
# From marine metapopulations to larval dispersal models (and back to metacommunities?)

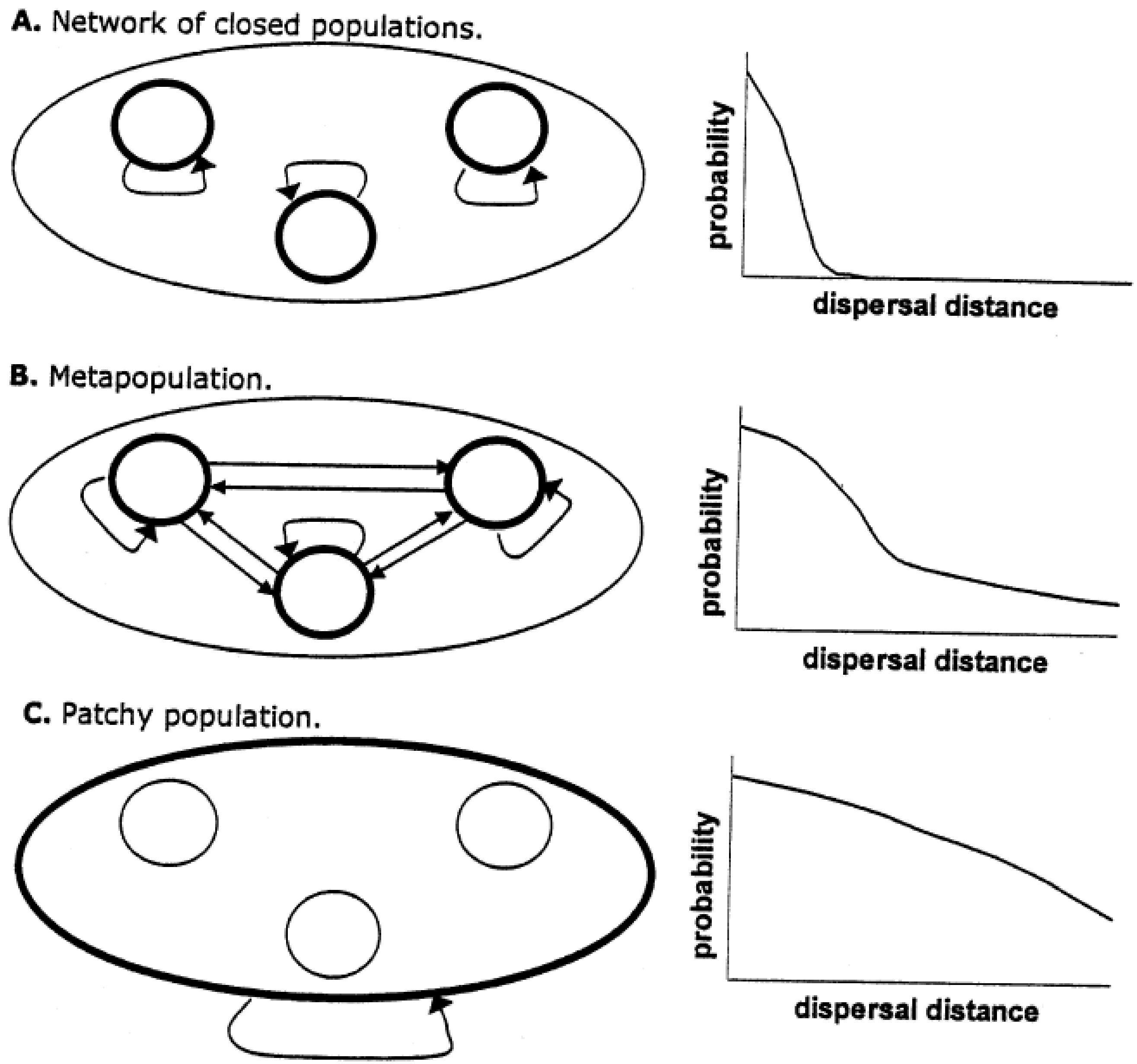
**Christophe Lett**

# What is a metapopulation?

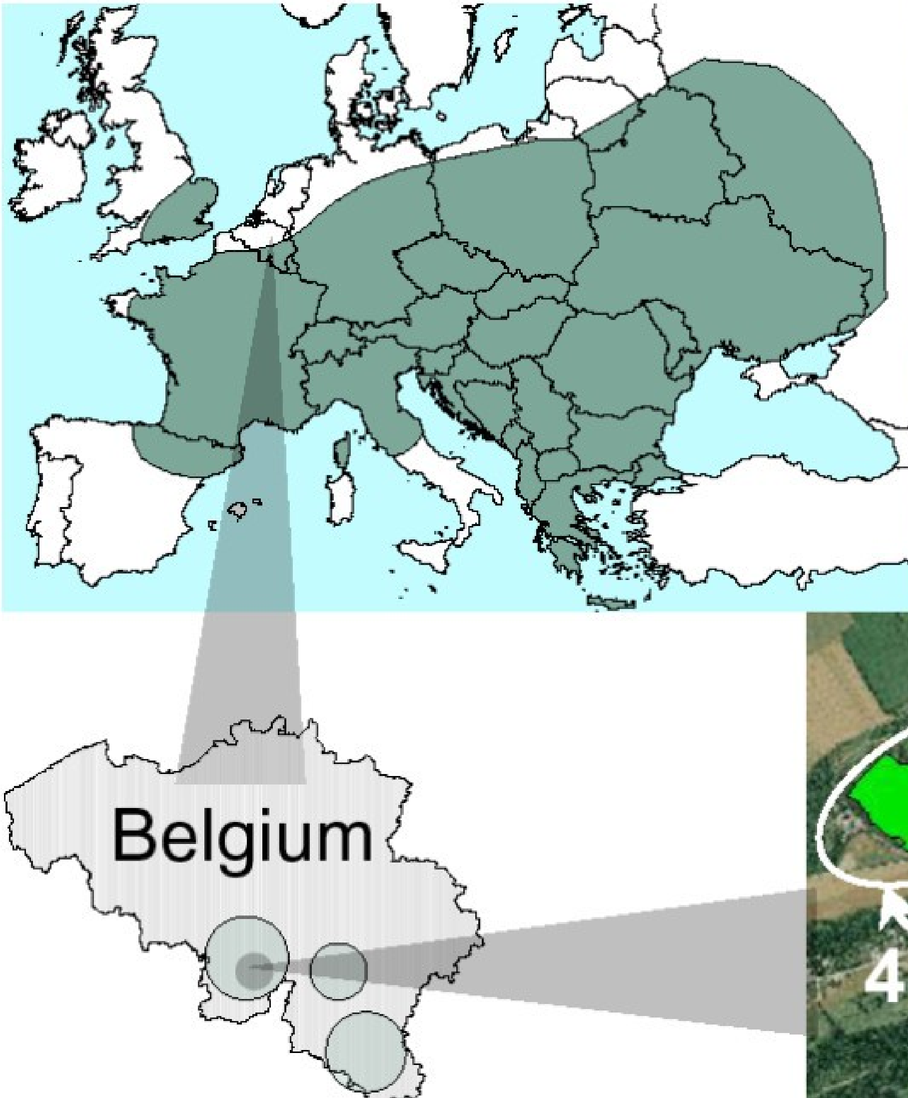
- “population of populations” (Levins 1970)
- “set of local populations which interact via individuals moving among populations” (Hanski and Gilpin 1991)
- “system in which (1) local populations inhabit discrete habitat patches and (2) interpatch dispersal is neither so low as to negate significant demographic connectivity nor so high as to eliminate any independence of local population dynamics, including a degree of asynchrony with other local populations” (Sale et al. 2006)

