf and Caribbean Fisheries Institute, 46: 744–758.
- Carruthers, R. T., and Hordyk, A. R. 2018. The Data-Limited Methods Toolkit (DLMtool): an R package for informing management of data-limited populations. Methods in Ecology and Evolution, 9: 2388–2395.
- Cayré, P., and Diouf, T. 1980. Croissance de la thonine (*Euthynnus alletteratus*) (Rafinesque, 1810) établie a partir de coupes transversales du premier rayon de la nageoire dorsale. Collected Volume of Scientific Papers of ICCAT, 15: 337–345.
- Cayré, P., Amon Kothias, J. B., Diouf, T., and Stretta, J. M. 1993. Biology of tuna. In Resources, Fishing and Biology of the Tropical Tunas of the Eastern Central Atlantic. Ed. by A. Fonteneau and J. Marcille. FAO Fisheries Technical Paper, 292. FAO, Rome, Italy. 354 pp.
- Chen, S., and Watanabe, S. 1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi, 55: 205–208.
- Chrysafi, A., and Kuparinen, A. 2016. Assessing abundance of populations with limited data: lessons learned from data-poor fisheries stock assessment. Environmental Reviews, 1: 1–44.
- Clark, W. G. 2002. F35% revisited ten years later. North American Journal of Fisheries Management, 22: 251–257.

- Collette, B. B., and Nauen, C. E. 1983. FAO Species Catalogue, Vol. 2 Scombrids of the World. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fisheries Synopsis, 125. 137 pp.
- Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., Elfes, C. *et al.* 2011. High value and long life—double jeopardy for tunas and billfishes. *Science*, 333: 291–292.
- Cope, J. M. 2017. Natural Mortality Estimators—The Barefoot Ecologist's Toolbox. http://barefootecologist.com.au/shiny_m (last accessed 1 April 2018).
- Diouf, T. 1980. Peche et biologie de trois Scombridae exploités au Sénégal: *Euthynnus alletteratus*, *Sarda sarda* et *Scomberomorus tritor*. Thèse de doctorat 3ème cycle, Université de Bretagne Occidentale, France. 159 pp.
- Dowling, N. A., Wilson, J. R., Rudd, M. B., Babcock, E. A., Caillaux, M., Cope, J., Dougherty, D. *et al.* 2016. FishPath: a decision support system for assessing and managing data- and capacity-limited fisheries. *In* Assessing and Managing Data-limited Fish Stocks, pp. 59–96. Ed. by T. J. Quinn II, J. L. Armstrong, M. Baker, J. Heifetz, and D. Witherell. Alaska Sea Grant Program, University of Alaska, Fairbanks.
- FAO. 2016. The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all. Food and Agriculture Organization. Rome. 200 pp. <http://www.fao.org/3/a-i5555e.pdf> (last accessed 1 October 2017).
- Frota, L. O., Costa, P. A. S., and Braga, A. C. 2004. Length-weight relationships of marine fishes from the central Brazilian coast. *Naga, WorldFish Center Quarterly*, 27: 20–26.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk Evaluation and Biological Reference Points for Fisheries Management, 120, pp. 67–82. Ed. by S. J. Smith, J. J. Hunt, and D. Rivard. Canadian Special Publication of Fisheries and Aquatic Sciences. 442 pp. NRC Research Press, Canada.
- Grudtsev, M. E., and Korolevich, L. I. 1986. Studies of frigate tuna *Auxis thazard* (Lacepede) age and growth in the eastern part of the Equatorial Atlantic. *Collective Volume of Scientific Papers of ICCAT*, 25: 269–274.
- Hajje, G., Hattour, A., Hajje, A., Cherif, M., Allaya, H., Jarbou, O., and Bouain, A. 2012. Age and growth of little tunny, *Euthynnus alletteratus* (Rafinesque, 1810), from the Tunisian Mediterranean coasts. *Cahiers de Biologie Marine*, 53: 113–122.
- Hattour, A. 2009. Les thons mineurs tunisiens: étude biologique et pêche. *Collective Volume of Scientific Papers of ICCAT*, 64: 2230–2271.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., and Prince, J. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES Journal of Marine Science*, 72: 217–231.
