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1 **Guidelines for larval dispersal simulations: flow field**  
2 **representation versus biological traits**

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10 • connectivity  
11 • larval behaviour  
12 • NW Mediterranean  
13 • *Paramuricea clavata*

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**Abstract**

The natural mechanism for sessile species resilience after major population disturbance is larval dispersal during reproduction. Modelling larval dispersal when processes controlling dispersal are accounted for, is a powerful tool to anticipate connectivity patterns among populations. However, simulations performance might be altered considerably by either flow representation in the underlying hydrodynamical simulations or the inclusion of larval traits. Here, we assessed how behaviour, ocean model resolution and temporal variability in the ocean dynamics influence connectivity patterns among coastal rocky locations, some of them being designated as MPAs. We combined a fine (0.3 km) and coarser (1.5 km) resolution ocean model, with or without the negatively buoyant behaviour of *Paramuricea clavata* larvae, with different turbulence intensity, in three years and for pelagic larval duration (PLD) ranging from 1 to 28 days. Ocean model resolution was the most influential factor on the resulting connectivity levels. The results were also equally influenced by buoyancy, PLD and temporal variability, in the fine resolution configuration, while turbulence could be neglected. Based on these results, guidelines for coastal biophysical modelling are proposed.

**1 Introduction**

Anticipating the impact of the on-going global change on the already altered ocean biodiversity is a major challenge for designing conservation measures in the next decade (ONU SGD 14, IPBES 2030 work program, <https://ipbes.net/o4-supporting-policy>). Among conservation measures, the Aichi Convention on Biological Diversity (CBD, 2010) defined the objective of reaching 10% of ocean surface designated as Marine Protected Areas (MPAs) by 2020. However, designating efficient MPAs requires incorporating knowledge and understanding of mechanisms regulating species spatial distribution such as dispersal (Urban et al., 2016).

The Mediterranean coastline is characterized by an alternance of Marine Protected Areas (MPAs) and non-protected areas (MedPAN, 2017). MPAs provide benefits to out-

41 side areas and in particular, many studies have shown the efficacy of MPAs on the con-  
42 servation of fishes through the spillover of juvenile and adult fishes (see Grüss et al. (2011)  
43 for a review). The effect of MPAs on the conservation of sessile species whose reproduc-  
44 tion implies a dispersive phase mediated by ocean circulation poses the question of an-  
45 ticipating population connectivity within a geographically fragmented network. To this  
46 end, larval dispersal numerical models incorporating knowledge and understanding of  
47 mechanisms regulating dispersal are essential tools (Lett et al., 2008; Paris et al., 2013).

48 Larval dispersal simulations first require hydrodynamical models to provide a re-  
49 liable and validated description of the flow and its variability at the spatio-temporal scales  
50 relevant for both dispersal processes at larval scale and regional connectivity estimates  
51 at population scale. Connectivity studies have used a variety of ocean circulation mod-  
52 els, from coarse-resolution global models (10 km, Treml et al. (2008); Wood et al. (2014))  
53 to high-resolution regional models (100 m to 1 km, Guizien et al. (2012, 2014); Briton  
54 et al. (2018)). Ocean circulation models have been validated against diagnostic variables  
55 such as sea surface temperature and salinity, heat content, sea level, mass transport, tur-  
56 bulent kinetic energy or vorticity (Fox-Kemper et al., 2019). However, such validation  
57 can be insufficient to ensure that simulated velocities used in the larval dispersal sim-  
58 ulations are representative of the advection and diffusion experienced by larvae in the  
59 flow (Pineda et al., 2007). When the flow field simulations are accurate, the specificity  
60 of larval dispersal simulations ultimately depends on the knowledge of biological traits  
61 such as location and timing of larval release in parental populations and larval traits im-  
62 portant for dispersal (Scheltema, 1986). Among these, pelagic larval duration (PLD, here-  
63 inafter) has been extensively tested in dispersal simulations (Siegel et al., 2003; Edwards  
64 et al., 2007; Guizien et al., 2012). Despite larval position in the water column likely al-  
65 ters dispersal patterns in three dimensional flows, two dimensional larval dispersal stud-  
66 ies are still frequent (Aguilar et al., 2019; Gamoyo et al., 2019; Hidalgo et al., 2019; Hock  
67 et al., 2019). When vertical larval position has been accounted for in simulations, it has  
68 been either prescribed (Donahue et al., 2015; Blanco et al., 2019; Criales et al., 2019)

69 or more recently it resulted from the interaction between a larval motility behaviour and  
70 the flow dynamics (Faillettaz et al., 2018; Kvile et al., 2018; Barbut et al., 2019; Munroe  
71 et al., 2018; Bode et al., 2019; Goodwin et al., 2019; McManus et al., 2020). In contrast,  
72 the sensitivity to release timing and larval release duration have been less studied (see  
73 Guizien et al. (2012)). Moreover, the relative importance of biological traits and flow field  
74 representation in altering dispersal patterns has not been frequently evaluated together  
75 (see Huret et al. (2007)).

76 In the present study, we chose the rocky and coralligenous habitat in the Ligurian  
77 sea as a case study for larval dispersal simulations sensitivity analysis. We estimated the  
78 sensitivity to different parameters of larval dispersal simulations. First we addressed the  
79 sensitivity to the choice of hydrodynamical model and in particular to its horizontal grid  
80 resolution. Second we addressed the temporal variability at different scales and finally,  
81 we addressed the parameters specific of larval dispersal simulations such as turbulence,  
82 larval behaviour, PLD and release timing, comparing an idealized neutrally buoyant species  
83 to *Paramuricea clavata* (Risso 1826). Eventually the sensitivities to the different param-  
84 eters were ranked by importance to suggest guidelines for larval dispersal simulations.

## 85 **2 Methods**

### 86 **2.1 Study background**

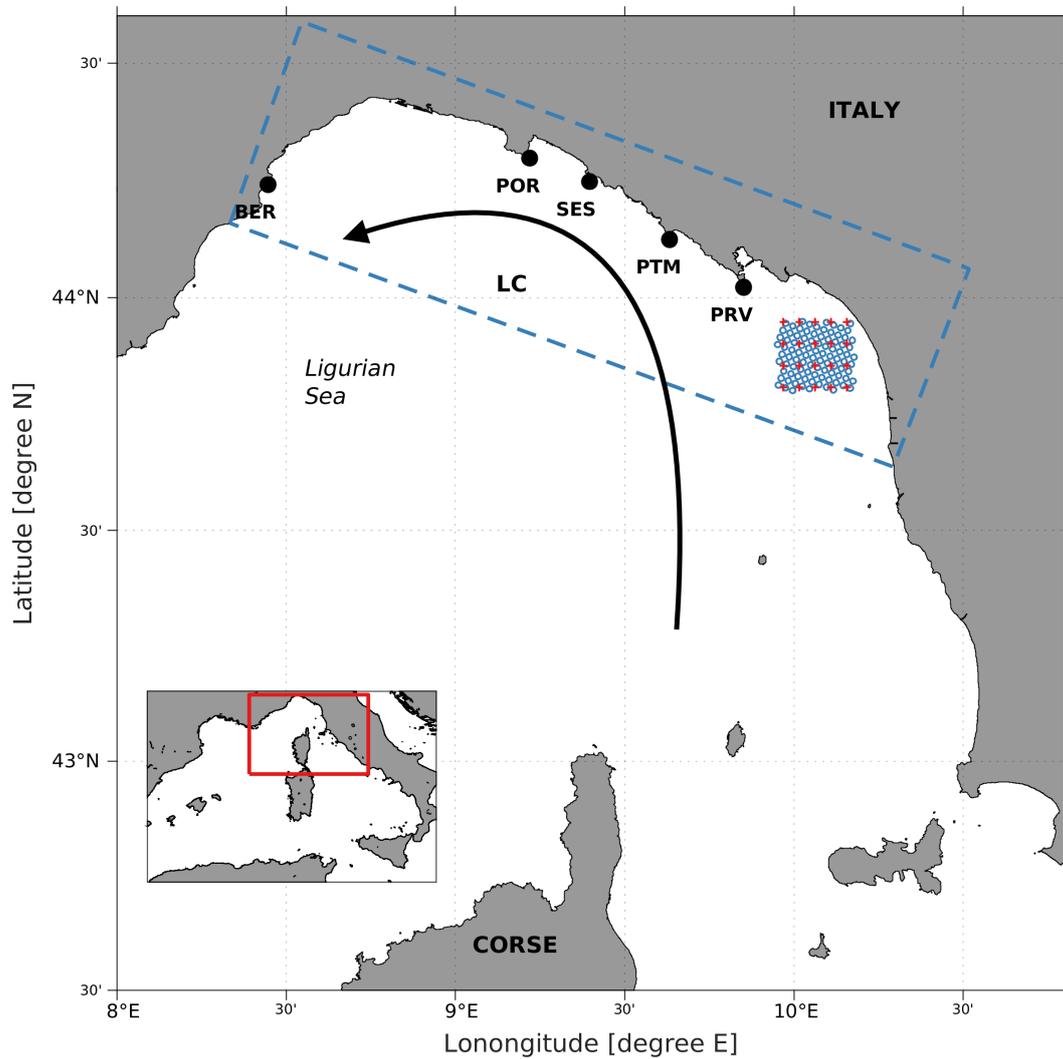
87 The Ligurian Sea extends between Italy and the north of Corsica in the Northwest-  
88 ern Mediterranean Sea (Astraldi & Gasparini, 1992). It is characterized by a mean cy-  
89 clonic circulation (Millot, 1999; Millot & Taupier-Letage, 2005) known as the Ligurian  
90 Current (LC) that flows west along the Italian coast toward France (Fig.1). Along the  
91 Ligurian coast, many MPAs have been established to foster the conservation of the rich  
92 biodiversity associated to coralligenous and rocky bottom habitats (Regional Natural  
93 Reserve of Bergeggi, Regional Natural Park of Portofino, Cinque Terre National Park,  
94 Regional Natural Park of Porto Venere, Fig.1). Coralligenous and rocky bottom habi-

95 tats are patchily distributed in the Ligurian sea (<http://srvcarto.regione.liguria>  
96 [.it/geoviewer2/pages/apps/geoportale/index.html?id=2121](http://srvcarto.regione.liguria.it/geoviewer2/pages/apps/geoportale/index.html?id=2121)).