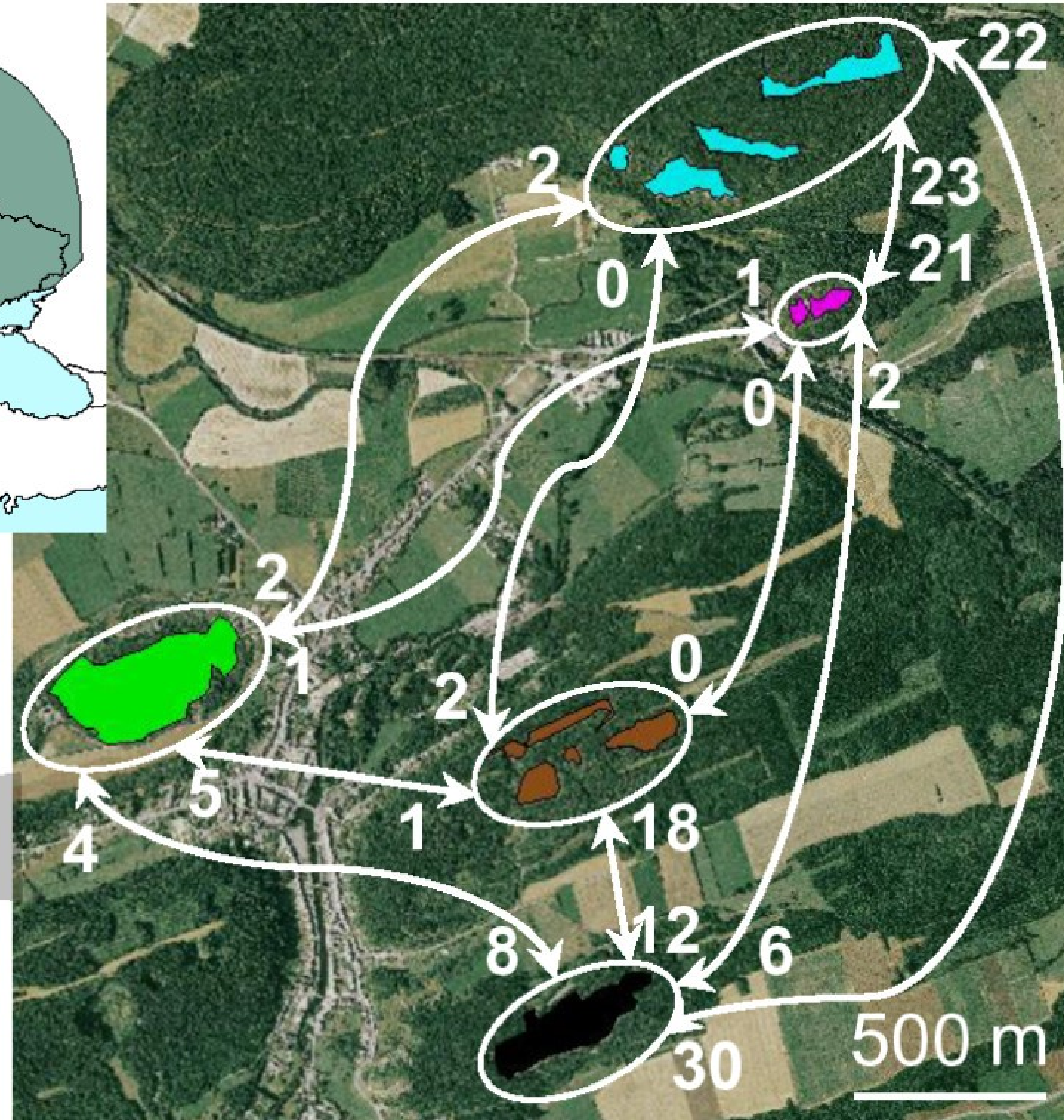
# What is a metapopulation?

Kritzer and Sale (2004)

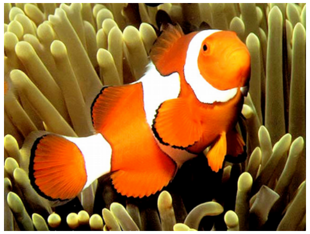


# *Polyommatus coridon*

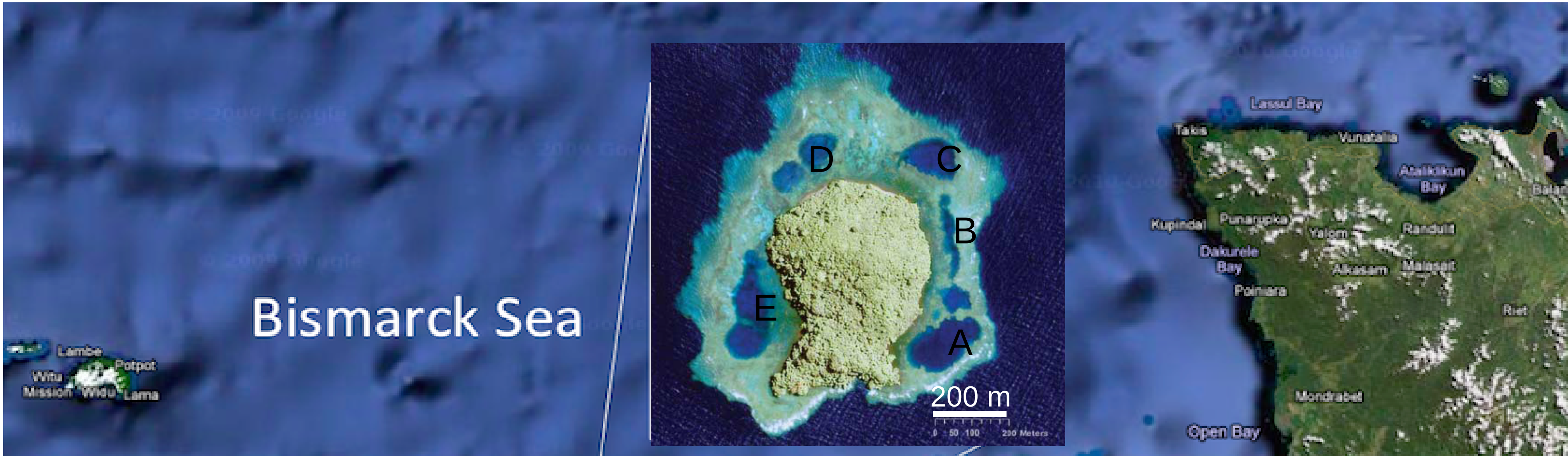



Vandewoestijne et al. (2008)



# *Amphiprion percula*




| | Settlement lagoon, December 2004 collection | | | | |
|---|---|---|---|---|---|
| | A ($n$ = 32) | B ($n$ = 20) | C ($n$ = 11) | D ($n$ = 32) | E ($n$ = 38) |
| Natal lagoon | | | | | |
| A | 12 | 3 | 1 | 1 | 1 |
| B | 3 | 1 | 0 | 3 | 3 |
| C | 0 | 1 | 0 | 0 | 2 |
| D | 2 | 2 | 3 | 4 | 5 |
| E | 0 | 1 | 1 | 0 | 6 |
| | Settlement lagoon, April 2005 collection | | | | |
| | A ($n$ = 29) | B ($n$ = 23) | C ($n$ = 18) | D ($n$ = 18) | E ($n$ = 37) |
| Natal lagoon | | | | | |
| A | 5 | 1 | 1 | 1 | 5 |
| B | 4 | 2 | 2 | 0 | 2 |
| C | 2 | 2 | 2 | 1 | 0 |
| D | 3 | 1 | 0 | 1 | 1 |
| E | 5 | 1 | 1 | 1 | 7 |

Lagoon A, 69 anemones ($n_{ane}$), 125 adults screened ($n_{scr}$); lagoon B, $n_{ane}$ = 38, $n_{scr}$ = 73; lagoon C, $n_{ane}$ = 29, $n_{scr}$ = 58; lagoon D, $n_{ane}$ = 59, $n_{scr}$ = 105; lagoon E, $n_{ane}$ = 75, $n_{scr}$ = 145.


