

THEORETICAL BIOLOGY FORUM

107 · 1-2 / 2014



PISA · ROMA

FABRIZIO SERRA EDITORE

MMXIV

Autorizzazione del Tribunale di Pisa n. 13 del 14 maggio 2012.
Già registrata presso il Tribunale di Genova: registrazione n. 22/96 del 2 maggio 1996.
Direttore responsabile: Fabrizio Serra

★

Amministrazione e abbonamenti
FABRIZIO SERRA EDITORE®
Casella postale n. 1, succursale n. 8, I 56123 Pisa
Uffici di Pisa: Via Santa Bibbiana 28, I 56127 Pisa,
tel. +39 050542332, fax +39 050574888, fse@libraweb.net
Uffici di Roma: Via Carlo Emanuele I, I 00185 Roma,
tel. +39 0670493456, fax +39 0670476605, fse.roma@libraweb.net

★

I prezzi ufficiali di abbonamento cartaceo e/o Online sono consultabili
presso il sito Internet della casa editrice www.libraweb.net.
Print and/or Online official subscription rates are available at Publisher's website www.libraweb.net.

I pagamenti possono essere effettuati tramite versamento su c.c.p. n. 17154550 indirizzato a:
FABRIZIO SERRA EDITORE® o tramite carta di credito (*American Express, Eurocard, Mastercard, Visa*).

*Suscriptions should be paid by cheque/international money order to
Fabrizio Serra editore, casella postale 1, succ. 8, I, 56123 Pisa, or by Bank transfer
(Monte dei Paschi di Siena, IBAN IT90G0103014009000000012660, swift code PASCITM1Y71),
or by credit card (American Express, Eurocard, Mastercard, Visa).*

★

Proprietà riservata · All rights reserved
© Copyright 2014 by Fabrizio Serra editore, Pisa · Roma.
*Fabrizio Serra editore incorporates the Imprints Accademia editoriale,
Edizioni dell'Ateneo, Fabrizio Serra editore, Giardini editori e stampatori in Pisa,
Gruppo editoriale internazionale and Istituti editoriali e poligrafici internazionali.*

www.libraweb.net

A norma del codice civile italiano, è vietata la riproduzione, totale o parziale
(compresi estratti, ecc.), di questa pubblicazione in qualsiasi forma e versione
(comprese bozze, ecc.), originale o derivata, e con qualsiasi mezzo a stampa o internet
(compresi siti web personali e istituzionali, academia.edu, ecc.), elettronico, digitale,
meccanico, per mezzo di fotocopie, pdf, microfilm, film, scanner o altro,
senza il permesso scritto della casa editrice.

*Under Italian civil law this publication cannot be reproduced, wholly or in part (included offprints, etc.),
in any form (included proofs, etc.), original or derived, or by any means: print, internet
(included personal and institutional web sites, academia.edu, etc.), electronic, digital, mechanical,
including photocopy, pdf, microfilm, film, scanner or any other medium,
without permission in writing from the publisher.*

ISSN 2282-2593
ISSN ELETTRONICO 1825-6538

CONTENTS

<i>Editorial</i>	9
ARTICLES	
PIERANNA FIETTA, ELVIRA COSTA, GIOVANNI DELSANTE, <i>Interleukins (ILS), a Fascinating Family of Cytokines. Part I: ILS from IL-1 to IL-19</i>	13
KATELL GUIZIEN, LORENZO BRAMANTI, <i>Modelling Ecological Complexity for Marine Species Conservation: the Effect of Variable Connectivity on Species Spatial Distribution and Age-structure</i>	47
GIANLUCA MARTELLONI, ALISA SANTARLASCI, FRANCO BAGNOLI, GIACOMO SANTINI, <i>Modeling Ant Battles by Means of a Diffusion-Limited Gillespie Algorithm</i>	57
GIULIA MENICHETTI, DANIEL REMONDINI, <i>Entropy of a Network Ensemble: Definitions and Applications to Genomic Data</i>	77
MARCO PELLEGRINI, GIUSEPPE PIRILLO, <i>On the Dinucleotide Circular Codes of Maximum Cardinality</i>	89
SERGIO PENNAZIO, <i>Elements of Plant Physiology in Theophrastus' Botany</i>	97
DUŠAN RISTANOVIĆ, BRATISLAV D. STEFANOVIĆ, NELA PUŠKAŠ, <i>Fractal Analysis of Dendrite Morphology of Rotated Neuronal Pictures: The Modified Box Counting Method</i>	109
ALESSIA ROSSI, SIMONE PANIGADA, MASSIMO ARRIGONI, MARGHERITA ZARNARDELLI, CRISTINA CIMMINO, LUIGI MARANGI, PIERO MANFREDI, GIOVANNI SANTANGELO, <i>Demography and Conservation of the Mediterranean Fin Whale (<i>Balaenoptera physalus</i>): What Clues can be obtained from Photo-Identification Data</i>	123
SUREYYA MERT SELIMOGLU, <i>Conscience Dilemma: to become a Bioengineer or to survive as a Biologist</i>	143
MASOMEH TAHERIAN, MEGERDICH TOOMANIAN, MOHAMMADREZA MOLAEI, <i>A Dynamical Model for Influenza under Seasonal Variables</i>	151
ARMANDO BAZZANI, PAOLO FREGUGLIA, <i>Dynamics on Genes Network Structures. An Ago-Antagonist Approach</i>	163
<i>Instructions for Authors</i>	171

