Connectivity and the structural complexity of marine populations: implications for protection & management

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Projects: HYDROGENCONNECT, ESCOLA, LINC, LAOP
Fluid transport in the ocean and the atmosphere plays an important role in many contexts and at different scales of space and time.

Global climate

Advection of fluid masses plays an important role in many contexts and at different scales of space and time.
Fluid transport in the ocean and the atmosphere

Pollutants spreading
Fluid transport in the ocean and the atmosphere
Networks and Geophysical Flows

Transport processes (fluid advection) in a continuous, time-dependent, 2 or 3-dimensional flow (ocean and atmosphere)

Set of point-like objects (nodes) and pairwise connections among them (links)
Network Theory 1: nodes

Discretization: from continuous to point-like

We define **nodes** as 2-dimensional boxes \{ B_i ; i=1, \ldots, N \} covering the whole domain.

- Equal area constraint: linear size = Δ
- Induced diffusion at box-size scale
Network Theory 2: links & weights

Given a starting time $t_0$ and we want to quantify the amount of fluid exchanged between each pair of nodes during a time interval $\tau$.

- A directional link is established when an exchange of fluid occurred among two nodes.

- The weight of such link will be proportional to the amount of fluid transported.
Lagrangian simulations

How to estimate the amount of fluid exchanged among different regions by currents/winds?

- Time dependent velocity field (2-dim)
- Fill each box $B_i$ with **ideal fluid particles** (tracers)

Velocity field:
Copernicus (NEMO): 1/16°, daily, 1987-2011
[Oddo et al. 2009]

RK4 algorithm:
trajectories of particles passively advected by the flow.

[Rossi et al. 2014]
[Ser-Giacomi et al. 2015]
Lagrangian Flow Networks

We give a coarse-grained (spatial scales fixed by the box-size $\Delta$) description of the flow dynamics.

DIRECTED + WEIGHTED + TEMPORAL

$P$ \rightarrow Adjacency Matrix

$B_i$ \rightarrow Node $i$

$P_{ij}$ \rightarrow Weight of link $i$-$j$

Transport/Adjacency/Connectivity matrix construction

Trajectories are used to build a transport matrix $P$

$$P_{ij} = \frac{\# \text{ tracers from box } i \text{ to box } j}{\# \text{ tracers of box } i}$$
• Out- & In-degree
• Out- & In-strength
• Centrality
• Betweenness
• Paths
• Communities
A dictionary among Networks and Geophysics

**Dynamical system perspective: dispersion and mixing**

How the fluid masses are dispersed and mixed by the flow?

\[
\lambda(x, t_0, \tau) = \lim_{||\delta_0|| \to 0} \left[ \frac{1}{\tau} \log \frac{||\delta(x, t_0 + \tau)||}{||\delta_0||} \right]
\]

Finite Time Lyapunov Exponents

A local measure of maximum separation between trajectories of infinitesimally close initial conditions.
Relating the **out-degree** of the node-i to the **length of the filament**, we found:

$$K_{out}(i) \approx \frac{\bar{L}}{\Delta} = \langle e^{\tau \lambda(x_0, t_0, \tau)} \rangle B_i$$

(Ser-Giacomi et al. 2015, Chaos)
Network entropies: dispersion & mixing

Pushing forward the analogy, a sequence of Renyi-like entropies is defined for each node $i$:

$$H_i^q(t_0, \tau) \equiv \frac{1}{(1 - q)|\tau|} \log \sum_{j=1}^{N} (P(t_0, \tau)_{ij})^q$$

They measure the diversity of the amounts of fluid sent by the node-$i$ to all the nodes connected to it.

- limit: $q \to 1$:

$$H_i^1(t_0, \tau) = -\frac{1}{\tau} \sum_{j=1}^{N} P(t_0, \tau)_{ij} \log P(t_0, \tau)_{ij}$$

Dispersion patterns from both measures agree and reflect most of known oceanographical features (eddies, fronts, filaments, etc...)

