1. INTRODUCTION

Large pelagic fish such as tuna and swordfish, which form the top of the marine food chain, are known to be affected by fishing pressure, pollution and climate change (Romeo et al. 2015, Woodworth-Jefcoats et al. 2019). Specifically, fishing pressure has been documented to impact stock dynamics in the Atlantic and Mediterranean regions, with ICCAT (International Commission for the Conservation of Atlantic Tunas) stock assessments frequently reporting overfished or fully exploited stocks. In particular, the Mediterranean swordfish *Xiphias gladius* L., 1758 is considered highly overfished, and a stock recovery program has been adopted to rebuild stock biomass to sustainable levels by the end of the current decade (ICCAT 2020). Pollution is also a common stressor for large pelagic fish, as pollutants such as plastics (Romeo et al. 2015) and heavy metals (Torres-Escribano et al. 2010, Gobert et al. 2017) are often found in their tissues, affecting their health and potentially their population dynamics (Damiano et al. 2011). Furthermore, climate change is expected to impact large pelagic fish, changing their habitat dis-
tribution and quality, spawning period and grounds, distribution and abundance. For instance, in modeling studies Lehodey et al. (2013) and Dueri et al. (2014) investigated the potential impacts of climate change on Pacific skipjack tuna *Katsuwonus pelamis* and both studies reported decreasing biomass after 2050. Furthermore, Silva et al. (2015) predicted a decline in swordfish relative abundance in the south Pacific, while Muhling et al. (2011) predicted a loss of spawning habitat for bluefin tuna in the Gulf of Mexico. Interestingly, Schartup et al. (2019) demonstrated that climate change can impact the accumulation of toxins in large fish, reporting increased methylmercury (MeHg) concentrations in the tissue of Atlantic bluefin tuna due to the rise of seawater temperature. In contrast, in a latitudinal study, Houssard et al. (2019) showed that higher sea surface temperature (SST) is associated with lower mercury (Hg) concentrations in 3 tuna species (bigeye, yellowfin and albacore).

Changes in populations of large pelagic fish can initiate trophic cascades (Heithaus et al. 2008), as top predators play a key role in marine ecosystem structure and dynamics through top-down control (Baum & Worm 2009). To examine how the life cycle and habitat characteristics (e.g. spawning areas, movements, migrations, physiology) and consequently the population dynamics of marine top predators are affected by seasonal and inter-annual variability of the environment (temperature, circulation and prey availability etc.) and by human pressures (e.g. fishing, pollution), there is a need to develop tools that can describe important processes (physical, biochemical and biological) that ultimately determine the dynamics of the ecosystem. Given the complexity of the combined effects of these processes, end-to-end models can be regarded as unique tools to deliver integrated approaches (Fulton 2010).

End-to-end models attempt to simulate the entire food web coupled with the related abiotic environment in a single framework (Travers et al. 2009). To date, several modelling frameworks have been characterized as end-to-end approaches, based on specific criteria regarding their forcing, scaling, coupling and interactions between associated ecosystem components (Travers et al. 2007). Representative examples focusing on large pelagic fish are SEAPODYM (spatial ecosystem and population dynamics model) and APECOSM (apex predators ecosystem model). Both have been implemented for studies of tuna species in the Indian and Pacific Oceans (e.g. Lehodey et al. 2008, 2018, Maury 2010), while SEAPODYM was also implemented for swordfish of the Indian Ocean (Dragon et al. 2014). Both SEAPODYM and APECOSM are Eulerian-density models that describe fish movement with advection-diffusion equations, reproducing the population dynamics of large predators at oceanic spatial scales driven by the biophysical variability obtained from coupled physical–biochemical models (Travers et al. 2007).

Another example of an end-to-end approach, although not focusing on large pelagic fish, is the Lagrangian-IBM (individual based model) OSMOSE (object-oriented simulator of marine ecosystems exploitation; Shin & Cury 2001). Recently, Moullec et al. (2019) performed a basin-scale implementation of OSMOSE in the Mediterranean Sea considering 100 interacting species (fish, cephalopods and crustaceans), including swordfish. Although the model results were consistent with ecosystem dynamics of the Mediterranean Sea, the authors state their approach was limited by simplifications regarding the description of life cycle characteristics. Thus, the model could be improved if somatic growth, currently modelled by Von Bertalanffy equations, and annual relative fecundity, currently fixed at a species specific value, were explicitly described by bioenergetics models. Indeed, full life cycle bioenergetics models can provide needed detail in end-to-end approaches, as they dynamically describe processes like growth and reproduction with respect to environmental characteristics such as temperature and prey availability. In bioenergetics models, organisms’ metabolism and physiology are taken into consideration by describing the different energy fluxes of an individual.

There are 2 types of mechanistic bioenergetic models commonly used in fisheries science: Wisconsin type or traditional bioenergetic models (Hanson et al. 1997) and dynamic energy budget (DEB) models (Kooijman 2000). Both have been used in many end-to-end modelling approaches (e.g. Rose et al. 2015, Gatti et al. 2017), and the APECOSM model referred to above uses a simplified version of DEB theory to represent basic physiological processes and control allocation of energy intake by organisms (Maury et al. 2007). Besides the advantages that such models provide when describing the growth and reproduction of individuals in a changing environment, one can use them to investigate the dynamics of the accumulation of pollutants (Stamatakis et al. 2020), as well as the impact of this accumulation on an organism’s metabolism through shifts in its energy balance (Cheng et al. 2018). Although various bioenergetic models exist for tuna species (e.g. Kirby 2005, Jusup et al. 2011, Aoki et al. 2020), there are no studies focusing on bioenergetics modelling of swordfish, except a simplified application of DEB (Kooijman...
2. MATERIALS AND METHODS

2.1. Model description

2.1.1. Life cycle

In the present Wisconsin type bioenergetics model, the life cycle of swordfish is composed of 6 life stages, based on diet, maturity and growth. The life cycle of an individual swordfish begins with the egg stage, which lasts for 3 d (Yasuda et al. 1978). Afterwards, the individual passes to the second stage of its life as an early larva, with an initial size of 3.2 mm, and begins feeding on zooplankton. When the individual reaches a length of 10 mm (ca. 2 wk; Govoni et al. 2003) it is considered a late larva that feeds on fish larvae. The transition to the juvenile stage happens at 118 mm lower fork jaw length (LFJL, Govoni et al. 2003). Until a length (LFJL) of 60 cm is reached, it is considered to be an early juvenile and grows linearly (Megalofonou et al. 1995). The transition from juvenile to adult occurs when a juvenile becomes 3.5 yr of age (age at first maturity for females, de la Serna et al. 1996). Finally, an adult is assumed to die at the age of 15.5 yr (Nakamura 1985). The main life stages and their duration are shown in Table 1.

2.1.2. Bioenergetics model

Bioenergetics models describe energy flow through an organism as a balance between consumption and energy losses such as respiration, specific dynamic action, excretion, egestion and reproduction. The growth of a swordfish can be estimated by the following differential equation that describes the swordfish round wet weight (W) rate as a range of change over time:

\[
\frac{1}{W} \frac{dW}{dt} = \left(C - R - SDA - E - F - A_{\text{repro}}\right) \frac{\text{CAL}_{\text{prey}}}{\text{CAL}_W} \tag{1}
\]

where \( C \) is the daily consumption rate, \( R \) is the respiration rate (standard metabolic rate + costs for activity), \( SDA \) is the specific dynamic action, \( E \) is excretion, \( F \) is egestion losses and \( A_{\text{repro}} \) represents the energy spent for reproduction. All components of the energy budget are in units of mass (e.g. g prey g fish \(^{-1}\) d \(^{-1}\)) converted by the caloric content of the swordfish prey (\( \text{CAL}_{\text{prey}} \)) and the caloric content of swordfish (\( \text{CAL}_W \)). The scaling of energy components as well as temperature dependence functions follow the Wisconsin type structure (Hanson et al. 1997) which has been applied for over 70 fish species (Deslauriers et al. 2017). Consumption rate \( (C) \) is a proportion \( (f) \) of maximum consumption \( (C_{\text{max}}): \ C = f \times C_{\text{max}} \), where \( f \) is a Hollings Type II functional response function varying between 0 and 1:

\[
f = \frac{X}{X + X_k} \tag{2}
\]

where \( X \) is food availability and \( X_k \) is the half saturation constant, representing the density of food at which food uptake is half of its maximum value. Given there are no estimates of prey patchiness, Hollings Type II was chosen over Type III, assuming a homogeneous prey distribution rather than a spa-
Table 1. Swordfish life stages modelled. LJFL: lower jaw fork length

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Thresholds</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>3 d</td>
<td>Yasuda et al. (1978)</td>
</tr>
<tr>
<td>Early larva</td>
<td>3.2 mm &lt; LJFL &lt; 10 mm</td>
<td>Govoni et al. (2003)</td>
</tr>
<tr>
<td>Late larva</td>
<td>10 mm &lt; LJFL &lt; 118 mm</td>
<td>Govoni et al. (2003)</td>
</tr>
<tr>
<td>Early juvenile</td>
<td>118 mm &lt; LJFL &lt; 600 mm</td>
<td>Megalofonou et al. (1995)</td>
</tr>
<tr>
<td>Late juvenile</td>
<td>600 mm &lt; LJFL</td>
<td>Megalofonou et al. (1995)</td>
</tr>
<tr>
<td>Adult</td>
<td>Age &gt; 3.5 yr</td>
<td>de la Serna et al. (1996)</td>
</tr>
</tbody>
</table>

temporally resolved patchy distribution. Maximum consumption ($C_{max}$) and respiration ($R$) are modelled as allometric functions of weight:

$$C_{max} = a_C W^{b_C} f_C(T)$$

(3)

$$R = a_R W^{b_R} f_R(T)$$

(4)

where $a_C$, $b_C$, $a_R$, $b_R$ are the intercepts and exponents for consumption and respiration. The effect of temperature on swordfish energy budget is modelled through a temperature dependent function for consumption, as this is described by Kitchell et al. (1977), using the auxiliary terms $V, S, Y$ and $Z$ (Box 1), which are parametrized by an optimum ($T_{opt}$) and maximum temperature ($T_{max}$):

$$f_C(T) = V Z^{1-V}$$

(5)

and an exponential $Q_1(T)$ temperature relationship for respiration (Politikos et al. 2011):

$$f_R(T) = e^{\frac{\log(Q_1(T) - T_{ref})}{T_{opt}}}$$

(6)

where $T$ is the ambient temperature and $T_{ref}$ is a reference temperature at which $f_R(T)$ is 1 (Politikos et al. 2011, Rose et al. 2015). Specific dynamic action (SDA) and excretion ($E$) are assumed to be constant proportions of assimilated energy:

$$SDA = a_{SDA} \times (C - F)$$

(7)

$$E = a_E \times (C - F)$$

(8)

where $a_{SDA}$ and $a_E$ are the intercepts for SDA and $E$ respectively. Egestion ($F$) is a direct proportion of consumption:

$$F = a_F \times C$$

(9)

where $a_F$ is the intercept for $F$. Energy spent on reproduction ($A_{repro}$) is discussed below (see Section 2.1.3).

