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Larval buoyancy matters: sinking changes larval
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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. In the present study, we show that connectivity patterns among *Paramuricea Clavata* populations in the Ligurian sea predicted using sinking behaviour agreed better with estimated gene flow than when using neutrally buoyant behaviour. Larval transport predictions taking into account sinking behaviour resulted in both open and closed populations, depending on their geographical location in the Tyrrhenean-Ligurian sea. Moreover, graph

analysis of larval transport probability among 18 populations highlights a cluster of four highly connected populations along the Ligurian coast between which, thanks to larval transport, rescue can happen. Current protection measures are implemented in those locations. Another location (Capraia Island) displayed similarly interesting properties for network resilience, and thus deserve protection.

Keywords: Larval dispersal modelling; connectivity; *Paramuricea clavata*; NW Mediterranean; larval behaviour; graph theory and conservation

1 Introduction

1 Anticipating the impact of the on-going climate change on the already altered ocean biodi-
2 versity is a major challenge for the next decade (ONU SGD 14, IPBES 2030 work program,
3 <https://ipbes.net/o4-supporting-policy>). To do so, models incorporating knowledge and
4 understanding of mechanisms regulating species spatial distribution such as dispersal will
5 be crucial to produce biodiversity maps for the future (Urban *et al.*, 2016). The Mediter-
6 ranean sea has been highlighted as a climate change hotspot (IPPC 2015). Over the last
7 decades, mass mortalities of conspicuous species have been increasingly reported in the
8 Mediterranean coastal ecosystems and related to climate anomalies (*Paramuricea clavata*:
9 Garrabou *et al.* 2009, *Pinna nobilis*: Vázquez-Luis *et al.* 2017). Severe population de-
10 pletion or local extirpation occurrences poses the question of species resilience (Holling,
11 1973). For sessile species, propagules dispersal which establishes connections among pop-
12 ulations is a key mechanism for species resilience (Hanski, 1998). As a metter of fact the
13 recovery of impacted populations have been observed, (Cupido *et al.*, 2008; Santangelo
14 *et al.*, 2015). Recovery was attributed to larval dispersal from less impacted populations
15 located in neighbouring Marine Protected Areas (MPA) (Padrón *et al.*, 2018a). Thus,
16 anticipating the recovery potential of impacted populations thanks to dispersal might
17 help optimize biodiversity management. Numerical simulations of larval dispersal be-
18 tween species-suitable habitats have the potential to forecast such population recovery
19 pathways.

20 Larval dispersal simulations require hydrodynamical models to provide a reliable and

21 validated description of the flow and its variability at the spatio-temporal scales relevant
22 for both dispersal processes and regional population connectivity estimates. Connectivity
23 studies have used a variety of ocean circulation models, from coarse-resolution global
24 models (10 kms, Treml *et al.* 2008; Wood *et al.* 2014) to high-resolution regional models
25 (100 m to 1 km, Guizien *et al.* 2006). Ocean circulation models are validated against
26 diagnostic variables such as sea surface temperature and salinity, heat content, mass,
27 sea level, meridional transport, turbulent kinetic energy or vorticity (Fox-Kemper *et al.*,
28 2019). However, such validation can be insufficient to ensure that simulated velocities
29 used for the larval dispersal simulations are representative of the advection and diffusion
30 experienced by larvae in the flow (Pineda *et al.*, 2007). Even when flow field simulations
31 are accurate, the specificity of larval dispersal simulations ultimately depends on the
32 knowledge of biological traits such as location and timing of larval release in parental
33 populations and larval traits important for dispersal (Scheltema, 1986). Among these,
34 pelagic larval duration has been extensively tested in dispersal simulations (Siegel *et al.*,
35 2003; Edwards *et al.*, 2007; Guizien *et al.*, 2012). In contrast, larval motility behaviour is
36 less often accounted for, despite being recognized as essential in regulating larval position
37 in the water column (Leis, 2007). Assuming neutrally buoyant larvae in dispersal studies
38 can be a reasonable hypothesis but it should be grounded on larval motility behaviour
39 experimental studies (Guizien *et al.*, 2006; Martínez-Quintana *et al.*, 2015). In fact, in
40 most larval dispersal modelling studies, the neutrally buoyant assumption is not based
41 on data but justified by the lack of knowledge on larval motility. The few species for
42 which larval motility behaviour has been documented are commercial species such as
43 oysters (North *et al.*, 2008) or scallop (Tremblay *et al.*, 1994) and species of tropical reef
44 fishes (review in Leis 2006). However, regardless of the larval behaviour implemented in
45 dispersal simulations larval transport predictions should be tested against independent
46 observations.

47 For most benthic invertebrates, the larval stage is difficult to identify at the species
48 level for two reasons: the larval stage is too small to be tagged and the loss during the
49 dispersive phase is so large that recollection is almost impossible. As a consequence, larval

50 transport observations of benthic invertebrates are very rare, and population genetics
51 is the main measurable effect of larval transport that keeps track of larvae population
52 origin (Lowe and Allendorf, 2010). Despite several works assuming the importance of
53 connectivity to favor the persistence of sessile benthic species, empirical validation of
54 larval dispersal simulations are still not that frequent (Padrón *et al.* 2018b; Bode *et al.*
55 2019). Moreover, the most appropriate population genetics metrics to test larval dispersal
56 simulations are debated (Bode *et al.*, 2019).

57 In the present study, we chose *Paramuricea clavata* (Risso 1826) in the Ligurian-North
58 Tyrrhenian shelf as a case study for larval dispersal simulations validation. The *Para-*
59 *muricea clavata* is a conspicuous octocoral species of the Mediterranean coralligenous
60 assemblage (Carpine *et al.*, 1975). Due to its role of ecosystem engineer (*sensu* Jones *et al.*
61 1994), and its patrimonial value linked to the beauty it gives to seascapes, *Paramuricea*
62 *clavata* has been used as a flag species for the detrimental effects of climate change in
63 the Mediterranean Sea. *P. clavata* is one of the tallest sessile Mediterranean species with
64 erected colonies as high as 1.3 m (Harmelin and Marinopoulos, 1994) and is found on
65 hard substrate from 10 to 200 m water depth (Gori *et al.*, 2017). In the Ligurian and
66 northern Tyrrhenian seas, populations are patchily distributed within the hard bottom
67 shallow habitats, posing the question if larval dispersal could ensure their resilience.