MODELLING ECOLOGICAL COMPLEXITY FOR MARINE SPECIES CONSERVATION: THE EFFECT OF VARIABLE CONNECTIVITY ON SPECIES SPATIAL DISTRIBUTION AND AGE-STRUCTURE

KATELL GUIZIEN · LORENZO BRAMANTI

*Laboratoire d'Ecogéochimie des Environnements Benthiques,
CNRS, Université Paris VI, UMR8222,
Avenue du Fontaulé, F-66651 Banyuls-sur-Mer (France)
E-mail: guizien@obs-banyuls.fr*

CONTENTS: 1. Introduction. 2. Material and Methods. 2.1. Age-class structured metapopulation model for benthic invertebrates. 2.2. Application to the Gulf of Lions: the soft-bottom and the hard-bottom species cases. 2.3. Simulations. 3. Results and Discussion. 4. Conclusive Remarks.

KEYWORDS: Larval dispersal, Metapopulation, Connectivity, Numerical simulation, Age-structure, Spatial distribution, Conservation, MPA.

ABSTRACT: Connectivity is currently emphasized as a key factor in conservation for its role in enhancing biodiversity of an area and giving benefit to the adjacent areas. For most marine species, connectivity is synonymous of larval dispersal. We applied a spatially explicit metapopulation model to test the hypothesis that larval dispersal can affect local demographical features, consequently misleading conservation practice in the marine environment. Simulations were carried out in the Gulf of Lions where coastal circulation displays highly variable tem-

poral and spatial submeso-scale structures. Two different benthic invertebrate species were considered: a soft bottom short lived species and a hard bottom long lived one. In the first case, simulations showed that highest densities at equilibrium do not inform on self-persistent populations location. In the second case, simulations showed that connectivity effects may result in out-of-equilibria demographical structure. We emphasized the caveats in the parameterization of demographical models when local demography is controlled by connectivity.

1. INTRODUCTION

THE role of connectivity in biodiversity resilience (defined as the long-term persistence of species) has been extensively studied theoretically in conservation biology and population ecology. Landscape connectivity is currently emphasized as an essential factor enhancing biodiversity and ecosystem services' [18] and their resilience to climate change [14].

In marine environment, connectivity is more than often arising from larval dispersal by the oceanic flow during reproduction. Due to the ongoing debate on

the best approaches to its estimation, connectivity has not yet been taken into account in the design of conservation measures. Marine connectivity is currently assessed either from genetic diversity structure or parentage analysis using molecular biology techniques or from larval dispersal patterns derived from oceanic circulation simulations.

In the context of conservation, connectivity estimates based on flow simulations are more promising tools. Being *process-based* instead of *state-based*, they enable forecasting connectivity changes as a result of both population and environmental dynamics. Effects of demography on connectivity are crucial in places where conservation measures aim to release a pressure on an ecosystem for which the baseline is unknown. Effects of environment on connectivity are essential in the context of the global climate change, which should modify current circulation patterns in the next century.

Process based dispersal description requires integration between the flow and species biological traits such as spawning timing, pelagic larval duration, motility behavior and mortality [12,7]. In the marine environment, oceanographic connectivity have been estimated on the basis of flow simulations and methods elucidating species persistence on the basis of the only connectivity matrices have been proposed, applying either graph theory [27] or eigenvalues decomposition [15]. However, local demography (recruitment success, adult mortality and fecundity) interacts with the regional spatial structure imposed by ocean circulation, and may compensate for oceanographic connectivity and finally affect density spatial distribution or local demographical structure [20]. Thus, assessing populations persistence requires to integrate oceanographic connectivity and local demography spatial-structure in metapopulation dynamics models.