- Hordyk, A. R. 2017. LBSPR: Length-Based Spawning Potential Ratio. R Package Version 0.1.3. <https://github.com/AdrianHordyk/LBSPR> (last accessed 10 July 2018).
- Hordyk, A. R., and Carruthers, T. R. 2018. A quantitative evaluation of a qualitative risk assessment framework: examining the assumptions and predictions of the Productivity Susceptibility Analysis (PSA). *PLoS One*, 13: e0198298.
- ICCAT. 2014. Report of the 2013 ICCAT North and South Atlantic Albacore stock assessment meeting. *Collective Volume of Scientific Papers of ICCAT*, 70: 830–995.
- ICCAT. 2017. Report of the 2017 Small tunas species group intersessional meeting, Miami, United States, 24–28 April 2017. *Collective Volume of Scientific Papers of ICCAT*, 74: 1–75.
- ICCAT. 2018. Report of the 2018 ICCAT Small tuna species group intersessional meeting, Madrid, Spain 2–6 April, 2018. *Collective Volume of Scientific Papers of ICCAT*, 75: 1–67.
- Jenkins, K. L. M., and McBride, R. S. 2009. Reproductive biology of wahoo, *Acanthocybium solandri*, from the Atlantic coast of Florida and the Bahamas. *Marine and Freshwater Research*, 60: 893–897.
- Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 820–822.
- Jensen, A. L. 1997. Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 987–989.
- Juan-Jordá, M. J., Mosqueira, I., Cooper, A. B., Freire, J., and Dulvy, N. K. 2011. Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences of the United States of America*, 108: 20650–20655.
- Juan-Jordá, M. J., Mosqueira, I., Freire, J., and Dulvy, N. K. 2015. Population declines of tuna and relatives depend on their speed of life. *Proceedings of the Royal Society B: Biological Sciences*, 282: 20150322.
- Juan-Jordá, M. J., Mosqueira, I., Freire, J., Ferrer-Jordá, E., and Dulvy, N. K. 2016. Global scombrid life history dataset. *Ecology*, 97: 809–809.
- Kahraman, A. E., Göktürk, D., Yildiz, T., and Uzer, U. 2014. Age, growth, and reproductive biology of Atlantic bonito (*Sarda sarda* Bloch, 1793) from the Turkish coasts of the Black Sea and the Sea of Marmara. *Turkish Journal of Zoology*, 38: 614–621.
- Kokkalis, A., Eikeset, A. M., Thygesen, U. H., Steingrund, P., and Andersen, K. H. 2017. Estimating uncertainty of data limited stock assessments. *ICES Journal of Marine Science*, 74: 69–77.
- Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. M. 2016. TMB: Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software*, 70: 1–21.
- Lucena-Frédou, F., Frédou, T., and Ménard, F. 2017. Preliminary Ecological Risk Assessment of small tunas of the Atlantic Ocean. *Collective Volume of Scientific Papers of ICCAT*, 73: 2663–2678.
- Lucena-Frédou, F., Kell, L., Frédou, T., Gaertner, D., Potier, M., Bach, P., Travassos, P. *et al.* 2017. Vulnerability of teleosts caught by the pelagic tuna longline fleets in South Atlantic and Western Indian Oceans. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 140: 230–241.
- Majkowski, J. 2007. Global Fishery Resources of Tuna and Tuna-like Species. FAO Fisheries Technical Paper, 483. FAO, Rome. 54 pp.
- McBride, R. S., Richardson, A. K., and Maki, K. L. 2008. Age, growth, and mortality of wahoo, *Acanthocybium solandri*, from the Atlantic coast of Florida and the Bahamas. *Marine and Freshwater Research*, 59: 799–807.
- Method, R. D., and Wetzel, C. R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142: 86–99.
- Method, R. D., Wetzel, C. R., and Taylor, I. 2018. Stock Synthesis User Manual. V3.30.12: 1–235. NOAA Fisheries, Seattle, WA. <https://vlab.ncep.noaa.gov/web/stock-synthesis>
- Nadon, M. O., Ault, J. S., Williams, I. D., Smith, S. G., and DiNardo, G. T. 2015. Length-based assessment of coral reef fish populations in the main and northwestern Hawaiian Islands. *PLoS One*, 10: e0133960.