Almany et al. (2007)
Planes et al. (2009)

# Levins (1969) metapopulation model

- $dp / dt = c\, p\, (1 - p) - e\, p$

  | | |
  |---|---|
  | $0 < p < 1$ | fraction of occupied patches |
  | $c > 0$ | colonisation rate |
  | $e > 0$ | extinction rate |

- Levins model is the same as the Logistic model

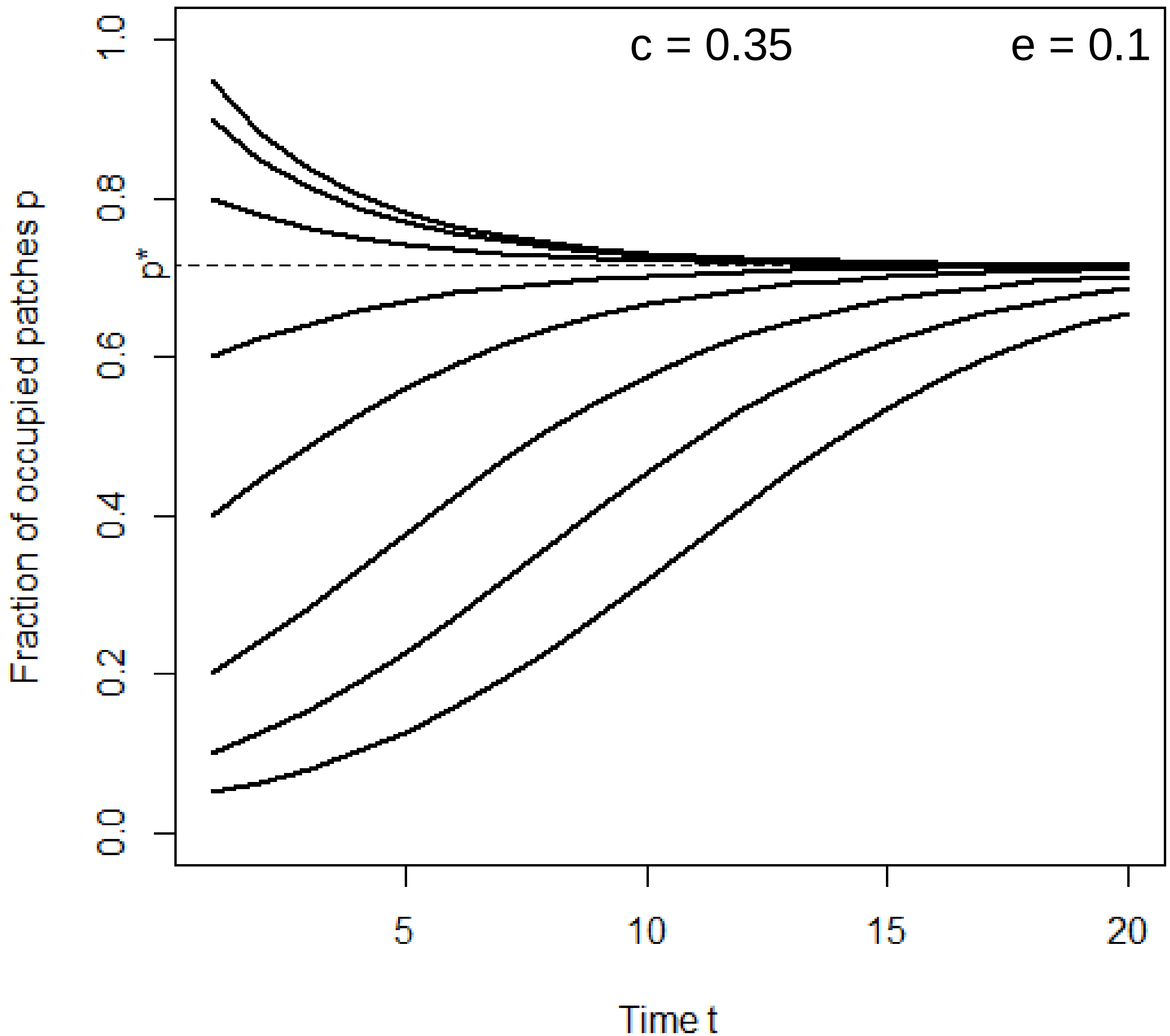
  $dp / dt = r\, p\, (1 - p / K)$

  with $r = c - e$ and $K = 1 - e / c$

- If $c > e$, $p^* = 1 - e / c > 0$ is a stable equilibrium

  If $c < e$, $p^* = 0$ is a stable equilibrium

# Levins (1969) metapopulation model



# Habitat loss in Levins model

- $dp / dt = c\, p\, (h - p) - e\, p$

| | |
|---|---|
| $0 < p < 1$ | fraction of occupied patches |
| $c > 0$ | colonisation rate |
| $e > 0$ | extinction rate |
| $0 < h < 1$ | fraction of habitable patches |

- This model is also the same as the Logistic model

  $dp / dt = r\, p\, (1 - p / K)$

  with $r = c\, h - e$ and $K = h - e / c$

- If $c\, h > e$, $p^* = h - e / c > 0$ is a stable equilibrium

  If $c\, h < e$, $p^* = 0$ is a stable equilibrium

# Limitations of Levins model

- A spatially-implicit metapopulation model

  infinite number of patches

  all patches are identical

  all patches are equally-connected

  → see e.g. Hanski and Ovaskainen (2000)

- Local (patch) dynamics are ignored

- Focuses on extinction-colonization

# Marine metapopulations

- “a useful concept?” (Grimm et al. 2003)
- “the unique feature of a metapopulation is the need to adopt two spatial scales to fully understand the system dynamics: the local patch scale and the regional patch network scale” (Kritzer and Sale 2004)

# Hastings and Botsford (2006)

- $N_{t+1} = C\,N_t$ with $c_{ij} = b_i\, p_{ij}\, a_j$

  $a_j$ propagule production per recruit in patch j

  $p_{ij}$ proportion of propagules produced in j settling in i

  $b_i$ proportion of settlers surviving as recruits in i

$$\begin{pmatrix} N_{1t+1} \\ N_{2t+1} \\ \dots \\ N_{nt+1} \end{pmatrix} = \underbrace{\begin{pmatrix} b_1 & 0 & \dots & 0 \\ 0 & b_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & \dots & b_n \end{pmatrix} * \underbrace{\begin{pmatrix} p_{11} & p_{12} & \dots & p_{1n} \\ p_{21} & p_{22} & \dots & p_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ p_{n1} & \dots & \dots & p_{nn} \end{pmatrix} * \underbrace{\begin{pmatrix} a_1 & 0 & \dots & 0 \\ 0 & a_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & \dots & a_n \end{pmatrix} * \underset{\text{recruits}}{\begin{pmatrix} N_{1t} \\ N_{2t} \\ \dots \\ N_{nt} \end{pmatrix}}}_{\text{propagules}}}_{\text{settlers}}}_{\text{recruits}}$$

