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Impact of environmental conditions on fish early-life stages, an Individual-Based Model approach

María-José Lagunes^{a,b,c,*}, Leo Berline^a, Marine Di Stefano^a, Vincent Rossi^a

^a*Aix Marseille Univ, Université de Toulon, CNRS, IRD,
MIO, , Marseille, 13228, , France*

^b*MARBEC, IRD, Univ Montpellier, CNRS, Ifremer, , Sète, 34200, , France*

^c*LEMAR, IRD, Univ Brest, CNRS, Ifremer, IUEM, , Plouzané, F-29280, , France*

Abstract

The duration and survival of dispersing fish Early-Life Stages (ELS) are influenced by biotic and abiotic factors. Moreover, current methods for estimating mortality rates based on laboratory experiments or field studies neglect key components, which can be investigated thanks to modeling. To address these gaps, a growth model is coupled with a Lagrangian model to simultaneously account for species-specific physiology, environmental variability and physical transport. Growth was modeled using Dynamic Energy Budget theory, coupled with a particle-tracking model that computes trajectories. Focusing on three species of Mediterranean coastal fishes, we first model their Pelagic Larval Durations (PLD) over realistic ranges of constant temperature and food density. Our modeling framework reproduces well the expected environmentally-driven variation of PLD. Then we estimated mortality as a function of spawning, using varying food density and

*Corresponding author

**Corresponding author

Email addresses: maria_jose.lagunes@ird.fr (María-José Lagunes),
vincent.rossi@mio.osupytheas.fr (Vincent Rossi)

temperature along dispersal trajectories. Mortality was estimated based on three criteria: time to metamorphosis, final position when metamorphosis occurs, and starvation. Variations of temperature and food density across the year induce seasonal variations of both PLDs and mortality rates, with slow growing species exhibiting higher mortality rates than those characterized by faster development. Our results showed that spawning phenology affects seasonal mortality rates, opening new opportunities to explicitly test the “match-mismatch” hypothesis.

Keywords: Biophysical modeling, DEB model, Lagrangian particle-tracking model, Early-Life Traits, Larval mortality, Pelagic Larval Duration

1. Introduction

2 The great majority of marine fishes undergo pelagic Early-Life Stages
3 (ELs, i.e.embryos and larvae), which are numerous (R-strategists) and dis-
4 perse largely in the ocean while juvenile and adult phases are more sedentary
5 (Thresher et al., 1989). To better understand and model the eco-evolutionary
6 dynamics of fish populations characterized by biphasic life cycles, stage-
7 specific source and sink terms (such as mortality) must be well-known (Mar-
8 shall and Morgan, 2011), as it has far-reaching implications for community
9 structure and species resilience to external perturbations (Cowen et al., 2007).
10 Historical efforts have been essentially devoted to estimating natural mortal-
11 ity in adults (Maunder et al., 2023) but large uncertainties remain regarding
12 the survival of fish ELS (Houde, 1997; White et al., 2014; Robert et al., 2023).
13 The study of fish ELS mortality is crucial for coastal fishes as it has large im-
14 pacts on recruitment and demographic connectivity (Cowen and Sponaugle,

15 2009), which are fundamental for population dynamics and fisheries man-
16 agement (Hidalgo et al., 2019). Moreover, the *Growth-Survival Paradigm*
17 recently reviewed by Robert et al. (2023) indeed postulates that recruitment
18 depends on growth and mortality during ELSs trajectory from spawning to
19 settlement, as well as the duration of this stage, which are our focus here.

20 Pelagic ELSs have the potential for large dispersal in the ocean, enduring
21 variable abiotic conditions. Dispersal is defined as the probability of an in-
22 dividual being successfully transported (under conditions favoring survival)
23 from the spawning site, where embryos are released, to the settlement site,
24 where post-metamorphosis larvae become juveniles to later recruit and re-
25 produce (Cowen et al., 2000; Pineda et al., 2007). As such, a combination of
26 transport-related processes, internal factors and external pressures (such as
27 predation, starvation, and thermal stress) would control the probability of
28 ELS survival, or ELS mortality rate (McGurk, 1986; Peck and Daewel, 2007;
29 Houde, 2008; Peck and Hufnagl, 2012). On one hand, the oceanic transport
30 of ELS is controlled by the location and period of spawning (Macpherson
31 and Raventos, 2006; Di Stefano et al., 2022), by turbulent advection due to
32 multi-scale ocean currents (Legrand et al., 2019), and eventually modulated
33 by the unpredictable swimming capacities of larvae (Cowen and Sponau-
34 gle, 2009). On the other hand, the space and time windows exploited by
35 dispersing ELSs dictate the environmental conditions they encounter, hav-
36 ing consequences for their development through thermally- or food-regulated
37 growth, as well as for their survival, through lethal temperatures or direct
38 predation (Lett et al., 2010; Dahlke et al., 2020).

39 The study of fish ELS has been challenging due to the difficulty associated

40 with observing them in the field and rearing them in the laboratory. In
41 consequence, coupled biological and physical models offer promising tools
42 to investigate ELS dynamics (Werner et al., 2001; Pethybridge et al., 2013;
43 Falcini et al., 2020; Flores-Valiente et al., 2023). Using Individual Based
44 Models (IBMs), when coupled with biophysical models, allows the estimation
45 of the Pelagic Larval Duration (PLD), defined as the time ELS spend as
46 embryos and larvae in the ocean, which is influenced by unfavorable transport
47 by currents, unsuitable temperatures, and an insufficient quantity of prey
48 (Knights, 2003; Macpherson and Raventos, 2006; Peck and Hufnagl, 2012;
49 Lacroix et al., 2018; Cabral et al., 2021; Rose et al., 2024). By estimating
50 the PLD, we can then study mortality, as organisms spending longer time in
51 the water column are more subject to encounter unfavorable environmental
52 conditions and/or predation pressure (Chambers and Leggett, 1987; Houde,
53 Edward, 1987; Peck and Hufnagl, 2012).

54 Given the importance of spawning periods in determining larval success,
55 this study tested how different spawning behaviors influence larval trajec-
56 tories and mortality rate. Our case study focuses on the Mediterranean sea,
57 where considering the typical seasonality of environmental conditions in tem-
58 perate seas, suggests that spawning strategies of Mediterranean fishes play
59 a role in determining larval trajectories, influencing their settlement or mor-
60 tality. Additionally, previous studies suggest that the majority of Mediter-
61 ranean coastal Teleosts have a 2-4 months spawning period, occurring from
62 the end of spring to early summer (Tsikliras et al., 2010). However, a recent
63 compilation of Mediterranean fishes' spawning behavior has shown that the
64 spawning periods may be misestimated because of a sampling bias towards

65 summer months (Di Stefano et al., 2024). To address this, we simulated ELS
66 trajectories for particles spawned during different spawning periods all year
67 round as species with a short, one peak spawning period concentrate their
68 reproductive effort into a specific window, to ensure that larvae encounter
69 adequate environmental conditions. In contrast, species with extended or
70 multiple spawning periods spread their reproductive effort across a larger
71 window, increasing the probability that at least some of the larvae will find
72 suitable environmental conditions (James et al., 2003; Tsikliras et al., 2010;
73 Peck and Hufnagl, 2012).