97 In these MPAs, the conspicuous octocoral species *Paramuricea clavata* has been  
98 used as a flag species for the conservation of the Mediterranean coralligenous assem-  
99 blage (Carpine & GRASSHOFF, 1975), due to its role of ecosystem engineer (sensu, Jones  
100 et al. (1994)), and its patrimonial value linked to the beauty it gives to seascapes. *P. clavata*  
101 is one of the tallest sessile Mediterranean species with erected colonies as high as 1.3 m  
102 (Harmelin & Marinopoulos, 1994) and is found on hard substrate from 10 to 200 m wa-  
103 ter depth (Gori et al., 2017). During reproduction, *P. clavata* releases eggs that get fe-  
104 cundated and mature during a few days at the colony surface. Once the maternal mu-  
105 cus is dissolved lecithotrophic planula larvae are released in the ocean currents. Off the  
106 Catalan coast, larval release happens during short events of a few days separated by 15  
107 days (Coma et al., 1995; Gori et al., 2007) in late June/early July. No information on  
108 the exact timing and occurrence of *P. clavata* larval release in the Ligurian Sea are avail-  
109 able in the scientific literature but several observations by recreational divers report a  
110 similar phenomenon in the month of July.

## 111 2.2 Fine resolution hydrodynamical simulations

112 The dynamic of the Ligurian sea is simulated using the Ligurian Integrated Mod-  
113 elling Effort, gcm (LIMEgcm, hereinafter Fig.1 blue dashed rectangle). LIMEgcm is based  
114 on the the Massachusetts Institute of Technology general circulation model (MITgcm, Marshall  
115 et al. (1997)). The MITgcm solves the Boussinesq form of the NavierStokes equations  
116 either on a generalized curvilinear grid or an orthogonal grid. The finite-volume discretiza-  
117 tion is rendered on a horizontal Arakawa C-grid with vertical  $z$ -levels. In this configu-  
118 ration the equation of state is due to (Jackett & McDougall, 1995), whereas advection  
119 for tracers is computed via a third-order direct spacetime flux limited scheme with zero



**Figure 1.** The Ligurian Sea with the main circulation branch and the release locations used in larval dispersal simulations, black circles ( Supp. Inf. Tab. 1). Blue dashed rectangle shows the LIMEgcm domain, red rectangle the LIME-ROMS domain. Blue circles and red crosses indicate the numerical grids of LIMEgcm and LIME-ROMS, respectively. For visualization purposes the LIMEgcm mesh is plotted every 6 grid point while the LIME-ROMS mesh is plotted every three grid point.

120 explicit diffusivity. The K-profile parameterization (KPP, Large et al. (1994)) is used with  
 121 a background vertical viscosity of  $n_\nu=10^{-5} \text{ m}^2\text{s}^{-1}$ .

122 The numerical domain was discretized with an orthogonal horizontal grid of 560  
 123 x 160 points. The horizontal mesh had a resolution of 300 m (Fig.1 blue circles) while  
 124 the vertical was discretized with 100 levels. The vertical resolution increased linearly from  
 125 1m to 20m in the first 20 levels, was kept constant at 20m for the following 50 levels, and  
 126 finally increased to 25m for the 30 deepest layers. The bathymetry is interpolated from  
 127 the EMODNET 1/8 arcminute product (Consortium, 2016). Realistic surface forcings  
 128 came from the hourly, Weather Research and Forecasting (WRF) model setup by the  
 129 University of Genoa (Cassola et al., 2015), while 6-hourly open boundary conditions were  
 130 derived from LIME-ROMS model outputs (Sciascia et al., 2019). Model outputs were  
 131 saved every three hours.

### 132 **2.3 Coarse resolution hydrodynamical simulations**

133 The circulation of the Ligurian Sea was simulated using the Ligurian Integrated  
 134 Modelling Effort (LIME-ROMS, Sciascia et al. (2019)). LIME-ROMS was based on the  
 135 Rutgers University kernel of the Regional Ocean Modelling System (ROMS, Haidvogel  
 136 et al. (2000); Shchepetkin and McWilliams (2005)). The numerical domain was discretized  
 137 with an horizontal grid of 590 x 314 points. The mesh was unevenly spaced and the most  
 138 resolved area(Fig.1 red rectangle), which includes the area of the Ligurian-Northern Tyrrhe-  
 139 nian shelf, had a horizontal resolution of  $1/64^\circ \times 1/64^\circ$  ( $\sim 1.5 \text{ km}$ , Fig.1 red crosses).  
 140 The vertical dimension was discretized with 50 sigma layers. Realistic surface forcings  
 141 came from the 3-hourly,  $0.25^\circ$  horizontal resolution ERA-Interim reanalysis fields (Dee  
 142 et al., 2011) available at the <http://apps.ecmwf.int/datasets/data/interim-full>  
 143 `-daily` link, while the daily open boundary values were derived from the Mediterranean  
 144 Forecasting System (MFS) SYS4a3 product (Delrosso et al., 2016). Model outputs were

145 saved every six hours. The reader is referred to Sciascia et al. (2019) for a detailed de-  
146 scription and validation of the model.

## 147 **2.4 Larval dispersal simulations**

148 Dispersal simulations of virtual larvae were performed independently using the LIME-  
149 ROMS (hereinafter, coarse) and LIMEgcm (hereinafter, fine) resolutions flow fields sim-  
150 ulated as described above.

151 The offline Lagrangian Transport model (LTRANS, Schlag and North (2012)) was  
152 selected to compute particle advection in the coarse resolution hydrodynamical fields for  
153 its capability to cope with sigma layers. The offline Connectivity Modelling System (CMS,  
154 Paris et al. (2013)) was selected to compute particle advection in the fine resolution hy-  
155 drodynamical fields for its capability to cope with z layers. Both Lagrangian models com-  
156 pute 3D trajectories using a 4th order Runge-Kutta for both neutrally buoyant and ac-  
157 tive (e.g. sinking, swimming) particles, eventually including turbulent diffusion.

158 In both larval dispersal simulation set ups, particles were released in five locations  
159 where *P. clavata* has been reported (Bergeggi (BER), Portofino (POR), Sestri Levante  
160 (SES), Punta Mesco (PTM), Porto Venere (PRV), Fig. 1, Supp. Inf. Tab. 1, Padrón et  
161 al. (2018)). Each population was described by ten release points, separated by 100 m.  
162 Particles were released  $\sim 3$  km away from the coast line, which represented two grid points  
163 of the coarse resolution flow field in order to avoid any retention bias due to the numer-  
164 ical boundary layer of this simulation. Particles were released 4 m above the bottom in  
165 the coarse resolution simulations and 2 m above the bottom in the fine resolution sim-  
166 ulations (Supp. Inf., Tab. 1). Particles were released every hour from June 15 at mid-  
167 night until July 15 at 11pm and tracked during 28 days after release. Tacking time step  
168 was 120 s in the coarse resolution flow field and 600 s in the fine resolution flow field. *P.*  
169 *calvata* populations suffered two mass mortality events in 1999 and 2003 (Cerrano et al.,  
170 2000; Cupido et al., 2008) and get to sexual maturation after at least four years (Coma

171 et al., 1995). Hence the reproductive events that more likely contribute to the popula-  
 172 tions found now at sea took place from 2004 onward. For the aforementioned reasons,  
 173 larval dispersal simulations were performed during three successive reproductive years  
 174 in the fine resolution flow field forcing (2004, 2005 and 2006) but only in two reproduc-  
 175 tive years in the coarse resolution flow field forcing (2004 and 2006 only, 2005 being hy-  
 176 drodynamically very close to 2004). In order to explore the sensitivity of larval disper-  
 177 sal simulations to the flow field resolution, to larval behaviour and flow turbulence in-  
 178 tensity, various simulations were performed as summarized in Tab. 1.

