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On the Calculation of Betweenness Centrality in Marine Connectivity Studies Using Transfer Probabilities

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Abstract

Betweenness has been used in a number of marine studies to identify portions of sea that sustain the connectivity of whole marine networks. Herein we highlight the need of methodological exactness in the calculation of betweenness when graph theory is applied to marine connectivity studies based on transfer probabilities. We show the inconsistency in calculating betweeness directly from transfer probabilities and propose a new metric for the node-to-node distance that solves it. Our argumentation is illustrated by both simple theoretical examples and the analysis of a literature data set.

Introduction the set of the set of

In the last decade, graph theory has increasingly been used in ecology and conservation studies $[1]$ and particularly in marine connectivity studies $(e.g., [2] [3] [4] [5] [6])$. Graphs are a mathematical representation of a network of entities (called nodes) linked ⁴ by pairwise relationships (called edges). Graph theory is a set of mathematical results $\frac{5}{5}$ that permit to calculate different measures to identify nodes, or set of nodes, that play ⁶ specific roles in a graph (e.g., $[7]$). Graph theory application to the study of marine connectivity typically consists in the representation of portions of sea as nodes. Then, ⁸ the edges between these nodes represent transfer probabilities between these portions of ⁹ \mathbf{s} ea. 10

Transfer probabilities estimate the physical dispersion of propagula [5] [9] [10] [11], $\frac{11}{2}$ nutrients or pollutants $[12]$, particulate matter $[13]$, or other particles either passive or $\frac{12}{2}$ interacting with the environment (see $[14]$ [15] and references therein). As a result, graph theory already proved valuable in the identification of hydrodynamical ¹⁴ provinces $[6]$, genetic stepping stones $[16]$, genetic communities $[4]$, sub-populations $[10]$, 15 and in assessing Marine Protected Areas connectivity [5].

In many marine connectivity studies, it is of interest to identify specific portions of 17 sea where a relevant amount of the transfer across a graph passes through. A well-known graph theory measure is frequently used for this purpose: betweenness $\frac{1}{19}$ centrality. In the literature, high values of this measure are commonly assumed to ²⁰ identify nodes sustaining the connectivity of the whole network. For this reason a high $_{21}$ value of betweenness has been used in the framework of marine connectivity to identify $\frac{2}{2}$ migration stepping stones $[2]$, genetic gateways $[16]$, and marine protected areas $\frac{23}{2}$ ensuring a good connectivity between them $[5]$.

Our scope in the present letter is to highlight some errors that can occur in ²⁵ implementing graph theory analysis. Especially we focus on the definition of edges when $_{26}$ one is interested in calculating the betweenness centrality and other related measures. 27 We also point out two papers in the literature in which this methodological $_{28}$ inconsistency can be found: [3] and [5]. $\frac{29}{29}$

In Materials and Methods we introduce the essential graph theory concepts for our $\frac{30}{20}$ scope. In Results we present our argument on the base of the analysis of a literature $\frac{31}{10}$ data set. In the last Section we draw our conclusions. $\frac{32}{2}$

$\mathbf{Materials} \text{ and } \mathbf{Methods} \qquad \qquad \text{33}$

A simple graph G is a couple of sets (V, E) , where V is the set of nodes and E is the set $\frac{34}{4}$ of edges. The set V represents the collection of objects under study that are pair-wise $\frac{35}{25}$ linked by an edge a_{ij} , with $(i,j) \in V$, representing a relation of interest between two of \bullet these objects. If $a_{ij} = a_{ji}$, $\forall (i,j) \in V$, the graph is said to be 'undirected', otherwise it \equiv is 'directed'. The second case is the one we deal with when studying marine $\frac{38}{100}$ connectivity, where the edges' weights represent the transfer probabilities between two ³⁹ zones of sea $(e.g., [3] [4] [5] [6])$.

If more than one edge in each direction between two nodes is allowed, the graph is 41 called multigraph. The number of edges between each pair of nodes (i,j) is then called 42 multiplicity of the edge linking i and j .

The in-degree of a node k, $deg^+(k)$, is the sum of all the edges that arrive in k: $deg^+(k) = \sum_i a_{ik}$. The out-degree of a node k, $deg^-(k)$, is the sum of all the edges that 45 start from k: $deg^{-}(k) = \sum_{j} a_{kj}$. The total degree of a node k, $deg(k)$, is the sum of the 46 in-degree and out-degree of k: $deg(k) = deg^{+}(k) + deg^{-}(k)$.