In this paper, we present results of numerical simulations of the spatio-temporal dynamics of a soft-bottom short-lived polychaete and a hard-bottom long-lived gorgonian in the Gulf of Lions obtained with a generic metapopulation model in which connectivity was the only parameter with a spatial structure and variable in time. A set of different connectivity spatial structures were estimated from larval dispersal simulations and were randomly applied in the metapopulation model to include the inter-annual variability of dispersal that arises from the conjunction of environmental (currents) and biological (spawning timing) variability [13]. The simulations showed that in absence of any spatial structure in local demographical parameters, state variables (spatial distribution of population density, demographical structure) displayed particular features, which may be attributed to local demography.

2. MATERIAL AND METHODS

2.1. Age-class structured metapopulation model for benthic invertebrates

Spatio-temporal dynamics of populations of benthic invertebrate with dispersive pelagic larval stage were simulated after modifying the generic metapopulation model of [15]. The original model describes explicitly, in discrete times and for a set of sites connected by larval transfer, the dynamics of density of individuals for the sedentary adult stage only (FIG. 1). Population density dynamics at a given site

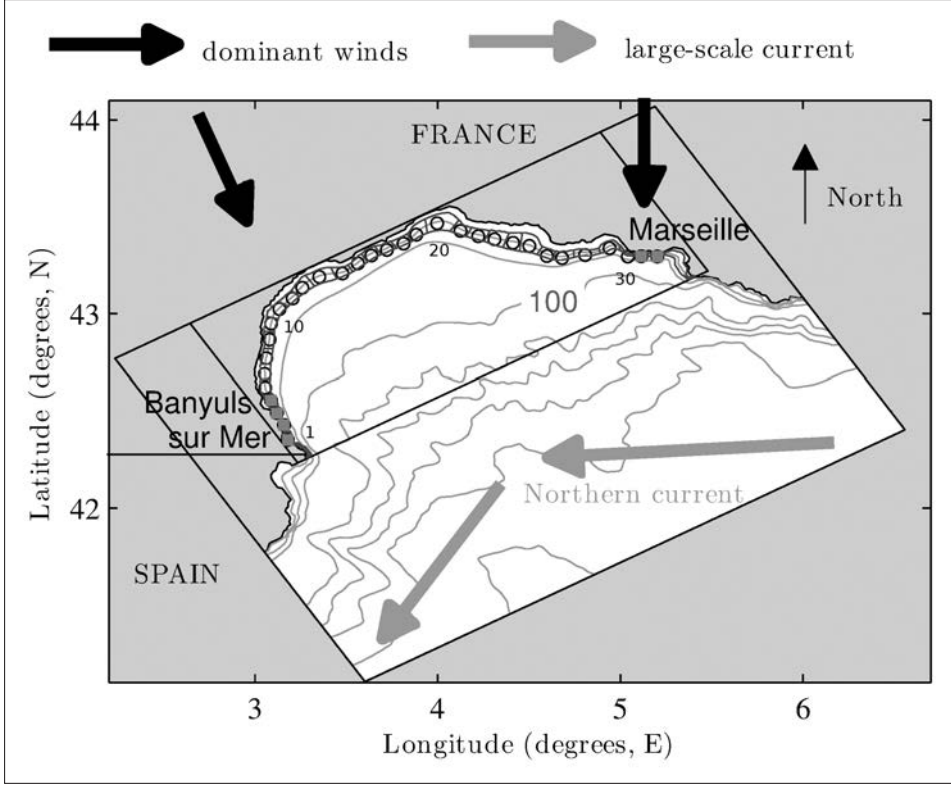


FIG. 1. Gulf of Lions (NW Mediterranean Sea) bathymetric map with depth contour displayed in grey lines (depth contours are 20, 50, 100, 500m and spacing is 500m below 500m deep). The nearshore habitat (depth between 10 and 30 m) was meshed into 32 sites in the center of which (indicated by circles) larvae were released for dispersal computations. Hollow circles indicate release points for short-lived species living in sandy beds while filled squares indicate release points for long-lived species living in hard-bottom. Solid boxes show the extension of the two nested computational domains (1500 m and 750 m resolution grids).

result from spatially structured local survivorship and reproductive success input potentially coming from all the other sites forming the metapopulation. The original model was modified to account for (1) size-structured populations, (2) recruitment limitation because of space availability at the destination site [22] (computed as the proportion of free space based on saturating density of adults $A_{\max} = 1/\alpha_A$, where α_A is the mean cross-sectionnal area of one adult), and (3) the variability in propagule transfer rate.