74 The objective of this study is to assess the effect of spawning behaviors on
75 the Pelagic Larval Duration and on ELS mortality rate. Our study employs
76 a mechanistic Dynamic Energy Budget (DEB) model to analyze ELS growth
77 and development forced by outputs from a physical/biogeochemical circula-
78 tion model, incorporating the spatio-temporal variability of environmental
79 conditions. Our study focuses on three well-known species on the Western
80 Mediterranean *Pagellus erythrinus*, *Diplodus sargus* (Sparidae family), and
81 *Sciaena umbra* (Sciaenidae family). These species were chosen based on
82 the availability of ecological data (ELSS dispersal traits)(Di Stefano et al.,
83 2024) and the availability of DEB parameters which suggested contrasting
84 physiologies. Moreover, they are targeted by artisanal and recreational fish-
85 ermen. First, we explored the effect of food density and temperature on
86 species' PLDs, using constant conditions. Then, using varying food density
87 and temperature from a Lagrangian model, we estimated PLDs and fish lar-
88 val mortality for different spawning months based on three criteria: time to
89 arrive at metamorphosis, final position when metamorphosis occurs and star-

90 vation. For practical reasons and due to the lack of data, predation mortality
91 and the larvae swimming capacities were neglected. Finally, we discussed the
92 effect of environmental conditions on ELS development and survival.

93 **2. Material and methods**

94 *2.1. Species-specific growth model*

95 Dynamic Energy Budget (DEB) theory describes the assimilation and
96 use of energy for maintenance, growth, maturity and reproduction during
97 an organism's life cycle according to environmental conditions (Kooijman,
98 2009). DEB theory considers three main life stages: embryos, juveniles,
99 and adults. Embryos do not feed nor reproduce; juveniles feed but do not
100 reproduce; adults feed and reproduce. Based on this theory, we simulated
101 growth and development of fish embryos and larvae, which are described by
102 three state variables: the structural volume V , the reserve energy E , and the
103 cumulative energy invested in maturity E_H . Equations describing the model
104 are presented in Table 1.

105 In this study, we used the extended DEB model to incorporate the larval
106 stage into the standard model as proposed by Lika et al. (2014). Thus the
107 model includes the embryo stage which starts at spawning (including the egg
108 and the yolk-sac larvae) and the larval stage, marked by the start of individual
109 exogenous feeding and ends with metamorphosis, when larvae transform into
110 juveniles (Figure 1). The transition from one stage to another occurs when
111 the energy accumulated in maturity (E_H) reaches the threshold E_H^b for birth
112 and E_H^j for metamorphosis. Considering this, in this study PLD is defined
113 as the time duration between spawning and metamorphosis.

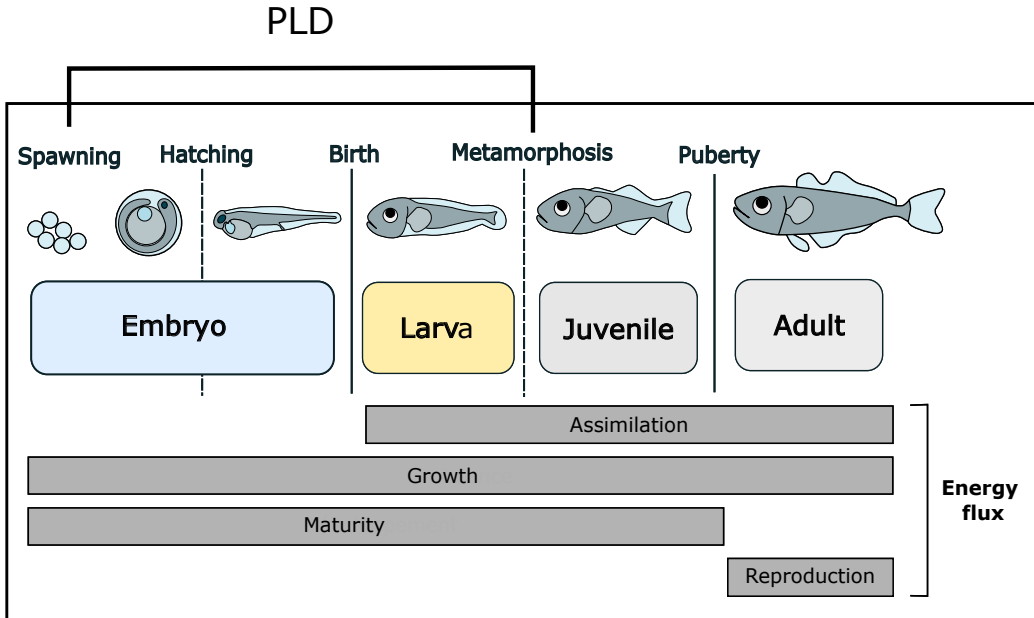


Figure 1: Fish life cycles stages according to DEB theory. PLD in this study is represented as the duration between spawning and metamorphosis processes.

114 Furthermore, the extended DEB model considers that at embryonic stage
 115 individuals are isomorphic, meaning that surface area is proportional to the
 116 volume to the power $2/3$, and that at larval stage they become V1-morphs,
 117 meaning that surface area is proportional to the structural volume (Kooi-
 118 jman, 2009, 2014). To follow this change in shape, the acceleration factor
 119 (s_M) must be implemented to adjust the maximum specific assimilation rate
 120 $\{\dot{p}_{Am}\}$ and energy conductance, \dot{v} based on the stage of development (Lika
 121 et al., 2014).

122 Equations describing individual growth and allowing for the estimation
 123 of mortality under different environmental conditions depend on two forcing
 124 variables: temperature and food density. Temperature T influences all rates

Table 1: Implemented equations of the standard DEB model for an organism. $[E]$ represents reserve density E/V with V the structural volume and E energy in reserve.

Equation	Definition
Physiological rates	
$\dot{p}_A = 0$	Embryos assimilation rate
$\dot{p}_A = c(T)f\{\dot{p}_{Am}\}V^{2/3}$	Larvae assimilation rate
$\dot{p}_C = [E]\frac{[E_G]\dot{v}V^{2/3} + \dot{p}_M}{\kappa[E] + [E_G]}$	Reserve mobilization rate
$\dot{p}_M = [\dot{p}_M]V$	Somatic maintenance rate
$\dot{p}_J = \dot{k}_J E_H$	Maturity maintenance rate
$\dot{p}_G = \kappa\dot{p}_C - \dot{p}_M$	Growth rate
$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$	Energy flux to maturation
State variables	
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	Energy in reserve
$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$	Structural body volume
$\frac{dE_H}{dt} = \dot{p}_R(E_H < E_H^p)$	Energy investment to maturation
$\frac{dE_R}{dt} = 0$	Energy investment to reproduction

125 through an Arrhenius function, defined as:

$$\dot{k}(T) = \dot{k}_{ref}c(T) \quad (1)$$

126 where \dot{k}_{ref} represents each physiological rate at the reference temperature
 127 T_{ref} (273 K). The term $c(T)$ refers to the correction factor of temperature:

$$c(T) = \exp\left[\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right] \quad (2)$$

128 with T_A the Arrhenius temperature (in Kelvin).

129 The second forcing variable is the scaled functional response f , which follows
130 a Holling Type II model with 0 being no food and 1 the maximal functional
131 response and is described as follows :

$$f = \frac{X}{K_X + X} \quad (3)$$

132 with X , food density and, K_X the species-specific half saturation constant
133 expressing the food density X , which provides half of the maximum uptake
134 rate (Kooijman, 2009).