# Hastings and Botsford (2006)

- $N_{t+1} = C\, N_t$ with $c_{ij} = b_i\, p_{ij}\, a_j$

  $a_j$ propagule production per recruit in patch j

  $p_{ij}$ proportion of propagules produced in j settling in i

  $b_i$ proportion of settlers surviving as recruits in i

- The model asymptotic dynamics is determined by the dominant eigenvalue $\lambda_C$ of matrix $C$

  $\lambda_C > 1$ persistence and stable spatial distribution

  $\lambda_C < 1$ global extinction

# Hastings and Botsford (2006)

- A “spatially structured population” model
- “The underlying model we use is not a conventional metapopulation model that would allow for stochasticity and extinctions and colonization.”
- “Our goals are to understand how the interplay between connectivity (dispersal) and local population dynamics allows persistence in a network of heterogeneous patches”

# Use of Hastings and Botsford (2006)

Self-persistence of local subpopulations  LEP * LR > 1
(Burgess et al. 2014)

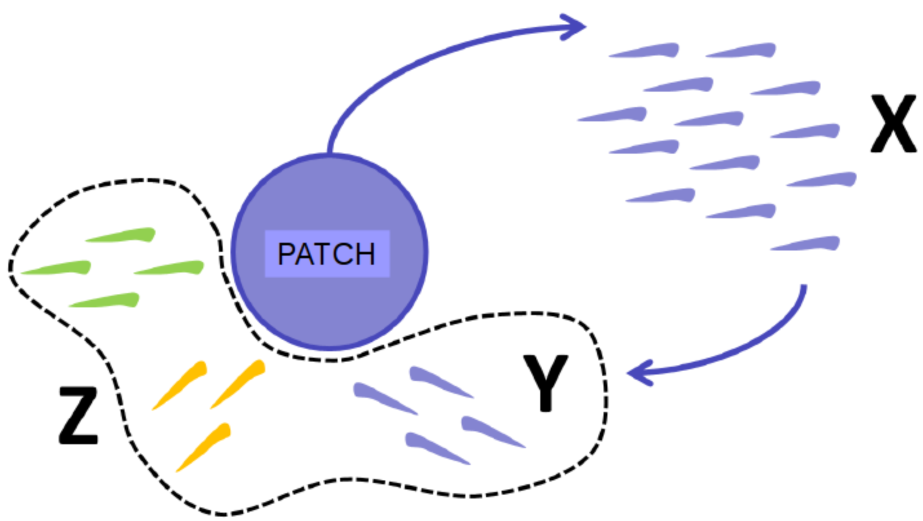
Global persistence of a metapopulation  LEP * LR / SR > 1
(Lett et al. 2015)

with

local retention      LR = Y / X

self-recruitment   SR = Y / Z

lifetime egg production LEP



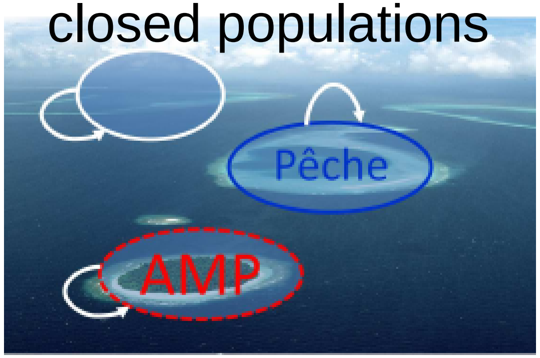
# Propagule dispersal

Terrestrial seed dispersal

Marine larval dispersal

# Dispersal scale

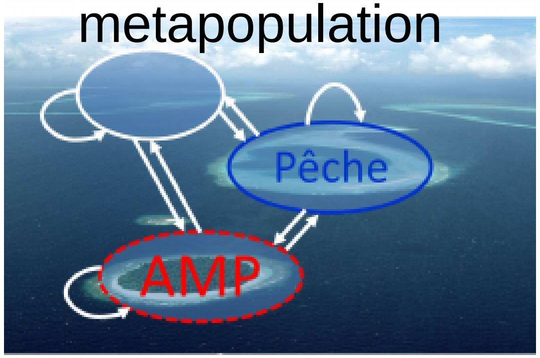
closed populations




dispersal distance << distance between patches

Marine Protected Area (MPA) benefits to conservation, not to exploitation

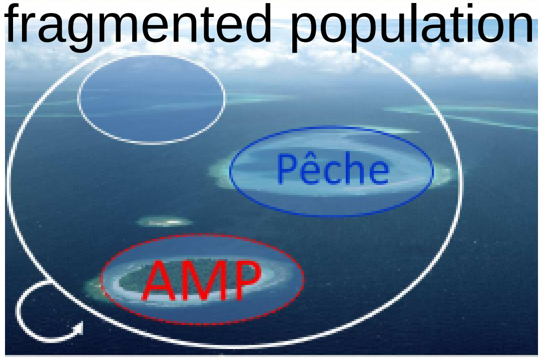
metapopulation




dispersal distance ≈ distance between patches

“Getting the right balance between reserve design for conservation and exploitation requires detailed understanding of dispersal patterns” (Jones et al. 2007)