The round wet weight ($W$) of swordfish is converted to LJFL using the length–weight relationship of Tserpes et al. (2017) for the Mediterranean swordfish ($W_{gg}$ (gilled and gutted weight) = $0.00000842 \times \text{LJFL}^{0.509}$, $W = 1.14 \times W_{gg}$). This relationship is based on a large dataset ($N = 23,529$), with LJFL ranging from 52 to 213 cm, and has been adopted by ICCAT for assessment purposes. In the absence of length–weight data for swordfish individuals smaller than 50 cm LJFL, this relationship was tested against data for small juvenile Atlantic blue marlin Makaira nigricans (Prince et al. 1991), assuming black marlin have similar growth rates to swordfish. Thus, the actual weight of a black marlin individual of 4.3 cm and one of 23 cm LJFL corresponds to 0.6 g and 0.1 kg respectively (Prince et al. 1991). This is ~27% smaller, in comparison to the predicted weight (0.83 g and 0.14 kg) using the Tserpes et al. (2017) relationship.

2.1.3. Reproductive buffer concept

One of the main assumptions of a DEB model (Kooijman 2000) is that the assimilated energy of an individual is stored in a reserve pool, from which a fixed part $\kappa$ is spent on maintenance and growth, while the remaining $1 - \kappa$ is stored to a reproductive buffer that adults use for egg production. Following Politikos et al. (2015) and Gkanasos et al. (2019), a similar concept is included in a Wisconsin type bio-energetic model and net energy $A$ is calculated in each model time step as $A = C - (R + SDA + E + F)$. If $A$ has positive values, an immature swordfish spends all net energy on growth (soma and gonads), while an adult swordfish stores a fixed part $\kappa g$ in a reproductive buffer ($E_{buffer}$) for spawning and the rest of it is spent on growth. When $E_{buffer}$ is enough for spawn-
ing \((E_{\text{buffer}} > E_{\text{batch}})\) and the sea surface temperature \((\text{SST})\) is higher than 24°C (Neilson et al. 2013), the swordfish release eggs with a spawning interval \((I_{\text{spawn}})\) of 3 d (Young et al. 2003, Poisson & Fauvel 2009b, Neilson et al. 2013) until the buffer is empty or the spawning season is over. If \(A\) is below zero, the simulated swordfish does not have enough energy for maintenance \((M = R + SDA + F + E)\) and thus the required energy is taken from the reproductive buffer. This utilization of energy initially stored for egg production to cover maintenance costs can be regarded as a representation of follicular atresia, which is a common process in fish (González-Kother et al. 2020), as well as in Mediterranean swordfish (Carnevali et al. 2019), frequently attributed to unfavorable environmental conditions (González-Kother et al. 2020). If energy stored in the buffer is not enough to satisfy needs for maintenance, the swordfish loses weight equal to \(|A| - E_{\text{buffer}}\).

The batch fecundity \((B_f)\) is assumed to vary between \(2 \times 10^6\) and \(10 \times 10^6\) oocytes depending on length and according to \(B_f = a_{\text{fec}} \times L F JL^{b_{\text{fec}}}\) (with \(a_{\text{fec}} = 7.013 \times 10^{-3}\) and \(b_{\text{fec}} = 3.994\); Arocha 2007). If the individual does not have enough energy to release the batch corresponding to its length, but does have enough to cover the energetic costs of the minimum batch \((B_{\text{min}} = 2 \times 10^6\); de la Serna et al. 1996, Arocha 2007), it is allowed to spawn. The reproductive buffer concept is schematically described in Fig. 1.

### 2.1.4. Vertical and horizontal movements

A series of studies have demonstrated that swordfish typically follow a diel vertical migration pattern, staying at depth during daytime and coming up to near surface waters at night (e.g. Abascal et al. 2010, Abecassís et al. 2012, Lerner et al. 2013, Sepulveda et al. 2018). This pattern is affected by external factors such as light intensity (Loefer et al. 2007), food availability, water temperature (Carey & Robison 1981) and oxygen (Takahashi et al. 2003), and therefore various depths are reported on a global scale: Evans et al. (2014) report >400 m in the daytime and 0–100 m at night in the central and eastern North Atlantic, Abascal et al. (2015) report 300–600 m in the daytime and above mixed layer depth at night for the South Pacific and Canese et al. (2008) report 250–650 m in the daytime and 0–10 m at night for the Mediterranean Sea. Considering the general pattern in those studies, it was assumed that juvenile and adult swordfish spend 12 h (19:00–07:00) in the 0–100 m layer and the other 12 h (07:00–19:00) below 100 m. Larval swordfish are assumed to be in the near surface layer (above 0.5 m; Govoni et al. 2003).

Considering the long distance horizontal movements of swordfish (Palko et al. 1981) and given that this study is restricted to the vertical dimension (1-D), it was assumed that simulated individuals remain at the spawning grounds during the summer months when spawning occurs \((\text{SST} > 24^\circ C)\) and could be

Fig. 1. Schematic representation of the bioenergetic model, including the adopted reproductive buffer concept
anywhere else in the Mediterranean Sea during all other seasons. Thus, during spawning the model is forced with a mean temperature over the spawning grounds, and for the rest of the year a mean temperature for the Mediterranean is used. In contrast, juvenile swordfish are assumed to experience a mean Mediterranean temperature, with larvae remaining within the spawning grounds until they become juveniles. Two known spawning grounds were examined in this study: one in the eastern Levantine Sea between the islands of Cyprus and Rhodes (Tserpes et al. 2008) and the second in the Tyrrenhenian Sea (Arocha 2007).

### 2.2. Parameterization

#### 2.2.1. Stomach content data: daily consumption rates

For the parameterization of the model's consumption compartment (as discussed below in Section 2.2.4), estimates of daily consumption rates were obtained from the stomach content data of Peristeraki & Tserpes (2001). The samples included 69 juvenile and adult swordfish (LFJL range: 68–214 cm) from the south Aegean Sea caught by commercial surface longline fisheries from January 1994 to September 1995. In their analysis, Peristeraki & Tserpes (2001) identified 1 cephalopod and 10 teleost families in the swordfish stomachs, while 15.94% of stomachs examined were completely empty. The frequency of occurrence (%FO), percentage abundance (%N) and percentage weight (%W) of identified families in the swordfish diet are shown in Table 2. These data can also be used to compute the index of relative importance (%IRI, Ceyhan & Akyol 2017), combining FO, N and W. In Table 2, the families identified in swordfish stomachs are sorted from the highest to lowest IRI. The first 6 families (Scombridae, Ommastrephidae, Belonidae, Carangidae, Clupeidae, Congrsideae) largely explain the diet of swordfish in the area, having a summed IRI of 99.51%.

To estimate the daily consumption rates of swordfish from stomach content data, the methods of Olson & Mullen (1986) were adopted. Cortés (1997) reviewed different methods of estimating fish consumption rates based on the analysis of stomach contents and concluded that the Olson-Mullen and Diana (1979) methods can be regarded as the most appropriate for estimating the daily ration of large fish, due to their flexibility dealing with the determination of gastric evacuation compared to other methods. Following Zambrano et al. (2019), the estimation of swordfish daily consumption rate is given by the following formula:

\[
r = \sum_{i=1}^{j} 12 \times \frac{1}{W} \times \frac{SW_i}{A_i}
\]

where \(r\) (g prey g predator\(^{-1}\) d\(^{-1}\)) is the daily consumption rate, \(W\) (g) is the round weight of the predator, \(SW_i\) (g) is the mean weight of stomach contents per prey category per predator, \(I\) is the number of identified prey categories and \(A_i\) (h) is the average time required to evacuate the average proportion of prey category \(i\). Values of \(A_i\) are those in Olson & Boggs (1986) estimated for the yellowfin tuna Thunnus albacares. The same values of \(A_i\) were also used for the estimation of swordfish daily ration by Zambrano et al. (2019) and Young et al. (2010). The ratio \(SW_i / A_i\) is multiplied by 12, assuming swordfish feed for 12 h per d (Young et al. 2010, Zambrano et al. 2019). Still, some bias is expected from this simplification, as the influence of the digestion of multiple meals and satiation limits on predation have the potential to influence both the amount consumed and digestion (Andersen & Beyer 2007). Finally, empty stomachs were included in the calculation (as zero daily ration) considering they reflect the natural feeding conditions of the population (Menard 2000, Zambrano et al. 2019).