179 The dispersal of neutrally buoyant particles was simulated using both the coarse  
 180 and fine resolution simulations. The dispersal of particles with a specific buoyancy was  
 181 carried out only with the fine resolution simulations in order to simulate the dispersal  
 182 of non-motile *P. clavata* larvae (Coma et al., 1995; Linares et al., 2008). Particle den-  
 183 sity was set to vary from 1.0282 to 1.0295, with an equivalent diameter of  $761 \cdot 10^{-6}$  m,  
 184 to achieve the sinking speed of  $0.056 \pm 0.021$  cm s<sup>-1</sup> at 20°C and a salinity of 38 psu  
 185 as measured experimentally (Guizien et al., 2020).

**Table 1.** Available larval dispersal simulations and their main parameters

	No Turbulence	Low Turbulence	High Turbulence
Neutrally Buoyant	2004 LIMEgcm	2004 LIMEgcm	2004 LIMEgcm
	2005 LIMEgcm	2005 LIMEgcm	2005 LIMEgcm
	2006 LIMEgcm	2006 LIMEgcm	2006 LIMEgcm
	2004 LIME-ROMS		
	2006 LIME-ROMS		
<i>P. clavata</i> buoyancy	2004 LIMEgcm	2004 LIMEgcm	2004 LIMEgcm
	2005 LIMEgcm	2005 LIMEgcm	2005 LIMEgcm
	2006 LIMEgcm	2006 LIMEgcm	2006 LIMEgcm

186 The effect of turbulence intensity on larval dispersal simulations was tested by re-  
 187 peating each simulation using the fine resolution flow field forcing without turbulence,  
 188 with low turbulent diffusivity ( $10^{-4} \text{ m}^2\text{s}^{-1}$ ) and high turbulent diffusivity ( $10^{-3}\text{m}^2\text{s}^{-1}$ )  
 189 (Tab. 1). Depending on whether turbulence was (was not) accounted for, twenty-five (one)  
 190 particles were released every hour during each larval release event summing up to a total  
 191 number of 180000 (7200) particles for each population. Similarly to what was done  
 192 in Guizien et al. (2006), the number of particles was increased by a factor twenty-five  
 193 to ensure the convergence of statistical properties when dispersion due to subgrid tur-  
 194 bulence is accounted for.

## 195 2.5 Larval connectivity estimates

196 Larval transport values between five locations in the Ligurian basin were calculated  
 197 as the proportion of particles released during a larval-release event from an origin loca-  
 198 tion that reached a destination location after a given dispersal duration (Pelagic Lar-  
 199 val Duration, PLD). Larval transport values were gathered to build connectivity matri-  
 200 ces, varying according to PLD, larval-release event, particle buoyancy (neutrally buoy-  
 201 ant and *P. clavata* buoyancy), turbulence level (high, low and no) and hydrodynamical  
 202 grid resolution (coarse and fine). Nine values of PLD were considered, starting from one  
 203 day, then 3.5 days up to 28 days with 3.5 days increments. The duration of each larval-  
 204 release event was set to three days, yielding a total of ten 3-day events spanning the 30  
 205 days long reproductive season of each year (2004-2006).

206 The intra-annual ( $VAR_{intra}$ ) and inter-annual ( $VAR_{inter}$ ) variance of any pair-  
 207 wise larval transport elements of the connectivity matrix  $T$  were computed as defined  
 208 in equations 1 and 2 for the coarse and fine resolution simulations and all PLDs.

$$VAR_{intra} = \frac{\sum_{y=1}^{N_y} \sum_{r=1}^{N_r} (T_r^y - \overline{T^y})^2}{N_r N_y} \quad (1)$$

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$$VAR_{inter} = \frac{\sum_{r=1}^{N_r} \sum_{y=1}^{N_y} (T_r^y - \overline{T_r})^2}{N_r N_y} \quad (2)$$

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where  $N_y$  is the number of years,  $N_r$  is the number of release events per year and  $\overline{T^y} = \sum_{r=1}^{N_r} T_r^y / N_r$  is the average connectivity across all release events of year  $y$  and  $\overline{T_r} = \sum_{y=1}^{N_y} T_r^y / N_y$  is the average connectivity across all years for the release event  $r$  in the year. Ratios  $\frac{VAR_{intra}}{VAR_{inter}}$  were computed for each pairwise connection among the five locations and summarized into boxplots for the five locations network.

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For all the PLDs, the effect of turbulence levels (high/low/no), particle buoyancy (neutrally buoyant/ *P. clavata* buoyancy) and the hydrodynamical grid resolution (coarse/fine) on larval transport estimates between any pairwise connection of the five locations network were computed as larval transport deviations from a same reference simulation set for each larval-release events and years. For each pairwise connection among the five populations, the deviations across larval-release events and years was described by its median, avoiding any normality assumption, to compare the effect of turbulence level, particle buoyancy and hydrodynamical grid resolution. The fine resolution neutrally buoyant simulations without turbulence for the years 2004-2006 was considered as the reference simulation set for all comparisons. All calculations and statistics were conducted in Matlab (R2018).

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### 3 Results

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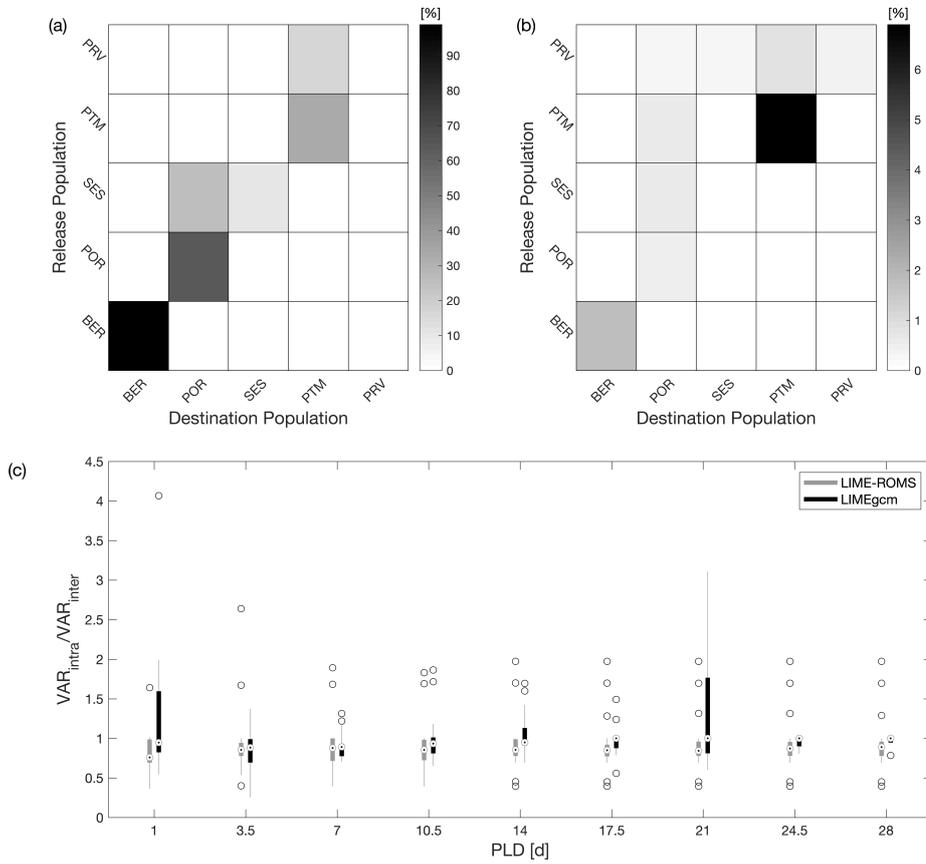
233

In the following, the effect of flow resolution, larval buoyancy and turbulence level on connectivity patterns will be presented for a PLD of 3.5 days as an example. In both fine and coarse resolution hydrodynamical simulations, the median larval transport among the five populations showed a northwestern drift (upper diagonal elements larger than lower diagonal ones) with larval export (off-diagonal elements) from PRV and SES dominating over local retention (diagonal elements) while retention rates dominated over any other connections in BER, POR and PTM (Fig. 2 a,b). However, apart this similarity,

234 the two sets of simulations differed largely. Firstly, larval retention values were ten times  
 235 larger in the coarse resolution simulations (max  $\sim 95\%$ ) than in the fine resolution sim-  
 236 ulations (max  $\sim 7\%$ ). Secondly, largest retention values were found in different loca-  
 237 tions (BER and POR in the coarse resolution and PTM in the fine resolution; Fig. 2 a,b).  
 238 Thirdly, more connections between populations appeared in the fine resolution simula-  
 239 tions compared to the coarse resolution simulations. Differences in the intensity of coastal  
 240 currents in the coarse and fine resolution hydrodynamical models support the differences  
 241 in larval transport estimates. Coastal currents were weaker in the coarse resolution hy-  
 242 drodynamical simulation compared to the fine resolution one (Supp. Inf. Fig. 1). Inter-  
 243 estingly, observations available in the area for the period May-June 2004 better agreed  
 244 with the order of magnitude of the fine resolution simulation than that of the coarse res-  
 245 olution one (Supp. Inf. Fig. 2).