fragmented population

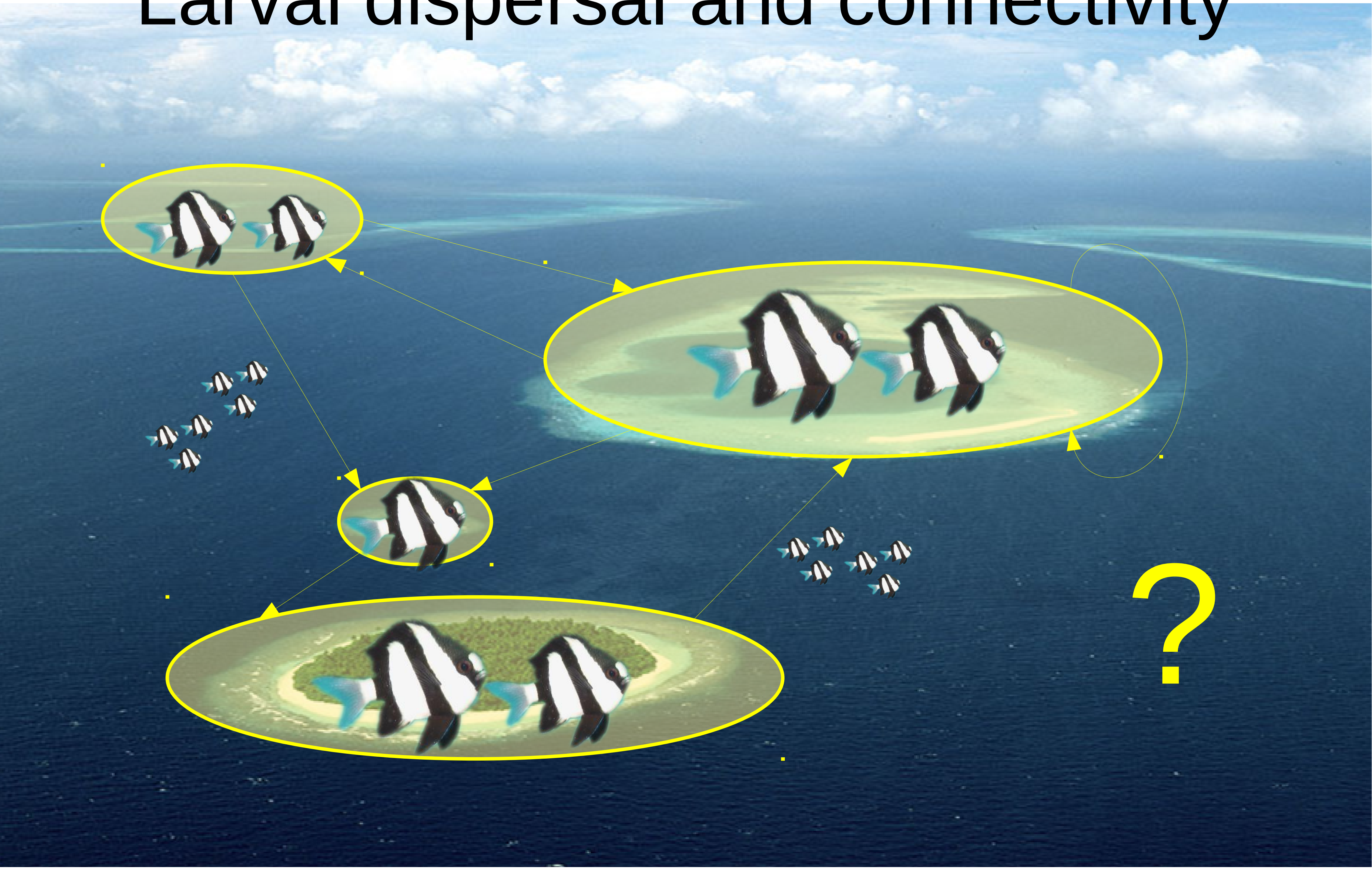



dispersal distance >> distance between patches

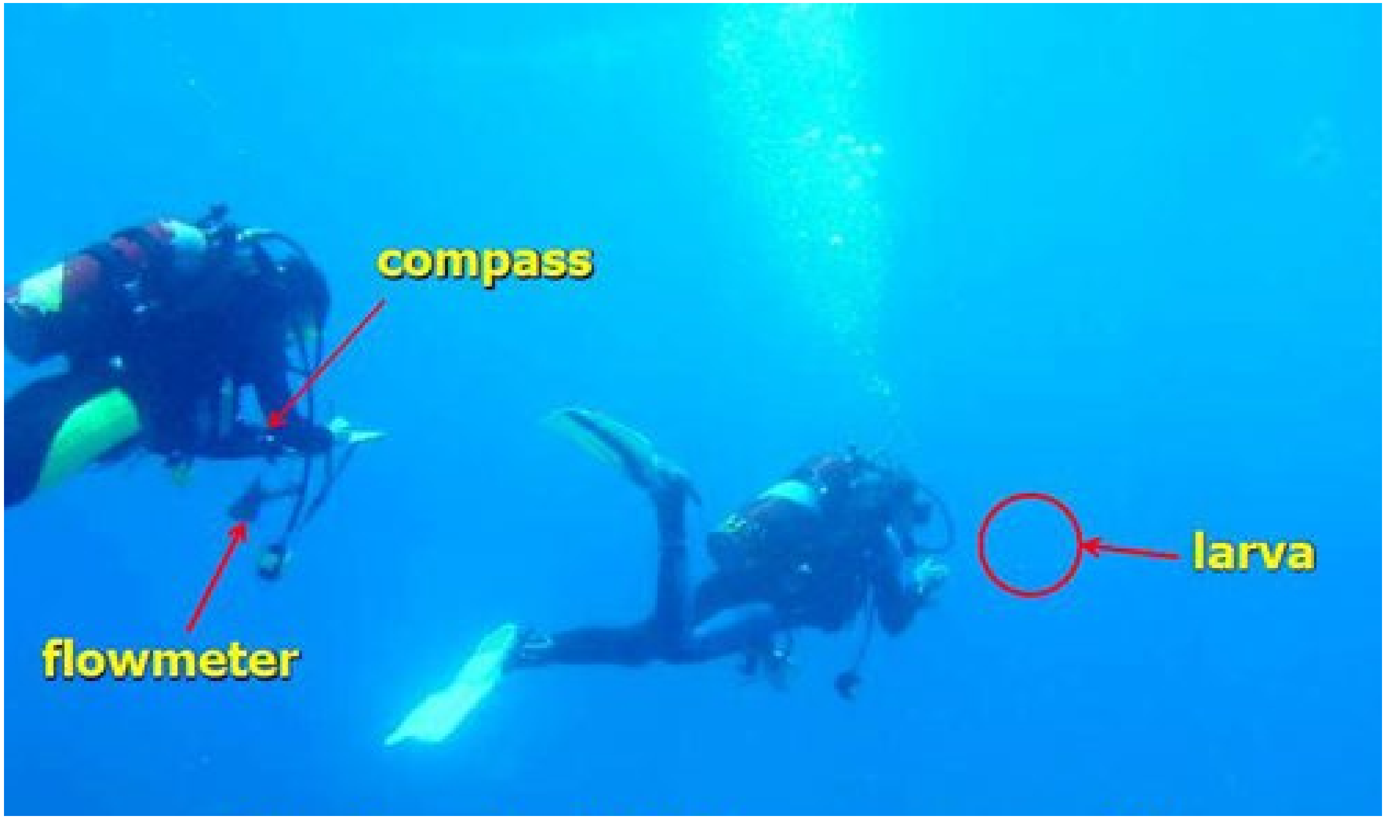
MPA benefits (to some extent) to conservation and exploitation, wherever it is located

Adapted from Kritzer and Sale (2004) courtesy of M. Cuif

# Larval dispersal and connectivity



# Observation: larval transport




Leis et al. (2006)