#### 2.2.2. Caloric content parameters

The caloric content of adult and juvenile swordfish was estimated using the equation of Hartman & Brandt (1995) for Perciformes assuming a percent dry weight of 24% (Mannan et al. 1961) that results in a caloric content of \(CAL = 7428\) J g\(^{-1}\). The caloric con-

<table>
<thead>
<tr>
<th>Family</th>
<th>%FO</th>
<th>%NO</th>
<th>%W</th>
<th>%IRI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scombridae</td>
<td>46.55</td>
<td>6.13</td>
<td>25.76</td>
<td>43.26</td>
</tr>
<tr>
<td>Ommastrephidae</td>
<td>32.76</td>
<td>5.75</td>
<td>34.85</td>
<td>38.76</td>
</tr>
<tr>
<td>Belonidae</td>
<td>6.9</td>
<td>49.23</td>
<td>6.44</td>
<td>11.19</td>
</tr>
<tr>
<td>Carangidae</td>
<td>10.34</td>
<td>4.98</td>
<td>7.96</td>
<td>3.89</td>
</tr>
<tr>
<td>Clupeidae</td>
<td>5.17</td>
<td>11.30</td>
<td>2.15</td>
<td>2.02</td>
</tr>
<tr>
<td>Congridae</td>
<td>5.17</td>
<td>0.57</td>
<td>2.84</td>
<td>0.51</td>
</tr>
<tr>
<td>Trichiuridae</td>
<td>1.72</td>
<td>2.61</td>
<td>2.61</td>
<td>0.22</td>
</tr>
<tr>
<td>Zeididae</td>
<td>1.72</td>
<td>0.19</td>
<td>0.77</td>
<td>0.048</td>
</tr>
<tr>
<td>Merluccidae</td>
<td>1.72</td>
<td>0.19</td>
<td>0.05</td>
<td>0.012</td>
</tr>
<tr>
<td>Macrorhamphosidae</td>
<td>1.72</td>
<td>0.19</td>
<td>0.01</td>
<td>0.010</td>
</tr>
<tr>
<td>Ophichthidae</td>
<td>1.72</td>
<td>0.19</td>
<td>0.01</td>
<td>0.010</td>
</tr>
</tbody>
</table>
tent of swordfish larvae was estimated using the ontogenetic pattern in percent dry weight and caloric content in fish early life stages found by Wuenschel et al. (2006). The latter is one of the few studies dealing with the energy density of larval fish, highlighting the importance of ontogeny. Although the studied species (spotted seatrout) is not closely related to swordfish, in the absence of any data on the caloric content of swordfish or any related species, Wuenschel et al.'s (2006) scaling for caloric content was used to capture increasing caloric content through ontogeny. Therefore, the percentage dry weight (%DW) was related to LFJL of swordfish and calculated as follows until %DW reached the value of 24% (i.e. LFJL = 95 mm) adopted for juvenile and adult swordfish:

\[
%\text{DW} = 5.97 \times \text{LFJL}^{0.3038} \quad (11)
\]

while caloric content of larva (CAL) corresponding to %DW values given by Eq. (11) was calculated by:

\[
\text{CAL} = -63.02 + 162.68 \times %\text{DW} \quad (12)
\]

The caloric content of swordfish prey (CAL\text{prey}) for all life stages is shown in Table 3. Swordfish feed on zooplankton (mainly copepods) as early larvae for approximately 15 d, and on fish larvae as late larvae (Govoni et al. 2003); juveniles and adults seem to have the same opportunistic feeding behavior (Neilson et al. 2013). For CAL\text{prey} for the late larval stage, the caloric content of anchovy larvae was adopted (Politikos et al. 2011). CAL\text{prey} of juvenile and adult swordfish was computed from the 6 most important identified prey families (Table 2) based on their IRI, using it as preference weight for each type of prey. Finally, the caloric content of 1 egg was set to CAL\text{egg} = 4330 J, assuming an egg diameter of 1.6 mm (Yasuda et al. 1978) and using the general scaling of Barneche et al. (2018) linking fish egg energy density with egg size (-1%) of warm bodied fish (Hill et al. 2008) and although they warm different parts of their body (Fritsches et al. 2005), it is assumed that such differentiations can be captured by adopting species specific parameters for consumption and respiration as discussed below.

It is assumed that, since swordfish early egg sack larvae are planktonic, they have zero energetic costs due to activity and their respiration rate is given by the general scaling that Clarke & Johnston (1999) found for the resting metabolic rate of teleost fish (modified to fit the units of the presented framework: \(R = 0.0088 \times W^{-0.2}\)). Early larval consumption is given by the scaling of Politikos et al. (2011) for the zooplankton feeder anchovy Engraulis encrasicolus (\(C = 0.41 \times W^{-0.31}\)). Late larvae and early juveniles are expected to have energetic costs due to activity and therefore their respiration is scaled as the early larvae’s but with an increased intercept, \(a_R\), to represent activity. To cover this energetic cost, more consumption is needed, hence the intercept of consumption for late larvae should also be higher than the 0.41 used for early larvae. Both exponents and intercepts of \(C\) and \(R\) (\(a_C, b_C, a_R, b_R\)) were calibrated for late juvenile and adult stages.

Besides exponents and intercepts, the calibration of \(C\) also includes the estimation of half saturation constant \(X_{0.5}\), which determines the dependence of swordfish feeding on prey availability (Eq. 2). In the absence of a swordfish forage model that would provide food density \(X\), Eq. (2) is transposed to:

\[
f = \frac{R_X}{r_X + 1} \quad (13)
\]

with \(r_X = X/X_{0.5}\) calibrated for each life stage of the individual.

Temperature dependence is regulated by 5 model parameters. Optimum temperature (\(T_{opt}\)) and refer-

### 2.2.3. Borrowed and calibrated parameters

In the absence of data on swordfish, some parameters expected to show relatively low sensitivity, such as those for excretion, egestion and specific dynamic action (Politikos et al. 2011), were borrowed from tuna bioenergetics (Olson et al. 2016; \(a_E = 0.06, \delta_S = 0.15, \delta_{SDA} = 0.15\)). Both billfishes and tunas belong to the small faction

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Prey: CAL\text{prey} (J g\text{-1})</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early larva</td>
<td>Copepods: 2580</td>
<td>Politikos et al. (2011)</td>
</tr>
<tr>
<td>Late larva</td>
<td>Fish larvae: 3120</td>
<td>Politikos et al. (2011)</td>
</tr>
<tr>
<td>Juvenile and adult</td>
<td>Combined: 6104</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Scombridae: 7500</td>
<td>Spitz &amp; Jouma‘a (2013)</td>
</tr>
<tr>
<td></td>
<td>Ommastrephidae: 4470</td>
<td>Estess et al. (2014)</td>
</tr>
<tr>
<td></td>
<td>Belonidae: 6200</td>
<td>Spitz et al. (2010)</td>
</tr>
<tr>
<td></td>
<td>Carangidae: 6500</td>
<td>Spitz &amp; Jouma‘a (2013)</td>
</tr>
<tr>
<td></td>
<td>Clupeidae: 7200</td>
<td>Spitz &amp; Jouma‘a (2013)</td>
</tr>
<tr>
<td></td>
<td>Congridae: 6900</td>
<td>Spitz et al. (2010)</td>
</tr>
</tbody>
</table>
ence temperature ($T_{\text{ref}}$) were determined by the mean temperature that the individual experiences in each life stage, assuming the simulated individual has adapted to the prevailing temperature of its habitat. In the absence of any relevant data, maximum temperature for consumption ($T_{\text{max}}$), above which consumption stops, was set to 30 and 31°C for adult and larva respectively, which is the upper limit of ambient temperatures in the habitat of swordfish (Boyce et al. 2008). Finally, thermal sensitivity $Q_{10}$ was set to 1.67, which is the estimation of Blank et al. (2007) for bluefin and yellowfin tunas. According to Kitchell et al. (1977), $Q_C$ approximates the $Q_{10}$ parameter, and thus $Q_C$ was calibrated and set to the value closest to $Q_{10}$ that gives the best model results when compared with consumption field data. Summarizing, there are 7 parameters that were calibrated across all life stages via comparison of the model output with observations: $a_C$, $b_C$, $r_X$, $a_R$, $b_R$, $\kappa_R$ and $Q_C$.

**2.2.4. Calibration methods**

Initially, parameters controlling consumption ($a_C$, $b_C$, $r_X$ and $Q_C$) were calibrated against mean daily consumption rates of various size classes (68–79 cm, 80–89 cm, 90–99 cm, 100–109 cm, 110–129 cm, 130–214 cm) as these are calculated in section 2.2.1. Afterwards, parameters of respiration ($a_R$, $b_R$), and $\kappa_R$ for reproduction, were calibrated to get the best fit between simulated growth and field LFJL-at-age observations of swordfish larvae (Govoni et al. 2003) and mixed sex juvenile/adult swordfish (Tserpes & Tsimenides 1995). Although data for growth and consumption come from different locations, swordfish of the Mediterranean are considered one genetically homogeneous population (Kotoulas et al. 1995, Chow & Takeyama 2000) and managed as a unique stock by ICCAT (ICCAT 2020). Thus, it was assumed that individuals in these datasets experienced the same environmental conditions (see Section 2.3). The dataset of larval growth (Govoni et al. 2003) from the western North Atlantic is unique globally. Thus, in the absence of any information about larval growth in the Mediterranean, this dataset was used to calibrate larval growth, assuming that growth at larval stages is similar in the Atlantic and Mediterranean stocks. Moreover, the simulated growth of the individual was also compared with the Govoni et al. (2003) larval growth model and the Tserpes & Tsimenides (1995) Von Bertalanffy model for juveniles and adults. In the absence of sufficient data on the reproductive output of swordfish, $\kappa_R$ was calibrated to get realistic annual egg production.