68 The Ligurian and North Tyrrhenian seas are the two basins forming the portion of the
69 Northwestern Mediterranean Sea between Italy and France and are connected through the
70 Corsica channel (Astraldi and Gasparini, 1992). Both basins are characterized by a mean
71 cyclonic circulation (Millot, 1999; Millot and Taupier-Letage, 2005). In the Ligurian sea,
72 this cyclonic circulation is known as the Ligurian (or Northern) Current and flows along
73 the Ligurian coast. We estimated recent gene flow over a few generations among coastal
74 populations of *P. clavata* in the Ligurian-north Tyrrhenian sea (Padrón *et al.*, 2018a) as
75 independent observations to test larval dispersal simulations. After selecting the most
76 likely larval motility behaviour to be incorporated in larval dispersal simulations, larval
77 transport patterns were simulated within a wider set of known or potential populations
78 extending to the southern part of the Tyrrhenean sea. The network of populations was

79 analyzed with graph theory metrics to identify the role of different populations in species
80 regional resilience.

81 **2 Material and Methods**

82 **2.1 Hydrodynamical simulations in the Northwestern**

83 **Mediterranean**

84 The circulation of the Ligurian and Tyrrhenian Seas was simulated using the Ligurian In-
85 tegrated Modelling Effort (Sciascia *et al.* 2019, LIME-ROMS hereinafter). LIME-ROMS
86 was based on the Rutgers University kernel of the Regional Ocean Modelling System
87 (ROMS, Shchepetkin and McWilliams 2005; Haidvogel *et al.* 2000). The numerical do-
88 main was discretized with an horizontal grid of 590 x 314 points. The mesh was unevenly
89 spaced and the most resolved area, which includes the area of the Ligurian-Northern
90 Tyrrhenian shelf, had a horizontal resolution of $1/64^\circ \times 1/64^\circ$ (~ 1.5 km). The vertical
91 dimension was discretized with 50 sigma layers. Realistic surface forcings came from the
92 3-hourly, 0.25° horizontal resolution ERA-Interim reanalysis fields (Dee et al., 2011) avail-
93 able at the <http://apps.ecmwf.int/datasets/data/interim-full-daily> link, while the daily
94 open boundary values were derived from the Mediterranean Forecasting System (MFS)
95 SYS4a3 product (Delrosso *et al.*, 2016). Model outputs were saved every six hours. The
96 reader is referred to Sciascia *et al.* (2019) for a detailed description and validation of the
97 model.

98 The genetic data used in the present study were collected in 2013 Padrón *et al.* (2018a).
99 Most of the sampled populations suffered two massive mortality events in 1999 and 2003
100 (Cerrano *et al.*, 2000; Cupido *et al.*, 2008). Given the sexual maturation of *P. clavata* of
101 at least 4 years (Coma *et al.*, 1995), the reproductive events that more likely contributed
102 to the population genetics used in the present study took place between 2004 and 2009.
103 These years were also characterized by an abrupt shift in the Western Mediterranean
104 circulation (Schroeder *et al.*, 2016) starting from 2005. The mean circulation in 2004
105 was similar to that of 2005, but differed between 2004 and 2006 with faster currents

106 across both basins in 2006 and in particular a faster Ligurian Current (LC). Moreover,
107 the atmospheric forcing (i.e. wind speed, air temperature and rain) were also different
108 between the two years with more rain and colder air temperature in 2004 compared
109 to 2006 (not shown). For the aforementioned reasons, in the following larval transport
110 simulations were performed for the years 2004 and 2006.

111 Figure 1 showed the mean summer (i.e. 15 June-15 August) horizontal velocity
112 vertically-averaged over the first 30 m of the water column, for 2004 (Fig.1a) and 2006
113 (Fig.1b). The model reproduced well the mean cyclonic circulation of the Ligurian and
114 Tyrrhenian Seas (Millot, 1999) and showed that the area was characterized by a strong
115 interannual variability with differences in the mean circulation between the two years.
116 In 2004 (Fig.1a), on top of the mean cyclonic circulation of the LC, large eddies and
117 recirculations were found. In 2006 (Fig.1b), the LC was faster and flowed following the
118 narrow continental shelf of the Ligurian coast and the mean circulation was considered
119 typical of the basin.

120 **2.2 Larval dispersal simulations**

121 Dispersal simulations of *P. clavata* larvae were performed with the offline Lagrangian
122 Transport model (LTRANS, Schlag and North 2012). Particles displacement due to
123 advection was calculated after integrating the LIME-ROMS hydrodynamical fields with
124 a 4th order Runge-Kutta scheme with timestep of 120s. LTRANS was selected over
125 other Lagrangian transport models for its capability to cope with sigma layers and to
126 compute 3D trajectories for both neutrally buoyant and active (e.g. sinking, swimming)
127 particles, eventually including turbulent diffusion. Particles were released in the locations
128 of seven *P. clavata* populations sampled by Padrón *et al.* (2018a) (Bergeggi, Portofino,
129 Sestri Levante, Punta Mesco, Porto Venere, Calafuria and Cerboli Island, red circles in
130 Figure 1, Table 1), together with 11 additional populations located along the Ligurian
131 and North Tyrrhenian shelf where *P. clavata* has been recorded (L. Bramanti, Personal
132 Communication, blue squares, Figure 1, Table 1). Each population was described by ten
133 release points, separated by 100 m. Particles were released two grid points away from