135

136 To simulate ELS growth and estimate mortality, we used the DEB param-
137 eters, obtained from the AddmyPet database (Table 2; https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/). The initial reserve energy E_0 of the
138 fish embryos depends on the mature female's conditions at the time of spawn-
139 ing. For each simulation, we considered an egg spawned from a mother with
140 the maximum functional response ($f = 1$) at a temperature of $T = 20^\circ C$.
141 The initial structural volume V_0 was estimated using $V_0 = W_d^0/d_V$, where
142 W_d^0 represents the initial dry weight and d_V represents the specific density
143 of the structure for dry weight. Lastly, the energy invested in maturity E_H^0
144 was set to 0.
145

146 *2.2. External forcing along dispersal trajectories*

147 To simulate Mediterranean environmental forcing conditions along ELS's
148 dispersal pathways, a Lagrangian transport model was used (Lett et al., 2008)
149 to obtain space- and time-dependent 3-dimensional trajectories. Then, food
150 density and temperature conditions along each trajectory are extracted from

Table 2: DEB parameters available in AddmyPet for the studied species.

Parameter	Symbol	Unit	<i>P. erythrinus</i>	<i>D. sargus</i>	<i>S. umbra</i>
Arrhenius temperature	T_A	K	8000	8000	8000
Specific assimilation rate	$\{\dot{p}_{Am}\}$	$J/d.cm^2$	26.2038	115	54.2356
Energy conductance	\dot{v}	cm/d	0.05087	0.059223	0.075943
Allocation fraction to soma	κ	-	0.9659	0.90162	0.92491
Volume-specific somatic maintenance	$[\dot{p}_M]$	$J/d.cm^3$	17.09	21	8.6618
Maturity maintenance rate coefficient	\dot{k}_J	$1/d$	0.002	0.002	0.00050435
Specific cost of structure	$[E_G]$	J/cm^3	5231	5220.37	5239.49
Maturity at birth	E_H^b	J	0.02744	0.128	0.1823
Maturity at metamorphosis	E_H^j	J	24.03	1.491	5.166

151 the 4-dimensional (longitude, latitude, depth, time) outputs of a biogeochem-
152 ical model ECO3M-Med coupled with the circulation model NEMO-Med12
153 ($1/12^\circ$ spatial resolution on a C-Arakawa grid). The NEMO (Nucleus for Eu-
154 ropean Modelling Ocean) model computes current velocities, temperature,
155 and salinity fields based on hydrostatic primitive equations. It is coupled
156 offline with ECO-3M-Med which simulates biogeochemical tracers and zoo-
157 plankton compartments, obtaining environmental data representative of the
158 Mediterranean pelagic seascape (Guyennon et al., 2015; Pagès et al., 2020).
159 Here, food consists of the biomasses of copepods, ciliates, and nanoflagellates
160 ($molCL^{-1}$). More concretely, for this study, based on the Ichthyop model,
161 Lagrangian trajectories were simulated using velocity and recording position

162 (latitude, longitude, depth), plus temperature and food density along each
163 particle’s trajectory on a daily basis. For this, a set of initial particles (885)
164 was seeded every 10 km along the western Mediterranean coastline (aligned
165 with the 10 m isobath) for the year 2005, with initial releases occurring every
166 15 days (twice a month). Transport was considered passive, as the effects of
167 egg buoyancy and fish larval swimming capacities were not included. This
168 choice was made as knowledge of species-specific active transport behaviors
169 is limited.

170 *2.2.1. Growth model and mortality estimation under constant environmental*
171 *conditions*

172 To quantitatively estimate the influences of the environment on PLD and
173 mortality, first simulations were carried out with constant temperature and
174 food conditions within each model run, varying these values across multiple
175 runs. We explored the range of sea water temperatures typical of the western
176 Mediterranean sea (13-28°C; García-Monteiro et al. (2022)) and a functional
177 response between 0 and 1.

178 Each simulation was run for a maximum duration equivalent to four times
179 the mean PLD (PLD_{mean}) of each species, as derived from a compilation of
180 observed early-life traits (Table 3, Di Stefano et al. (2024)). The time inter-
181 val from the start of simulations to birth and metamorphosis was recorded
182 based on the transitions between each development stage, as outlined in
183 the Subsection 2.1. Mortality was estimated using a *duration of develop-*
184 *ment* (PLD_{simu} , duration from spawning to metamorphosis) criterion: par-
185 ticles that did not reach birth or metamorphosis, as well as larvae for which
186 $PLD_{simu} > PLD_{mean} + 2std$ (standard-deviation), were considered dead.

Table 3: PLD and spawning periods from various sources, for the three species. PLD_{mean} and spawning months from Di Stefano et al. (2024). PLD literature from ¹ Micale et al. (2006), ² Macpherson and Raventos (2006), ³ Di Franco and Guidetti (2011), ⁴ Ducos et al. (2022), and ⁵ Millot et al. (2023).

Species	PLD literature (days)	PLD mean (days)	Spawning period
<i>P. erythrinus</i>	28-30 ¹	58	June-July
	43.9 ²		
<i>D. sargus</i>	27.6 ²	21	January-April
	21.95 ³		
<i>S. umbra</i>	25 ⁴	36	May-June
	35 ⁵		

187 *2.2.2. Growth and mortality under varying environment*

188 *Model setup.* Second simulations were done by integrating the DEB model
 189 with temperatures and the functional response associated with the food den-
 190 sity estimates obtained from the Lagrangian transport model (Subsection 2.2)
 191 in the Mediterranean sea (Figure 2), considering monthly spawning events.

192 Spawning events were modeled as the fortnightly particle releases on the
 193 1st and 15th of the month, with total number of particles for a monthly event
 194 being the sum of particles released on these two dates.

195 Firstly, to begin simulations of ELS trajectories, the half-saturation pa-
 196 rameter K_X is species-specific and depends on local conditions, thus, it has
 197 to be fitted using temperature and food. To achieve this, DEB simulations
 198 were conducted using a range of K_X values. Each simulation started at the
 199 spawning month with the highest number of observed occurrences (Table 3)
 200 for each species in the western Mediterranean (Di Stefano et al., 2024).

201 For each simulation (i initial positions, j the different K_X values), the

202 resulting $PLD_{simu;i,j}$ for each simulation was compared to the species-specific
 203 PLD_{mean} . The mean quadratic error, the so-called Standard-Error (SE) of
 204 all $PLD_{simu;i,j}$ was calculated across all simulations for each K_X value as :

$$SE_{i,j} = \frac{1}{N} \sum |PLD_{simu;i,j} - PLD_{mean}|^2 \quad (4)$$

205 Subsequently, the optimal K_X value was selected based on the lowest
 206 mean quadratic (\hat{SE}_j), and it was used for the following simulations. The
 207 values are for *P. erythrinus* $K_X = 4e-07$, for *D. sargus* $K_X = 2e-06$, and for
 208 *S. umbra* $K_X = 2e-06$.

209 *PLD and mortality.* From the simulated trajectories, time at birth and at
 210 metamorphosis, PLD_{simu} and the final position at time PLD_{simu} were recorded.
 211 Mortality was estimated based on three criteria (Fig. 2). The first *develop-*
 212 *ment* criterion considers $PLD_{simu} > PLD_{mean} + 2std$ as a limit for the
 213 ELS growth duration. The second *dispersal* criterion takes into account the
 214 bathymetry of the particle's final position at time PLD_{simu} , with lethal set-
 215 tlement happening offshore the 100 m isobath. Lastly, the third *starvation*
 216 criterion considers the feeding condition of larvae. Organisms that experi-
 217 enced extended periods without enough food may undergo starvation, which
 218 we considered as lethal. In the case of the larval DEB model, this occurs when
 219 energy mobilized from reserves is not sufficient to pay for somatic mainte-
 220 nance costs ($\kappa p_C < [p_M]V$) leading to structure break down, to pay for the
 221 remaining costs which leads to larval shrinking (Augustine et al., 2011).

