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Larval buoyancy matters: sinking changes larval transport predictions among *Paramuricea clavata* populations. manuscript for ICES: Journal of Marine Science

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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

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

Larval dispersal simulations require hydrodynamical models to provide a reliable and

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

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

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

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

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

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

2 Material and Methods

2.1 Hydrodynamical simulations in the Northwestern Mediterranean

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

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

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

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

2.2 Larval dispersal simulations

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

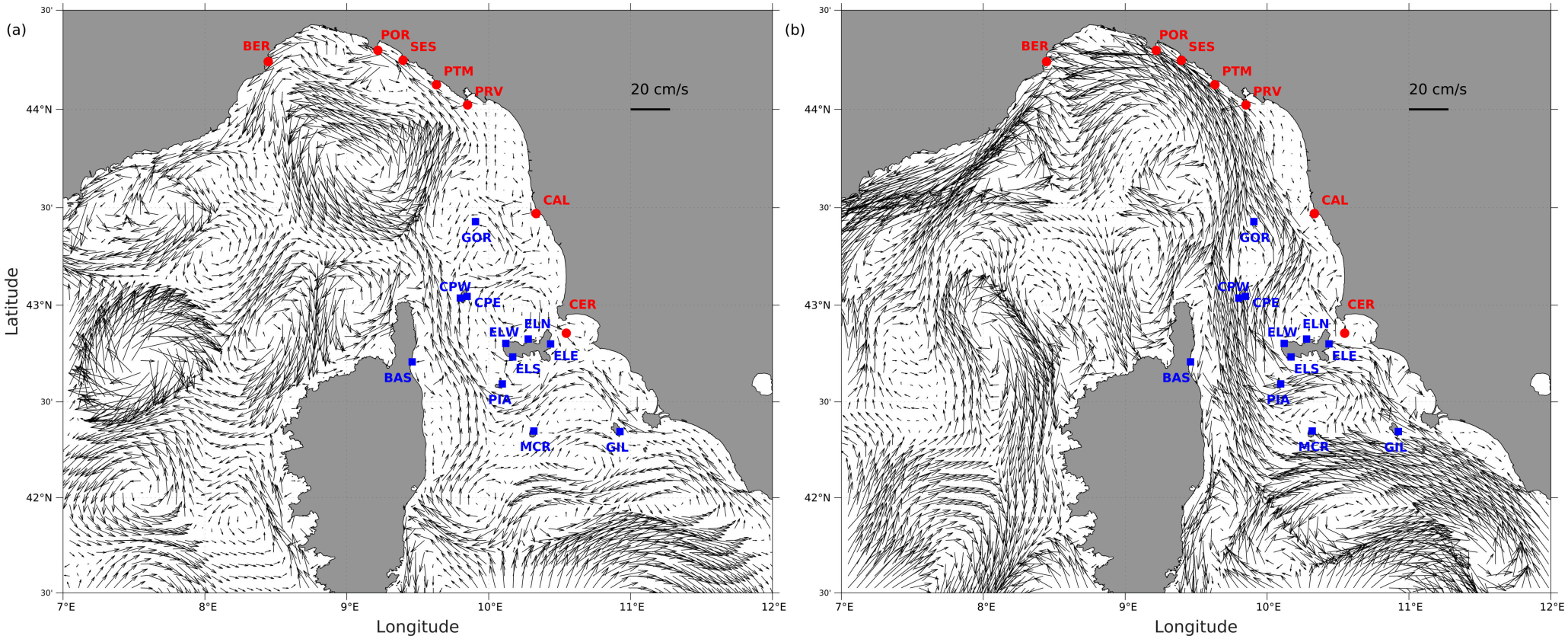


Figure 1: LIME-ROMS depth averaged (0-30 meters) horizontal velocity for the period June 15th-August15th of (a) 2004 and (b) 2006. Overlaid on top of the currents are the populations of *P. clavata* simulated in the larval dispersal sets (Table 1). Red squares represent locations where samples were collected, 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	2 8.9
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.

the coast line (i.e. $\sim$ 3 km) in order to avoid any retention bias due to the numerical boundary layer.