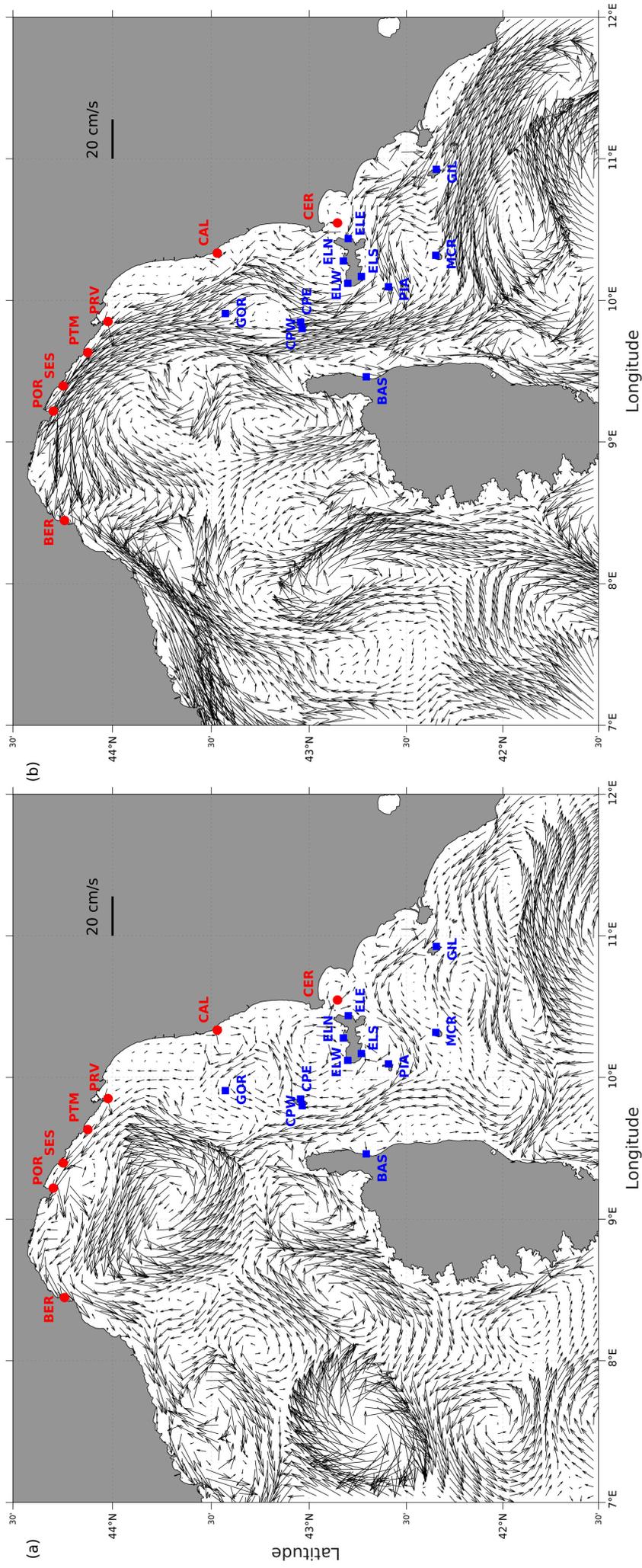


Figure 1: LIME-ROMS depth averaged (0-30 meters) horizontal velocity for the period June 15th-August 15th of (a) 2004 and (b) 2006. Overlaid on top of the currents are the populations of *P. clavata* simulated in the larval dispersal sets (Table 1). Red squares represent locations where samples were collected, blue circles locations where *P. clavata* populations are present but not sampled in this study.

Abbreviation	Name	Lat [deg N]	Lon [deg E]	Depth [m]
BER	Bergeggi	44.24	8.45	39.6
POR	Portofino	44.30	9.22	40.4
SES	Sestri Levante	44.25	9.40	40.5
PTM	Punta Mesco	44.12	9.63	37.9
PRV	Porto Venere	44.02	9.85	27.7
GOR	Gorgona Island	43.43	9.91	41.8
CAL	Calafuria	43.47	10.33	38.6
CPW	Capraia Island - West	43.04	9.80	29.4
CPE	Capraia Island - East	43.04	9.85	29.7
ELW	Elba Island - West	42.80	10.12	35.3
ELN	Elba Island - North	42.82	10.28	28.9
ELS	Elba Island - South	42.73	10.17	31.7
ELE	Elba Island - East	42.80	10.44	31.1
CER	Cerboli Island	42.85	10.55	39.9
BAS	Bastia	42.71	9.46	29.0
PIA	Pianosa Island	42.59	10.09	28.4
MCR	Montecristo Island	42.35	10.32	34.0
GIL	Giglio Island	42.34	10.92	28.3

Table 1: Latitude, Longitude and average depth of the simulated populations across the Ligurian-Tyrrhenian basin.

134 the coast line (i.e. ~ 3 km) in order to avoid any retention bias due to the numerical
135 boundary layer.

136 Off the Catalan coast *P. clavata* larvae are released in summer, late June/early July,
137 during short events of a few days separated by 15 days (Coma *et al.*, 1995; Gori *et al.*,
138 2007). No information on the exact timing and occurrence of *P. clavata* larval release
139 in the Ligurian Sea are available in the scientific literature but several observations by
140 recreational divers report this phenomenon in the month of July. For this reason, in
141 each of the ten points forming a population, particles were released every hour in the 30
142 days between June 15th and July 15th for both 2004 and 2006. Depending on whether
143 turbulence was (was not) accounted for, thirty (one) particles were released in each lar-
144 val release episodes summing up to a total number of particles of 21600 (7200) for each
145 population. The number of particles was increased by a factor thirty to ensure the conver-
146 gence of statistical properties when dispersion due to subgrid turbulence was accounted
147 for (Guizien *et al.*, 2006).