Commonly, in bioenergetics models $\kappa_R$ is assumed to be a constant value throughout the mature life of an individual. Here, preliminary sensitivity experiments with the model showed that a constant value of $\kappa_R$ leads to decreased energy investment in reproduction from the beginning of maturity. This is in conflict with life history theory (Stearns 1992) and the recent findings of Barneche et al. (2018) in which the opposite is demonstrated. Although some empirical observations imply rule of increasing energy investment to reproduction through aging is not universal (Fitzhugh et al. 2012), there is no information to support that this rule is not valid for swordfish. Thus, $\kappa_R$ was set to increase gradually with age, so swordfish energy investment in reproduction increases through aging at least until some point of late maturity. Thus, $\kappa_R$ was calibrated separately for each year of age (4, 5, etc.). The necessity for such an assumption derives from the fact that maintenance costs, which increase with age, are subtracted before the energy partition between growth and reproduction. Other DEB models, which keep a constant value of $\kappa_R$ through aging, first partition energy between soma and reproduction and then partition somatic energy between growth and maintenance.

**2.3. Environmental forcing**

Temperature datasets were obtained from model outputs and satellite data. Daily temperature in the 0–100 m layer and below 100 m over the period between 2003 and 2017 was extracted from the simulation of a 3-dimensional (3-D) Mediterranean basin-scale hydrodynamic model (Kalarray et al. 2020) based on the Princeton Ocean Model (POM; Blumberg & Mellor 1983). The climatological daily mean temperature in each layer was computed and used to drive the swordfish bioenergetics model. Since POM prediction of SST is less accurate without applying data assimilation techniques (Korres et al. 2007), and given that SST is critical for this study as it controls spawning pattern and affects larval metabolism, SST was obtained from satellite data provided by Copernicus Marine Environmental Monitoring Service (CMEMS) over a 16 yr period (2003–2018) from a product with daily (nighttime) temporal resolution and 0.05° spatial resolution. The product was built from a consistent reprocessing of the level-3 (merged
multi-sensor, L3) climate data record provided by the ESA Climate Change Initiative (CCI) and Copernicus Climate Change Service (C3S) initiatives, but also includes as input an adjusted version of the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder dataset version 5.3 to increase the input observation coverage (Buongiorno Nardelli et al. 2013). The nighttime SST products were chosen to avoid potential bias related to solar radiation (diurnal fluctuation in SST) that can occur during the daytime from surface heating (Raitos et al. 2010).

Furthermore, in all simulations, except where otherwise indicated, \( r_\text{S} \) (food satiation level, see Section 2.2.4) was modified daily, within a random sequence of a normal distribution around its calibrated value, so that simulated individuals experience different situations of food availability, varying from zero to maximum. This can be regarded as a simplification, as any temporal or spatial variability is not taken into account. However, swordfish are a highly opportunistic species and feed on a wide range of prey with different habitats, life traits and seasonality in their abundance and thus prey biomass does not differ among seasons (Young & Drake 2002). Additionally, preliminary analysis of consumption rates from Peristeraki & Tserpes’ (2001) data did not reveal any seasonal pattern in swordfish feeding. Thus the rational of using stochastic food availability to force the model seems reasonable as a first approximation, assuming it represents the mean state of realistic conditions. Finally, it is assumed that swordfish feed over the entire year, including during the spawning season.

2.4. Sensitivity analysis

To estimate model uncertainty with regard to parameterization, a series of sensitivity experiments were performed. Initially, the effect of each parameter was measured using the sensitivity index, \( S_A(p_s) \) proposed by Kitchell et al. (1997):

\[
S_A(p_s) = \frac{\Delta A}{A_s} \cdot \frac{p_s}{\Delta p}
\]

(14)

where \( p_s \) and \( \Delta p \) are the nominal value of the parameter and the input deviation respectively, whilst \( A_s \) and \( \Delta A \) are the nominal variable and output deviation response due to \( \Delta p \). To calculate \( S_A(p_s) \), each parameter was increased/decreased by 1%, keeping all other parameters at their nominal values. Temperature parameters were perturbed by 0.5°C, spawning interval \( (I_{\text{spawn}}) \), was perturbed by 1 d, and life stage transition lengths/ages were perturbed by 10%. Moreover, the model was tested assuming a minimum batch \( (B_{\text{min}}) \) of \( 1 \times 10^6 \) and \( 3 \times 10^6 \) instead of the adopted value of \( B_{\text{min}} = 2 \times 10^6 \) (100% perturbation). All applied perturbations were chosen to keep simulated growth in a realistic range of LFJL indicated by field observations.

To further investigate the sensitivity of the model, an envelope of alternative values of the most sensitive parameters was built, within ranges at which growth remains inside the limits of field observations. A model run was performed for each possible combination of them, and the mean and standard deviation of the model outputs (growth and reproduction) were calculated, representing the uncertainty of the model due to the perturbed parameters (Hatzonikolakis et al. 2017). This can be used as an ensemble model simulation, to provide a range of expected results due to variability that cannot be captured by a single-state model (Araújo & New 2007).

2.5. Evaluation of resulting reproduction

To further evaluate the annual egg production estimated here, data from the latest stock assessment for the Mediterranean swordfish (ICCAT 2020) were used. While the bioenergetics model simulates the growth and reproduction of an individual, the estimated egg production may be adopted to assess some aspects of swordfish population dynamics that can be compared with stock assessment findings as an additional model evaluation. For this reason, a preliminary projection of the energy budget model to a fixed swordfish population was applied.

The model was initialized with \( N \) individuals in the egg life stage on 15 July, and the simulation continued until the individuals reached recruitment size (>60 cm, less than 1 yr). Different mortality rates \( (M) \) were applied at each life stage of the individuals. In the absence of mortality rates for early life stages of swordfish, the general scaling of Pepin (1991) was used for eggs and larvae with length less than 15 mm:

\[
M_{\text{egg}} = 0.030 \times e^{0.18T}
\]

(15)

\[
M_{\text{lar}} = 5.17 \times G^{0.74} \times L^{-1.17}
\]

(16)

where \( M_{\text{egg}} \) is the daily natural mortality \( (d^{-1}) \) of eggs, \( T \) stands for ambient temperature, \( M_{\text{lar}} \) is the daily natural mortality \( (d^{-1}) \) of larvae, \( G \) is the growth rate \( (mm \ d^{-1}) \) and \( L \) is the length \( (mm) \). \( M_{\text{lar}} \) was applied to fish of length of 15 mm and less because this is the length range of the species.
(Scomber scombrus and S. japonicus) most related to swordfish in the dataset of Pepin (1991). In addition to the model of Pepin (1991), the model of McGurk (1986) and constant values of natural mortalities of eggs and larvae were also tested and the model of Pepin (1991) gave the best results. Carpi et al. (2017) also tested various general models for the natural mortality of fish larvae in European sardine and reached the same conclusion. For fish larger than 15 mm, the natural mortality rate was defined based on the Lorenzen (1996) empirical relationships, which have been previously used in ICCAT’s stock assessment for swordfish (ICCAT 2017):

\[ M = 4.65 \times W^{-0.309} \]  

(17)

where \( M \) is the annual natural mortality rate (yr\(^{-1}\)) and \( W \) (g) is the round wet weight. Mortality rates adopted through aging are shown in Fig. 2.

The abundance of mature females occurring in the Mediterranean Sea at the beginning of the spawning season of 2017 was calculated, assuming a percentage of 50% females under age 4, 60% at age 4 and 70% at age 5 (no individuals older than 5 yr were reported in the stock assessment). From these, assuming an increasing percentage of maturity from the age of 2 (15%) to 3 (65%) and older than 4 (100%), a total of 144,380 mature females was calculated in 2017. Assuming that each mature female will spawn an annual number of eggs (\( N_{\text{egg}} \)) as simulated by the bioenergetics model for ages 4 and 5, a total egg production of \( N = 144,380 \times N_{\text{egg}} \) is found in the Mediterranean Sea. Applying mortality rates (Eqs. 15–17) to \( N \) should result in a number of recruited fish (>60 cm) comparable to the stock assessment for 2018.

### 2.6. Model runs

The model was initialized in the middle of the reproductive season (15 July) from the egg life stage and 16 yr simulations were performed to complete the life cycle of the individual. For the main results (growth and reproduction) the 16 yr simulation was performed twice, the first with the Levantine Sea as the spawning ground and the second with spawning occurring in the Tyrrhenian Sea. Results regarding energy budget and consumption, as well the sensitivity analysis described above, were performed assuming that spawning occurs in the Tyrrhenian Sea, since preliminary simulations showed insignificant changes in these results between the 2 alternatives for spawning ground. Finally, to calibrate the consumption compartment against mean consumption rates per size class, as described in Section 2.2.4, one more simulation was performed with constant food availability (constant \( r_X \)).

### 3. RESULTS

#### 3.1. External forcing (temperature)

Climatological mean SST obtained from satellite data and climatological mean temperature fields at 0–100 m and below 100 m depth extracted from the POM 3-D hydrodynamic model for the Tyrrhenian and Levantine Seas are shown in Fig. 3. The temperature below 100 m is relatively constant, showing very small fluctuations (~±0.015) around its mean (approximately 13.7°C in the Tyrrhenian Sea and 14.3°C in the Levantine Sea). On an annual basis, the 0–100 m layer in Levantine Sea (mean ± SD 17.8 ± 1.1°C) is warmer than Tyrrhenian Sea (16.09 ± 1.38°C). When compared with the mean Mediterranean Sea temperatures in the 0–100 m layer (16.99 ± 1.42°C), the Levantine Sea is warmer, except during the period from August to November, when the 2 time series are almost identical. A com-
Hatzonikolakis et al.: Swordfish bioenergetics model

Comparison of the SST in the 2 spawning grounds illustrates that the Levantine Sea is characterized by warmer surface waters. However, during summer when the SST is higher than 24°C, the difference is minimal. In both areas, the spawning period begins in mid-June. In the Tyrrhenian Sea, it terminates during late September, while in the Levantine Sea it ends in mid-October.