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

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

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

2.3 Correlation between larval transport and gene flow matrices

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

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

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

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

3 Results

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

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

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

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

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

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

3.2 Regional connectivity patterns exhibit both closed and open populations

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

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

4 Discussion

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

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

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

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

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

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

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

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

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

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

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

5 Supplementary material

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

6 Acknowledgments

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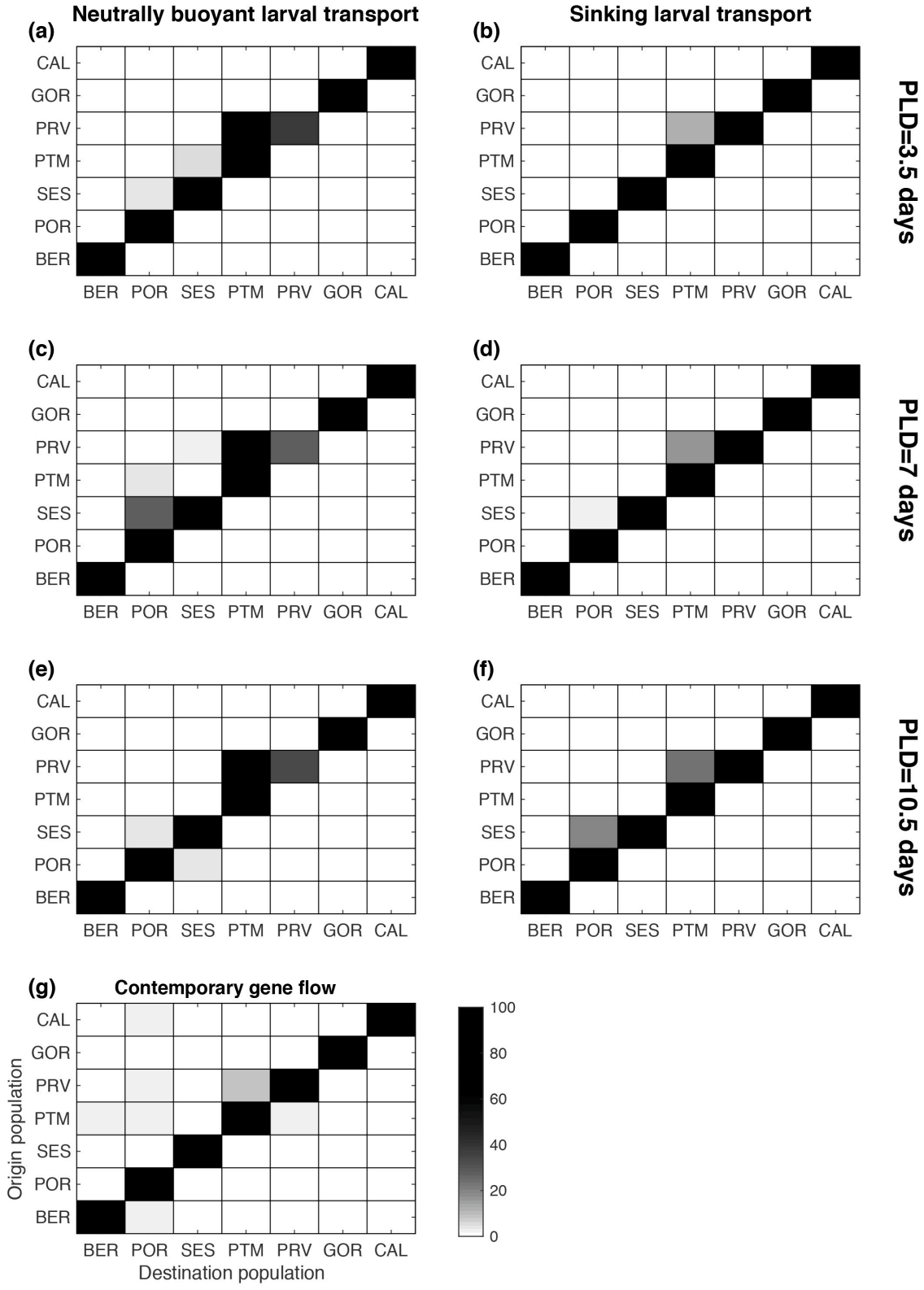


Figure 2: Panels (a,c,e): connectivity matrices for different PLDs for the larval-release event among the neutrally buoyant simulations set with the highest R^2. Panels (b,d,f): connectivity matrices for different PLDs for the larval-release event among the sinking simulations set with the highest R^2.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