222 Total mortality is estimated as the ratio of final dead particles to the
 223 initial number of particles for each month and expressed as a percentage.
 224 First, mortality is estimated independently based on the three criteria: *de-*

225 *velopment* mortality, *dispersal* mortality and *starvation* mortality. The total
226 mortality is then calculated as the intersection of the fulfilled criteria.

227 Based on the exponential mortality model (Mendiola et al., 2006), daily
228 mortality rates (z , expressed in day^{-1}) were estimated for each month of
229 spawning and then the annual daily mortality rate was calculated as the
230 average of the whole period.

$$z = \ln(N_0/N_t)/t \quad (5)$$

231 with N_0 initial number of particles, N_t final number of particles and t , num-
232 ber of days for each month.

233

234 To evaluate the environmental conditions that embryos and larvae ex-
235 perience, we analyzed the food density and temperatures encountered by
236 each living particle throughout their trajectory from the time of spawning
237 until PLD_{simu} . Additionally, to better understand the cause of success or
238 failure of recruitment, we compared the PLD_{simu} between living and dead
239 particles (those who underwent metamorphosis outside of the coastal area),
240 and examined the food and temperatures encountered by dead particles.

241 2.3. Spawning duration

242 In consideration of the diverse spawning behaviors reported in the lit-
243 erature for Mediterranean fish and the effect this can have in ELS growth
244 and survival (James et al., 2003; Tsikliras et al., 2010; Peck and Hufnagl,
245 2012), one-peak spawning lasting 2, 4 and 8 consecutive months in 2005 were
246 analyzed. The total initial particles of each spawning duration corresponds
247 to the total number sum of all initial particles for the given months (e.g.

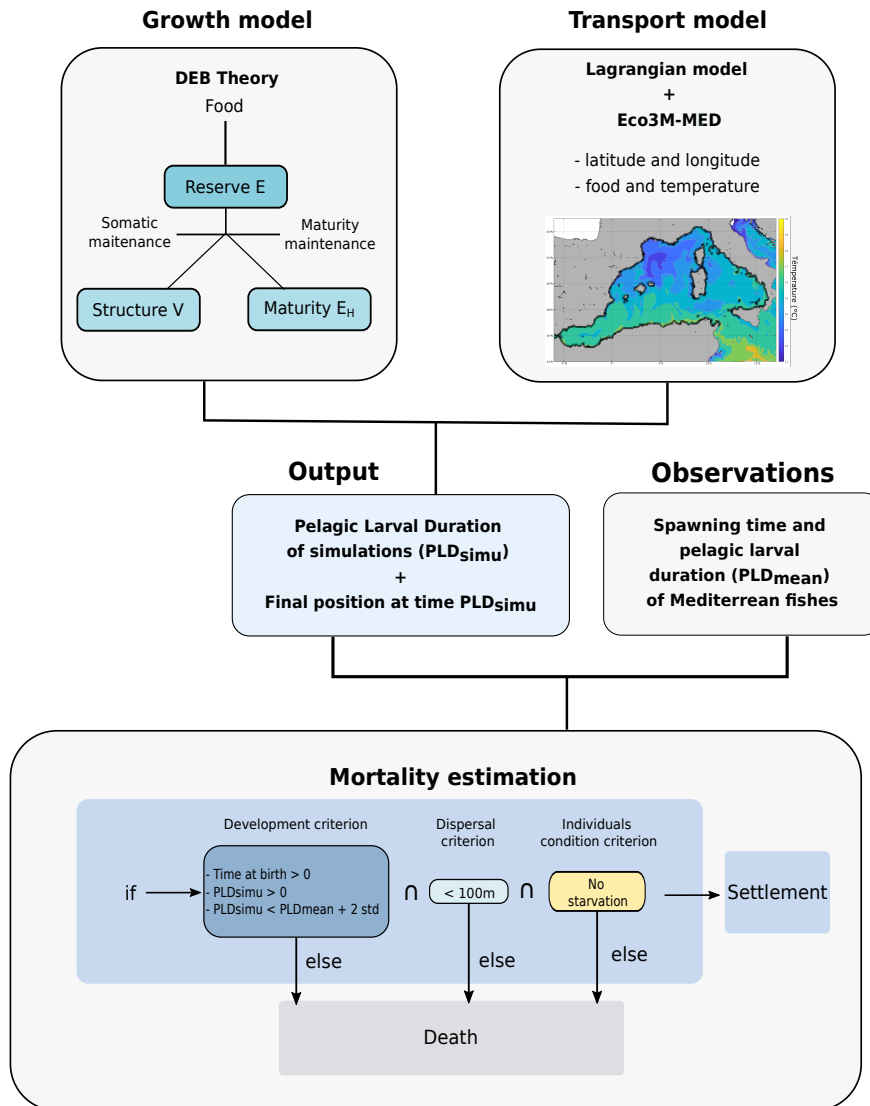


Figure 2: Integration of the physiological growth model (from the DEB theory) with the Lagrangian model, coupled to larval and adult observations (Di Stefano et al., 2024), in order to estimate PLD_{simu} and fish ELS mortality.

248 885 particles every 15 days, 1770 for each month. Totaling 3540 particles for
249 the 2-month duration configuration). Subsequently, total mortality percent-
250 ages were estimated for each duration based on the intersection of the three
251 criteria, along with the associated standard deviation and the average daily
252 mortality rate.

253 3. Results

254 3.1. Simulations with constant environmental conditions

255 For all three species in constant conditions, simulations showed an in-
256 crease of PLD_{simu} when temperatures or food density decreased, indicating
257 a slower development (Figure 3). Lower temperatures and insufficient food
258 density resulted in larvae not reaching metamorphosis before the prescribed
259 end of the simulation (4 times PLD_{mean}). In other words, it leads to infinite
260 PLDs that increase total mortality due to development duration being slower
261 than those allowing ELS survival and subsequent metamorphosis. Further-
262 more, estimated PLD_{simu} under the same temperature and functional re-
263 sponse varied across species. *Diplodus sargus* exhibited a faster development
264 with PLD_{simu} ranging from 6 to 83 days, while *Pagellus erythrinus* had a
265 broader range from 49 to 231 days. Such differences are linked to parameter
266 values (Table 2), as *P. erythrinus* invests more energy to attain metamor-
267 phosis than *D. sargus* and *S. umbra*.