3.2. Model parameterization

The parameter set of all energy budget components is summarized in Table 4. Intercepts and exponents of $C$ and $R$ of early larvae were parameterized as discussed in section 2.2.4. For late larvae and early juveniles, the same exponents were assumed, while intercept $a_C$ was 4.7 higher in late larva and intercept $a_R$ was 1.5 and 7.5 higher for late larvae and early juveniles respectively, which is attributed to activity. Late juveniles and adults have the same intercepts and exponents but a different consumption satiation level, considered in terms of $r_x = (X/X_k)$ or $f$. This is reasonable, considering that mature and larger swordfish consume more and larger prey (higher values of prey availability $X$, Zambrano et al. 2019).

Based on the mean temperatures that individual swordfish experience, the optimum temperature $T_{opt}$ and reference temperature $T_{ref}$ were set to 25.7°C for larvae and 15.5°C for juveniles and adults. The latter is very close to estimates from Canese et al. (2008), who found that adult swordfish prefer temperatures between 14 and 15°C in the Messina Strait. Finally, the slope for temperature dependence, $Q_C$, was set to 1.7.

3.3. Consumption

Simulated consumption rates versus estimates based on stomach content data are shown in Fig. 4. The simulated consumption rates are in reasonable agreement with the estimates from field data, with the mean simulated consumption closely related to the mean field consumption rates for the different size classes ($r^2 = 0.893$, $p = 0.0067$) but slightly overestimated (bias = 6%). Moreover, most of the field data estimates (64 of 69) are found within the range of maximum simulated consumption rate ($C$ with $f = 1$). The simulated consumption follows an exponential decrease, approaching a steady state of 0.03 kg prey kg swordfish$^{-1}$ d$^{-1}$ at the end of the juvenile life stage ($W = 30$ kg).

Fig. 3. Temperature fields used for the forcing of the bioenergetics model: (a) sea surface temperature (SST), (b) 0–100 m layer and (c) below 100 m layer in the Levantine Sea (red), Tyrrhenian Sea (green) and Mediterranean Sea overall (blue). Mean SST for Mediterranean Sea is not presented (see Section 2.1.4)
Table 4. Parameter set used for each energy budget component at each life stage. E: early larva, LL: late larva, EJ: early juvenile, LJ: late juvenile, A: adult. A dash (−) indicates that the parameter is not used in the specific life stage.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>EL</th>
<th>LL</th>
<th>Value</th>
<th>EJ</th>
<th>LJ</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a_C )</td>
<td>Intercept for consumption</td>
<td>0.41&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.15&lt;sup&gt;i&lt;/sup&gt;</td>
<td>2.15&lt;sup&gt;i&lt;/sup&gt;</td>
<td>7.77&lt;sup&gt;i&lt;/sup&gt;</td>
<td>7.77&lt;sup&gt;i&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>( b_C )</td>
<td>Exponent for consumption</td>
<td>−0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>−0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>−0.31&lt;sup&gt;i&lt;/sup&gt;</td>
<td>−0.486&lt;sup&gt;i&lt;/sup&gt;</td>
<td>−0.486&lt;sup&gt;i&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>( r_X / f )</td>
<td>Satiation level / functional response function</td>
<td>0.35 / 0.26&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.35 / 0.26&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.67 / 0.40&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.89 / 0.47&lt;sup&gt;i&lt;/sup&gt;</td>
<td>1 / 0.5&lt;sup&gt;i&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>( a_R )</td>
<td>Intercept for respiration</td>
<td>0.0088&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.5 × 0.0088&lt;sup&gt;i&lt;/sup&gt;</td>
<td>7.5 × 0.0088&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.611&lt;sup&gt;i&lt;/sup&gt;</td>
<td>0.611&lt;sup&gt;i&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>( b_R )</td>
<td>Exponent for respiration</td>
<td>−0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>−0.439&lt;sup&gt;i&lt;/sup&gt;</td>
<td>−0.439&lt;sup&gt;i&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>
| \( \kappa_R \) | Fraction of assimilated energy to reproductive buffer | – | – | – | – | – | 0.5−0.8<sup>i</sup>
| \( t_{spawn} \) | Spawning interval | – | – | – | – | 3<sup>i</sup> | |
| SST<sub>eggs</sub> | Sea surface temperature for spawning | – | – | – | – | 24<sup>i</sup> | |
| \( T_{opt} \) | Optimum temperature | 25.7<sup>i</sup> | 25.7<sup>i</sup> | 15.5<sup>i</sup> | 15.5<sup>i</sup> | 15.5<sup>i</sup> | |
| \( T_{ref} \) | Reference temperature | 25.7<sup>i</sup> | 25.7<sup>i</sup> | 15.5<sup>i</sup> | 15.5<sup>i</sup> | 15.5<sup>i</sup> | |
| \( T_{max} \) | Maximum temperature | – | 31<sup>b</sup> | 30<sup>b</sup> | |
| \( Q_{10} \) | Thermal sensitivity | – | 1.67<sup>e</sup> | |
| \( Q_C \) | Slope for temperature dependence | – | 1.7<sup>b</sup> | |
| \( \alpha_{D_A} \) | Specific dynamic action intercept | – | 0.15<sup>d</sup> | |
| \( \alpha_{E} \) | Egestion intercept | – | 0.15<sup>c</sup> | |
| \( \alpha_{E} \) | Excretion intercept | – | 0.06<sup>c</sup> | |

<sup>a</sup>Politikos et al. 2011; <sup>b</sup>Clarke & Johnston 1999; <sup>c</sup>Olson et al. 2016; <sup>d</sup>Olson & Boggs 1986; <sup>e</sup>Blank et al. 2007; <sup>f</sup>Yasuda et al. 1978; <sup>g</sup>Neilson et al. 2013; <sup>h</sup>Boyce et al. 2008; <sup>i</sup>calibrated; \( \kappa_R = 0.5 \text{ for ages 3.5–6 yr, 0.6 for ages 7–8 yr, 0.7 for ages 8–9 yr, 0.8 for ages >9 yr} \)

Fig. 4. Swordfish daily consumption simulated and estimated from stomach content data. Red circles represent the estimated consumption rate from stomach content analysis, while red stars represent the mean consumption rates for each size class (68–79, 80–89, 90–99, 100–109, 110–119, 120–129 and 130–214 cm with an average weight of 4.9, 7.3, 11.5, 14.8, 17.8, 23.7, and 54.4 kg, respectively); error bars represent standard deviation (SD) of the same rates. Lines indicate simulated consumption: the black line represents mean consumption with stable food availability, the blue line represents maximum consumption (with \( f = 1 \)) and the cyan line represents consumption with food availability varying randomly daily.
Fig. 5. Swordfish juvenile and adult growth (LFJL: lower jaw fork length). Simulated growth with spawning occurring in the Tyrrhenian Sea and in the Levantine Sea is represented by the blue and black lines, respectively. Individual observations are represented by red circles, means of LFJL for each year of age are represented by red stars and error bars represent SD. The cyan line shows the Von Bertalanffy growth curve from Tserpes & Tsimenides (1995).

Fig. 6. Simulated growth (LFJL: lower jaw fork length) of larval stages in the Tyrrhenian (blue) and Levantine (black) Sea, compared with growth observations (red circles, Govoni et al. 2003), and the larval growth model (green line; Govoni et al. 2003).
3.4. Growth

The simulated swordfish LFJL for both scenarios (spawning occurring in the Levantine and Tyrrhenian Seas) is shown in Fig. 5 against observations and the Von Bertalanffy model from Tserpes & Tsimenides (1995). Larval growth is also shown (Fig. 6) against observations and the growth model by Govoni et al. (2003). Overall, the simulated LFJL for both adults ($r^2 = 0.991$, $p < 0.0001$) and larvae ($r^2 = 0.827$, $p < 0.0001$) is well correlated with observations and is closely related to the growth models of Tserpes & Tsimenides (1995) and Govoni et al. (2003). Swordfish growth appears linear for early life stages (Megalofonou et al. 1995, Govoni et al. 2003), with a growth rate of 0.5 mm d$^{-1}$ for early larvae, 5 mm d$^{-1}$ for late larvae and 2.07 mm d$^{-1}$ for early juveniles. The latter is close (~10% lower) to the 2.3 mm d$^{-1}$ found by Megalofonou et al. (1995) for juvenile swordfish with LFJL between 51 and 74 cm. Finally, the mean growth rate for adults is 0.23 mm d$^{-1}$.

The lower temperatures at the 0−100 m layer in the Tyrrhenian Sea (16.09 ± 1.38°C) as compared to those in the Levantine Sea (17.8 ± 1.1°C), are closer to the optimum temperature for swordfish ($T_{opt}$) and therefore have a slightly positive impact on adult growth. Larval growth is very similar in the 2 areas as the divergence in SST during the summer months is not significant (Fig. 3).

3.5. Energy budget

The energy allocation of swordfish in terms of kJ spent on each energy budget component throughout their life cycle for the Tyrrhenian Sea scenario is shown in Fig. 7. The increasing energy demands as the swordfish grows are clearly illustrated, with the individual consuming and spending a total of $0.39 \times 10^6$ kJ during the first year of its life, which increases to $3.8 \times 10^6$ kJ during the fifteenth year. Most of the energy consumed is spent on respiration (52.7–62.2%), followed by losses due to excretion (14%), specific dynamic action (12.9%) and egestion (5.16%). In Fig. 8, the energy costs for growth and reproduction are shown as percentages of consumption. The simulated individual shows a decrease in percentage energy costs for growth as it passes from larva to juvenile and adult stages, with a simultaneous increase in metabolic costs. Before maturity, the entire energy surplus is directed to growth, with the individual spending 15.17, 8.2 and 6.3% of consumed energy for somatic growth during the first, second
and third year respectively. After maturity (fourth year and beyond), the available energy directed to somatic growth continuously decreases and stabilizes at 1.49% during the tenth year. Simultaneously, reproduction gains priority and a significant amount of available energy (3.88–4.96%) is allocated for egg production.