246 Intra-annual variability (between different larval release events within the same year,  
 247  $VAR_{intra}$ ) and inter-annual variability (between the same larval release event in differ-  
 248 ent years,  $VAR_{inter}$ ) were the same order of magnitude, whatever the PLD and hydro-  
 249 dynamical resolution (5% maximum in the fine resolution and 30% maximum in the coarse  
 250 resolution, Supporting Information Fig. 3). The median of the intra-annual to inter-annual  
 251 ratio across all PLD was 0.93 for the fine resolution and 0.85 for the coarse resolution,  
 252 in the neutrally buoyant case without turbulence, considering years the 2004 and 2006  
 253 only (Fig. 2c). For the fine resolution simulations adding the year 2005 yielded to a me-  
 254 dian intra-annual to inter-annual ratio across all PLDs of 0.88. When varying turbulence  
 255 and buoyancy for the fine resolution simulations, the intra-annual and inter-annual vari-  
 256 ance stayed the same order of magnitude, with a median intra-annual to inter-annual  
 257 ratio of  $\sim 0.8$  (Supp. In., Fig. 2).

258 The sensitivity of larval transport estimates to refining the resolution of the hy-  
 259 drodynamical simulations (Fig.3 a) was compared to incorporating the specific buoyancy  
 260 of *P. clavata* (Fig.3 b) and to incorporating different intensity of turbulence (Fig.3 c,d)



**Figure 2.** Median connectivity matrix for the larval release events of 2004 and 2006 for the neutrally buoyant simulations without turbulence and a PLD of 3.5 days. Panel (a) represents the coarse resolution simulation and panel (b) the fine resolution simulations. Box plot of the  $VAR_{intra}/VAR_{inter}$  for different PLDs for the coarse resolution (Panel (c), grey bars) and high resolution (Panel (c), black bars) simulations.  $VAR_{intra}/VAR_{inter}$  were calculated for larval release events of 2004 and 2006 for the neutrally buoyant simulations without turbulence.

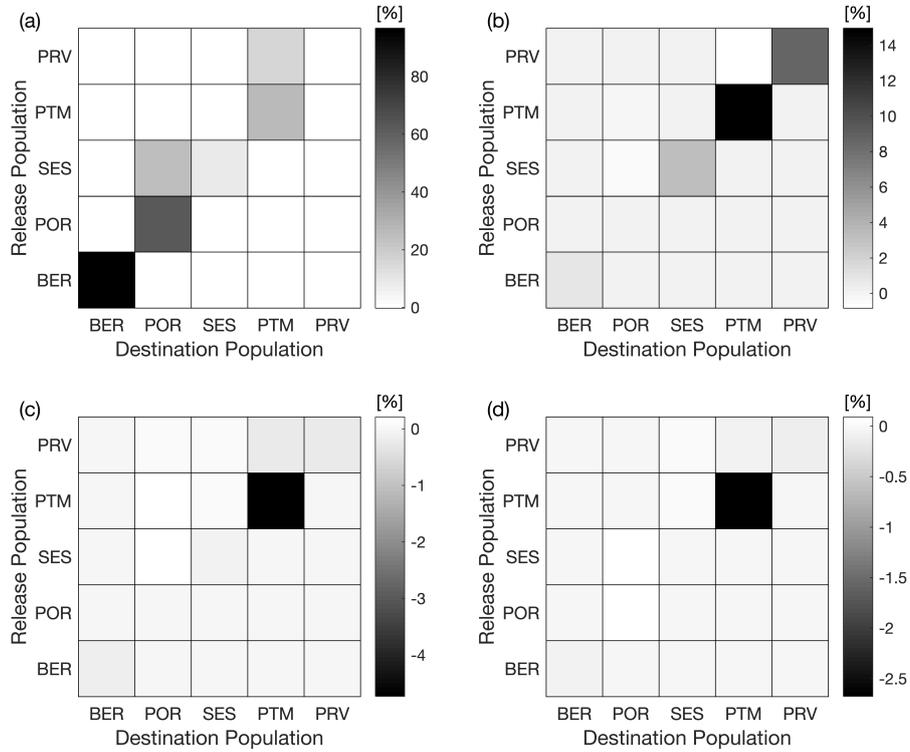
261 for a PLD of 3.5 days. A clear hierarchy can be drawn with the effect of the hydrody-  
262 namical resolution being an order of magnitude higher (median deviation up to 90%) than  
263 that of incorporating the specific buoyancy (median deviation up to 14%) and two or-  
264 ders of magnitude higher than the effect of including turbulence dispersal, whatever the  
265 level (median deviation up to 5 % for the two levels of turbulence tested). More specif-  
266 ically, the effect of incorporating the specific *P. clavata* buoyancy mainly affected the re-  
267 tention rates in PTM, PRV and to a lower extent in SES (Fig.3 b). The effect on all other  
268 connections was similarly negligible. The effect of turbulence dispersal only affected re-  
269 tention in PTM (Fig.3 c,d).

270 The above results were true for all simulations with short PLD (1-7 days). For longer  
271 PLD (10.5-28 days), sensitivity to the specific buoyancy of *P. clavata* and to turbulence  
272 intensity were significantly reduced, although specific buoyancy effect remained preva-  
273 lent (Fig.4). While the specific buoyancy continued to affect mainly retention rates when  
274 the PLD increase from 3.5 days to 28 days (although in different locations, Fig.3b and  
275 Fig.4b), the effect of turbulence mainly affected distant connections (import for BER,  
276 Fig.4c and d).

277 Finally, varying the PLD from the reference value of 3.5 days to 1 or 7 days affected  
278 larval transport estimates of the same order of magnitude as those obtained by incor-  
279 porating *P. clavata* buoyancy for the same PLD (Fig.5). Reducing the PLD from 3.5 days  
280 to 1 day only increased the retention rates (Fig. 5a) while extending the PLD from 3.5  
281 to 7 days not only decreased retention rates but also distant connections from SES to  
282 POR and from PRV to PTM (Fig. 5b).

## 283 4 Discussion

284 In the present study we tested the sensitivity of larval transport simulations among  
285 coastal populations in the Ligurian Sea to different parameters. The horizontal resolu-  
286 tion of the hydrodynamical model was found to have the strongest effect on larval trans-



**Figure 3.** Median transfer deviation matrix for all the larval release events of 2004-2006 and a PLD of 3.5 days. Deviations are computed between (a) neutrally buoyant coarse resolution simulations without turbulence, (b) *P. clavata* buoyancy fine resolution simulation without turbulence, (c) neutrally buoyant fine resolution simulation with low turbulence, (d) neutrally buoyant fine resolution simulation with high turbulence and the reference fine resolution neutrally buoyant simulation without turbulence.

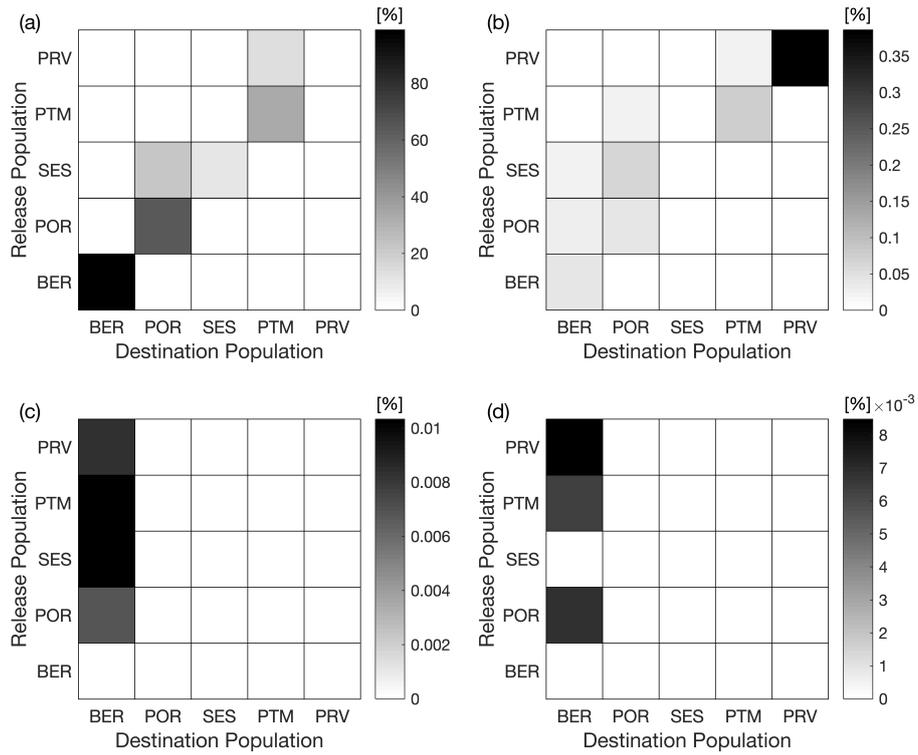


Figure 4. Same as 3 but for a PLD of 28 days

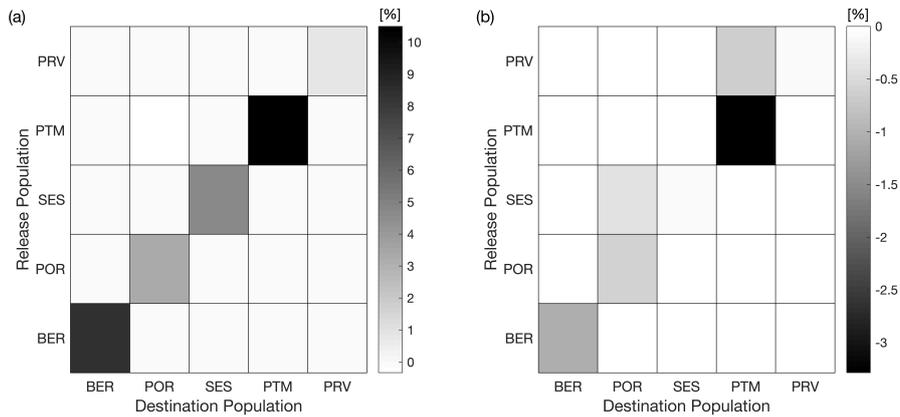


Figure 5. Median transfer deviation matrix for all the larval release events of the 2004-2006 fine resolution neutrally buoyant simulations without turbulence. Deviations are computed between (a) a PLD of 1 day, (b) a PLD of 7 days and a PLD of 3.5 days.