148 Particles were released 1 m above the bottom, at a depth between 25 and 45 m,

149 depending on the local bathymetry (Table 1). *P. clavata* larvae are less than 1 mm long,
150 lecithotrophic and do not undergo any ontogenetic development. The main competency
151 period was less than 20 days (Guizien *et al.*, 2020). Thus, particles were tracked up to
152 21 days after their release. During the pelagic stage, larvae display very limited motility
153 activity, eventually crawling and settling on rigid surface (Coma *et al.*, 1995; Linares
154 *et al.*, 2008). *P. clavata* larval motility behaviour was limited to free fall as a recent
155 experimental study reported less than 5% of swimming activity frequency. Larval free
156 fall speed at 20°C was 0.056 ± 0.021 cm s⁻¹, as a result of larval body density ranging
157 from 1.025 to 1.034 during the first 30 days of larval life (Guizien *et al.*, 2020). Given
158 that in summer surface waters are mostly warmer than 20°C across the whole basin,
159 assuming a sinking behaviour for *P. clavata* larvae seems reasonable. However, water
160 temperature in some part of the basin can still be lower than 20°C especially at the
161 beginning of the reproductive season (mid June) or offshore, and the free fall speed of *P.*
162 *clavata* larvae is expected to decrease in colder waters. For these reasons, two ensemble
163 of simulations were performed, one assuming *P. clavata* larvae drift passively as neutrally
164 buoyant particles and another applying a constant sinking speed of 0.5 mm s⁻¹. In the
165 latter case, vertical turbulent diffusion was included to depict settling hindering, while
166 turbulence was neglected in the neutrally buoyant dispersal case.

167 **2.3 Correlation between larval transport and gene flow**

168 **matrices**

169 Larval transport values between *P. clavata* populations in the Ligurian-North Tyrrhenian
170 shelf were calculated as the proportion of particles released during a larval-release event
171 from an origin population that reached a destination population after a given dispersal
172 duration (Pelagic Larval Duration, PLD). Larval transport values were gathered to build
173 connectivity matrices, varying according to PLD, larval-release event and larval buoyancy.
174 Six values of PLD from 3.5 up to 21 days with 3.5 days increments were considered. The
175 duration of each larval-release event was set to three days, yielding a total of ten 3-day
176 events during the 30 days reproductive season of 2004 and 2006.

177 In total, twenty connectivity matrices (ten for each year), each one corresponding to a
178 3-day larval-release event, were built for the two larval buoyancies (neutrally buoyant and
179 sinking) and for the six PLD values, summing up to 240 connectivity matrices. Variances
180 of larval transport values among the seven populations arising from the timing of each
181 larval-release event, larval behaviour or inter-annual variability were computed for each
182 PLD (Briton *et al.*, 2018).

183 Connectivity matrices depicting larval transport for different larval buoyancy, larval-
184 release event and PLD were tested against recent gene flow estimated among the seven
185 populations studied by Padrón *et al.* (2018a). Recent gene flow over the last few genera-
186 tions was calculated on the multilocus genotypes assessed in the seven populations in the
187 form of matrices containing migration rates including a proxy of self-recruitment using
188 the BayesAss 3.0 software (Wilson and Rannala, 2003). As gene flow measures focus on
189 destination population and larval transport measures focus on source populations, com-
190 paring gene flow and larval transport requires data transformation (Padrón *et al.*, 2018b).
191 Hence, gene flow was transformed into the proportion of migrants that left a source pop-
192 ulation and arrived at each destination population and larval transport matrices were
193 normalized by removing the proportion of larvae dispersed outside the seven populations
194 sampled for genetics as this proportion was not included in the gene flow assessment.

195 The significance of the Pearson product-moment correlations between the contempo-
196 rary gene flow and any of the 240 variants of recent larval transport matrices, was tested.
197 A Mantel test (Mantel, 1967) was performed based on the 5040 possible permutations,
198 after modifying the random QAP.m Matlab routine by Rombach (2011). Whenever the
199 Mantel test indicated a significant correlation between the recent gene flow and the larval
200 transport, the determination coefficient was computed. The statistical distribution of
201 the determination coefficients for a same PLD, behaviour and year was described by its
202 quantiles. Highest determination coefficient were used to select the PLDs and buoyancy
203 condition yielding the best agreement between larval transport simulations and gene flow
204 estimates from population genetics observations. All statistical analyses were conducted
205 in Matlab (R2018).

2.4 Analysis of the network formed by Tyrrhenian-Ligurian *P. clavata* populations

The weighted directed network formed by the 18 *P. clavata* populations (nodes) connected by larval transport probabilities (edges) for the PLDs and buoyancy condition yielding the best agreement between larval transport simulations and gene flow estimates was analyzed. Five node metrics taken from graph theory were computed to rank the 18 populations according to different networking features: (1) degree centrality, (2) total strength, (3) clustering coefficient, (4) betweenness centrality and (5) bridging centrality. Degree centrality is the number of connections of a population in the network. Populations displaying more outgoing connections than in-going ones are identified as sources. Total strength is the total larval transport departing or arriving in a population of the network. Populations displaying more outgoing flow than in-going one are identified as sources. Clustering coefficient of a population is the average larval transport within all possible groups of 3 populations involving that population (Fagiolo, 2007). Large values of clustering coefficient depicted those populations with most tightly connected neighbourhood, often called small worlds. Betweenness centrality of a population is the proportion of the network shortest paths that passes through that population. In the case of a larval transport network, shortest path are detected after transforming larval transport probabilities into distances (Costa *et al.*, 2017). Thus, large values of betweenness centrality depicted those populations through which passes the largest larval transport. Bridging centrality is the product of betweenness centrality and bridging coefficient, the latter accounting for the average probability of leaving the direct neighborhood (Woochang *et al.*, 2008). Thus, large values of bridging centrality depicted those populations that are on the border of population cluster and within which larval transport is large. The five metrics were computed for all populations and for the twenty larval transport connectivity matrices variants using the TATOO Matlab toolbox (connecTivity grAph Theory TOOLbox, Andrea Costa vs_2017.12.18 https://www.researchgate.net/profile/Andrea_Costa10, andrea.costa@pusan.ac.kr). Finally, each population of the network was described by two statistics (median and 75 percentile) for each of the five metrics.