In a graph, there can be multiple ways (called paths) to go from a node i to a node j $\frac{4}{9}$ passing by other nodes. The weight of a path is the sum of the weights of the edges $\frac{50}{50}$ composing the path itself. In general, it is of interest to know the shortest or fastest $\frac{51}{100}$ path σ_{ij} between two nodes, i.e. the one with the lowest weight. But it is even more \sim instructive to know which nodes participate to the greater numbers of shortest paths. In $\frac{53}{10}$ fact, this permits to measure the influence of a given node over the spread of $\frac{54}{54}$ information through a network. This measure is called betweenness value of a node in $\frac{55}{55}$ the graph. The betweenness value of a node k, $BC(k)$, is defined as the fraction of \sim shortest paths existing in the graph, σ_{ij} , with $i \neq j$, that effectively pass through k, σ_{ij} $\sigma_{ij}(k)$, with $i \neq j \neq k$:

$$
BC(k) = \sum_{i \neq k \neq j} \frac{\sigma_{ij}(k)}{\sigma_{ij}} \tag{1}
$$

with $(i,j,k) \in V$. Note that the subscript $i \neq k \neq j$ means that betweenness is not s influenced by direct connections between the nodes. Betweenness is then normalized by \sim the total number of possible connections in the graph once excluded node k : $\frac{61}{100}$ $(N-1)(N-2)$, where N is the number of nodes in the graph, so that $0 \le BC \le 1$.

Although betweenness interpretation is seemingly straightforward, one must be careful in its calculation. In fact betweenness interpretation is sensitive to the node-to-node metric one chooses to use as edge weight. If, as frequently the case of the ϵ marine connectivity studies, one uses transfer probabilities as edge weight, betweenness σ loses its original meaning. Based on additional details –personally given by the authors $\overline{68}$

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of [3] and [5]– on their methods, this was the case in those studies. In those cases, edge \bullet weight would decrease when probability decreases and the shortest paths would be the π sum of edges with lowest value of transfer probability. As a consequence, high $\frac{71}{71}$ betweenness would be associated to the nodes through which a high number of $\frac{72}{2}$ improbable paths pass through. Exactly the opposite of betweenness original purpose. $\frac{73}{2}$ Hence, defining betweenness using Equation 1 (the case of $[3]$ and $[5]$) leads to an inconsistency that affects the interpretation of betweenness values.

Alternative definitions of betweenness accounting for all the paths between two $\frac{76}{6}$ nodes and not just the most probable one have been proposed to analyze graphs in η which the edge weight is a probability $[8]$ and avoid the above inconsistency.

Herein, we propose to solve the inconsistency when using the original betweenness $\frac{80}{20}$ definition of transfer probabilities by using a new metric for the edge weights instead of $\frac{1}{81}$ modifying the betweenness definition. The new metric transforms transfer probabilities $\frac{1}{2}$ a_{ij} into a distance in order to conserve the original meaning of betweenness, by ensuring \approx that a larger transfer probability between two nodes corresponds to a smaller $\frac{84}{100}$ node-to-node distance. Hence, the shortest path between two nodes effectively is the $\frac{1}{1000}$ most probable one. Therefore, high betweenness is associated to the nodes through $\frac{86}{100}$ which a high number of probable paths pass through.

In the first place, in defining the new metric, we need to reverse the order of the 88 probabilities in order to have higher values of the old metric a_{ij} correspond to lower \bullet values of the new one. In the second place we also consider three other facts: (i) transfer \sim probabilities a_{ij} are commonly calculated with regards to the position of the particles $\frac{91}{2}$ only at the beginning and at the end of the advection period; (ii) the probability to go $\frac{92}{2}$ from i to j does not depend on the node the particle is coming from before arriving in i; $\frac{1}{93}$ and (iii) the calculation of the shortest paths implies the summation of a variable ⁹⁴ number of transfer probability values. Note that, as the a_{ij} values are typically $\qquad \qquad$ calculated on the base of the particles' positions at the beginning and at the end of a \qquad 96 spawning period, we are dealing with paths whose values are calculated taking into $\frac{97}{97}$ account different numbers of generations. Therefore, the transfer probabilities between $\frac{98}{960}$ sites are independent from each other and should be multiplied by each other when $\frac{99}{99}$ calculating the value of a path. Nevertheless, the classical algorithms commonly used in $_{100}$ graph theory analysis calculate the shortest paths as the summation of the edges 101 composing them (e.g., the Dijkstra algorithm, [17] or the Brandes algorithm [18]). $_{102}$ Therefore, these algorithms, if directly applied to the probabilities at play here, are $\frac{103}{200}$ incompatible with their independence.