287 port followed by larval behaviour and PLD, while turbulence was found to have a sec-  
288 ond order effect. Thanks to the progresses in ocean modelling availability and perfor-  
289 mances, larval transport predictions are now frequently used to explore the functioning  
290 of marine populations and help understanding their spatial distribution (reviewed in Swearer  
291 et al. (2019)). Assessing the accuracy of larval transport predictions is more than often  
292 qualitative (Barbut et al., 2019; Crosbie et al., 2019). However, quantifying the improve-  
293 ment of larval transport simulations thanks to the improvement in ocean modelling (i.e.  
294 resolution, forcing) and larval traits knowledge (i.e. behaviour, PLD, release events) is  
295 a preliminary to asses the accuracy of larval transport predictions.

296 It has been recurrently argued that including larval motility behaviour was key to  
297 improve the realism of larval dispersal predictions, and led to develop tracking softwares  
298 specific for larval dispersal studies (Lett et al., 2008; Schlag & North, 2012; Paris et al.,  
299 2013). This is particularly relevant for the dispersal of fish larvae that can orient them-  
300 selves (Faillettaz et al., 2018). For many benthic invertebrates species which are unable  
301 to outcompete flow speeds by swimming, only larval buoyancy and motility behaviour  
302 regulate their position in the water column (Leis, 2007). Yet, knowledge about larval motil-  
303 ity behaviour is still restricted to a limited number of species, mainly commercial species  
304 such as oysters (North et al., 2008), scallop (Tremblay et al., 1994), red coral (Martínez-  
305 Quintana et al., 2015) or tropical reef fish species (review in Leis (2006)). Behaviour ef-  
306 fect on larval transport estimates was either explored in sensitivity studies confronting  
307 simulations with different hypothetical behaviours (Donahue et al., 2015; Blanco et al.,  
308 2019) or in projections studies to inform about populations functioning or management,  
309 as a replacement of observations (Munroe et al., 2018; Goodwin et al., 2019; McManus  
310 et al., 2020). The present study confirmed the importance of motility behaviour in lar-  
311 val dispersal predictions, the inclusion of a sinking speed of about 0.5 mm/s altered lar-  
312 val dispersal pattern by 10% for short PLD.

313           However, other larval traits alter dispersal patterns in simulations. Several recent  
314 works performed 2D or 3D dispersal varying PLD only (Aguilar et al., 2019; Gamoyo  
315 et al., 2019; Hidalgo et al., 2019). In the present study, a PLD increase from 1 to 3.5 days  
316 resulted in 10% deviation in dispersal patterns, similar to the effect of *P. clavata* behaviour.  
317 PLD is a very uncertain parameter as environmental mortality processes occurring dur-  
318 ing dispersal, such as predation or starvation for planktotrophic larvae, are underesti-  
319 mated in the laboratory (Rumrill, 1990). For instance, for the white gorgonian *Eunicella*  
320 *singularis*, the most frequent effective PLD determined by comparing dispersal patterns  
321 simulations with population genetics (Padrón et al., 2018) lies in the lower range of po-  
322 tential PLDs determined experimentally (Guizien et al., 2020). For the red gorgonian  
323 *P. clavata*, population genetics indicated short distance dispersal are the most frequent,  
324 but long distance migrants have been observed (Mokhtar-Jamaï et al., 2011), suggest-  
325 ing that the larger potential PLD observed in laboratory experiments (Guizien et al.,  
326 2020) may also contribute to population genetics. In conclusion, despite an accurate rep-  
327 resentation of motility behaviour, the output of larval dispersal studies can be signifi-  
328 cantly impacted by uncertainty on PLD estimates, resulting from ecosystemic interac-  
329 tion.

330           Nevertheless deviation among dispersal patterns of similar order of magnitude as  
331 the effect of behaviour and PLD was obtained when varying another larval trait, the re-  
332 lease timing within the current reproductive season. Such deviation was expected from  
333 the interaction of the short release event duration of *P. clavata* with the natural short  
334 term variability of ocean flows in the area. A similar result was obtained in the Gulf of  
335 Lion where connectivity patterns variability increased when release event duration de-  
336 crease (Guizien et al., 2012). In this area, such effect was even more significant as wind  
337 forcing explains most of the coastal circulation (Briton et al., 2018). As a consequence,  
338 despite larval behaviour and PLD might be better ascertained, uncertainty on disper-  
339 sal patterns will remain larger for species releasing larvae or gametes during short pulses,  
340 compared to species releasing propagules regularly over long periods.

341 The coastal circulation in the Ligurian Sea is characterized by high variability of  
342 the currents at different temporal scales from seasonal (Astraldi & Gasparini, 1992) to  
343 climatic (Astraldi & Gasparini, 2013) in particular the years from 2004 to 2009 were char-  
344 acterized by an abrupt shift in the Western Mediterranean circulation (Schroeder et al.,  
345 2016) starting from 2005. The present study has pinpointed that in such cases, larval  
346 dispersal studies should include estimating connectivity variance with intra-annual vari-  
347 ability and not only with inter-annual variability. In fact the seasonal and climatic vari-  
348 ability equally affect larval dispersal patterns suggesting that yearly averages should be  
349 avoided.

350 Aside to the temporal variability of the hydrodynamical forcing, the importance  
351 of spatial resolution of the hydrodynamical ocean model in affecting the dispersal pat-  
352 terns of larval transport simulations was questioned in several studies (Guizien et al.,  
353 2006; Huret et al., 2007; Andutta et al., 2012; Putman & He, 2013) and reviewed in Swearer  
354 et al. (2019). A recent sensitivity study reported after comparing two ocean model res-  
355 olution of 4 km and 1.6 km, with and without larval vertical behaviour in different years,  
356 that inter-annual variability was the most influential factor in dispersal simulations of  
357 fish larvae in the North sea (Kvile et al., 2018). The present study showed in contrast  
358 that the most influential factor in the coastal Ligurian population was ocean model res-  
359 olution as retention increased dramatically when decreasing the horizontal cell size from  
360 1.5 km to 300 m. Such bias is to be expected in coarse resolution ocean models when  
361 the habitat lies within the coastal boundary layer where the model representation of the  
362 flow is inaccurate due to both their coarse resolution and their lack of coastal ocean pro-  
363 cess parameterization (Holt et al., 2010; Griffies & Treguier, 2013; Holt et al., 2017). The  
364 large deviation in connectivity fluxes found in the present study when increasing ocean  
365 model resolution questions the reliability of past studies of coastal habitat connectivity  
366 using basin or Ocean General Circulation ocean Models (OGCM) (Corell et al., 2012;  
367 Andreollo et al., 2013). However, those models still have an interest for connectivity stud-  
368 ies to delineate well-connected oceanic regions, when care is taken of releasing particles

369 outside this artefactual coastal numerical boundary layer (Rossi et al., 2014). Delineat-  
370 ing such well-connected regions is essential to identify areas in which ocean circulation  
371 model downscaling should be performed to study specific populations connectivity. To  
372 this respect, including turbulence into dispersal simulations is expected to be less im-  
373 portant when the cell size decrease as mesoscale and sub-mesoscale processes will be re-  
374 solved (Guizien et al., 2006; Huret et al., 2007). In the present study, the effect of tur-  
375 bulence on connectivity patterns was clearly negligible when resolving the coastal cir-  
376 culation at 300 m in comparison to the effect of biological traits.

377 In conclusion, we formulate the following guidelines for larval dispersal simulations:

- 378 • Ensure that the grid resolution is sufficient to resolve the coastal dynamics around  
379 the reproductive population where larvae are released. In such a case, multiply-  
380 ing dispersal tracks to account for turbulence effect can be avoided, reducing com-  
381 putational costs. Coastal dynamics may be very different from place to place but  
382 this study showed that, at least for the Ligurian Sea, horizontal resolutions in the  
383 order of a few hundred meters should be employed.
- 384 • Assess the variability of connectivity patterns arising from uncertainty on release  
385 timing by simulating multiple release events. Multiple release events should at least  
386 span over the reproductive season within a year or over multiple years, when inter-  
387 annual climatic variability dominates over short term climatic variability. As a guide,  
388 we suggest a number of release events equal to the ratio of the duration of the re-  
389 productive season divided by the duration of a single release event. Such proce-  
390 dure would ensure to estimate confidence level for the different connectivity pat-  
391 terns.
- 392 • Assess the variability of connectivity patterns arising from uncertainty on PLD  
393 by simulating multiple dispersal duration, spanning the range of potential PLDs.  
394 Such procedure would ensure to estimate most likely PLDs by comparing simu-

395 lated connectivity patterns with observed ones, baring in mind that retention sen-  
 396 sitivity to PLD is the largest for short PLD.