The model in matricial form is:

$$A(t+1) = \min (r C(t) [A(t) F] + A(t) S, A_{\max}) \quad (1)$$

where $A(t)$ is a matrix $R^p \times R^c$ which elements A_{ij} are the spatial density of individuals in each site $i \in [1, p]$ and of each age class $j \in [1, c]$ at time t , F is a matrix $R^c \times R^c$ [larva per adult] containing the propagule production rate of each age class j (>1 as first

age class are not sexually mature) in first column and zero elsewhere, C is a matrix $R^P \times R^P$ [no units] which elements C_{ki} are the propagule transfer rate from site i to site k , r [adult per larva] is the recruitment success, S [no units] is a matrix $R^C \times R^C$ which elements S_{+i} are survival rate between classes and $(+1)$ i.e. proportion of individuals of class i that survive during a year, and A_{\max} is the site carrying capacity.

Propagule transfer rates are the elements of a connectivity square matrix C and are defined as the proportion of larvae coming from a source site (columns) and arriving at a settlement site (rows), multiplied by the ratio of source to settlement site surfaces. Recruitment success accounts for all mortality losses during the first year, and includes mortality during larval dispersal, settlement and part of juveniles stage.

2.2. Application to the Gulf of Lions: the soft-bottom and the hard-bottom species cases

The Gulf of Lions is a micro-tidal, relatively wide continental shelf, delimited by a steep shelf break along which the northern current flows from East to West (FIG. 1). This large-scale thermohaline flow generates a strong barrier to inputs inside the Gulf, which support the assumption that populations located inside the Gulf form a metapopulation. The Gulf of Lions includes soft-bottom habitat with patches of rocky beds [1]. In order to evidence the effect of variable and spatially structured connectivity on local demography, two species were selected, a short-lived one inhabiting soft-bottom and a long-lived one inhabiting hard-bottom.

The Mediterranean red coral (*Corallium rubrum*) was chosen as hard bottom species case, because an exhaustive work on its population dynamics have been performed [25, 24, 3] and extensive data on its demographic features can be found in literature [9, 26, 23, 4, 2]. It is a long-lived, slow growing precious gorgonian endemic to the Mediterranean and neighboring Atlantic areas (30), distributed in dense monospecific patches within the coralligenous assemblages. Harvesting of colonies due to the hard skeleton used in jewelry industry brought many coastal populations near to local extirpation [2, 24, 28]. Life cycle is composed by a sessile phase and a dispersal larval phase. Adult colonies undergo sexual reproduction and larvae are internally brooded by female colonies. Larval release happens once a year in summer [26]. In the present work we used life table data from [24]. Red coral populations with oldest individuals of 13 years were described by their spatial density in thirteen age classes, fecundity increased with age class from 2 to 250 larvae/colonial individual and survival rate varied not monotonically between 20% and 100%. Recruitment success, which could not be determined from observations lacking the actual number of larvae settling in a site, was set to 10%. Site saturating capacity was set to 70 colonial individuals m^{-2} , based on maximum densities observed in the field.

The polychaete *Ditrupa arietina* is an epifauna free-living serpulid (non-attached) living in sandy beds. It is present along the coasts of the Gulf of Lions (France) and along the Catalan coasts (Spain) between 20m and 30m water depth [11]. Past [17] and ongoing surveys in Banyuls Bay have shown the occurrence of high population densities (up to 20,000 ind m^2) at some sites. However, abundance and population structure exhibit wide temporal and spatial fluctuations, with local extirpations in

the bay of Banyuls-sur-Mer [16]. Most of the life traits of this species in the Gulf of Lions are known [17, 6]. This species has on average a two-year life span after recruitment and most growth occurs during the first year. These worms first reproduce when they are at least one year old. No significant recruitment was observed on the sea bed before March in 2000 and 2001, nor before April in sediment traps from 1993 to 1996. Worm populations were described by their spatial density within a single age classe from 6 months to 2-yr old, fecundity was set to 500 larvae/individual (based on 10^4 eggs/female, a sex ratio of 1:1 and a fertilization rate of 10%) and survival rate was set to 10% based on a 2-year life span. Recruitment success, which could not be determined from observations lacking the actual number of larvae settling in a site, was set to the minimum value enabling metapopulation persistence, that is 3%. Site saturating capacity was set to 25,000 individuals m^{-2} , based on a worm cross-sectional area of $4 \cdot 10^{-5} \text{ m}^2$.

Thirty-two contiguous sites spanning the 10 to 30 m isobaths were defined along the gulf to describe the spatial distribution of the two species (FIG. 1): *Ditrupa arietina* was found in the soft-bottom of all the 32 sites while *Corallium rubrum* was found in the hard-bottom of only 4 sites in the western tip (Banyuls Sur Mer) and 2 sites in the eastern tip (Marseille). The connectivity matrix, with local retention rates on the diagonal, and transfer rates between distant sites outside the diagonal, was quantified from Lagrangian larval dispersal simulations. Simulations of larval dispersal in the Gulf of Lions used three-dimensional currents and turbulent kinetic energy computed at a resolution of $750 \text{ m} \times 750 \text{ m}$ after interpolation between hourly outputs [12]. The Gulf of Lions hydrodynamics is driven by the interaction between strong northern winds, the large-scale northern current and to a lesser extent to density-stratification (either thermal or saline), which results in highly variable coastal upwellings and meso-scale gyres [19, 21]. As wind climate in the Gulf of Lions does not exhibit a marked seasonality but a strong weekly variability, we assumed that wind-driven circulation do not exhibit a marked seasonality, albeit the thermal stratification.