268 Additionally, the models reproduced reasonably well the PLD_{mean} of the
269 three species and the few observed PLDs taken from the literature (Table 3,
270 Fig. 3) that overall fall within the range of the simulated values. *P. ery-*
271 *thrinus* has a mean duration of 58.25 days, which is represented in an area

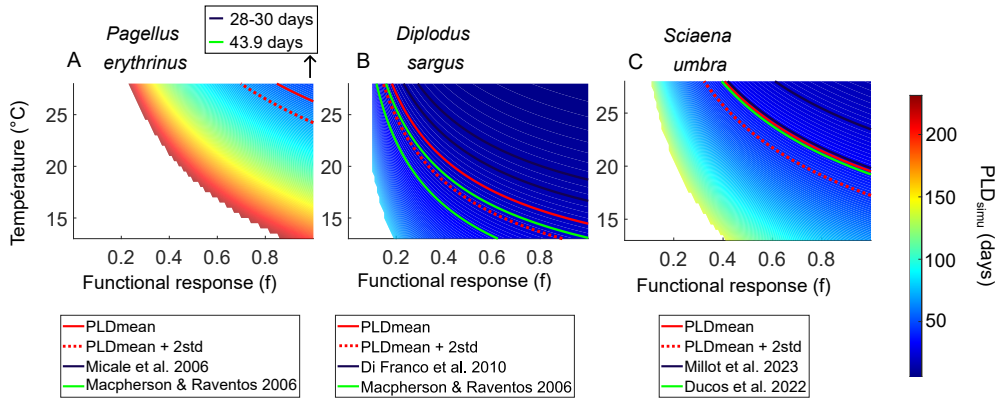


Figure 3: PLD_{simu} under constant conditions for a range of temperatures (13-28°C) and functional response ($f = 0 - 1$). Red continuous line represents the PLD_{mean} , the red dotted line represents the development criterion of mortality ($PLD_{mean} + 2std$) and in dark blue and green are the conditions associated with the PLD reported in different studies. White area represents conditions where larvae did not reach metamorphosis. Note that for *Pagellus erythrinus*, the few PLDs reported in the literature were shorter than the simulated ones.

272 characterized by high temperatures and a high level of functional response.
 273 In contrast, *D. sargus* displayed a mean duration of 21.13 days, represented
 274 for a broader range of temperatures and levels of functional response. When
 275 considering the *development* criterion in constant conditions, we observe a
 276 similar pattern of variability across species. *P. erythrinus*, a species with
 277 a long development, exhibited a limited range of viable conditions, charac-
 278 terized by a high level of functional response between $\sim 0.65-1$ and elevated
 279 temperatures ranging from 25-28 °C. In contrast, *D. sargus* demonstrated a
 280 broader range of viable conditions with values of functional response ranging
 281 from ~ 0.25 to 1 and across all temperatures tested. At an intermediary point,
 282 our models showed that *S. umbra* individuals survive over an intermediate

283 range of conditions.

284 3.2. PLD and ELS mortality estimates by coupled models

285 Using simulations with varying food density and temperature dynamics in
286 the western Mediterranean PLDs (Fig. 4) and total mortality (Fig. 5) were
287 obtained for one-peak spawning behavior every month of 2005. PLD_{simu}
288 estimates for the three species for living particles (Fig. 4) showed a winter
289 maximum, a decrease in late winter/early spring and an increase in the fall,
290 with the shortest PLDs simulated in late spring-early summer. When com-
291 paring the average PLD (Fig. 4) with the values obtained from the literature
292 (Table 3), we observe that the average estimated PLD aligns with the aver-
293 age from those reported in previous studies. However, there are differences
294 among studies (e.g. for *Sciaena umbra*, 10 days between studies).

295 Associated with these seasonal variations of PLDs, mortality estimates
296 based on the *development* criterion showed similar seasonal cycles with the
297 lowest mortality modeled in late spring / early summer (Fig. 5). Conversely,
298 mortality associated with ELS dispersal showed the opposite pattern, reach-
299 ing their maximum during summer but with a less marked seasonality. Mor-
300 tality caused by a long period of starvation did not occur here. Finally, total
301 mortality percentages for all species displayed a bi-modal pattern, reaching
302 its minimum ($\simeq 35-60\%$) during the late spring-early summer periods, and
303 larger values ($\simeq 40-100\%$) during the rest of the year.

304 When comparing mortality between species, slow development species
305 such as *P. erythrinus* presented higher total mortality and daily mortality
306 rates (50-100%; Fig. 5A and 0.057 d^{-1} ; Table 4) in comparison to fast de-
307 velopment species such as *S. umbra* whose total and daily mortality rates

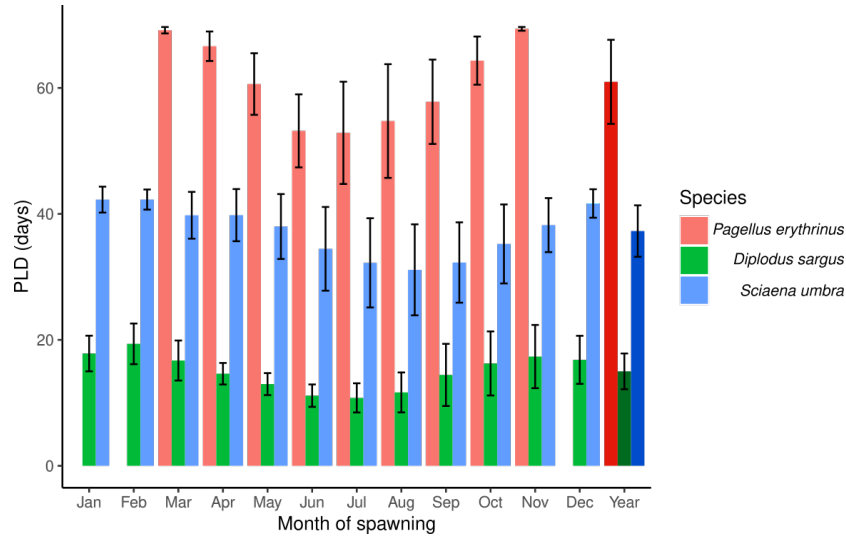


Figure 4: Average PLD estimate of alive ELS particles for *P. erythrinus* (A) in red, *D. sargus* (B) in green and *S. umbra* (C) in blue for each month of 2005, black error bars represent the associated standard deviations. Bars on the right represent the annual mean of all PLDs.

308 are lower (Fig. 5C), or *D. sargus* with the lowest total mortality across the
 309 months and the lowest daily mortality rate (60% maximum; Fig. 5B) and
 310 0.017 d^{-1}). Furthermore, as mentioned in Section 3.1, *D. sargus* survived
 311 under more variable conditions than *S. umbra* and *P. erythrinus*. The lat-
 312 ter, for example at low food and high temperature (Fig. 3), presented a
 313 decreasing PLD_{simu} insufficient to survive in comparison to *D. sargus*.

314 Additionally, by taking into consideration the *development criterion*, statis-
 315 tics of temperature, food density and PLD_{simu} associated to alive and dead
 316 larvae were evaluated (Fig. 6). This analysis suggested that between April
 317 and September, temperatures encountered by larvae were elevated (around
 318 $20\text{-}25^\circ\text{C}$) and PLD_{simu} decreased for the three species, while being associated

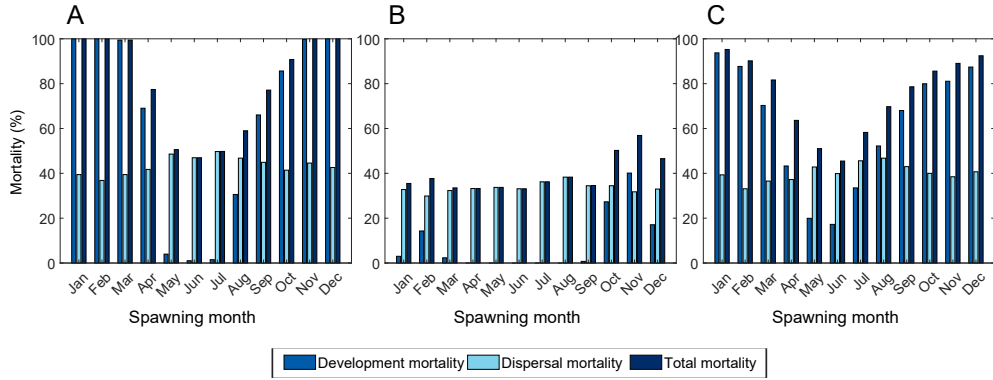


Figure 5: ELS mortality percentage estimates for *P. erythrinus* (A), *D. sargus* (B) and *S. umbra* (C) for monthly spawning events (considering simulations initialized on the 1st and 15th of each month) over 2005. Note the partitioning of the different mortality sources: dispersion mortality (light blue), development mortality (blue), which have been estimated independently, and the total mortality (dark blue) considering the intersection of both criterions.