- 397 • Include larval motility behaviour (buoyancy and swimming speed) prior to assess-  
 398 ing PLD effect in dispersal patterns for a specific species. This behaviour should  
 399 be based on experimentally derived parameters, including inter-individual vari-  
 400 ability, to reduce uncertainty on dispersal patterns.

## 401 **Supporting Information**

402 Supporting Information are available in online version of the manuscript.

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## 409 **References**

- 410 Aguilar, L. A., Matthews, S. A., Ayre, D. J., & Minchinton, T. E. (2019). Modelling  
 411 the differences between el nio and la nia years and planktonic larval dura-  
 412 tion on dispersal across the southeast australian biogeographic barrier. *Geo:*  
 413 *Geography and Environment*, 6(1), e00074. doi: 10.1002/geo2.74
- 414 Andrello, M., Mouillot, D., Beuvier, J., Albouy, C., Thuiller, W., & Manel, S. (2013,  
 415 07). Low connectivity between mediterranean marine protected areas: A bio-  
 416 physical modeling approach for the dusky grouper epinephelus marginatus.  
 417 *PLOS ONE*, 8(7), 1-15. doi: 10.1371/journal.pone.0068564
- 418 Andutta, F. P., Kingsford, M. J., & Wolanski, E. (2012). 'sticky water' enables the  
 419 retention of larvae in a reef mosaic. *Estuarine, Coastal and Shelf Science*, 101,

- 420 54-63. doi: <https://doi.org/10.1016/j.ecss.2012.02.013>
- 421 Astraldi, M., & Gasparini, G. (1992). The seasonal characteristics of the circulation  
422 in the north mediterranean basin and their relationship with the atmospheric-  
423 climatic conditions. *Journal of Geophysical Research: Oceans*, *97*(C6), 9531–  
424 9540.
- 425 Astraldi, M., & Gasparini, G. P. (2013). The seasonal characteristics of the circula-  
426 tion in the tyrrhenian sea. In *Seasonal and interannual variability of the west-  
427 ern mediterranean sea* (p. 115-134). American Geophysical Union (AGU). doi:  
428 10.1029/CE046p0115
- 429 Barbut, L., Groot Crego, C., Delerue-Ricard, S., Vandamme, S., Volckaert, F. A. M.,  
430 & Lacroix, G. (2019). How larval traits of six flatfish species impact connectiv-  
431 ity. *Limnology and Oceanography*, *64*(3), 1150-1171. doi: 10.1002/lno.11104
- 432 Blanco, M., Ospina-Álvarez, A., Navarrete, S. A., & Fernández, M. (2019). Influence  
433 of larval traits on dispersal and connectivity patterns of two exploited marine  
434 invertebrates in central chile. *Marine Ecology Progress Series*, *612*, 43–64. doi:  
435 10.3354/meps12870
- 436 Bode, M., Leis, J. M., Mason, L. B., Williamson, D. H., Harrison, H. B., Choukroun,  
437 S., & Jones, G. P. (2019). Successful validation of a larval dispersal  
438 model using genetic parentage data. *PLoS biology*, *17*(7), e3000380. doi:  
439 <https://doi.org/10.1371/journal.pbio.3000380>
- 440 Briton, F., Cortese, D., Duhaut, T., & Guizien, K. (2018). High-resolution modelling  
441 of ocean circulation can reveal retention spots important for biodiversity con-  
442 servation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(4),  
443 882-893. doi: 10.1002/aqc.2901
- 444 Carpine, C., & GRASSHOFF, M. (1975). Les gorgonaires de la méditerranée. *Bul-  
445 letin de l'Institut Océanographique de Monaco*, *71*, 1140.
- 446 Cassola, F., Ferrari, F., & Mazzino, A. (2015, October). Numerical simulations of  
447 Mediterranean heavy precipitation events with the WRF model: A verification

- 448 exercise using different approaches. *Atmospheric Research*, *164*, 210-225. doi:  
 449 10.1016/j.atmosres.2015.05.010
- 450 CBD. (2010). Strategic plan for biodiversity 2011–2020..
- 451 Cerrano, C., Bavestrello, G., Bianchi, C., Cattaneo-vietti, R., Bava, S., Morganti,  
 452 C., ... Sponga, F. (2000). A catastrophic mass-mortality episode of gorgoni-  
 453 ans and other organisms in the ligurian sea (north-western mediterranean),  
 454 summer 1999. *Ecology Letters*, *3*(4), 284-293. doi: [https://doi.org/10.1046/  
 455 j.1461-0248.2000.00152.x](https://doi.org/10.1046/j.1461-0248.2000.00152.x)
- 456 Coma, R., Ribes, M., Zabala, M., & Gili, J.-M. (1995). Reproduction and cycle  
 457 of gonadal development in the mediterranean gorgonian paramuricea clavata.  
 458 *Marine Ecology Progress Series*, *117*(1/3), 173–183. doi: [http://dx.doi.org/  
 459 10.3354/meps117173](http://dx.doi.org/10.3354/meps117173)
- 460 Consortium, E. B. (2016). *Emodnet digital bathymetry (dtm 2016)*. Author. doi: 10  
 461 .12770/c7b53704-999d-4721-b1a3-04ec60c87238
- 462 Corell, H., Moksnes, P.-O., Engqvist, A., Döös, K., & Jonsson, P. R. (2012). Depth  
 463 distribution of larvae critically affects their dispersal and the efficiency of  
 464 marine protected areas. *Marine Ecology Progress Series*, *467*, 29–46. doi:  
 465 <https://doi.org/10.3354/meps09963>
- 466 Criales, M. M., Chérubin, L., Gandy, R., Garavelli, L., Ghannami, M. A., & Crow-  
 467 ley, C. (2019). Blue crab larval dispersal highlights population connectivity  
 468 and implications for fishery management. *Marine Ecology Progress Series*,  
 469 *625*, 53–70. doi: 10.3354/meps13049
- 470 Crosbie, T., Wright, D. W., Oppedal, F., Johnsen, I. A., Samsing, F., & Dempster,  
 471 T. (2019). Effects of step salinity gradients on salmon lice larvae behaviour  
 472 and dispersal. *Aquaculture Environment Interactions*, *11*, 181–190. doi:  
 473 10.3354/aei00303
- 474 Cupido, R., Cocito, S., Sgorbini, S., Bordone, A., & Santangelo, G. (2008). Re-  
 475 sponse of a gorgonian (paramuricea clavata) population to mortality events:

- 476 recovery or loss? *Aquatic Conservation: Marine and Freshwater Ecosystem,*  
 477 *18*, 984–992.
- 478 Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., ...  
 479 Vitart, F. (2011). The era-interim reanalysis: configuration and performance  
 480 of the data assimilation system. *Quarterly Journal of the Royal Meteorological*  
 481 *Society, 137*(656), 553–597. doi: 10.1002/qj.828
- 482 Delrosso, D., Clementi, E., Grandi, A., Tonani, M., Oddo, P., Feruzza, G. G., &  
 483 Pinardi, N. (2016). *Towards the mediterranean forecasting system my-*  
 484 *ocean v5: numerical experiments results and validation.* Retrieved from  
 485 <http://hdl.handle.net/2122/11435>
- 486 Donahue, M. J., Karnauskas, M., Toews, C., & Paris, C. B. (2015, 06). Location isn't  
 487 everything: Timing of spawning aggregations optimizes larval replenishment.  
 488 *PLOS ONE, 10*(6), 1-14. doi: 10.1371/journal.pone.0130694
- 489 Edwards, K., Hare, J., Werner, F., & Seim, H. (2007). Using 2-dimensional dispersal  
 490 kernels to identify the dominant influences on larval dispersal on continental  
 491 shelves. *Marine Ecology Progress Series, 352*, 77–87. doi: 10.3354/meps07169
- 492 Faillettaz, R., Paris, C. B., & Irisson, J.-O. (2018). Larval fish swimming be-  
 493 havior alters dispersal patterns from marine protected areas in the north-  
 494 western mediterranean sea. *Frontiers in Marine Science, 5*, 97. doi:  
 495 10.3389/fmars.2018.00097
- 496 Fox-Kemper, B., Adcroft, A., Bning, C. W., Chassignet, E. P., Curchitser, E.,  
 497 Danabasoglu, G., ... Yeager, S. G. (2019). Challenges and prospects  
 498 in ocean circulation models. *Frontiers in Marine Science, 6*, 65. doi:  
 499 10.3389/fmars.2019.00065
- 500 Gamoyo, M., Obura, D., & Reason, C. J. C. (2019). Estimating connectivity  
 501 through larval dispersal in the western indian ocean. *Journal of Geophysical*  
 502 *Research: Biogeosciences, 124*(8), 2446-2459. doi: 10.1029/2019JG005128
- 503 Goodwin, J. D., Munroe, D. M., Defne, Z., Ganju, N. K., & Vasslides, J. (2019). Es-