235 **3 Results**

236 **3.1 Larval transport for sinking larvae with short PLD** 237 **explains gene flow**

238 Larval behaviour affected the particles spatial distribution, both horizontally and verti-
239 cally, in the dispersal simulations. Neither the neutrally buoyant nor the constant sinking
240 behaviour led to a constant depth distribution of the particles as a function of time. In
241 particular, the sinking particles can be found at different depths along their tracks, de-
242 pending on the larval-release event or year (Supplementary Figure 1). Particles could
243 either spread across the first 100 meters of the water column or aggregate at some spe-
244 cific depths (Supplementary Figure 1). As a result, larval transport values varied largely
245 among simulations with different behaviours, but also between years and larval-release
246 event. The standard deviation of larval transport values among release events reached
247 3 times the mean value in some origin/destination populations pair. The inter-annual
248 variability and the variability due to the different behaviour had the same order of magni-
249 tude. The ratio between the variance of larval transport values between the two years and
250 between the two behaviours ranged from 0.35 to 1.76 depending on the origin/destination
251 populations pair. The median value of this ratio in all populations pairs varied between
252 0.9 and 1 across all PLDs. The variability of larval transport values due to larval-release
253 timing was lower than the one arising from the two aforementioned factors. The ratio
254 between the variance of larval transport values between the two years and among the
255 release events ranged from 1.4 to 4.2, with a median value of about 2 across all PLDs.

256 Larval transport simulated for each behaviour and for each release event were com-
257 pared with the recent gene flow estimated among the seven populations sampled by
258 Padrón *et al.* (2018a). Larval transport for the release event that best correlated (i.e.
259 highest determination coefficient) with gene flow showed high retention (i.e. diagonal
260 elements) for both larval behaviours in agreement with estimated gene flow (Fig.2). How-
261 ever, the two behaviours differed with respect to larval transport among POR, SES, PTM
262 and PRV (i.e. off-diagonal elements). For the neutrally buoyant case, in PRV larval trans-

263 port to PTM in higher than local retention. For the sinking case in contrast, PRV to
264 PTM larval transport was lower than PRV local retention whatever the PLD, as observed
265 in gene flow estimates. Yet, for PLD larger than 7 days other connections appeared in
266 the simulations that are not present in the gene flow estimates mainly between SES and
267 POR. These connections varied in strength with PLD and behaviour.

268 Albeit 2004 and 2006 differed in their hydrodynamical features (Fig.1), the sinking
269 behaviour better explained the estimated gene flow than the neutrally buoyant behaviour
270 in both years (Fig.3). The median determination coefficients between simulations for 3.5-
271 day PLD and gene flow estimates were > 0.9 for the sinking behaviour and < 0.7 for the
272 neutrally buoyant behaviour. The effect of behaviour on the determination coefficient
273 between simulations and observations decreased more rapidly in 2004 than in 2006 as the
274 PLD increased (Fig.3). However, in each year the simulated larval transport after 3.5
275 days with sinking behaviour correlated with gene flow estimates with $R^2 \sim 1$ in at least
276 one larval-release event (whiskers box plot, Fig.3).

277 Hence, the sinking behavior for a 3.5-day PLD was selected to simulate larval transport
278 within the extended network.

279 **3.2 Regional connectivity patterns exhibit both closed and** 280 **open populations**

281 The 18 populations connected by larval transport after 3.5 days with sinking behaviour
282 were divided into two groups: four populations (POR, SES, PTM and PRV) were open,
283 with more than two connections with other populations of the network (Fig.4a). The other
284 14 populations were more closed with maximum one connection with another population
285 (Fig.4a). Among the four open populations the number of connections was limited to a
286 maximum of five (PTM, Fig.4a). Connection intensity further differentiated those four
287 populations from the other 14 as large values of larval transport probabilities occurred
288 frequently among them (Fig.4b). Interestingly, when only the number of connections
289 was considered, PRV was the only source among these four populations while when
290 larval transport probabilities were taken into account, SES appeared as a more important

291 source than PRV. POR and SES total strength varied largely among larval-release events
292 as displayed by the difference between the 50% and 75% percentiles. These four Ligurian
293 populations built up a tightly connected neighbourhood, with POR as the topographical
294 center. The neighborhood was connected to the rest of the network by equally important
295 populations (SES, PTM, PRV, Fig.4c). Among these four populations, SES displayed
296 the largest betweenness centrality (i.e. largest larval transport of the network) but only
297 in < 25% of the larval-release events (Fig.4d). It is worth noting that the large larval
298 transport passing through SES in some larval-release events was not found in gene flow
299 estimates. Surprisingly, comparable larval transport to the one passing in SES was found
300 in one Tyrrhenian population with low number of connections (CPE, Fig.4d).

301 4 Discussion

302 In the present study, we tested the correlation between larval transport simulations and
303 gene flow patterns among *P. Clavata* populations in the Ligurian and Northern Tyrrhe-
304 nian seas accounting for two different buoyancy (neutral and negative). The sinking
305 behaviour established experimentally (Guizien *et al.*, 2020) together with short disper-
306 sal duration was singled out based on consistently higher correlations throughout the
307 entire reproductive period and the two years. Difference in correlations was driven by
308 the prevalence of self-recruitment over transport in *P. Clavata* populations along the
309 Ligurian coast, particularly between Portovenere and Punta Mesco. Larval transport
310 simulations using the sinking behaviour with 3.5-day dispersal duration among a set of
311 known or potential *P. Clavata* populations extending into the Tyrrhenian sea further
312 suggested that population connectivity was limited to the portion of coast comprised
313 between Portovenere and Portofino.