- Pitcher, T. J., Watson, R., Forrest, R., Valtýsson, H., and Guénette, S. 2002. Estimating illegal and unreported catches from marine ecosystems: two case studies. *Fish and Fisheries*, 3: 317–339.
- Pons, M., Branch, T. A., Melnychuk, M. C., Jensen, O. P., Brodziak, J., Fromentin, J. M., Harley, S. J. *et al.* 2017. Effects of biological, economic and management factors on tuna and billfish stock status. *Fish and Fisheries*, 18: 1–21.
- Pons, M. 2018. Stock Status and Management in Tuna Fisheries: From Data-rich to Data-poor. University of Washington, ProQuest Dissertations Publishing, 2018: 10846859. 186 pp. <https://search.proquest.com/docview/2126689812?accountid=14784> (last accessed 15 November 2018).
- Pons, M., Melnychuk, M. C., and Hilborn, R. 2018. Management effectiveness of large pelagic fisheries in the high seas. *Fish and Fisheries*, 19: 260–270.

- Prince, J., Victor, S., Kloulchad, V., and Hordyk, A. 2015. Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. *Fisheries Research*, 171: 42–58.
- Ramírez-Arredondo, I. 1993. Aspectos reproductivos de la carachana pintada, *Euthynnus alletteratus* (Pisces: Scombridae) de los alrededores de la Isla de Picua, Estado Sucre, Venezuela. *Boletín del Instituto Oceanográfico de Venezuela*, 32: 69–78.
- Ramírez-Arredondo, I., Silva, J., and Marchán, F. 1996. Relación longitud peso y factor de condición en *Euthynnus alletteratus* (Rafinesque 1810), (Pisces: Scombridae) de los alrededores de las Islas los Testigos, Venezuela. *Boletín del Instituto Oceanográfico de Venezuela*, 35: 63–68.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> (last accessed 1 August 2017).
- Rudd, M. B. 2018. LIME: Length-based Integrated Mixed Effects (LIME) assessment method. R package version 2.1.0. <https://github.com/merrillrudd/LIME> (last accessed 10 July 2018).
- Rudd, M. B., and Thorson, J. T. 2018. Accounting for variable recruitment and fishing mortality in length-based stock assessments for data-limited fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 1019–1035.
- Saber, S., Ortiz de Urbina, J., Lino, P. G., Gómez-Vives, M. J., Coelho, R., Lechuga, R., and Macías, D. 2017. Biological Samples Collection for Growth and Maturity Studies EU Portugal and Spain: Northeastern Atlantic and Western Mediterranean. ICCAT, Madrid. 41 pp.
- Santana, J. C., Delgado de Molina, A., and Ariz, J. 1993. Estimación de una ecuación talla-peso para *Acanthocybium solandri* (Cuvier, 1832), capturado en la Isla de el Hierro (Islas Canarias). *Collective Volume of Scientific Papers of ICCAT*, 40: 401–405.
- SCRS. 2018. Report of the Standing Committee on Research and Statistics (SCRS) (Madrid, Spain—1 to 5 October 2018). ICCAT, Madrid. 469 pp.
- SEDAR. 2014a. SEDAR 38 Stock Assessment Report. South Atlantic King Mackerel. Southeast, Data, and Assessment Review Stock Assessment Report. 502 pp. http://sedarweb.org/docs/sar/SEDAR_38_SA_SAR.pdf (last accessed 10 July 2018).
- SEDAR. 2014b. SEDAR 38 Stock Assessment Report. Gulf of Mexico King Mackerel. Southeast, Data, and Assessment Review Stock Assessment Report. 465 pp. http://sedarweb.org/docs/sar/SEDAR_38_Gulf_SAR.pdf (last accessed 10 July 2018).
- Then, A. Y., Hoenig, J. M., Hall, N. G., and Hewitt, D. A. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science*, 72: 82–92.
- Viana, D., Branco, I., Fernandes, C., Fischer, A., Carvalho, F., Travassos, P., and Hazin, F. 2013. Reproductive biology of the wahoo, *Acanthocybium solandri* (Teleostei: Scombridae) in the Saint Peter and Saint Paul Archipelago, Brazil. *International Journal of Plant and Animal Sciences*, 2: 49–57.

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