- 504           timating connectivity of hard clam (*mercenaria mercenaria*) and eastern oyster  
505           (*crassostrea virginica*) larvae in barnegat bay. *Journal of Marine Science and*  
506           *Engineering*, 7(6), 167. doi: 10.3390/jmse7060167
- 507 Gori, A., Bavestrello, G., Grinyó, J., Dominguez-Carrió, C., Ambroso, S., & Bo, M.  
508           (2017).       Animal forests in deep coastal bottoms and continental shelf of the  
509           mediterranean sea.       In S. Rossi, L. Bramanti, A. Gori, & C. Orejas (Eds.),  
510           *Marine animal forests: The ecology of benthic biodiversity hotspots* (pp. 1–27).  
511           Cham: Springer International Publishing. doi: 10.1007/978-3-319-17001-5\_5-1
- 512 Gori, A., Linares, C., Rossi, S., Coma, R., & Gili, J.-M.   (2007).   Spatial variabil-  
513           ity in reproductive cycle of the gorgonians *paramuricea clavata* and *eunicella*  
514           *singularis* (anthozoa, octocorallia) in the western mediterranean sea. *Marine*  
515           *Biology*, 151(4), 1571–1584. doi: 10.1007/s00227-006-0595-7
- 516 Griffies, S. M., & Treguier, A. M. (2013). Chapter 20 - ocean circulation models and  
517           modeling. In G. Siedler, S. M. Griffies, J. Gould, & J. A. Church (Eds.), *Ocean*  
518           *circulation and climate* (Vol. 103, p. 521-551). Academic Press. doi: [https://](https://doi.org/10.1016/B978-0-12-391851-2.00020-9)  
519           doi.org/10.1016/B978-0-12-391851-2.00020-9
- 520 Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M., & Botsford, L. W.   (2011).  
521           Consequences of adult and juvenile movement for marine protected areas. *Bi-*  
522           *ological Conservation*, 144(2), 692–702.   doi: [https://doi.org/10.1016/j.biocon](https://doi.org/10.1016/j.biocon.2010.12.015)  
523           .2010.12.015
- 524 Guizien, K., Belharet, M., Marsaleix, P., & Guarini, J. M.   (2012).   Using larval  
525           dispersal simulations for marine protected area design: Application to the  
526           gulf of lions (northwest mediterranean). *Limnology and Oceanography*, 57(4),  
527           1099-1112. doi: 10.4319/lo.2012.57.4.1099
- 528 Guizien, K., Belharet, M., Moritz, C., & Guarini, J. M. (2014). Vulnerability of ma-  
529           rine benthic metapopulations: implications of spatially structured connectivity  
530           for conservation practice in the gulf of lions (nw mediterranean sea). *Diversity*  
531           *and Distributions*, 20(12), 1392-1402. doi: <https://doi.org/10.1111/ddi.12254>

- 532 Guizien, K., Brochier, T., Duchene, J., Koh, B.-S., & Marsaleix, P. (2006). Dispersal  
533 of *owenia fusiformis* larvae by wind-driven currents: turbulence, swimming be-  
534 haviour and mortality in a three-dimensional stochastic model. *Marine Ecology  
535 Progress Series*, *311*, 47–66. doi: 10.3354/meps311047
- 536 Guizien, K., Viladrich, N., Martínez-Quintana, Á., & Bramanti, L. (2020). Survive  
537 or swim: different relationships between migration potential and larval size in  
538 three sympatric mediterranean octocorals. *Scientific reports*, *10*(1), 1–12. doi:  
539 10.1038/s41598-020-75099-1
- 540 Haidvogel, D. B., Arango, H. G., Hedstrom, K., Beckmann, A., Malanotte-Rizzoli,  
541 P., & Shchepetkin, A. F. (2000). Model evaluation experiments in the North  
542 Atlantic Basin: simulations in nonlinear terrain-following coordinates. *Dyn.  
543 Atmos. Oceans*, *32*(3-4), 239–281. doi: 10.1016/S0377-0265(00)00049-X
- 544 Harmelin, J.-G., & Marinopoulos, J. (1994). Population structure and partial  
545 mortality of the gorgonian *paramuricea clavata* (risso) in the north-western  
546 mediterranean (france, port-cros island). *Marine life*, *4*(1), 5–13.
- 547 Hidalgo, M., Rossi, V., Monroy, P., Ser-Giacomi, E., Hernández-García, E., Guijarro,  
548 B., . . . Reglero, P. (2019). Accounting for ocean connectivity and hydrocli-  
549 mate in fish recruitment fluctuations within transboundary metapopulations.  
550 *Ecological Applications*, *29*(5), e01913. doi: 10.1002/eap.1913
- 551 Hock, K., Doropoulos, C., Gorton, R., Condie, S. A., & Mumby, P. J. (2019). Split  
552 spawning increases robustness of coral larval supply and inter-reef connec-  
553 tivity. *Nature communications*, *10*(1), 1–10. doi: [https://doi.org/10.1038/  
554 s41467-019-11367-7](https://doi.org/10.1038/s41467-019-11367-7)
- 555 Holt, J., Hyder, P., Ashworth, M., Harle, J., Hewitt, H. T., Liu, H., . . . Wood, R.  
556 (2017). Prospects for improving the representation of coastal and shelf seas in  
557 global ocean models. *Geoscientific Model Development*, *10*(1), 499–523. doi:  
558 10.5194/gmd-10-499-2017
- 559 Holt, J., Wakelin, S., Lowe, J., & Tinker, J. (2010). The potential impacts of cli-

- 560 mate change on the hydrography of the northwest european continental shelf.  
 561 *Progress in Oceanography*, 86(3), 361-379. doi: [https://doi.org/10.1016/](https://doi.org/10.1016/j.pocean.2010.05.003)  
 562 [j.pocean.2010.05.003](https://doi.org/10.1016/j.pocean.2010.05.003)
- 563 Huret, M., Runge, J. A., Chen, C., Cowles, G., Xu, Q., & Pringle, J. M. (2007).  
 564 Dispersal modeling of fish early life stages: sensitivity with application to at-  
 565 lantic cod in the western gulf of maine. *Marine Ecology Progress Series*, 347,  
 566 261–274. doi: <https://doi.org/10.3354/meps06983>
- 567 Jackett, D. R., & McDougall, T. J. (1995). Minimal Adjustment of Hydrographic  
 568 Profiles to Achieve Static Stability. *Journal of Atmospheric and Oceanic Tech-*  
 569 *nology*, 12(2), 381-389. doi: [10.1175/1520-0426\(1995\)012<0381:MAOHPT>2.0](https://doi.org/10.1175/1520-0426(1995)012<0381:MAOHPT>2.0.CO;2)  
 570 [.CO;2](https://doi.org/10.1175/1520-0426(1995)012<0381:MAOHPT>2.0.CO;2)
- 571 Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engi-  
 572 neers. *Oikos*, 69(3), 373–386. doi: [doi.org/10.2307/3545850](https://doi.org/10.2307/3545850)
- 573 Kvile, K. Ø., Romagnoni, G., Dagestad, K.-F., Langangen, Ø., & Kristiansen,  
 574 T. (2018, 04). Sensitivity of modelled North Sea cod larvae transport  
 575 to vertical behaviour, ocean model resolution and interannual variation in  
 576 ocean dynamics. *ICES Journal of Marine Science*, 75(7), 2413-2424. doi:  
 577 [10.1093/icesjms/fsy039](https://doi.org/10.1093/icesjms/fsy039)
- 578 Large, W. G., McWilliams, J. C., & Doney, S. C. (1994). Oceanic vertical mixing: A  
 579 review and a model with a nonlocal boundary layer parameterization. *Reviews*  
 580 *of Geophysics*, 32(4), 363-403. doi: <https://doi.org/10.1029/94RG01872>
- 581 Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? In *Advances in*  
 582 *marine biology* (Vol. 51, p. 57 - 141). Academic Press. doi: [https://doi.org/10](https://doi.org/10.1016/S0065-2881(06)51002-8)  
 583 [.1016/S0065-2881\(06\)51002-8](https://doi.org/10.1016/S0065-2881(06)51002-8)
- 584 Leis, J. M. (2007). Behaviour as input for modelling dispersal of fish larvae: be-  
 585 haviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny  
 586 meet hydrography. *Marine Ecology Progress Series*, 347, 185–193. doi:  
 587 [10.3354/meps06977](https://doi.org/10.3354/meps06977)