314 Larval transport predictions are now frequently used to explore the functioning of ma-
315 rine populations and help understanding their spatial distribution, thanks to progresses in
316 ocean modelling tools availability and performance (reviewed in Swearer *et al.* 2019). Yet,
317 larval behaviour is still not systematically discussed, with several recent works assuming

318 2D or 3D dispersal without incorporating behaviour (Aguilar *et al.*, 2019; Gamoyo *et al.*,
319 2019; Hidalgo *et al.*, 2019). Even when larval behaviour was included, its added value was
320 very rarely quantitatively assessed. Behaviour effect on larval transport estimates was
321 either explored in sensitivity studies confronting simulations with different hypothetical
322 behaviours (Donahue *et al.*, 2015; Blanco *et al.*, 2019) or in projections studies to inform
323 about populations functioning or management, as a replacement of observations (Munroe
324 *et al.*, 2018; Goodwin *et al.*, 2019; McManus *et al.*, 2020). While some sensitivity studies
325 focused on finding most influential factors between flow and behaviour in larval trans-
326 port estimates (Faillettaz *et al.*, 2018; Kvile *et al.*, 2018), assessing the accuracy of larval
327 transport predictions is more than often qualitative only (Barbut *et al.*, 2019; Crosbie
328 *et al.*, 2019). Yet, quantifying the improvement of larval transport simulations thanks
329 to the incorporation of empirically obtained larval behaviour against independent sets
330 of genetic observations is key to assess the accuracy of larval transport predictions (Bode
331 *et al.*, 2019). However, quantitative assessment of larval transport predictions versus pop-
332 ulation genetics is subject to a number of limitations linked to population demography
333 (Bohonak, 1999). Gene flow inferences at the population level, like the one used in the
334 present study cumulates multiple reproductive events occurring in different demographic
335 context, while larval transport was simulated at the scale of a single-reproductive event.
336 Parentage analysis is potentially the most appropriate genetic metrics to compare with
337 larval transport, provided that larval transport is simulated for the sampled cohort of off-
338 spring (Segura-Garcia *et al.*, 2019). Indeed, comparing parentage analysis of individuals
339 of different ages hence corresponding to different recruitment events with larval trans-
340 port corresponding to a single-reproductive event could potentially fail when recruitment
341 exhibits large temporal variability (Cuif *et al.*, 2015).

342 The present study also pinpoints that inferring larval behaviour from field observa-
343 tions (i.e. genetic analysis, larval vertical distribution) can be misleading. Indeed larval
344 transport depends on its interaction with the ocean flow in the area of observations.
345 Sampling a subset of populations only can jeopardize conclusions (Lowe and Allendorf,
346 2010). For *P. clavata* populations in the Ligurian sea the comparison between gene flow

347 assessment and larval transport simulations could have resulted in very different outcome
348 if the population sampled for the genetic analysis had been Bergeggi, Sestri Levante and
349 Calafuria only. Based on these locations, the simulated connectivity matrices with neu-
350 tral or sinking behavior would have been similar, rendering the test against gene flow
351 inconclusive regarding behaviour importance. Similarly, using larval vertical distribution
352 observed at sea as a behaviour descriptor in simulations should be avoided (Criales *et al.*,
353 2019). Although sinking behavior was simplified in the present simulations to a constant
354 free fall speed neglecting any inter-individual buoyancy variability, the vertical distribu-
355 tion of larvae in the simulations was not constant in space and time. For these reasons,
356 we suggest to document species behaviour independently of ocean flow in a specific set-
357 ting and test its relevancy in different ocean flow conditions (different years or regions,
358 Herbert *et al.* 2012; Blanco *et al.* 2019; Fobert *et al.* 2019).

359 Another reason for confronting larval transport to gene flow with caution is because
360 they do not integrate the same phases along a species life cycle. Indeed, settlement and
361 post-settlement processes can strongly alter the gene flow resulting from larval transport.
362 Among these processes, density-dependent recruitment limitations are frequent in benthic
363 populations due to lack of space (Roughgarden *et al.*, 1985; McGrorty and Goss-Custard,
364 1993). This process likely limited gene flow between healthy and densely populated
365 populations of long-living species such as *P. clavata* and lead to the conclusion that
366 *P. clavata* dispersal potential is in the order of tens of meters (Mokhtar-Jamaï *et al.*,
367 2011). The present study indicates that larval transport of sinking larvae can result in
368 efficient gene flow over a distance of tens of kilometers for a dispersal duration of 3.5
369 days. The good agreement between larval transport and gene flow found in the present
370 study further suggested that the mass mortality events that affected some Ligurian *P.*
371 *clavata* populations enabled to observe the potential for sinking larvae.

372 Environmental mortality processes occurring during dispersal, such as predation, are
373 embedded in the PLD used in larval dispersal simulations. Thus, it is expected that
374 effective PLD incorporated in larval transport simulations should be lower than larval
375 survival expectancy observed in laboratory experiments, in which environmental mortal-

376 ity is limited. The effective PLD leading to best agreement between larval transport and
377 gene flow (3.5 days) was indeed considerably lower than the survival expectancy of 70
378 days reported for *P. clavata* and *E. singularis* larvae (Guizien et al submitted). A similar
379 result was found for the white gorgonian *Eunicella singularis* in the Gulf of Lion (Padrón
380 *et al.*, 2018b). We suggest that comparing larval transport incorporating experimentally
381 documented larval behaviour and gene flow could be a methodology to infer mortality
382 risk at sea, particularly due to predation.

383 In the present study, a same species-specific larval behaviour resulted in different
384 population status in terms of openness or closeness of a population, with different impor-
385 tance with respect to species resilience, reflecting the geographical variations of the flow.
386 When interested in the capacity of a meta-population to recover from disturbance, poorly
387 connected populations are not ideal. Low input from other populations not only limit
388 demographical recovery but also lead to genetic loss because gene sorting process at each
389 reproduction causes a drift to dominant allele (Padrón and Guizien, 2015). In contrast,
390 highly connected networks which are robust to local perturbation, may also spread more
391 rapidly local evolution at a regional scale if a trade-off between local and regional scale
392 resilience exists (Nosil *et al.*, 2009). Migration (gene flow) is generally considered a ho-
393 mogenizing force that limits adaptation (Slatkin, 1987). On the contrary, populations of
394 species with limited dispersal ability among fragmented habitats may evolve local adapta-
395 tion, because gene flow is low. Local adaptation might have positive demographic effects,
396 increasing population fitness and thus reducing the risk of local extinction in stable en-
397 vironments. However, this fragmentation can also have negative effects by limiting the
398 spread of adaptive mutations, and thus constraining adaptation (Cowen and Sponaugle,
399 2009). Non-homogeneous gene flow among *P. Clavata* populations observed in this study
400 may reinforce the stability of the metapopulation in the region, and help explaining the
401 resilience after several local mass mortality events.