A possible workaround could be to not use the algorithms in [17] and [18] and use ¹⁰⁵ instead the 10^{th} algorithm proposed in [19]. Therein, the author suggests to define the $_{106}$ betweenness of a simple graph via its interpretation as a multigraph. He then shows 107 that the value of a path can be calculated as the product of the multiplicities of its $\frac{1}{108}$ edges. When the multiplicity of an edge is set equal to the weight of the corresponding 109 edge in the simple graph, one can calculate the value of a path as the product of its $\frac{110}{20}$ edges' weights a_{ij} . However, this algorithm selects the shortest path on the basis of the \Box number of steps (or hop count) between a pair of nodes (Breadth-First Search 112 algorithm $[20]$. This causes the algorithm to fail in identifying the shortest path in $\frac{1}{113}$ some cases. For example, in Fig 1 it would identify the path ACB (2 steps with total $_{114}$ probability 1×10^{-8}) when, instead, the most probable path is ADEB (3 steps with 115 total probability 1×10^{-6}). See Table 1 for more details.

However, by changing the metric used in the algorithms, it is possible to calculate 118 the shortest path in a meaningful way with the algorithms in $[17]$ and $[18]$. In 119 particular, we propose to define the weight of an edge between two nodes i and j as: $\frac{120}{20}$

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Fig 1. Example of graph in which the 10^{th} algorithm in [19] would fail to identify the shortest path between A and B (ADEB) when using a_{ij} as metric.

$$
d_{ij} = \log\left(\frac{1}{a_{ij}}\right) \tag{2}
$$

This definition is the composition of two functions: $h(x) = 1/x$ and $f(x) = \log(x)$. 121 The use of $h(x)$ allows one to reverse the ordering of the metric in order to make the 122 most probable path the shortest. The use of $f(x)$, thanks to the basic properties of 123 logarithms, allows the use of classical shortest-path finding algorithms while dealing $_{124}$ correctly with the independence of the connectivity values. In fact, we are $de\ facto$ 125 calculating the value of a path as the product of the values of its edges. 126

It is worth mentioning that the values $d_{ij} = \infty$, coming from the values $a_{ij} = 0$, do 127 not influence the calculation of betweenness values via the Dijkstra and Brandes 128 algorithms. Note that d_{ij} is additive: $d_{il} + d_{lj} = \log\left(\frac{1}{a_{il} \cdot a_{lj}}\right) = \log\left(\frac{1}{a_{ij}}\right) = d_{ij}$, for any 129 $(i,l,j) \in V$ thus being suitable to be used in conjunction with the algorithms proposed 130 by [17] and [18]. Also, note that both a_{ij} and d_{ij} are dimensionless. 131

Equation 2 is the only metric that allows to consistently apply the algorithms in $[17]$ 132 and $\left|18\right|$ to transfer probabilities. Other metrics would permit to make the weight $\frac{133}{133}$ decrease when probability increases: for example, $1 - a_{ij}$, $1/a_{ij}$, $-a_{ij}$, $\log(1 - a_{ij})$. 134 However, the first three ones do not permit to account for the independence of the ¹³⁵ transfer probabilities along a path. Furthermore, $log(1 - a_{ij})$ takes negative values as 136 $0 \le a_{ij} \le 1$. Therefore, it cannot be used to calculate shortest paths because the 137 algorithms in [17] and [18] would either endlessly go through a cycle (see Fig 2a and ¹³⁸ Table 2) or choose the path with more edges (see Fig 2b and Table 2), hence arbitrarily $_{139}$ lowering the value of the paths between two nodes. 140

$\textbf{Results}$

The consequences of the use of the raw transfer probability (a_{ij}) rather than the 142 distance we propose (d_{ij}) are potentially radical. To show this, we used 20 connectivity $\frac{1}{43}$ matrices calculated for [21]. They were calculated from Lagrangian simulations using a ¹⁴⁴

	Path	Probability	Weight using $\log(1/a_{ij})$ Hop count	
Figure 1		ADEB $(1 \times 10^{-2})^3 = 1 \times 10^{-6}$	13.8	
		ACB $(1 \times 10^{-4})^2 = 1 \times 10^{-8}$	18.4	

Table 1. Paths and respective probabilities, weights and hop count for the graph in Fig 1.