### 3.6. Reproduction

Annual egg production throughout an individual’s lifetime for swordfish spawning in the Levantine and Tyrrhenian Seas, obtained from the bioenergetics model results, is shown in Fig. 9. The annual egg production is higher in the Tyrrhenian Sea (14.9–37.2 × 10⁶ eggs) than in the Levantine Sea (14.72–33.5 × 10⁶ eggs). The difference between the 2 areas can be attributed to the lower temperature in the 0–100 m layer in the Tyrrhenian Sea, which is favorable for somatic growth (Fig. 3) and consequently egg production. In both areas, there is a trend of increasing egg production as the swordfish grows, and after the tenth year, annual egg production stabilizes at about 39 × 10⁶ eggs and 34 × 10⁶ eggs in the Tyrrhenian and Levantine Seas, respectively. Annual egg production is the result of a varying number of 4 to 6 spawning events per season, which, assuming a spawning interval of 3 d, corresponds to 12–18 d of spawning activity annually.

The predicted annual egg production is further supported by the preliminary population experiment described in Section 2.5, where the model is initialized with \( N = 144,380 \times N_{egg} \) individuals in the egg life stage and \( N_{egg} (17.6 \times 10^6) \) is the average annual egg production at Ages 4 and 5 across the Tyrrhenian and Levantine Seas, taken from the bioenergetics model. Applying the mortality rates given by Eqs. (15–17) results in a total of 907,670 fish surviving to the length of 60 cm and 861,210 to the length of 70 cm. This is in good agreement with the Mediterranean swordfish stock assessment for 2018 (ICCAT 2020), where a total of 872,478 recruits was estimated, with recruit defined as fish of length between approximately 60 and 70 cm.

### 3.7. Sensitivity analysis

The calculated sensitivity indices \( S_a(p_3) \) describing the effect of each model parameter on growth and reproduction are shown in Table 5. Indices >1, considered to have a significant impact on the tested output (Kitchell et al. 1997), are highlighted. For growth, these are the exponents and intercepts for consumption and respiration (i.e. \( a_C, b_C, a_R, b_R \)), the reference
temperature for respiration (\(T_{\text{ref}}\)) and the caloric content of prey (\(\text{CAL}_f\)). Annual egg production is sensitive to the same parameters in addition to coefficients for egestion (\(a_F\)) and specific dynamic action (\(s_{\text{SDA}}\)); however, the latter two have a much weaker impact, as indicated by \(S_{\Delta}(p_S)\), which is close to 1. Perturbations affecting growth also affect reproduction and in fact are amplified 3 to 5 times. This is in accord with the divergence in growth and reproduction between the 2 simulations, with spawning occurring in the Tyrrhenian or Levantine Sea. The lower temperatures in the Tyrrhenian Sea had a positive impact on both growth and annual egg production. Furthermore, parameters that directly control reproduction (i.e. \(\kappa_R\), \(I_{\text{spawn}}\), \(\text{SST}_{\text{egg}}\), \(\text{CAL}_{\text{egg}}\), \(B_{\text{fmin}}\)) have a relatively small effect on annual egg production, particularly spawning interval (\(I_{\text{spawn}}\)) and minimum batch fecundity (\(B_{\text{fmin}}\)), which have almost zero effect on annual egg production. Life stage transition lengths and ages were found to have very small impacts (\(S_{\Delta}(p_S) \approx 0\)) on both growth and reproduction.

The model results are mostly sensitive to parameters that control the balance between consumption and respiration and define the net energy available for spawning and growth. The most sensitive parameters by far are the exponents for consumption (\(b_C\)) and respiration (\(b_R\)), followed by \(a_C\), \(\text{CAL}_P\), \(\text{CAL}_{\text{egg}}\) and \(T_{\text{opt}}\). Since \(\text{CAL}_P\) and \(a_C\) have the same impact on the model results (since they are multiplied, see Eqs. 1 & 3), \(\text{CAL}_P\) was excluded from the ensemble experiment. In order to keep most model runs (and the standard deviation of all runs) inside the limits of

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Effect on growth</th>
<th>Effect on reproduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a_C)</td>
<td>3.050</td>
<td>-3.191</td>
</tr>
<tr>
<td>(a_R)</td>
<td>-2.799</td>
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<td>(b_C)</td>
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<td>(b_R)</td>
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</tr>
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</tr>
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</tr>
<tr>
<td>(Q_{\text{10}})</td>
<td>-0.099</td>
<td>0.003</td>
</tr>
<tr>
<td>(I_{\text{spawn}})</td>
<td>0.002</td>
<td>0.003</td>
</tr>
<tr>
<td>(\text{SST}_{\text{egg}})</td>
<td>0.066</td>
<td>0.175</td>
</tr>
<tr>
<td>(\text{CAL}_M)</td>
<td>-0.004</td>
<td>0.702</td>
</tr>
<tr>
<td>(\text{CAL}_{\text{egg}})</td>
<td>0.242</td>
<td>0.247</td>
</tr>
<tr>
<td>(L_{\text{hatch}})</td>
<td>0.046</td>
<td>0.055</td>
</tr>
<tr>
<td>(L_{\text{lar}})</td>
<td>0.031</td>
<td>-0.035</td>
</tr>
<tr>
<td>(L_{\text{juv}})</td>
<td>0.042</td>
<td>-0.042</td>
</tr>
<tr>
<td>(Y_{\text{mat}})</td>
<td>0.049</td>
<td>-0.052</td>
</tr>
<tr>
<td>(B_{\text{fmin}})</td>
<td>0.055</td>
<td>0.055</td>
</tr>
</tbody>
</table>

Table 5. Sensitivity indices \(S_{\Delta}(p_S)\) for growth (LFJL: lower jaw fork length) and reproduction (annual egg production) for each parameter of the model. Parameters where \(|S_{\Delta}(p_S)| > 1\), considered to indicate high sensitivity, are highlighted. \(L_{\text{hatch}}\): length at hatching, \(L_{\text{lar}}\): transition length for late larva, \(L_{\text{juv}}\): transition length for early juvenile, \(L_{\text{juv}}\): transition length for late juvenile, \(Y_{\text{mat}}\): transition age for adult, \(B_{\text{fmin}}\): minimum batch fecundity, \(\text{CAL}_P\): caloric content of swordfish, \(\text{CAL}_{\text{egg}}\): caloric content of swordfish eggs. All other parameters are described in Table 4. Grey shading: indices >1, considered to have a significant impact on output.
observed LFJL, small perturbations were necessary. Thus, intercepts ($a_C$ and $a_R$) and $T_{ref}$ were perturbed by 0.6% and exponents by 0.2%. All possible combinations of these parameter values were adopted and a model run was performed for each, leading to a total of $32 \times 2^5$ model runs. The mean and standard deviation of all outputs was calculated and plotted for all 32 runs in Fig. 10.

For growth, mean and SD of all model runs are closely related to observations, indicating that per-
turbations applied to the tested parameters are inside a realistic framework. Uncertainty due to the selected values of the tested parameters, as defined by SD, increases as the simulated individual grows. For reproduction, uncertainty increases from the fourth to the tenth year of age, but remains stable during the rest of the model runs. The pattern presented in Fig. 9, with annual egg production increasing until the tenth year and stabilizing afterwards, is also present in the ensemble experiment of Fig. 10, illustrated by the mean and SD of all runs. Moreover, the range of annual egg production estimated from the ensemble (mean ± SD 16.8 ± 3.1 × 10^6 in the fourth year of age) can be regarded as realistic, taking into account the relationship found between growth and reproduction through the calculation of parameter sensitivity indices and that the range of growth remains inside the variability of observations.

### 4. DISCUSSION

A Wisconsin type bioenergetics model was developed to study the growth and reproduction of Mediterranean swordfish. Simulated growth and consumption were calibrated against observations, while the resulting reproduction was evaluated indirectly using spawning stock biomass and recruitment data (for 2017 and 2018 respectively) from the most recent stock assessment. Despite knowledge gaps regarding the bioenergetic budget of swordfish and the constraints of specific limitations, the model is evaluated at its most vital points and its results concerning growth and egg production can be regarded as reliable. Furthermore, the study highlights the importance of bioenergetics in the reproduction of swordfish, suggesting that each individual’s spawning period lasts ~15 d, while the commonly reported spawning season of the whole population is ~90 d (Arocha 2007).

### 4.1. Growth and reproduction

The bioenergetics simulation curve for growth is well correlated with the observations and the Von Bertalanffy curve from Tserpes & Tsimenides (1995). However, the latter is only applicable for commercial-sized fish (>60–70 cm) and cannot take into account any differentiation among individuals due to different environmental characteristics. The bioenergetics model describes growth throughout the entire life cycle of an individual, controlled by external forcing environmental variables (food availability, temperature), and considering physiological aspects and reproductive effort.

The estimated number of spawned batches (between 4 and 6), assuming a spawning interval of 3 d, indicates that an individual is reproductively active for a period between 12 and 18 d, resulting in a varying annual egg production between 15 × 10^6 and 40 × 10^6. The exact number of spawning events, and thus the time interval during which swordfish remain reproductively active, is largely controlled by the adopted value of minimum batch fecundity (B_{fmin}), for which we used the minimum reported value found in literature for the Mediterranean stock (~2 × 10^6, de la Serna et al. 1996). As an alternative, we tested the model adopting the minimum batch fecundity reported for the North Atlantic stock (~1 × 10^6, Arocha 2007) which resulted in an increased number of spawning events (between 6 and 8). Still, the annual egg production did not significantly change, showing very low sensitivity to B_{fmin} (sensitivity analysis, Table 5).