319 with the lowest total mortality (Fig. 5). In fall and winter, PLDs lengthen in
 320 concert with cooling temperatures. Remarkably, the months when seawater
 321 temperatures spanned 10-18°C coincides with highest mortality for the three
 322 species, with some species having less tolerance to low temperatures. None
 323 of the larvae of *P. erythrinus* survived during January-February (Fig. 6A)
 324 with a mean temperature of $\sim 14^{\circ}\text{C}$, in contrast with *D. sargus*, with 40% of

Table 4: Mean daily mortality rate (z_{my}) for the three species and the associated standard deviation (n=12 months).

Species	z_{my} (d^{-1})	std
<i>Pagellus erythrinus</i>	0.057	0.076
<i>Diplodus sargus</i>	0.017	0.005
<i>Sciaena umbra</i>	0.054	0.026

325 larvae not surviving when experiencing temperatures between 11-13°C. Con-
326 cerning food availability, a weaker seasonal cycle was simulated but there
327 was no obvious relationship nor concomitant evolutions with our prognostic
328 variables (PLD or mortality). It is probably related to the fact that food is
329 not a limiting factor here, as indicated in the previous section.

330 3.3. Effect of spawning behavior

331 When exploring different spawning duration, the total mortality percent-
332 ages and daily mortality rate patterns illustrated in Fig. 7 are similar to
333 those represented in Fig. 5. There is a decrease in total mortality percentage
334 throughout the year, with minimum mortality in late-spring early-summer,
335 and an increase in mortality in fall and winter. Moreover, as the spawning
336 duration extends, the variability in mortality diminishes, resulting in less
337 variable total mortality. Regarding differences among species, *Pagellus ery-*
338 *thrinus* and *Sciaena umbra* exhibited total, mean and daily mortality rates
339 higher and more variable than that of *Diplodus sargus*, across all considered
340 spawning durations. When comparing total mortality percentages with cur-
341 rent knowledge on species' spawning periods (Table 3), the tested months
342 and duration configurations indicate a potential successful dispersal.

343 4. Discussion

344 4.1. Estimating mortality

345 The offline coupling of a biophysical model of environmental conditions
346 into a growth species-specific model allows us to explore the effect of different
347 conditions on larval mortality considering individual trajectories. Larvae

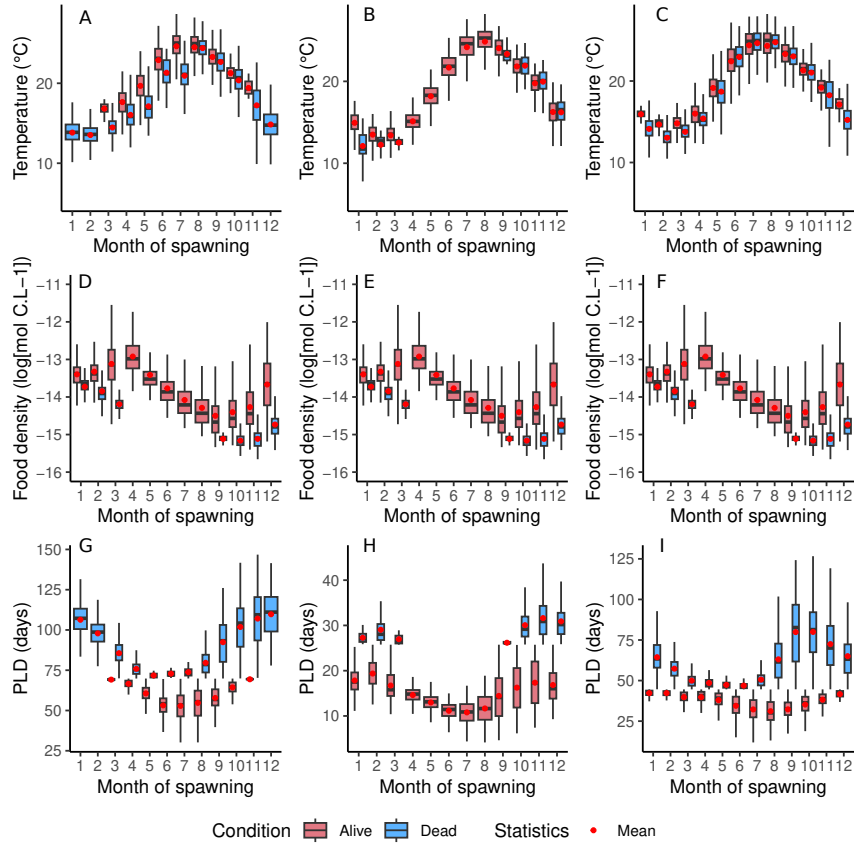


Figure 6: Environmental conditions and PLD of *P. erythrinus* (A, D, G), *D. sargus* (B, E, H) and *S. umbra* (C, F, I) of alive and dead larvae for monthly spawning events (considering simulations of the 1st and 15th of each month) over 2005. First row: temperature ($^{\circ}\text{C}$); second row: food density (mol.C.L^{-1}); third row: PLD_{simu} (days). Boxplot range represents the 25th and 75th percentile and the median is represented by a horizontal bar; the red dot represents the mean value.

348 experiencing increasing temperatures associated with late-spring and early
 349 summer spawning months had a faster development and lower mortality in
 350 comparison to low-temperature spawning periods (Fig. 6 and Fig. 7). Our