Spawning was simulated by releasing thirty neutrally buoyant larvae in the center of each of the sites forming the metapopulation, on the 20 m isobath, every hour during 100 days in spring [13]. The final positions of larvae after two, three, four and five weeks were processed to compute the proportion of larvae coming from the center of any site which arrives in each of the thirty-two sites. Connectivity matrices were then built for ten consecutive 10-day spawning periods for years 2004 and 2006, and for each of the four different pelagic larval durations.

For the worm *Ditrupa arietina*, composite connectivity matrices were built assuming 50% of larvae had a 4-week pelagic larval duration, and 25% of larvae had a 3-week or 5-week pelagic larval duration, to describe a competency period extending from 3 to 5 weeks [6]. For the coral *Corallium rubrum*, 2-week connectivity matrices were built to describe a competency period peaking at 2-weeks, although this information is uncertain [29, and authors personal observations]. The twenty variant matrices for each species were used to describe the temporal variability of connectivity arising from a conjunction between meteorological variability and the timing of spawning during a reproductive season.

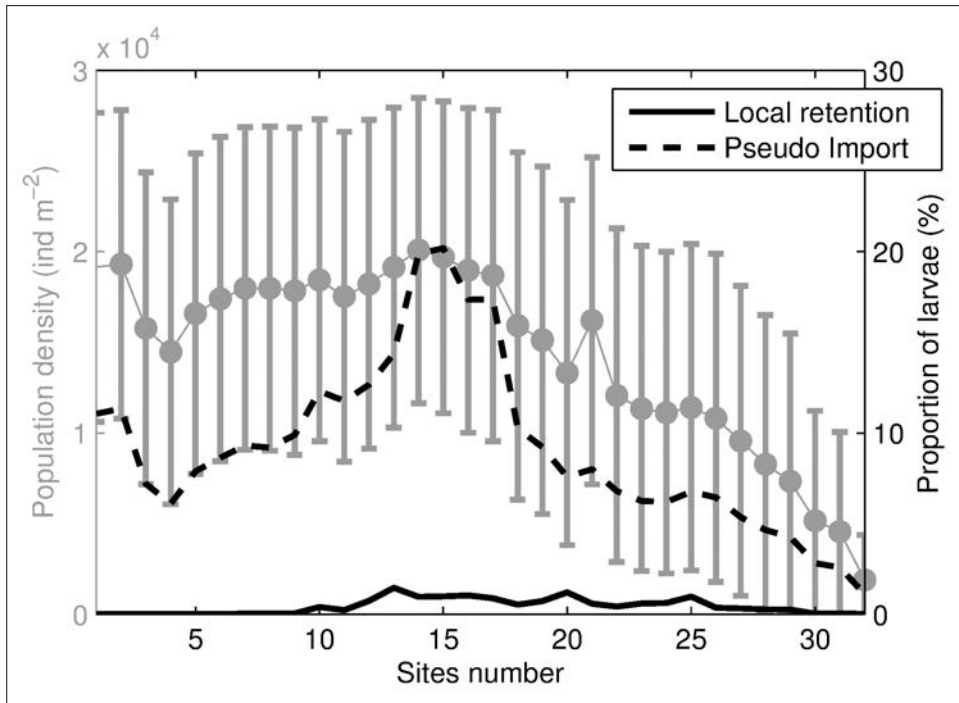


FIG. 2. *Ditrupa arietina* populations density in the 32 sites describing the spatial extent of the Gulf of Lions metapopulation (filled circle, error bars display the standard deviation of population density among 500 stochastic simulations). Local retention rate (solid line) and pseudo-import rate (sum of connectivity matrix rows, dashed line) in the 32 sites averaged over the twenty connectivity matrix variants that were picked up randomly in the stochastic simulations.

2.3. Simulations

For both species, simulations with yearly random selection of the connectivity matrix were carried out over a 100 years, starting with a uniform spatial density equal to the site carrying capacity. For the soft-bottom short-lived species, 100-yr simulations were replicated 500 times to test the relationship between the spatial structure of the average connectivity and the spatial distribution of individuals, averaged over the 500 simulations between year 91 and 100.