Some previous efforts attempt to estimate the potential annual egg production of swordfish at the individual level (Table 6). However, none of them was for the Mediterranean swordfish and none took into account the swordfish energy budget. The estimate in our study follows the bioenergetics ap-

<table>
<thead>
<tr>
<th>Area</th>
<th>Estimated annual egg production</th>
<th>Batch fecundity</th>
<th>LFJL (cm)</th>
<th>Spawning season</th>
<th>Spawning interval (d)</th>
<th>Spawning events</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific Ocean</td>
<td>21–42 × 10^6</td>
<td>1.66 × 10^6</td>
<td>194.8</td>
<td>Dec–Feb</td>
<td>1.78–3.02</td>
<td>12–25(^a)</td>
<td>Young &amp; Drake (2002)</td>
</tr>
<tr>
<td>North Atlantic Ocean</td>
<td>159 × 10^6</td>
<td>1.73 × 10^6</td>
<td>179</td>
<td>Dec–Jun</td>
<td>2.3</td>
<td>92(^a)</td>
<td>Arocha &amp; Lee (1996)</td>
</tr>
<tr>
<td>Indian Ocean</td>
<td>–</td>
<td>4.3 × 10^6</td>
<td>225</td>
<td>Oct–Apr</td>
<td>2.8</td>
<td>76(^a)</td>
<td>Poisson &amp; Fauvel (2009b)</td>
</tr>
<tr>
<td>Mediterranean Sea</td>
<td>20 × 10^6</td>
<td>2-4 × 10^6</td>
<td>158</td>
<td>Jun–Sep</td>
<td>3</td>
<td>6(^b)</td>
<td>This study</td>
</tr>
</tbody>
</table>

\(^a\)Assuming the individual will spawn the whole spawning season at the specified spawning interval (Arocha & Lee 1996, Young & Drake 2002, Poisson & Fauvel 2009b); \(^b\)Derived from the bioenergetics model.
proach, and besides the SST threshold and spawning interval, takes into account the energy requirements needed for swordfish to release a batch \( (A_{\text{buffer}} \times \text{batch fecundity} \times \text{caloric content of one egg}) \). Based on observations of growth, batch fecundity and consumption rates, it is demonstrated that swordfish are not capable of spawning for long periods of time. In their assessment of potential annual egg production, Young & Drake (2002, p. 34) noted that individuals might have a shorter spawning period than the one commonly considered for the whole population and if this were the case, there should be ‘a turnover of fish on the spawning ground’. The same is implied by Poisson & Fauvel (2009a), who found larger individuals were first to reach the spawning ground, followed by younger fish later in the spawning season, and it was unlikely for an individual to spawn for the whole season (Poisson & Fauvel 2009b). Similar to our approach, Jusup et al. (2011) used a bioenergetics model to demonstrate that Pacific bluefin tuna are capable of spawning an average of 9 batches per year, indicating that an individual can be reproductively active for 18 to 40.5 d, even though a longer spawning period is commonly reported for the population.

Comparisons of energy allocation to growth and reproduction can be made with other studies on large pelagic fish with similar life traits, like dolphinfish and tuna spp. (Figs. 11 & 12, Table A1 in the Appendix). Our findings suggest that at egg sack larva stage (<15 mm), swordfish energy allocation to growth is similar to that of dolphinfish. This changes at a later point of development (<20 cm), as swordfish channel more energy to growth than dolphinfish, resulting in higher growth rates (Govoni et al. 2003). The energy allocation of late juvenile swordfish is comparable to yellowfin tuna at 5.8 to 11 kg (Estess et al. 2017) and to Pacific bluefin tuna at 10.4 to 12.4 kg (Estess et al. 2014). Allocation to growth in juvenile swordfish is most similar to energetic demands of growth for yellowfin tuna, considering that at the same sizes and similar temperatures (16.1 ± 4.9°C for

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**Fig. 11.** Energy allocated to growth as a percentage of consumed energy at immature life stages of large pelagic fish. SWO: swordfish *Xiphias gladius* (this study), DLF: dolphinfish *Coryphaena hippurus* (Benetti 1992), YFT: yellowfin tuna *Thunnus albacares* (Estess et al. 2017), PFT: Pacific bluefin tuna *Thunnus orientalis* (Estess et al. 2014). EL: early larva, LL: late larva, EJ: early juvenile, LJ: late juvenile, DW: dry weight, W: wet weight. Red whiskers for DLF indicate range given by Benetti (1992). Estess et al. (2014) and Estess et al. (2017) used temperatures 19.9 ± 0.9°C (mean ± SD), while Benetti (1992) used 25–27°C. All 3 studies are outcomes from tank experiments. Percentages for swordfish are calculated in the interval specified by the indicated weight range from models runs with spawning occurring in the Tyrhenian Sea, which correspond to 27.02 ± 0.1°C (mean ± SD) for DW = 0.304–2.85 mg, 24.1 ± 4.9°C for W = 4.2–43.7 g, 16.1 ± 4.9°C for W = 5.8–11 kg and 15.2 ± 1.2°C for W = 10.4–12.4 kg. For more details, please see Table A1.
swordfish vs. 19.9 ± 0.9°C for yellowfin), swordfish have a similar allocation to growth (~8% lower). Still, at this size range, swordfish have higher growth rates (0.77 mm d⁻¹) than yellowfin tuna (0.38–0.42 mm d⁻¹, Estess et al. 2017), attributed to the lower caloric content of swordfish adopted here (7.4 kJ g⁻¹), as compared to the caloric content of yellowfin tuna (7.9 kJ g⁻¹, Estess et al. 2017). At the adult stage, energy allocation to growth and reproduction of swordfish is most similar to the Pacific bluefin tuna’s partitioning. Specifically, swordfish allocate (daily) 0–9 and 0–10.6% of assimilated energy to growth and reproduction, respectively, depending on size and temperature. The comparable percentages for Pacific bluefin tuna, as predicted by the DEB model of Aoki et al. (2020), are 0–9.3 and 1.1–9.1%, assuming constant ambient temperature. Finally, our results indicate that swordfish have a lower investment in reproduction than Atlantic bluefin and skipjack tuna, but higher than yellowfin tuna.

Regarding the costs of reproduction, the buffer concept used has some differences to the reproductive buffer of the DEB modelling framework for tuna spp. (Jusup et al. 2011, Aoki et al. 2020). In the presented modelling framework, when maintenance costs are covered, all energy stored in the reproductive buffer is converted to eggs, while in Aoki et al. (2020) and Jusup et al. (2011) a fixed 95% fraction of the reproductive buffer is converted to eggs. Moreover, in DEB terminology, wet weight (W) of our framework refers to reserves plus structure. In DEB models, the reproductive buffer is added in the calculation of weight. In the examples shown in Fig. 12, the percent of weight added by the reproductive buffer accounts for 9, 13 and 0% of Pacific bluefin, Atlantic bluefin and skipjack tuna, respectively (Aoki et al. 2020).

4.2. Limitations and future development

Generally, the parameterization of a model is a source of uncertainties (Araújo & New 2007). Here, some parameters (Q₁₀, aE, aF, aSDA) were borrowed from related species with similar life traits (tuna spp.) which is a common method in bioenergetics modelling (Petersen et al. 2008); however, considering their
low impact on the model outputs of the sensitivity analysis, the related uncertainties cannot be significant. On the other hand, the parameters controlling consumption \((a_C, b_C, r_S)\), respiration \((a_R, b_R, Q_{10})\) and reproduction \((\kappa_R)\) were calibrated via comparison with observations. Among them, \(a_C, b_C, a_R\) and \(b_R\) have the most significant impact on growth and reproduction, as demonstrated by the sensitivity analysis (Table 5). Since consumption was fitted with observation from the field and reproduction was evaluated through the population experiment (Section 2.5), the most uncertain and sensitive parameters are the intercept and exponent for respiration \(a_R, b_R\). However, considering growth was in good agreement with observations and respiration is the most important loss term, the scaling of \(a_R\) and \(b_R\) should be also realistic. Furthermore, the ensemble experiment showed how the model reacts to small changes in these parameters, providing the range of values at which the results remain realistic. Thus any uncertainties due to the factors discussed above, if minimized by collection of more field data in the future, can be overcome by changing the values of the most sensitive parameters \((a_C, b_C, a_R, b_R)\) in the range specified by the ensemble experiment.

Another uncertainty in the results is related to the consumption rates, which are estimated from stomach contents. Although these were estimated with a method considered among the most plausible for large pelagic fish (Olson & Mullen 1986), the evacuation rates used here are rates for yellowfin tuna. Still, these rates are considered reliable for such estimations in tunas, billfishes and dolphins, as these fishes share the same high performance physiology and rates of digestion (Brill 1996, Olson & Galvan-Magana 2002). Thus, the same evacuation rates have been previously used for daily ration estimates of swordfish (Young et al. 2010, Zambrano et al. 2019), dolphinfish (Olson & Galvan-Magana 2002, Varela et al. 2017), striped marlin (Abitia-Cardenas et al. 2011) and tuna spp. (Griffiths et al. 2009, Young et al. 2010). Apart from uncertainties related to the evacuation rates, uncertainties to the relatively small \((N = 69)\) and old dataset (data from January 1994 to September 1995) used for the analysis might be more important and thus more data should be analyzed in the future to get more robust results.