Fig 2. a) Example of network in which the metric $log(1 - a_{ij})$ would fail because of a cycle (ED). b) Example of network in which the metric $log(1 - a_{ij})$ would fail by taking the longest path possible (ADEFB instead of ACB).

3D circulation model with a high horizontal resolution of 750 m [22]. Spawning was simulated by releasing 30 particles in the center of each of 32 reproductive sites 146 (hereafter identified as nodes) for benthic polychaetes alongshore the Gulf of Lion (NW ₁₄₇) Mediterranean Sea), on the 30 m isobath, every hour from January 5 until April 13 in $_{148}$ 2004 and 2006. Note that the connectivity matrices' values strongly depend on the ¹⁴⁹ circulation present in the Gulf during the period of the dispersal simulations. The ¹⁵⁰ typical circulation of the Gulf of Lion is a westward current regime [25]. This was the ¹⁵¹ case of matrices $\#7,\#11,\#12,\#15,\#17$. However, other types of circulation are often $_{152}$ observed. In particular matrix $#1$ was obtained after a period of reversed (eastward) 153 circulation. Indeed, this case of circulation is less frequent than the westward ¹⁵⁴ circulation [26]. Matrices $\#14$, $\#10$ and $\#13$ correspond to a circulation pattern with 155 an enhanced recirculation in the center of the gulf. Finally, matrices $\#2, \#3, \#5, \#6,$ 156 $\#8, \#9, \#14, \#16, \#18, \#19, \#20$ correspond to a rather mixed circulation with no $_{157}$ clear pattern. The proportions of particles coming from an origin node and arriving at a ¹⁵⁸ settlement node after 3, 4 and 5 weeks were weight-averaged to compute a connectivity 159

	Path	Probability	Weight using $log(1 - a_{ij})$
Figure 2a	ADEDEDEB	$\rightarrow 0$	$\rightarrow -\infty$
	ACFB	$(1 \times 10^{-3})^3 = 1 \times 10^{-9}$	-3×10^{-3}
Figure 2b	ADEFB	$(1 \times 10^{-3})^4 = 1 \times 10^{-12}$	-4×10^{-3}
	ACB	$(1 \times 10^{-3})^2 = 1 \times 10^{-6}$	-2×10^{-3}

Table 2. Paths and respective probabilities and weights for the networks in Fig 2.

matrix for larvae with a competency period extending from 3 to 5 weeks.

As an example, in Fig 3 we show the representation of the graph corresponding to $_{161}$ matrix #7. The arrows starting from a node i and ending in a node j represent the $_{162}$ direction of the element a_{ij} (in Fig 3a) or d_{ij} (in Fig 3b). The arrows' color code represents the magnitude of the edges' weights. The nodes' color code indicates the ¹⁶⁴ betweenness values calculated using the metric a_{ij} (in Fig 3a) or d_{ij} (in Fig 3b).

In Fig 3a the edges corresponding to the lower 5% of the weights a_{ij} are represented. 166 These are the larval transfers that, though improbable, are the most influential in $_{167}$ determining high betweenness values when using a_{ij} as metric. In Fig 3b the edges 168 corresponding to the lower 5% of the weights d_{ij} are represented. These are the most 169 probable larval transfers that —correctly— are the most influential in determining high 170 betweenness values when using d_{ij} as metric. While in Fig 3a the nodes with highest $\frac{1}{171}$ betweenness are the nodes 31 (0.26), 27 (0.25) and 2 (0.21); in Fig 3b the nodes with $\frac{172}{172}$ highest betweenness are nodes 21 (0.33) , 20 (0.03) and 29 (0.03) .