3. RESULTS AND DISCUSSION

Using a spatially explicit metapopulation model in the Gulf of Lions, we investigated how the spatio-temporal variability of connectivity affects individuals spatial distribution and generate patterns which may be erroneously attributed to local demographic features.

Results of the simulations for the short-lived species living in sandy beds showed that notwithstanding the same demographic features was applied in all the 32 sites, after 90 years, the populations density along the Gulf of Lions were not similar (FIG.

3). Density were larger in the western part of Gulf of Lions (sites 1 to 16) compared to the eastern part (sites 17 to 32). Interpreting such spatial distribution from a closed population point of view would lead to conclude that either survival, fecundity or local recruitment rate is larger in the western part of the Gulf of Lions, suggesting a better quality of the habitat in this area. In fact, *Ditrupa arietina* is known to exhibit recurrent local extirpations in the western part of the Gulf of Lions due to recruitment failure caused by sediment destabilization during easterly swell [16]. A companion study [13] showed that the short-lived species persistence in the Gulf of Lions would not be threatened by recruitment failure occurring every year in the western area. In fact, large densities were found in western sites (1 to 10) where average local retention rates were very low (sink sites), and particularly lower than between sites 20 and 25, where densities were not as large. Densities were correlated ($R = 0.84$, $p < 0.01$) with the averaged pseudo-import rate that is the sum of connectivity matrix rows (cumulative proportion of settling larvae to a site assuming that population density in all sites was the same). Thus, spatial distribution of the short-lived species do not even reflect self-persistent sites, but only the rescue effect through connectivity as long as the species is present in the region. This example points out a risk in guiding conservation decision from species density spatial distribution, as higher densities may solely depict sink sites, in which conservation of reproducers is completely useless, as densities in those sites is driven by rescue from distant reproductive populations. On the contrary, sites displaying lower densities (site 19 to 21) may be good candidate for self-persistent marine protected areas with a benefit to the entire region through the spreading of individuals [13].

Results of the simulations for the long-lived species living in scarce hard-bottoms showed that notwithstanding the same population dynamics model based on the same demographic features was applied in all the 6 sites, after 20 years the different populations have different structures (FIG. 3). Being the starting conditions and demographic parameters the same for all the sites, the differences in population structure are due to the variability in the connectivity matrix. The sites in Marseille (FIG. 3 E, F) are characterized by higher retention rates and their structure resembles the one of a population in steady state. Among the sites around Banyuls (FIG. 3 A, B, C, D), characterized by lower retention rates, only one present a structure typical of a population in steady state (FIG. 3 C) while the others are characterized by different structures (FIG. 3 A, B, D). It is worth to notice that the outcome showed in FIG. 3, if examined in a population dynamics framework, namely not considering the existence of a metapopulation, could have been interpreted in a different way.

In a population dynamics framework, where population is considered demographically closed, shapes of population structure such as the ones showed in FIG. 3, could be interpreted as a result of local events. Population C, E and F could have been considered as populations in steady state, not affected by any disturbance since at least 13 years (the life span of the population). The structure of population A could have been interpreted as the effect of a heavy harvesting almost destroying the entire population. The structure of population B could have suggested a heavy harvesting happened after the reproductive period, as suggested by the peak in the recruitment class (FIG. 3 B). Finally, the structure of population D, with classes 3