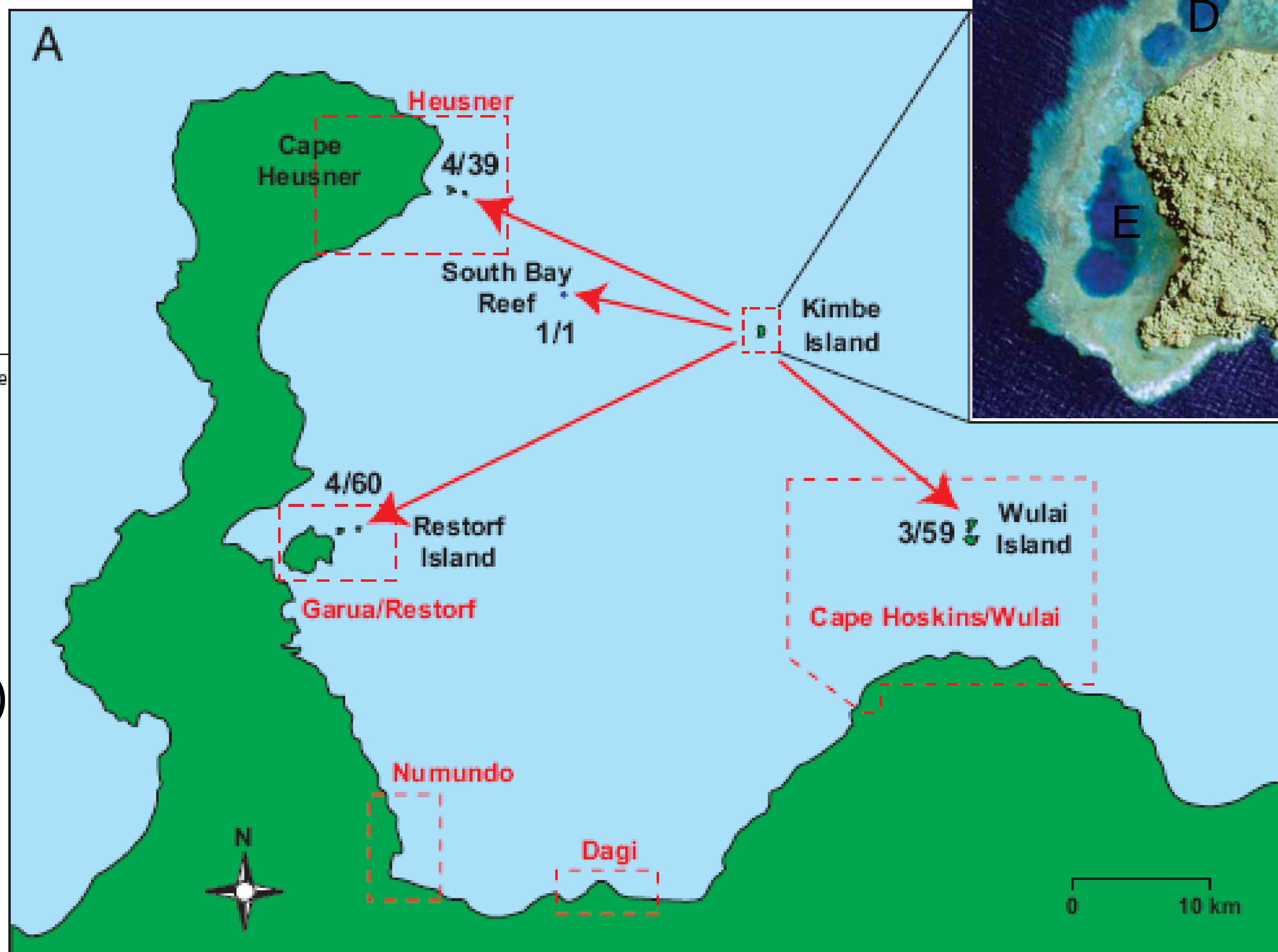
# Observation: larval dispersal

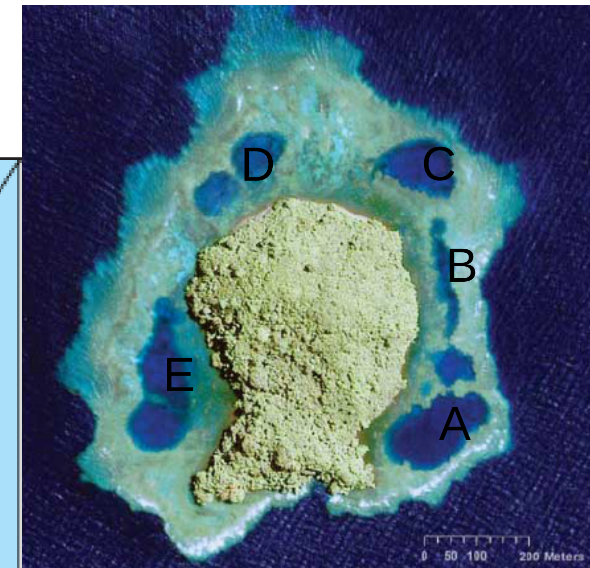
Mass coral spawning  (Sale et al. 2010)

# Observation: larval connectivity

| | Settlement lagoon, December 2004 collection | | | | |
|---|---|---|---|---|---|
| | A ($n$ = 32) | B ($n$ = 20) | C ($n$ = 11) | D ($n$ = 32) | E ($n$ = 38) |
| Natal lagoon | | | | | |
| A | 12 | 3 | 1 | 1 | 1 |
| B | 3 | | | | |
| C | 0 | | | | |
| D | 2 | | | | |
| E | 0 | | | | |
| | A ($n$ = 29) | | | | |
| Natal lagoon | | | | | |
| A | 5 | | | | |
| B | 4 | | | | |
| C | 2 | | | | |
| D | 3 | | | | |
| E | 5 | | | | |

Lagoon A, 69 anemones ($n_{ane}$), 125 adults screene
E, $n_{ane}$ = 75, $n_{scr}$ = 145.



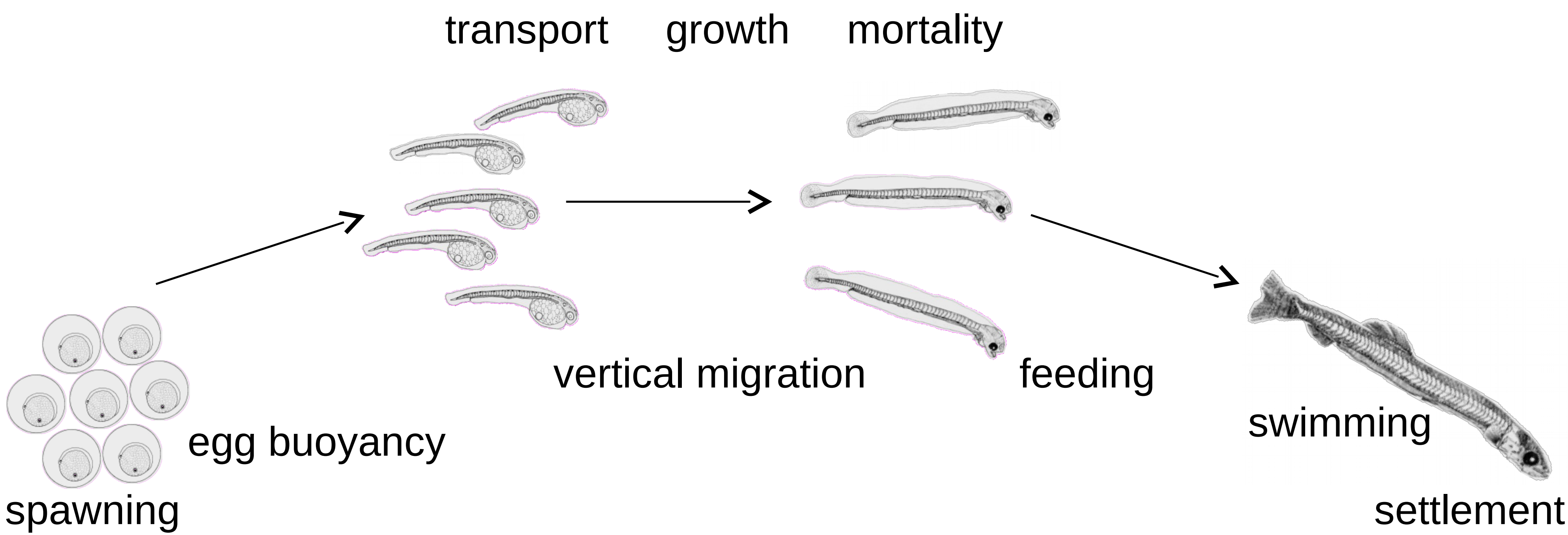




Jones et al. (2005)

Almany et al. (2007)

Planes et al. (2009)

# Larval dispersal




" … a complex process … determined by many factors operating and interacting on multiple time and spatial scales … " (Pineda et al. 2009)