402 Non-homogeneous connectivity also poses the question of how to optimize geograph-
403 ically protection measures (e.g. Marine Protected Areas). Results of the present study
404 suggest that current protection measures in the Ligurian sea should be efficient for the

405 conservation of *P. clavata* at a regional scale as they are implemented in locations with
406 high betweenness and bridging centrality. Such properties are expected to be associated
407 in metapopulation to prevailing dispersal pathways and stepping stones, thus playing a
408 key role in populations recovery (Rozenfeld *et al.*, 2008; Trembl *et al.*, 2008). The study
409 pinpoints that Capraia Island could similarly contribute to the network, and thus deserve
410 protection. Finally, larval dispersal models, after validation against gene flow, could be
411 used to explore new connections between known populations and potential habitats, both
412 natural and artificial, regardless of the presence of the species. In particular, connections
413 present in larval transport simulations should not be disregarded even if not visible in
414 gene flow and incorporated in meta-population models. Such procedure would enable to
415 forecast dynamical species distribution resulting from the coupling between local demog-
416 raphy and regional exchange among populations in marine spatial planning scenarios.

417 **5 Supplementary material**

418 Supplementary material is available at the ICESJMS online version of the manuscript.

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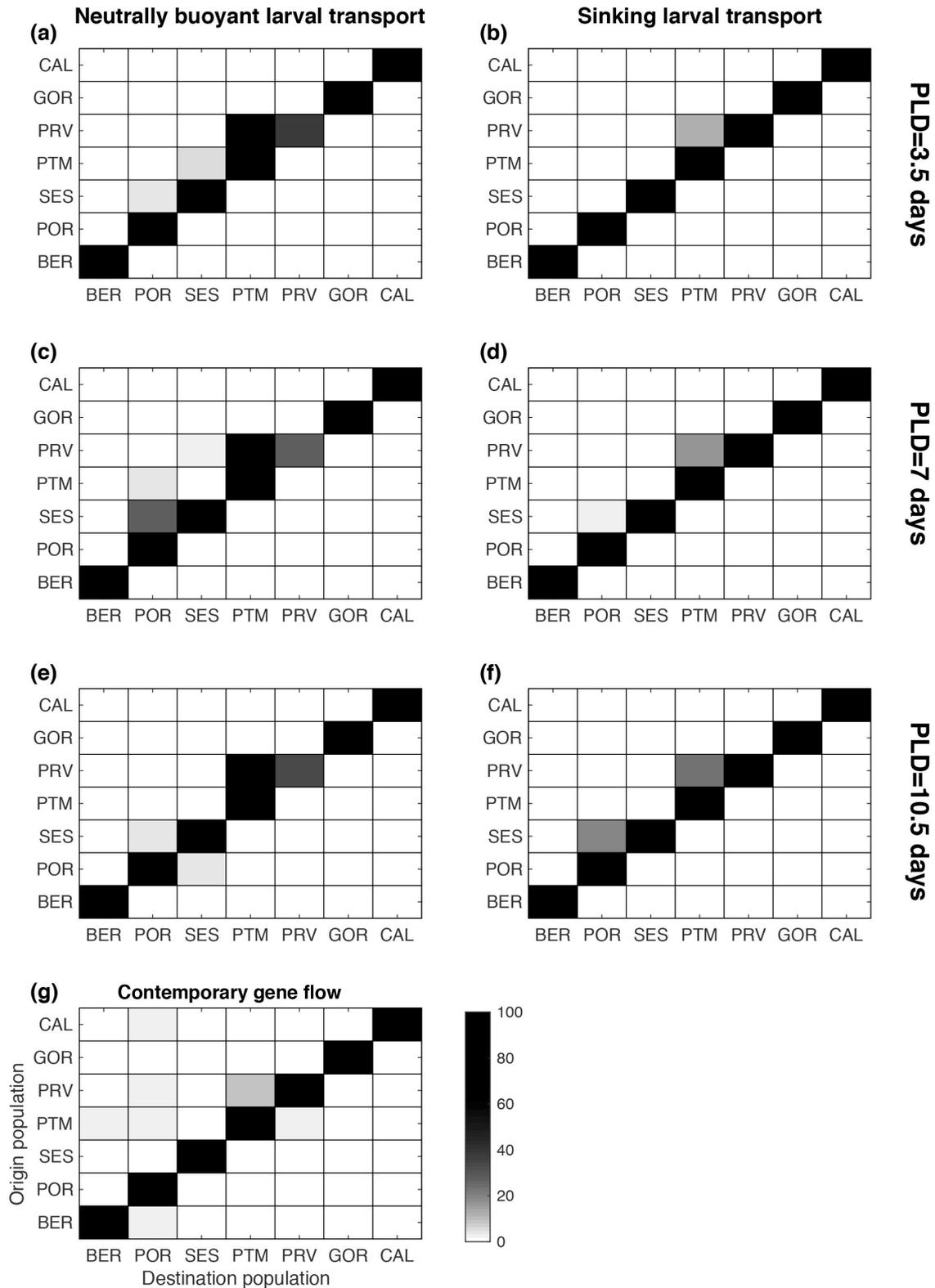


Figure 2: Panels (a,c,e): connectivity matrices for different PLDs for the larval-release event among the neutrally buoyant simulations set with the highest R^2 . Panels (b,d,f): connectivity matrices for different PLDs for the larval-release event among the sinking simulations set with the highest R^2 . Panel (g): observed gene flow among the seven Ligurian-Tyrrhenian populations.