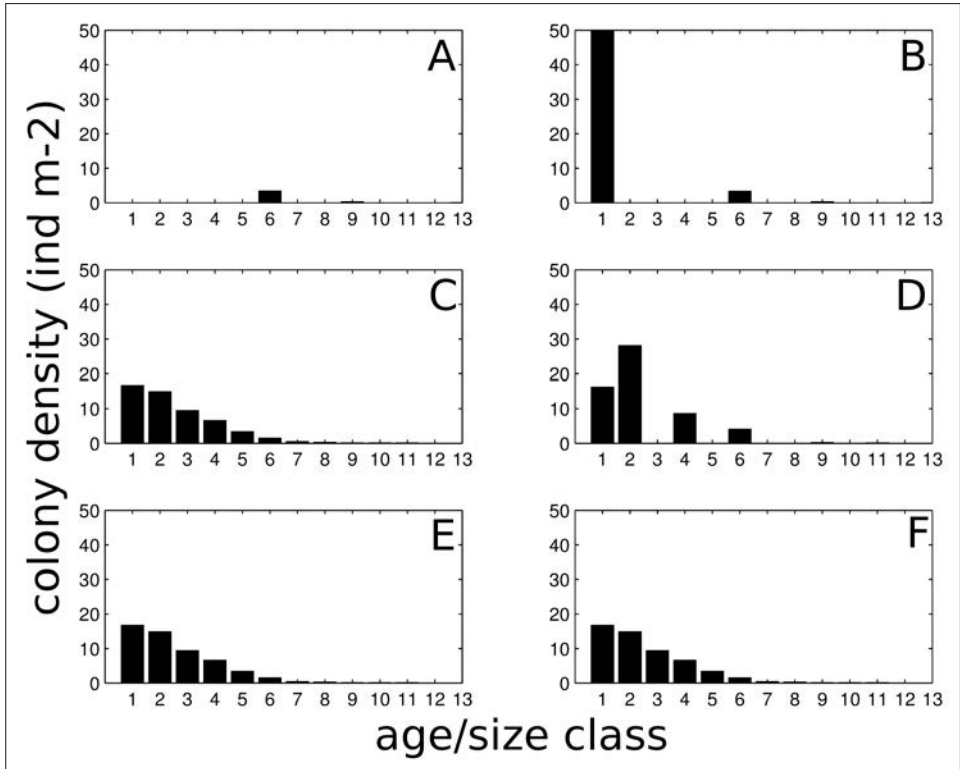


FIG. 3. Population structure (density of colony for each age/size class) after 20 years in Banyuls sites (A, B, C, D) and Marseille sites (E, F).

and 5 missing, could have been interpreted as a result of a recruitment failure in two years, putatively due to an increase in water temperature during the period of settlement. This scenario really happened in 1999 and 2003 in the northern ligurian sea when the temperature increase of the water column in September resulted in a reduced recruitment rate [10, 8, 5].

4. CONCLUSIVE REMARKS

Our results showed that connectivity can affect population spatial distribution and demographic structure, which could be locally misinterpreted if the existence of a metapopulation system is not taken into account. Our conclusions suggest that metapopulation framework have to be taken into account when planning conservation and/or management plans.

ACKNOWLEDGMENTS

We thank METEO FRANCE for supplying atmospheric forcings and the Banque Hydro for supplying rivers discharge data for hydrodynamical simulations. We thank

the national platform Sirocco and P. Marsaleix for its support in the hydrodynamical simulations set up.

This work was funded by the French National Program LITEAU IV of the Ministère de l'Ecologie et de l'Environnement Durable under project RocConnect – Connectivité des habitats rocheux fragmentés du Golfe du Lion (de Marseille au Cap de Creus) et son rôle dans la persistance régionale de trois espèces de gorgonaires (PI, K. Guizien, Project Number 12-MUTS-LITEAU-1-CDS-013).

LITERATURE CITED

1. Aloisi JC, Got H, Monaco A. *Carte géologique du précontinent languedocien au 1/250000^{ième}*. Enschede (Netherlands): International Institute for Aerial survey and Earth sciences (ITC); 1973.
2. Bramanti L, Vielmini I, Rossi S, Tsounis G, Iannelli M, Cattaneo-Vietti R, Priori C, Santangelo G. *Demographic parameters of two populations of red coral (Corallium rubrum) in the North Western Mediterranean*. Marine Biology. 2014. Doi: 10.1007/s00227-013-2383-5.
3. Bramanti L, Santangelo G, Iannelli M. *Mathematical modelling for conservation and management of gorgonians corals: young and olds, could they coexist?* Ecological Modelling. 2009; 20 (21): 2851-2856.
4. Bramanti L, Rossi S, Tsounis G, Gili JM, Santangelo G. *Settlement and early survival of red coral on settlement plates: some clues for demography and restoration*. Hydrobiologia. 2007; 580: 219-224.
5. Bramanti L, Magagnini G, De Maio L, Santangelo G. *Recruitment, early survival and growth of the Mediterranean red coral Corallium rubrum (L 1758), a 4-year study*. Journal of Experimental Marine Biology and Ecology. 2005; 314: 69-78.
6. Charles F, Jordana E, Amouroux JM, Grémare A, Desmalades M, Zudaire L. *Reproduction, recruitment and larval metamorphosis in the serpulid polychaete Ditrupa arietina (O.F. Müller)*. Estuarine, Coastal and Shelf Science. 2003; 57, 435-443.
7. Cowen RK, Sponaugle S. *Larval dispersal and marine population connectivity*. Annual Review of Marine Science. 2009; 1, 443-466.
8. Garrabou J, Coma R, Bensoussan N, Chevaldonné P et alii. *Mass mortality in NW Mediterranean rocky benthic communities: effects of the 2003 heat wave*. Glob Change Biol. 2009; 15: 1090-110.
9. Garrabou J, Harmelin JG. *A 20-year study on life-history traits of a harvested long-lived temperate coral in NW Mediterranean: insights into conservation and management needs*. J An Ecol. 2002; 71: 966-978.
10. Garrabou J, Perez T, Sartoretto S, Harmelin JG. *Mass mortality event in red coral Corallium rubrum populations in the Provence region (France, NW Mediterranean)*. Mar Ecol Prog Ser. 2001; 217: 263-272.
11. Grémare A, Sardà R, Medernach L, Jordana E, Pinedo S, Amouroux JM, Martin D, Nozais C, Charles F. *On the dramatic increase of Ditrupa arietina O.F. Müller (Annelida: Polychaeta) along the French and Spanish Catalan coasts*. Est Coast Shelf Sci. 1998; 47, 447-457.
12. Guizien K, Brochier T, Duchêne J-C, Koh B-S, Marsaleix P. *Dispersal of Owenia fusiformis larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a three-dimensional stochastic model*. Marine Ecology Progress Series. 2006; 311, 47-66.
13. Guizien K, Belharet M, Guarini JM, Moritz C. *Marine benthic metapopulations vulnerability: implications of spatially structured connectivity for conservation practice*. Divers. Distrib. 2014; 20: 1392-1402.