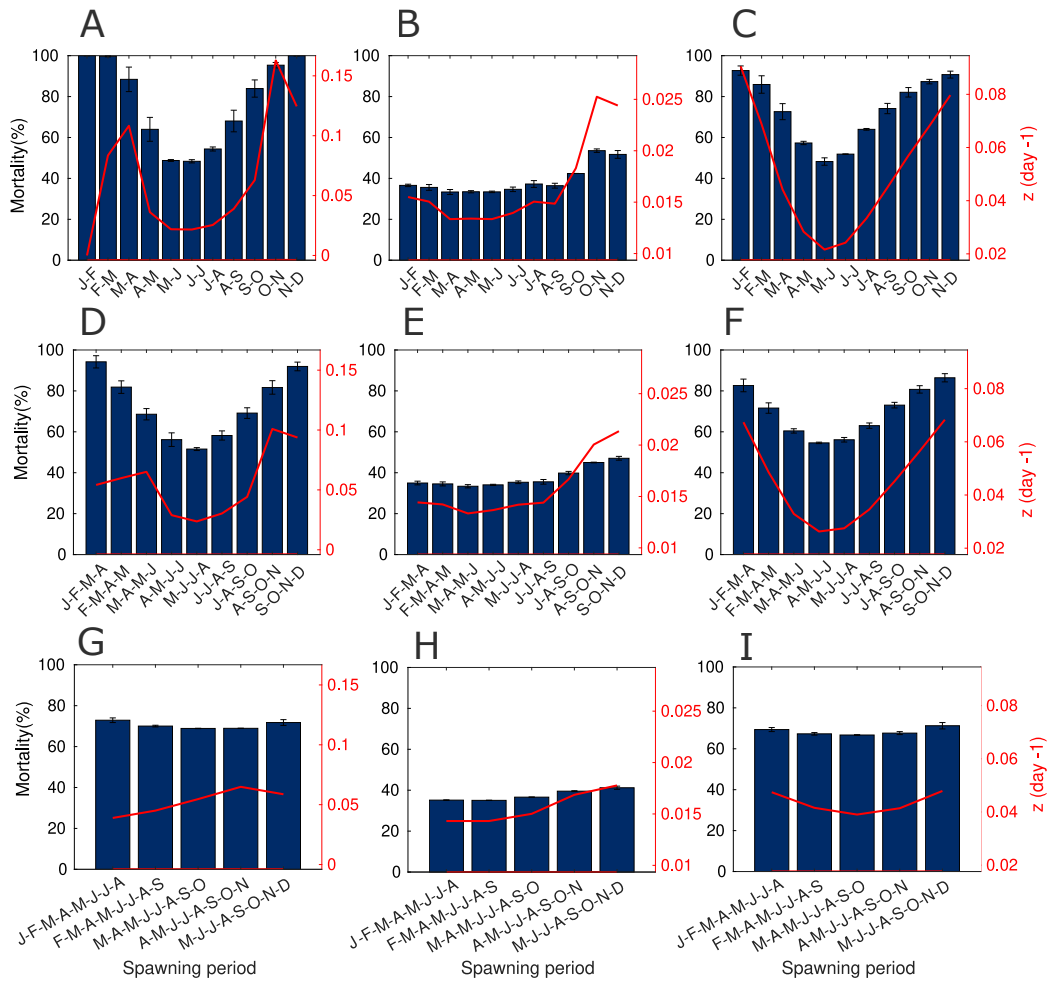


Figure 7: Early-life stages total mortality percentages (%) for *Pagellus erythrinus* (A, D, G), *Diplodus sargus* (B, E, H) and *Sciaena umbra* (C, F, I) for spawning durations of 2 (first row), 4 (second row) and 8 (third row) months and the associated daily mortality rate (red line, in d^{-1}).

351 simulated PLDs show that the mean PLD_{simu} (Fig 4) decreases for each
 352 species as temperature increases throughout the year from 13-28°C (Fig. 6).
 353 This is consistent with a reduction of the PLD when water temperature
 354 increases (Raventos et al., 2021), leading to a higher recruitment percentage

355 and a lower mortality (Lett et al., 2010). Specifically, Raventos et al. (2021)
356 reported a decline of 20-25% of the measured PLD of Mediterranean species
357 when simulating increasing temperatures from 14 to 28°C.

358 Food availability is also a source of mortality; however this condition was
359 never met as the reserve quantity to cover maintenance cost was always suf-
360 ficient. Nonetheless, fluctuations of food density, particularly during periods
361 of low food availability, may have caused growth limitations, increasing time
362 to metamorphosis and thus contributing indirectly to total mortality. Previ-
363 ous modeling studies using DEB-Ichthyop have shown sensitivity of Peruvian
364 anchovy growth to temporal food density variations thus showing that food
365 may not be the cause of mortality but a limiting factor when considering
366 temporal variation (Flores-Valiente et al., 2023). However, special attention
367 has to be taken as food assimilation is highly dependent on the parameters
368 K_X , here estimated as a function of the most recurrent spawning month for
369 each species. Re-evaluating this parameter thus have an effect on mortality
370 estimation due to starvation conditions or change in PLD_{simu} , as species
371 with higher K_X take longer to reach metamorphosis.

372 The *dispersal criterion* results in mortality estimates that were lower in
373 winter when species develop slowly and higher in spring-summer when tem-
374 peratures and food density results in a fast development. This may indicate
375 complex interactions between the seasonal variability of temperature, food
376 availability and of the oceanic circulation (Pinardi and Masetti, 2000), with
377 larvae spawned in summer having greater probabilities to be exported outside
378 of the coastal area. Indeed, the Northern Current in the Mediterranean sea
379 is stronger in winter than summer, limiting the cross shelf transport (Birol

380 et al., 2010; Bourg et al., 2024) and this generalizes to other coastal currents.
381 These results are in accordance with the *fast growth-high survival* hypothesis
382 stating that faster growing species experience less mortality as they spend
383 less time in the water column exposed to predation, harsh environment or
384 unfavorable advection (Houde, Edward, 1987; Houde, 1997; Robert et al.,
385 2023).

386 Mortality of planktonic organisms is currently estimated based on size
387 dependent models and catch-curve estimations established on length or age
388 with daily mortality rates varying between $z \simeq 1 d^{-1}$ and $0.01 d^{-1}$ (Peterson
389 and Wroblewski, 1984; Pepin, 1991; Houde, 1997; Pepin, 2016). Previous
390 studies have coupled a DEB model with Ichthyop trajectories, estimating
391 larval recruitment with different physical and biological processes, using a
392 constant mortality rate (Flores-Valiente et al., 2023). In our study, the use
393 of a coupled model allows us to simultaneously account for individual, spa-
394 tial, and temporal variability driven by intertwined biological and physical
395 factors and to separately quantify mortality percentages based on these com-
396 ponents. Following these methods, our estimated z ranged between 0.02 for
397 faster development species such as *D. sargus* and 0.06 for slow development
398 species such as *P. erythrinus*. These estimates are within the lower range
399 of previously published values (Peterson and Wroblewski, 1984; Pepin, 1991;
400 Houde, 1997; Pepin, 2016); for instance, it is an order of magnitude below
401 those reported for other species using advection models and common mor-
402 tality estimation methods (White et al., 2014).

403 4.2. Model implementation evaluation

404 Using parameters values available in the AddmyPet (AmP) database for
405 simulations of embryo and larval growth under constant conditions allowed
406 the simulation of realistic ranges of PLDs for three Mediterranean fish species.
407 The discrepancies between PLD_{mean} and PLD_{simu} may result from differ-
408 ences in approaches and data used. AmP parameters used to simulate growth
409 and to estimate PLD_{simu} were derived from various sources, including meso-
410 cosm experiments for *P. erythrinus* and *S. umbra* and data of adult otoliths
411 collected in the wild for *D. sargus* (Gordoa and Molí, 1997; Lika et al., 2014).
412 In mesocosm studies, ELS are reared under controlled conditions to optimize
413 larval growth, often resulting in faster development than in wild populations
414 (Papandroulakis et al., 2014), hence suggesting larger errors for PLD_{simu} of
415 *P. erythrinus* and *S. umbra*, than for *D. sargus*. Moreover, PLD_{mean} for
416 all three species was mainly estimated from in-situ observations (Di Stefano
417 et al., 2024), which implies PLD estimations closer to what one would expect
418 in the wild. In practice, both PLD estimates have distinct sources of error
419 that are difficult to evaluate and integrate in a coupled model.

420 The simulated PLD and mortality results from the species-specific pa-
421 rameters. Differences in PLD_{simu} , are linked to peculiar parameters' values
422 in Table 2 (Kooijman, 2009). Indeed, *P. erythrinus* invests more energy to
423 attain metamorphosis than *D. sargus* and *S. umbra*. Moreover, the different
424 mortality percentages for *Diplodus sargus* are the results from high assimila-
425 tion rates and small acceleration factor, resulting in rapid development and
426 low mortality with little variations of mortality among spawning behaviors.
427 In comparison, *Sciaena umbra* was distinguished as an intermediate species

428 with slower development and a metabolic acceleration parameter comparable
429 to fast-growing species such as *D. sargus*. However, it has a lower maximum
430 assimilation rate, meaning that the assimilation of food takes longer, which
431 lengthens PLDs and results in higher total mortality than *D. sargus*.