It should be noted that the simulated reproduction (maturity, energy allocation for egg production etc.) represents the energetics of a female swordfish while the simulated length represents mixed sex growth. Swordfish provide an example of sexual dimorphism in fish (DeMartini et al. 2007), with females having higher growth rates after an estimated age of 3 yr (Tserpes & Tsimenides 1995) and maturing later (~3.5 yr) than males (~2 yr, ICCAT 2008). In most fish species, females grow faster despite having higher energetic costs for reproduction, most likely due to reduced activity costs (Pauly 2019). The model presented here could simulate the energetics of males and females separately, most likely by adopting a lower value of energy allocated to the reproductive buffer, \(\kappa_R\), for males (Kirby 2005) combined with higher respiration costs due to higher activity. Indeed, Bozynski & Pauly (2017, p.15) demonstrated that ‘higher activity levels reduce growth and lead to earlier maturation, at smaller sizes’. However, in a more computationally demanding 3-D model application describing swordfish population dynamics, having both male and female agents would increase the computational load without gaining much in content. Thus, for computational efficiency, a mixed population is commonly used (e.g. Rose et al. 2015), and the reproduction of the whole population is described by taking into account reported sex ratios.

Commonly, bioenergetics models simulate activity costs as a function of swimming speed and weight (Politikos et al. 2011, Rose et al. 2015) or by applying a constant multiplier to respiration (Hanson et al. 1997). In the modelling framework presented, activity costs were embedded, as a first approximation, in respiration costs and were not modelled separately. Theoretical functions of activity costs with weight, swimming speed (Ohlberger et al. 2005, Rose et al. 2015) and consumption (Boisclair & Leggett 1989) can be tested in the future to provide more detail when describing the respiration of swordfish. If we assume that the resting metabolic rate of swordfish is given by the general scaling of Clarke & Johnston (1999), then active metabolism (resting metabolic rate + costs for activity) would be 9 to 10 times higher than resting metabolic rate. This is higher than the multiplier usually adopted for activity (~1–3), although it has been demonstrated that activity costs could be higher and more variable (Boisclair & Tang 1993). For swordfish, high activity costs are expected, considering the unique adaptation of the species for hunting in deep and cold waters (i.e. warming eyes and brain; Fritsches et al. 2005).

Furthermore, our study highlights important knowledge gaps regarding the physiology and energetics of fish larvae, especially for swordfish but also in general. Critical knowledge, such as length–weight relationships and energy density of fish larvae, is scarce and limited to a small number of species. Energy density is difficult to measure (Wuenschel...
et al. 2006), while length–weight relationships are more complicated in fish larvae than juvenile and adult fish, and as a result, the general allometric model \( W = a \times L^b \) is considered inappropriate for fish larvae (Pepin 1995). In the present study, the only available information for swordfish larvae was length at hatching and growth rate in terms of length, and although the model sufficiently reproduces the observed length, the calculated weight and consumption rate of swordfish larvae could not be validated as no information could be found in the literature. Future studies that focus on the physiology and behavior of swordfish larvae can improve the predictions of the presented model, especially if implemented to simulate population dynamics (Peck & Hufnagl 2012).

Despite limitations and uncertainties, the model results are in reasonable agreement with available observations at the individual level, providing a promising basis from which a population model can be developed in the future. Forcing functions used here represent the mean state of conditions that would be used in a spatially explicit model of swordfish at the Mediterranean scale. To integrate the individual model developed to a dynamic population modelling approach, 2 more basic steps are needed: the development of a sub-model that will reproduce temporal and spatial distribution of swordfish prey at the Mediterranean scale and the simulation of swordfish movements and migrations in the horizontal layer.

5. CONCLUSIONS

Here, we developed a bioenergetics model which describes in detail the full life cycle of the Mediterranean swordfish \( Xiphias gladius \). This step provides a fundamental module for the development of an end-to-end framework focused on the threatened Mediterranean swordfish. For instance, when developing an IBM to study climate change in fish, it is essential to combine it with life history models that provide sufficient detail throughout their complex life history (Petitgas et al. 2013). In contrast with simpler models like the Von Bertalanffy model, which partially covers the life history of an individual isolated from its surrounding environment, the presented model is an effort to describe an individual fish’s physiology in all life stages driven by a changing environment. Thus, a future projection of the model developed to the population level in a spatially explicit simulated environment will allow us to test habitat stability and potential for survival of Mediterranean swordfish in relation to environmental changes, thereby providing a useful tool for scenario testing (e.g. climate change or pollution scenarios), management and forecasting.

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Appendix.

Table A1. Energy allocation (to growth and reproduction) of swordfish through different life stages compared to the partitioning of other large pelagic fish. N.d.: no data available; dash (–): no allocation to reproduction (assumed for immature life stages). Growth and reproduction: To make comparisons with other studies, percentages of energy allocated to growth and reproduction for immature life stages are a fraction of consumed energy, while for adult stages they are a fraction of assimilated energy (consumption minus egestion and excretion). Growth: ± values are ranges. Temperature: Mean ± SD or range. Length: Fork length (FL) for tunas and dolphin fish and lower-jaw fork length (LFJL) for swordfish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life stage</th>
<th>Growth (%)</th>
<th>Reproduction (%)</th>
<th>Temperature (°C)</th>
<th>Weight</th>
<th>Length</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swordfish</td>
<td>Larva</td>
<td>48</td>
<td>–</td>
<td>27.0 ± 0.1</td>
<td>0.304–2.85 mg$^b$</td>
<td>6.7–13.1 mm</td>
<td>Bioenergetics modelling</td>
<td>This study</td>
</tr>
<tr>
<td>Dolphinfish</td>
<td>Larva</td>
<td>45 ± 5</td>
<td>–</td>
<td>25–27</td>
<td>0.304–2.85 mg$^b$</td>
<td>7–15 mm</td>
<td>Tank experiments</td>
<td>Benetti (1992)</td>
</tr>
<tr>
<td>Swordfish</td>
<td>Larva-Juvenile</td>
<td>50</td>
<td>–</td>
<td>24.1 ± 4.9</td>
<td>4.2–43.7 g</td>
<td>7.3–15.6 cm</td>
<td>Bioenergetics modelling</td>
<td>This study</td>
</tr>
<tr>
<td>Dolphinfish</td>
<td>Juvenile</td>
<td>35 ± 11</td>
<td>–</td>
<td>25–27</td>
<td>4.2–43.7 g</td>
<td>6.5–18.5 cm</td>
<td>Tank experiments</td>
<td>Benetti (1992)</td>
</tr>
<tr>
<td>Swordfish</td>
<td>Juvenile</td>
<td>7.2$^a$</td>
<td>–</td>
<td>16.1 ± 4.9</td>
<td>5.8–11 kg</td>
<td>77.5–96.6 cm</td>
<td>Bioenergetics modelling</td>
<td>This study</td>
</tr>
<tr>
<td>Yellowfin tuna</td>
<td>Juvenile</td>
<td>7.8$^a$</td>
<td>–</td>
<td>19.9 ± 0.9</td>
<td>5.8–11 kg</td>
<td>67.9–82.5 cm</td>
<td>Tank experiments</td>
<td>Estess et al. (2017)</td>
</tr>
<tr>
<td>Swordfish</td>
<td>Juvenile</td>
<td>10.3$^a$</td>
<td>–</td>
<td>15.2 ± 1.2</td>
<td>10.4–12.4 kg</td>
<td>93.9–109.2 cm</td>
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<td>This study</td>
</tr>
<tr>
<td>Pacific bluefin tuna</td>
<td>Juvenile</td>
<td>12.4$^a$</td>
<td>–</td>
<td>19.9 ± 0.9</td>
<td>10.4–12.4 kg</td>
<td>nd</td>
<td>Tank experiments</td>
<td>Estess et al. (2014)</td>
</tr>
<tr>
<td>Swordfish</td>
<td>Adult</td>
<td>5.4–1.2 (7.5–0)$^c$</td>
<td>3.9–6 (0–10.6)$^c$</td>
<td>15.6 ± 1.7</td>
<td>34.4–149 kg</td>
<td>139–224 cm</td>
<td>Bioenergetics modelling</td>
<td>This study</td>
</tr>
<tr>
<td>Atlantic bluefin tuna</td>
<td>Adult</td>
<td>11.4–3.9</td>
<td>1.1–15.9</td>
<td>18.4</td>
<td>nd</td>
<td>116.2–265 cm</td>
<td>Bioenergetics modelling</td>
<td>Aoki et al. (2020)</td>
</tr>
<tr>
<td>Pacific bluefin tuna</td>
<td>Adult</td>
<td>9.3–0</td>
<td>1.1–9.1</td>
<td>25.5</td>
<td>nd</td>
<td>152.2–250 cm</td>
<td>Bioenergetics modelling</td>
<td>Aoki et al. (2020),</td>
</tr>
<tr>
<td>Skipjack tuna</td>
<td>Adult</td>
<td>11.4–0</td>
<td>5.0–12.3</td>
<td>27</td>
<td>nd</td>
<td>42.8–100 cm</td>
<td>Bioenergetics modelling</td>
<td>Aoki et al. (2020),</td>
</tr>
<tr>
<td>Yellowfin tuna$^d$</td>
<td>Adult</td>
<td>17.5–1.4</td>
<td>2.4–3.2</td>
<td>nd</td>
<td>nd</td>
<td>nd</td>
<td>Bioenergetics modelling</td>
<td>Kirby (2005)</td>
</tr>
</tbody>
</table>

$^a$Percentages are calculated in the interval specified by weight range; $^b$Dry weight (DW); $^c$Percentages are calculated in annual interval. Percentages in the parentheses are calculated in daily interval; $^d$In Kirby (2005)’s results, no length or weight of simulated yellowfin tuna are shown, only age. The range of growth and reproduction values shown here are for simulated fish of 2.25–7 yr.