$t_0 =$July 1st 2011  $\tau = 15$ days
Introduction

Human mobility & smart cities
Introduction

Characterizing the structure and connectivity of marine populations = foundations of spatial conservation planning

Protection

Implementation of coastal & pelagic reserves
[Lester et al. 2009; Game et al. 2010; Kaplan et al. 2010; Pala, 2013; Guidetti et al. 2013]

Management

Assessment of “spatialized” fish stocks
[Colleter et al. 2012; Kough et al. 2014]
Characterizing marine populations and their connectivities

**Population Connectivity** = Exchanges of individuals (larvae & adults) among sub-populations [Cowen and Sponaugle, 2009]

- **CLOSED** subpopulation (limited exchanges)
- **OPEN** subpopulation (significant exchanges)
  - **SOURCE** subpopulation (exports more than imports)
  - **SINK** subpopulation (imports more than exports)

It structures genetically marine populations (**Genetic Connectivity**) and influences demographic rates (**Demographic Connectivity**) [Palumbi 2003]
Population Connectivity = F (spawning strategy + larval dispersal + habitat availability + adult movements + etc...)  

[Cowen and Sponaugle, 2009]

BUT for most marine species: **territorial adults** (limited movements) and **planktonic pelagic larvae** (efficient dispersion by ocean currents).

**OBJECTIVES:**

Characterize **larval transport and dispersal** at multiple scales to reveal marine population structures and connectivity, providing key information to **protect** and **manage** marine ecosystems.
Materials & Methods

Framework analogies

Ecological Objectives
Describe the **direction** and **quantity** of larvae transported between sub-populations (e.g. habitat patches)

Network Theory Equivalent
Describe the **direction** and **strength** of the links existing between all the nodes of our transport network
Lagrangian Flow Network
2-dimensional trajectories
(3D under development)

Materials & Methods

Parameters
Oceanic domain
Velocity field
Node size
Pelagic Larval Duration
Spawning time
Depth

1. Grid Construction
2. Lagrangian Engine
3. Matrix Construction
4. OUTPUTS: connectivity analyses

4a
4b
4c
BIOLOGICAL PARAMETERS & ASSUMPTIONS

- Larvae with passive horizontal drift (future implementation of realistic larval traits).
- Starting time $t_0 \sim$ spawning, considering seasonal & successive spawning events.
- Tracking duration $\tau \sim$ Pelagic Larval Duration (PLD).
- Larval production, mortality & success of recruitment are assumed homogeneous in space & time (easy to modulate due to spatial discretization and post-processing of matrices).

Probabilistic connectivity matrix

($\sim$ adjacency matrix) built from millions of trajectories.

$\in [0,1]$ Averaged analyses of ensemble of matrices

A FEW CASE-STUDIES

1) Generic parameters: ecosystem approach to connectivity
2) Specific parameters: connectivity of a target species
Mean" biological traits of mediterranean species.

Parameters:
- PLD: 15 – 90 days.
- 2 main spawning seasons.
- Successive and random spawning events.

Ecosystem Approach to connectivity

[Guidetti et al. 2013; Dubois et al. 2016]
Community detection with *Infomap*: finds the sets of nodes strongly connected among them and weakly connected with the rest.

- Hydrodynamical provinces in which larvae are more likely to disperse within each other than among them for a given time-scale.

- Hydrodynamical provinces evolve in space and time.
- Boundaries match multi-scale oceanic processes.
Hydrodynamical provinces

Mean partition of the ocean

How to give an average description of the main transport features across many years?

Post-average

Run infomap on each matrix and count boundaries occurrence

→ Identification of recurrent frontal systems and stable oceanic units (gyres, extended continental shelves…) which organise larval dispersion across the basin.

[Rossi et al. 2014]
Large variability of dispersion potential.

Small surfaces: favoring retention (e.g. Adriatic, Aegean, Gulf of Lyon…).