432 The estimation of ELS mortality was based on three criteria and existing
433 knowledge of fish ELS growth (Fig. 2). The *development* criterion was set
434 as $PLD_{mean} + 2std$ due to proven intra-specific variability of the PLD in
435 other species, exhibiting variations across spatial and temporal scales (Bay
436 et al., 2006; Di Franco and Guidetti, 2011). To account for this variabil-
437 ity, we considered the upper limit of variation, representing the maximum
438 time larvae can delay metamorphosis under varying environmental conditions
439 (Searcy and Sponaugle, 2000). However, the mean and standard deviation
440 values used here were derived from a compilation of observed PLDs col-
441 lected in various areas of the western Mediterranean Sea (Di Stefano et al.,
442 2024) that may not represent well the full range of plasticity expected from
443 dispersal traits in such variable marine environments. Thus, dividing the
444 Mediterranean in different areas according to spawning and settlement be-
445 havior (Di Stefano et al., 2022), as well as oceanographical regions (Ayata
446 et al., 2018), and using the PLD according to these zones may result in more
447 realistic mortality estimates. For instance, theoretical expectations are to
448 model higher mortality in oligotrophic regions due to low food availability
449 potentially leading to starvation, and lower mortality in zones characterized
450 by more favorable environmental conditions.

451 As for the *starvation* criterion that does not appear significant in this
452 study, it may be due to the estimation of K_X , that depends on the food out-

453 put. Indeed, significant uncertainties remain regarding the total zooplankton
454 from the Eco3M-MED model, which is used as a proxy of food density. First,
455 due to the model spatial resolution (~ 8 km), modeled food is not as variable
456 as in reality. Second, it is possible that the model overestimates the amount
457 of food available for ELS growth and development (Guyennon et al., 2015;
458 Pagès et al., 2020). To illustrate this, future simulations with different food
459 availability scenarios in the Mediterranean may be of interest.

460 Regarding the *dispersal* criterion, we considered the bathymetry at po-
461 sition PLD_{simu} . As larvae may decrease swimming capacities before meta-
462 morphosis (Ducos et al., 2022), and given that the three studied species are
463 demersal, we assumed that larvae would not have the swimming capabili-
464 ties to return to the settlement site if the metamorphosis occurs at depths
465 exceeding 100 m (Rochette et al., 2012). Even so, using maximum larvae
466 bathymetry and settlement species-specific sites could improve the reliability
467 of modeled mortality estimates.

468 Finally, using the coupled growth biophysical model has allowed us to test
469 different spawning strategies and explore their impacts on dispersal success.
470 Our findings provide insights on how various spawning strategies, along with
471 species-specific characteristics, can result in contrasted mortality estimates
472 and daily mortality rates, exemplifying the classical match-mismatch hypoth-
473 esis (Peck et al., 2012). Our simulations also suggest that spawning periods
474 differing from those commonly reported for Mediterranean species (typically
475 late spring-early summer)(Tsikliras et al., 2010; Mouine et al., 2012) may be
476 more viable than previously thought.

477 *4.3. Models' limitations and future improvements*

478 Observations were used here to validate the main models' outputs, namely
479 our simulated PLDs (see also Fig. 3) and mortality estimates (see also Section
480 4.1). The large spreads exemplified in the range of values found in the liter-
481 ature suggest that both the mortality and typical durations of ELSs are still
482 not well constrained or understood. To narrow down these uncertainties, a
483 more thorough collection of datasets derived from different sources (e.g. lab-
484 oratory experiments, compilation of field and aquaculture data) should help
485 refine our knowledge of larval traits (Mounier et al., 2020). Additionally, the
486 quantity of initial energy E_0 provided by the mother at the time of spawning
487 was considered identical among particles, without considering the effect of
488 the individual reproductive outputs on offspring conditions (Maddams and
489 McCormick, 2012; Burton et al., 2013). This effect could be simulated based
490 on biotic or abiotic factors experienced by the mother as for example, eggs
491 that begin their dispersal with lower energy content may be more susceptible
492 to long periods of starvation, resulting in a decrease in PLD and therefore
493 an increase in mortality (Augustine et al., 2011). Similarly, the inclusion
494 of larval swimming capacities, which was not considered here, could improve
495 trajectory estimates, and thus change the abiotic conditions encountered dur-
496 ing dispersal (e.g. increasing the number of settled fish) (Berenshtein et al.,
497 2018; Faillettaz et al., 2018; Leis, 2020).

498 In this study, we considered mortality sources related to development
499 time, advection, and starvation. However, one mortality factor not accounted
500 for here is the effect of lethal temperatures. High temperatures can accelerate
501 ELS development time up to a certain limit, beyond which enzyme activity

502 becomes inhibited (Kooijman, 2009; Illing et al., 2020; Flores-Valiente et al.,
503 2023). Including an upper thermal limit based on the species-specific ther-
504 mal thresholds could improve estimates of PLDs and mortality. Additionally,
505 another important source of mortality for fish ELS is predation, which has
506 been neglected in this study. Such a term could be included in this type
507 of modeling by setting a function of mortality based on length (i.e. “bigger
508 is better”) and/or growth rate (i.e. “growth-dependent” mortality) of the
509 organism (Cowan, 1996). Alternatively, predator-prey fields could be evalu-
510 ated to study prey-predator interactions; however, these interactions remain
511 a challenge due to a mismatch in model resolutions (Peck and Hufnagl, 2012).

512 **5. Conclusions**

513 We modeled the Pelagic Larval Duration and mortality of Fish ELS using
514 a multidisciplinary approach thanks to the off-line coupling of two Individual-
515 Based Models simulating larval physiology and current-driven dispersal. The
516 spatially- and temporally-explicit forcing variables (e.g. seawater tempera-
517 ture, planktonic food and currents) were provided by an external state-of-the-
518 art coupled biogeochemical-hydrodynamical model. Focusing on three dem-
519 ersal coastal Mediterranean fishes, our study allowed us to estimate ELSs’
520 duration and mortality under constant conditions within the ranges reported
521 in the literature, while exemplifying significant differences among species re-
522 lated to physiological parameters. When considering the full variability of
523 conditions encountered during dispersal in a highly heterogeneous seascape,
524 we analyzed how simulated growth and mortality vary over a realistic sea-
525 sonal cycle while testing different spawning phenology. Counter-intuitive

526 results suggest that this framework is well adapted to investigate further the
527 classical “match-mismatch” hypothesis and the complex growth-survival re-
528 lationship (Robert et al., 2023). Finally, while just one exemplary year was
529 used here, such coupled models can be run over longer periods to decipher
530 the variability of ELS survival, and the processes behind it, at inter-annual
531 as well as climatic time-scales (Rose et al., 2024).

532 **6. CRediT authorship contribution statement**

533 **MJL:** Investigation, Conceptualization, Methodology, Visualization, Writ-
534 ing - Original Draft, Writing - Review & Editing. **LB:** Funding acquisition,
535 Supervision, Conceptualization, Writing - Review & Editing. **MDS:** Re-
536 sources, Writing - Review & Editing. **VR:** Funding acquisition, Supervision,
537 Conceptualization, Writing - Review & Editing.

538 **7. Declaration of Competing Interests**

539 The authors declare that they have no known competing financial inter-
540 ests or personal relationships that could have appeared to influence the work
541 reported in this paper.

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