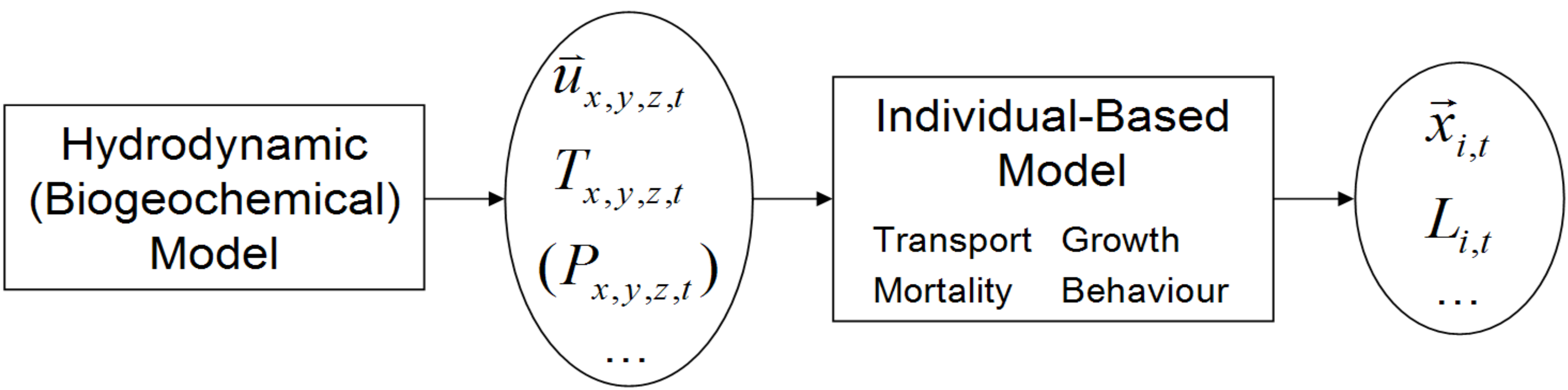
# Larval dispersal modelling

- Physics: hydrodynamic model

  ROMS  Regional Ocean Modelling System

  MARS  Model for Applications at Regional Scale

- Biology: individual-based model




Lett et al. (2009)

# Larval dispersal modelling

- Transport

  Advection + stochastic term (diffusion)

- Growth

  Stage duration, size or weight = f(T), bioenergetic model

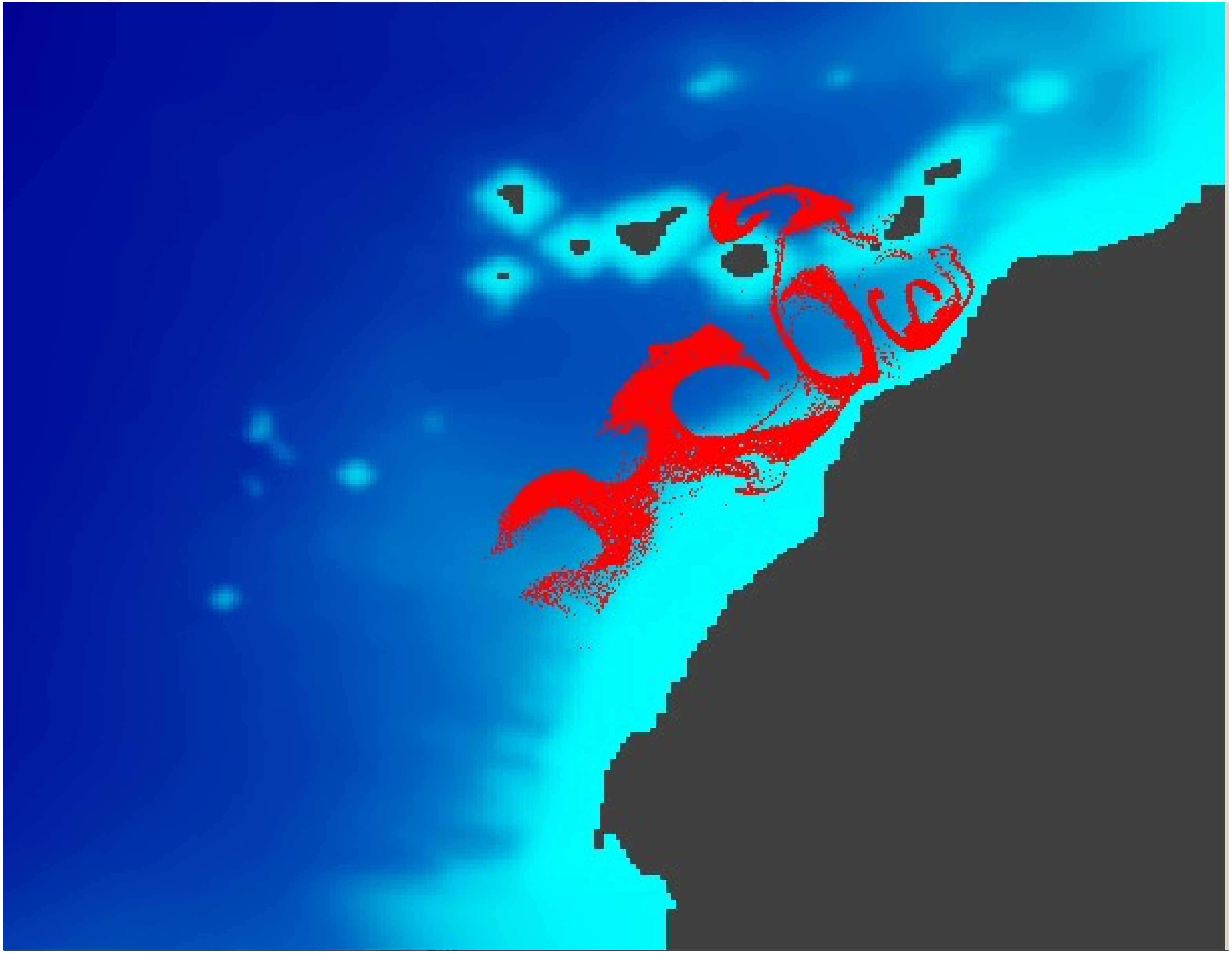
- Mortality

  Constant or function of age, size, T, etc.

- Behaviour

  Buoyancy for eggs, vertical migration for larvae (DVM, function of age, stage, size, etc.), swimming

# Larval dispersal simulation



# Anchovy in South Africa

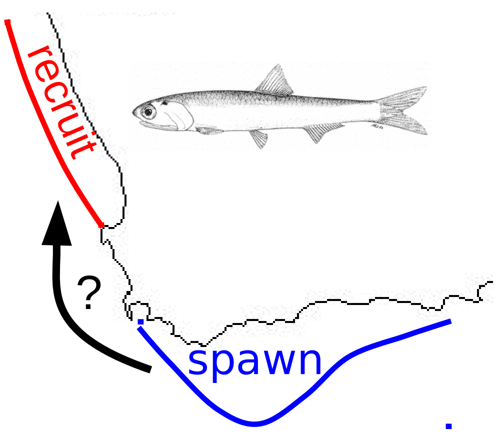
- A suite of models of increasing complexity

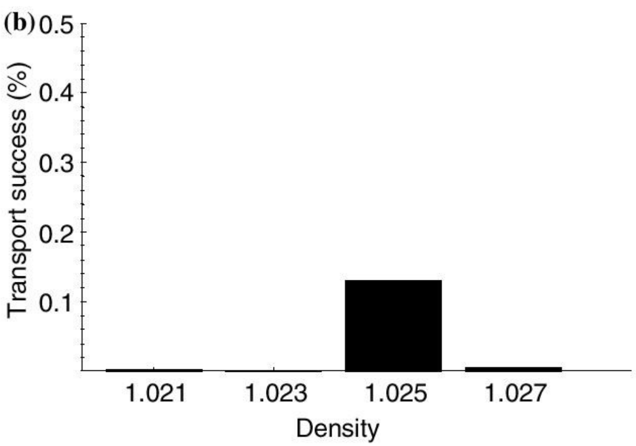
  passive transport (Huggett et al. 2003)