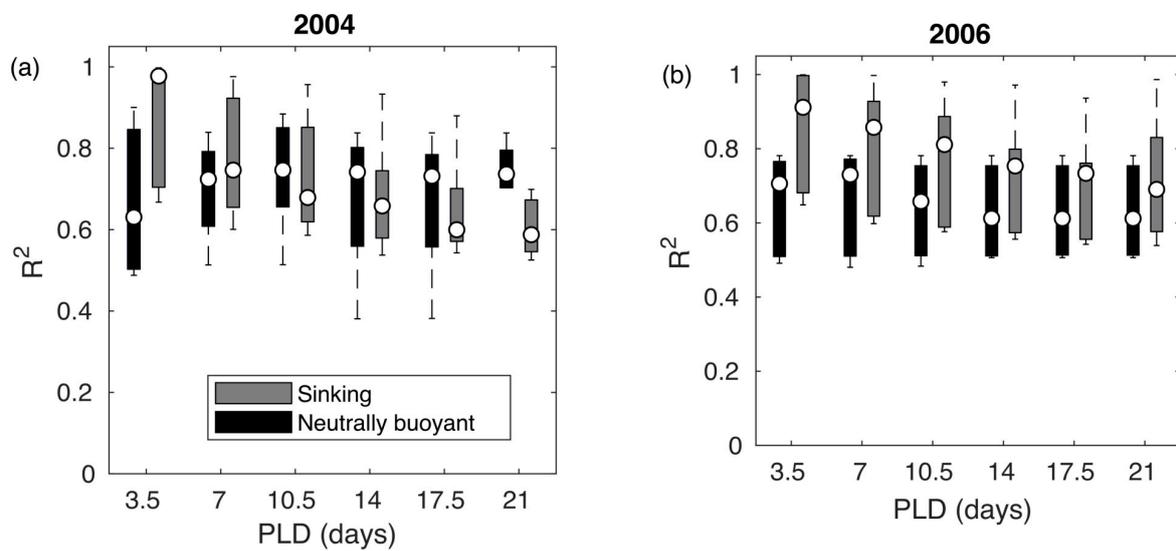


Figure 3: Box plot of the significant determination coefficient (R^2) between larval transport simulations and observed gene flow for different PLDs. Black bars represent neutrally buoyant simulations, grey bars the sinking simulations. Circles inside the bars represent the median value. The determination coefficient is obtained averaging over both 2004 and 2006.

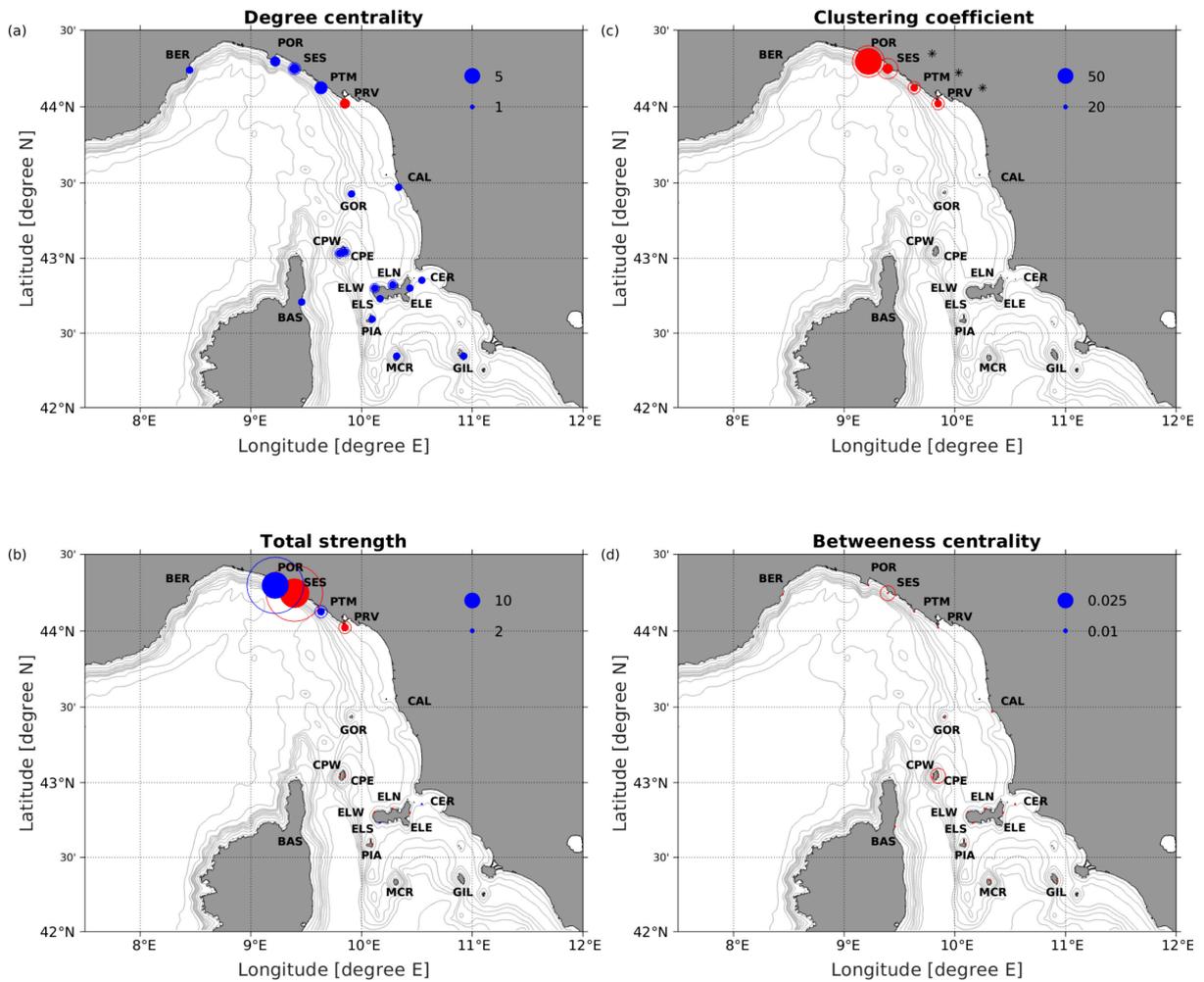


Figure 4: Graph analysis metrics for the complete network of *P. clavata* populations in the Ligurian-Tyrrhenian basin for a PLD of 3.5 days. In all the panels filled circles represent the median value and the contour around each circle represent the 75% percentile. For the panels where two colors are presents, blue (red) circles represent sinks (sources). Panels: (a) Degree centrality; (b) Total strength; (c) clustering coefficient, overlaid bridging centrality (black asterisk); (d) Betweenness centrality.