14. Heller NE, Zavaleta ES. *Biodiversity management in the face of climate change: a review of 22 years of recommendation*. Biol. Cons. 2009; 142, 14-32.
15. Hastings A, Botsford LW. *Persistence of spatial populations depends on returning home*. Proc Nat Acad Sci. 2006; 103(15): 6067-6072.
16. Labruno C, Grémare A, Guizien K, Amouroux JM. *Long-term comparison of soft bottom macrobenthos in the bay of Banyuls-sur-mer (Northwestern Mediterranean sea): a reappraisal*. J Sea Res. 2007; 58, 125-143.
17. Medernach L, Jordana E, Grémare A, Nozais C, Charles F, Amouroux JM. *Population dynamics, secondary production and calcification in a Mediterranean population of Ditrupa arietina (Annelida: Polychaeta)*. Mar Ecol Prog Ser. 2000; 199, 171-184.
18. Millennium Ecosystem Assessment. *Ecosystems and Human well-being: Biodiversity synthesis*. Washington, DC: World Resources Institute; 2005.
19. Millot C. *The Gulf of Lion's hydrodynamics*. Continental Shelf Research. 1990; 10(9-11): 885-894.
20. Moilanen A. 2011. *On the limitations of graph-theoretic connectivity in spatial ecology and conservation*. J. App. Ecol. 2011; 48, 1543-1547.
21. Petrenko A, Leredde Y, Marsaleix P. 2005. *Circulation in a stratified and wind-forced Gulf of Lions, NW Mediterranean Sea: in situ and modeling data*. Continental Shelf Research. 2005; 25(1): 7-27.
22. Roughgarden J, Isawa Y, Baxter C. *Demographic theory for an open marine population with space-limited recruitment*. Ecology. 1985; 66: 54-67.
23. Santangelo G, Bramanti L, Rossi S, Tsounis G, Vielmini I, Lott C, Gili JM. *Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral Corallium rubrum*. Journal of Experimental Marine Biology and Ecology. 2012; 411: 7-13.
24. Santangelo G, Bramanti L, Iannelli. *Population dynamics and conservation biology of the over-exploited Mediterranean Red coral*. Journ Theor Biol. 2007; 244: 416-423.
25. Santangelo G, Maggi E, Bramanti L, Bongiorno L. *Demography of the overexploited Mediterranean red coral (Corallium rubrum L. 1758)*. Scientia Marina. 2004; 67 (Suppl 3): 199-204.
26. Santangelo G, Carletti E, Maggi E, Bramanti L. *Reproduction and population of the sexual structure of the overexploited Mediterranean red coral Corallium rubrum*. Mar. Ecol. Prog. Ser. 2003; 248: 99-108.
27. Treml EA, Halpin PN, Urban DL, Pratson LF. *Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation*. Landscape Ecology. 2008; 23: 19-26.
28. Tsounis G, Rossi S, Bramanti L, Santangelo G. *Management hurdles for sustainable harvesting of Corallium rubrum*. Marine Policy. 2013; 39: 361-364.
29. Vighi M. *Etude sur la reproduction du Corallium rubrum (L.)*. Vie et Milieu. 1972; 23: 21-32.
30. Zibrowius H, Montero M, Grasshoff M. *La ripartition du Corallium rubrum dans l'Atlantique*. Thetis. 1984; 11: 163-170.

SET IN DANTE MONOTYPE BY
FABRIZIO SERRA EDITORE, PISA · ROMA.
PRINTED AND BOUND BY
TIPOGRAFIA DI AGNANO, AGNANO PISANO (PISA).

★

December 2014

(CZ 2 · FG 21)