Large surfaces: favoring larval export (e.g. islands, narrow shelves with boundary currents…).

Sizing and spacing guidelines (large/distant or small/nearby?): in accord with basin-scale dispersal patterns.

[Rossi et al. 2014]
Implications: scales & structures of larval dispersal

Lagrangian dynamical biogeography

Pre-average
Average matrices & run Infomap once

→ Impacts on Population Genetics:

- Help designing adequate sampling for genetics studies.
- Are these hydrodynamic provinces consistent with genetic clusters?
Local analyses

**RETENTION** (self-persistence)

**LOCAL RETENTION (LR)**
Proportion of locally produced settlement to local larval release [Bostford et al. 2009]

\[
LR_i = P_{i,i}
\]

**SELF-RECRUITEMENT (SR)**
Ratio of locally produced settlement to settlement of all origins at a given site [Bostford et al. 2009]

\[
SR_i = \frac{P_{i,i}}{\sum_{x=1}^{N} P_{x,i}}
\]

**EXCHANGE** (network persistence)

**SOURCE-SINK**

\[
SS_i^{\text{flux}} = \frac{IN_i^{\text{flux}}}{IN_i^{\text{flux}} + OUT_i^{\text{flux}}}
\]
Spatial distribution of **RETENTION** indices

**MEAN SELF-RECRUITMENT**
(PLD = 30 days)

Spatial distribution of **EXCHANGE** indices

**MEAN SOURCE-SINK**
(PLD = 60 days)

[Dubois et al. 2016]
• In summer: Western shores are sinks and Eastern coast behaves as source; well explained by the dipole upwelling/downwelling forced by the summer Northerlies.

[Dubois et al. 2016]

⇒ Impacts on **Population Genetics**: characterizing the genetic structures of source/sink populations.
Impact for MPAs design

• Characterizing the exchange and retention of all sites to implement future MPAs?

• Connectivity proxies are relevant information for managers and scientists to optimize MPAs design in accord with conservation objectives.
Sensitivity & robustness

Robustness of connectivity diagnostics to node-size

[Monroy et al. 2017]
Sensitivity & robustness

→ Connectivity proxies for long PLDs are more robust against biological uncertainties (PLD and spawning date) than for short PLDs.

→ Mass-spawners releasing propagules over short periods (2-10 days), daily release must be simulated (connectivity fluctuations due to variable currents).

→ Average connectivity estimates for species that spawn repeatedly over longer durations (few weeks to few months) remain robust even using longer periodicity (5-10 days).

[Monroy et al. 2017]
Use the Lagrangian Flow Network to investigate the impact of connectivity processes on population structure of Hake in the Western Mediterranean.

**European Hake** (*Merluccius merluccius*):
- exploited demersal fish, important landings
- largely distributed, PLD of about 40 days → potential for large dispersal
- larvae drifting at the subsurface.
Variable connectivity for Hake subpopulations

How are connected the 6 *a-priori* identified sub-populations?

Observations (annual trawl surveys)

**Mean connectivity – autumn 1987**

**Inter-annual variability**
exchange and retention of Hake’s larvae within the metapopulation

Hidalgo et al. 2009
Hake’s recruitment = f (larval retention & exchange + environment)
**Implications:**

Fisheries assessment should consider connectivity processes!
Conclusions & Perspectives

- Numerically cheap code and flexible “network” architecture (spatial dimension: very useful to compare to biological observations).

- Further applications in Marine Ecology (biological traits, non-conservative dynamics) and Oceanography (plastics and pollutants transport).


- Biogeochemistry: modelling sinking particles.
Thanks for your attention!

Questions?

http://ifisc.uib-csic.es/users/vincent

(will be moved soon onto the MIO website)


Dubois et al. 2016. Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. *GEB*.


Hidalgo, Rossi et al. 2017. Reconciling ocean connectivity and hydroclimate with the management of transboundary metapopulations, under review.