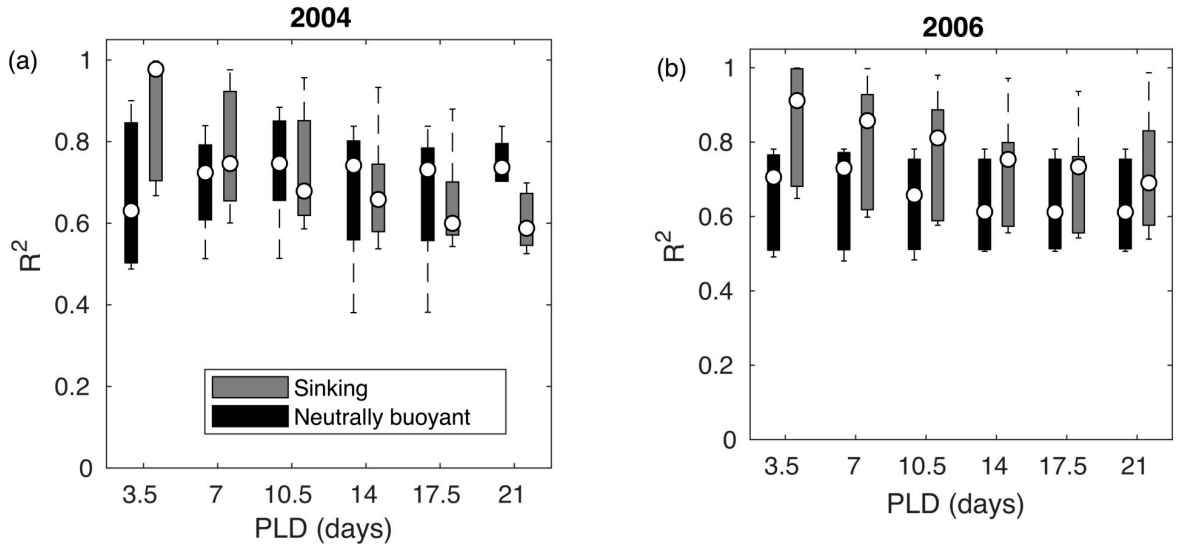


Figure 3: Box plot of the significant determination coefficient (R^2) between larval transport simulations and observed gene flow for different PLDs. Black bars represent neutrally buoyant simulations, grey bars the sinking simulations. Circles inside the bars represent the median value. The determination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

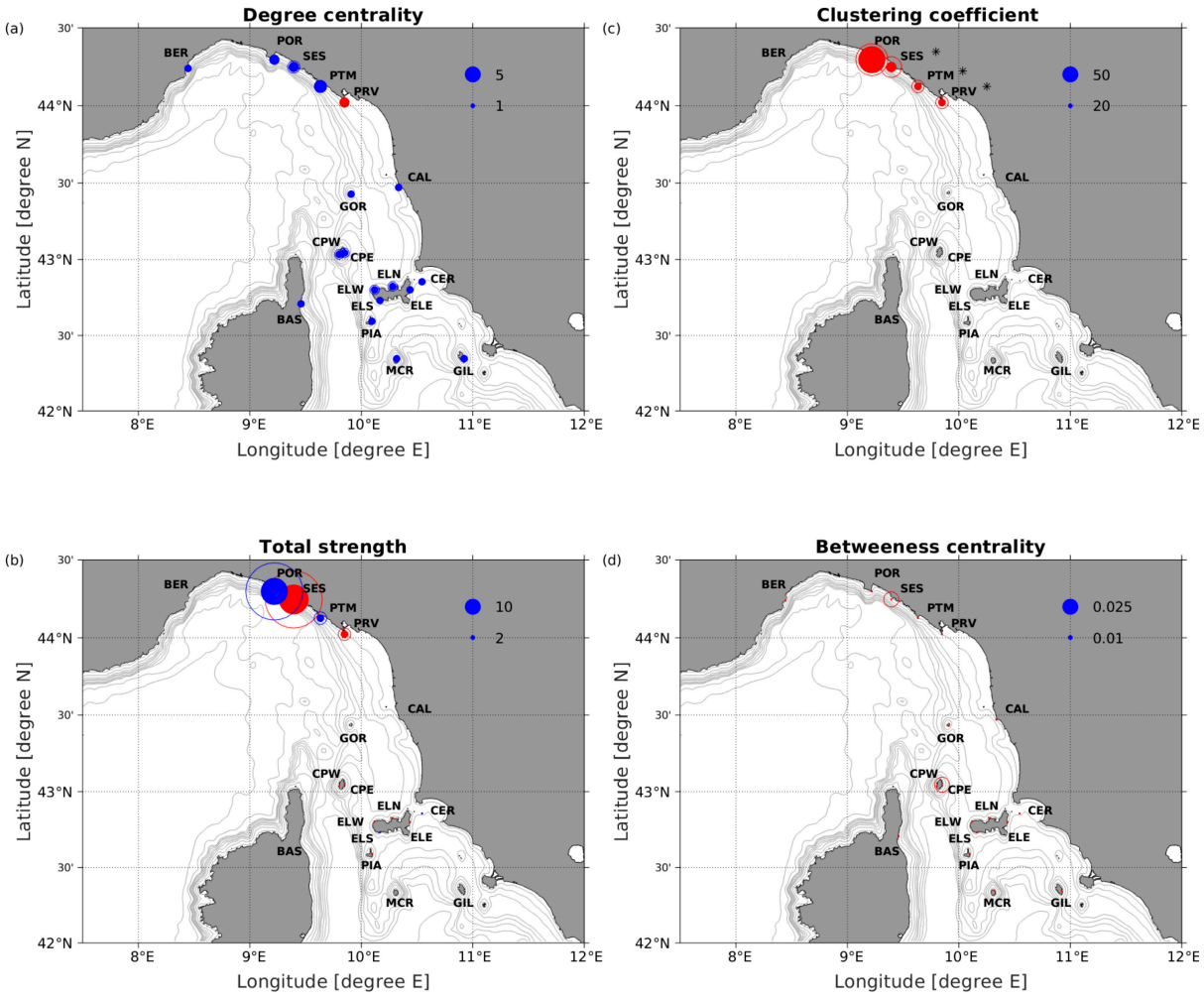


Figure 4: Graph analysis metrics for the complete network of *P. clavata* populations in the Ligurian-Tyrrhenian basin for a PLD of 3.5 days. In all the panels filled circles represent the median value and the contour around each circle represent the 75% percentile. For the panels where two colors are 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.