Furthermore, it is expected to have a positive correlation between the degree of a $_{174}$ node and its betweenness (e.g., [23] and [24]). However, we find that the betweenness 175 values, calculated on the 20 connectivity matrices containing a_{ij} , have an average 176 correlation coefficient of -0.42 with the total degree, -0.42 with the in-degree, and 177 -0.39 with the out-degree. Instead, betweenness calculated with the metric of Equation 178 2 has an average correlation coefficient of 0.48 with the total degree, 0.45 with the ¹⁷⁹ in-degree, and a not significant correlation with the out-degree (p-value > 0.05).

As we show in Fig 4, betweenness values of the 32 nodes calculated using the two $_{181}$ node-to-node distances a_{ij} and $\log(1/a_{ij})$ are drastically different between each other. 182 Moreover, in 10 out of 20 connectivity matrices, the correlation between node ranking 183 based on betweenness values with the two metrics were not significant. In the 10 cases ¹⁸⁴ it was (p-value < 0.05), the correlation coefficient was lower than 0.6 (data not shown). 185 Such partial correlation is not unexpected as the betweenness of a node with a lot of 186 connections could be similar when calculated with a_{ij} or d_{ij} if among these connections 187 there are both very improbable and highly probable ones, like in node 21 in the present 188 test case. Furthermore, it is noticeable that if one uses the a_{ij} values (Fig 4a), the 189 betweenness values are much more variable than the ones obtained using d_{ij} (Fig 4b). 190 This is because, in the first case, the results depend on the most improbable connections ¹⁹¹ that, in the ocean, are likely to be numerous and unsteady.

Conclusion and the conclusion of the concl

We highlighted the need of methodological exactness inconsistency in the betweenness 194 calculation when graph theory to marine transfer probabilities. Indeed, the ¹⁹⁵ inconsistency comes from the need to reverse the probability when calculating shortest ¹⁹⁶

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Fig 3. Representation of matrix $#7$ from [21], the right side colorbars indicate the metric values. a) Results obtained by using a_{ij} as edge weight, b) results obtained by using d_{ij} as edge weight. In a) the lowest 5% of edges weights are represented. In b) the lowest 5% of edges weights are represented. Note the change in the colorbars' ranges.

connectivity matrices obtained with Lagrangian simulations by [21]. a) Results obtained by using a_{ij} as edge weight; b) results obtained by using d_{ij} . Note the change in the colorbars' ranges.

paths. If this is not done, one considers the most improbable paths as the most ¹⁹⁷ probable ones. We showed the drastic consequences of this methodological error on the ¹⁹⁸ analysis of a published data set of connectivity matrices for the Gulf of Lion $[21]$.

On the basis of our study, it may be possible that results in $[3]$ and $[5]$ might also be 200 affected. A re-analysis of $[3]$ would not affect the conclusions drawn by the authors $\frac{201}{201}$ about the small-world characteristics of the Great Barrier Reef as that is purely 202 topological characteristics of a network. About [5], according to Marco Andrello ²⁰³ (personal communication), due to the particular topology of the network at study, which ²⁰⁴ forces most of the paths -both probable or improbable- to follow the Mediterranean large-scale steady circulation (e.g., [27]). As a consequence, sites along the prevalent \qquad 206 circulation pathways have high betweenness when using either a_{ij} or d_{ij} . However, $_{207}$ betweenness values of sites influenced by smaller-scale circulation will significantly vary ²⁰⁸ according to the way of calculating betweenness. ²⁰⁹

To solve the highlighted inconsistency, we proposed the use of a node-to-node metric ²¹⁰ that provides a meaningful way to calculate shortest paths and \sim as a consequence— \sim 211 betweenness, when relying on transfer probabilities issued from Lagrangian simulations ²¹² and the algorithm proposed in $[17]$ and $[18]$. The new metric permits to reverse the $\frac{213}{213}$ probability and to calculate the value of a path as the product of its edges and to ²¹⁴ account for the independence of the transfer probabilities. Moreover, this metric is not ²¹⁵ limited to the calculation of betweenness alone but is also valid for the calculation of ²¹⁶ every graph theory measure related to the concept of shortest paths: for example, ²¹⁷ shortest cycles, closeness centrality, global and local efficiency, and average path 218 length [28]. 219

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