- 588 Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., & Blanke, B.  
 589 (2008). A lagrangian tool for modelling ichthyoplankton dynamics. *Environ-*  
 590 *mental Modelling & Software*, 23(9), 1210-1214. doi: [https://doi.org/10.1016/](https://doi.org/10.1016/j.envsoft.2008.02.005)  
 591 [j.envsoft.2008.02.005](https://doi.org/10.1016/j.envsoft.2008.02.005)
- 592 Linares, C., Coma, R., Mariani, S., Daz, D., Hereu, B., & Zabala, M. (2008).  
 593 Early life history of the mediterranean gorgonian paramuricea clavata: im-  
 594 plications for population dynamics. *Invertebrate Biology*, 127(1), 1-11. doi:  
 595 [10.1111/j.1744-7410.2007.00109.x](https://doi.org/10.1111/j.1744-7410.2007.00109.x)
- 596 Marshall, J., Adcroft, A., Hill, C., Perelman, L., & Heisey, C. (1997). A finite-  
 597 volume, incompressible Navier Stokes model for studies of the ocean on parallel  
 598 computers. *J. Geophys. Res.*, 102(C3), 5753-5766. doi: [10.1029/96JC02775](https://doi.org/10.1029/96JC02775)
- 599 Martínez-Quintana, A., Bramanti, L., Viladrich, N., Rossi, S., & Guizien, K.  
 600 (2015). Quantification of larval traits driving connectivity: the case of  
 601 corallium rubrum (l. 1758). *Marine Biology*, 162(2), 309–318. doi:  
 602 [10.1007/s00227-014-2599-z](https://doi.org/10.1007/s00227-014-2599-z)
- 603 McManus, M. C., Ullman, D. S., Rutherford, S. D., & Kincaid, C. (2020). North-  
 604 ern quahog (*mercenaria mercenaria*) larval transport and settlement modeled  
 605 for a temperate estuary. *Limnology and Oceanography*, 65(2), 289-303. doi:  
 606 [10.1002/lno.11297](https://doi.org/10.1002/lno.11297)
- 607 MedPAN, U. (2017). *Map-spa/rac (2017). the 2016 status of marine protected ar-*  
 608 *eas in the mediterranean: Main findings.* [https://drive.google.com/file/](https://drive.google.com/file/d/1-an1aHCqHP1xAJGHaRgKXqZ4-rTPbBzR/view)  
 609 [d/1-an1aHCqHP1xAJGHaRgKXqZ4-rTPbBzR/view.](https://drive.google.com/file/d/1-an1aHCqHP1xAJGHaRgKXqZ4-rTPbBzR/view)
- 610 Millot, C. (1999). Circulation in the western mediterranean sea. *Journal of Marine*  
 611 *Systems*, 20(1), 423–442.
- 612 Millot, C., & Taupier-Letage, I. (2005). Circulation in the mediterranean sea.  
 613 In A. Saliot (Ed.), *The mediterranean sea* (pp. 29–66). Berlin, Heidelberg:  
 614 Springer Berlin Heidelberg. doi: [10.1007/b107143](https://doi.org/10.1007/b107143)
- 615 Mokhtar-Jamaï, K., Pascual, M., Ledoux, J.-B., Coma, R., Féral, J.-P., Garrabou,

- 616 J., & Aurelle, D. (2011). From global to local genetic structuring in the red  
 617 gorgonian *paramuricea clavata*: the interplay between oceanographic condi-  
 618 tions and limited larval dispersal. *Molecular Ecology*, *20*(16), 3291-3305. doi:  
 619 10.1111/j.1365-294X.2011.05176.x
- 620 Munroe, D. M., Haidvogel, D., Caracappa, J. C., Klinck, J. M., Powell, E. N., Hof-  
 621 mann, E. E., ... Hart, D. R. (2018). Modeling larval dispersal and con-  
 622 nectivity for atlantic sea scallop (*placopecten magellanicus*) in the middle  
 623 atlantic bight. *Fisheries Research*, *208*, 7 - 15. doi: [https://doi.org/10.1016/](https://doi.org/10.1016/j.fishres.2018.06.020)  
 624 [j.fishres.2018.06.020](https://doi.org/10.1016/j.fishres.2018.06.020)
- 625 North, E. W., Schlag, Z., Hood, R. R., Li, M., Zhong, L., Gross, T., & Kennedy,  
 626 V. S. (2008). Vertical swimming behavior influences the dispersal of simu-  
 627 lated oyster larvae in a coupled particle-tracking and hydrodynamic model  
 628 of chesapeake bay. *Marine Ecology Progress Series*, *359*, 99–115. doi:  
 629 10.3354/meps07317
- 630 Padrón, M., Costantini, F., Bramanti, L., Guizien, K., & Abbiati, M. (2018). Ge-  
 631 netic connectivity supports recovery of gorgonian populations affected by  
 632 climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*,  
 633 *28*(4), 776-787. doi: [10.1002/aqc.2912](https://doi.org/10.1002/aqc.2912)
- 634 Paris, C. B., Helgers, J., van Sebille, E., & Srinivasan, A. (2013). Connectivity  
 635 modeling system: A probabilistic modeling tool for the multi-scale tracking  
 636 of biotic and abiotic variability in the ocean. *Environmental Modelling &*  
 637 *Software*, *42*, 47-54. doi: <https://doi.org/10.1016/j.envsoft.2012.12.006>
- 638 Pineda, J., Hare, J. A., & Sponaugle, S. (2007, September). Larval transport  
 639 and dispersal in the coastal ocean and consequences for population con-  
 640 nectivity. *Oceanography*, *20*. Retrieved from [https://doi.org/10.5670/](https://doi.org/10.5670/oceanog.2007.27)  
 641 [oceanog.2007.27](https://doi.org/10.5670/oceanog.2007.27) doi: [10.5670/oceanog.2007.27](https://doi.org/10.5670/oceanog.2007.27)
- 642 Putman, N. F., & He, R. (2013). Tracking the long-distance dispersal of marine  
 643 organisms: sensitivity to ocean model resolution. *Journal of the Royal Society*

- 644 *Interface*, 10(81), 20120979. doi: <https://doi.org/10.1098/rsif.2012.0979>
- 645 Rossi, V., Ser-Giacomi, E., López, C., & Hernández-García, E. (2014). Hydro-  
 646 dynamic provinces and oceanic connectivity from a transport network help  
 647 designing marine reserves. *Geophysical Research Letters*, 41(8), 2883-2891. doi:  
 648 <https://doi.org/10.1002/2014GL059540>
- 649 Rumrill, S. S. (1990). Natural mortality of marine invertebrate larvae. *Ophelia*,  
 650 32(1-2), 163-198. doi: 10.1080/00785236.1990.10422030
- 651 Scheltema, R. S. (1986). On dispersal and planktonic larvae of benthic invertebrates:  
 652 An eclectic overview and summary of problems. *Bulletin of Marine Science*,  
 653 39(2), 290-322. Retrieved from [https://www.ingentaconnect.com/content/  
 654 umrsmas/bullmar/1986/00000039/00000002/art00013](https://www.ingentaconnect.com/content/umrsmas/bullmar/1986/00000039/00000002/art00013)
- 655 Schlag, Z. R., & North, E. W. (2012). Lagrangian TRANSport model (LTRANS  
 656 v.2) User's Guide [Computer software manual].
- 657 Schroeder, K., Chiggiato, J., Bryden, H., Borghini, M., & Ismail, S. B. (2016).  
 658 Abrupt climate shift in the western mediterranean sea. *Scientific Reports*, 6.
- 659 Sciascia, R., Magaldi, M. G., & Vetrano, A. (2019). Current reversal and associated  
 660 variability within the corsica channel: The 2004 case study. *Deep Sea Research  
 661 Part I: Oceanographic Research Papers*, 144, 39 - 51. doi: [https://doi.org/10  
 662 .1016/j.dsr.2018.12.004](https://doi.org/10.1016/j.dsr.2018.12.004)
- 663 Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling  
 664 system (ROMS): a split-explicit, free-surface, topography-following-coordinate  
 665 oceanic model. *Ocean Modelling*, 9(4), 347 - 404. doi: [http://dx.doi.org/  
 666 10.1016/j.ocemod.2004.08.002](http://dx.doi.org/10.1016/j.ocemod.2004.08.002)
- 667 Siegel, D., Kinlan, B., Gaylord, B., & Gaines, S. (2003). Lagrangian descriptions of  
 668 marine larval dispersion. *Marine Ecology Progress Series*, 260, 83-96. doi: 10  
 669 .3354/meps260083
- 670 Swearer, S. E., Treml, E. A., & Shima, J. S. (2019). *H7 a review of biophysical mod-  
 671 els of marine larval dispersal.* Taylor & Francis.

- 672 Tremblay, M. J., Loder, J. W., Werner, F. E., Naimie, C. E., Page, F. H., & Sinclair,  
 673 M. M. (1994). Drift of sea scallop larvae *Placopecten magellanicus* on Georges  
 674 bank: a model study of the roles of mean advection, larval behavior and larval  
 675 origin. *Deep Sea Research Part II: Topical Studies in Oceanography*, 41(1), 7 -  
 676 49. doi: [https://doi.org/10.1016/0967-0645\(94\)90061-2](https://doi.org/10.1016/0967-0645(94)90061-2)
- 677 Treml, E. A., Halpin, P. N., Urban, D. L., & Pratson, L. F. (2008). Mod-  
 678 eling population connectivity by ocean currents, a graph-theoretic ap-  
 679 proach for marine conservation. *Landscape Ecology*, 23(1), 19–36. doi:  
 680 10.1007/s10980-007-9138-y
- 681 Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., . . .  
 682 Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate  
 683 change. *Science*, 353(6304). doi: 10.1126/science.aad8466
- 684 Wood, S., Paris, C. B., Ridgwell, A., & Hendy, E. J. (2014). Modelling dispersal  
 685 and connectivity of broadcast spawning corals at the global scale. *Global Ecol-  
 686 ogy and Biogeography*, 23(1), 1-11. doi: 10.1111/geb.12101