  + egg buoyancy (Parada et al. 2003)

  + larval vertical migration (Parada et al. 2008)

  + larval growth = f (T°, P, Z)  (Koné et al. 2013)



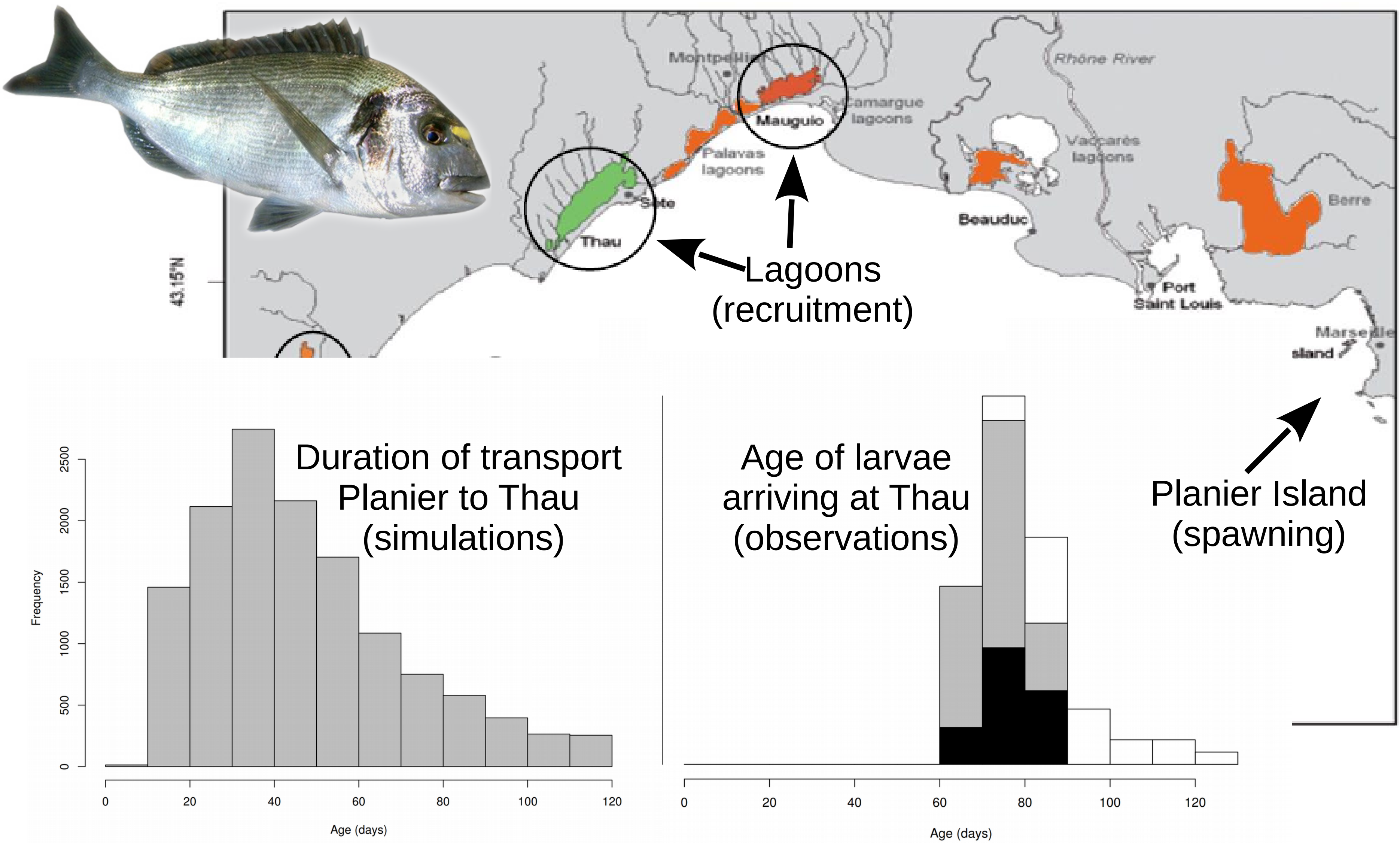




Mullon et al. (2003)

| Anchovy egg density | |
|---|---|
| mean | 1.02393 g.cm$^{-3}$ |
| median | 1.02386 |
| mode | 1.02406 |
| minimum | 1.02159 |
| maximum | 1.02747 |

van der Lingen (pers. com.)

# Gilthead seabream in the NW Med.



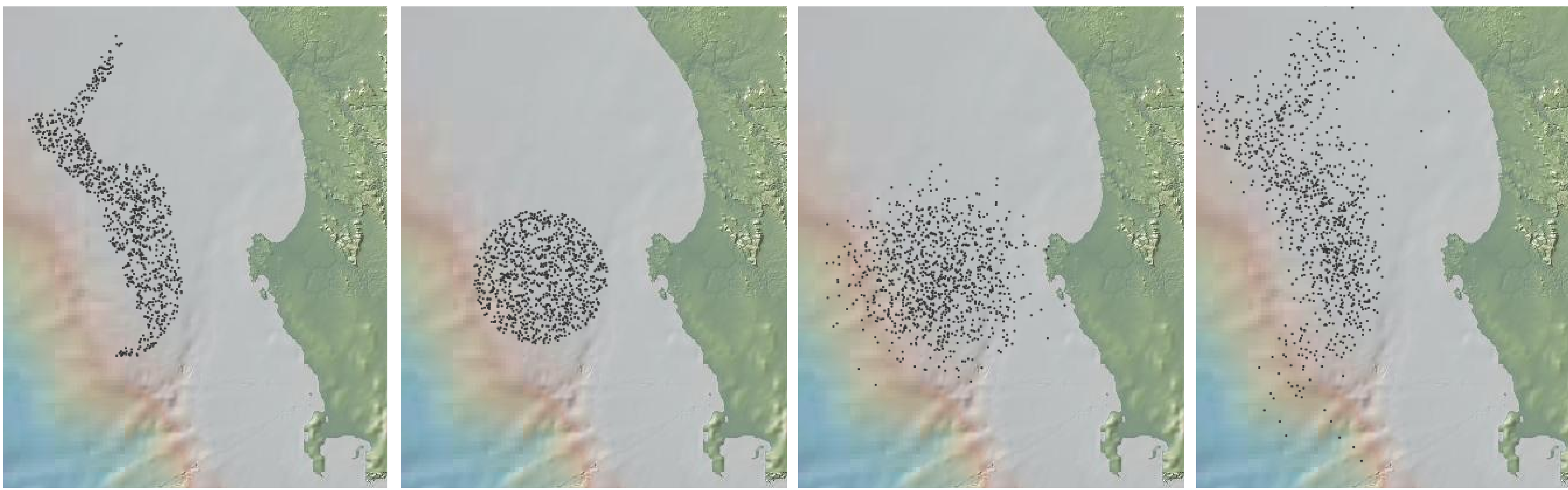

Lett et al. (2019)

# ICHTHYOP Simulating ichthyoplankton

An individual-based (Lagrangian) modelling tool developed in Java

Advection-diffusion and biological processes important for marine dispersal

Free and open source on the Web for 15 years http://www.ichthyop.org/



Advection
Diffusion

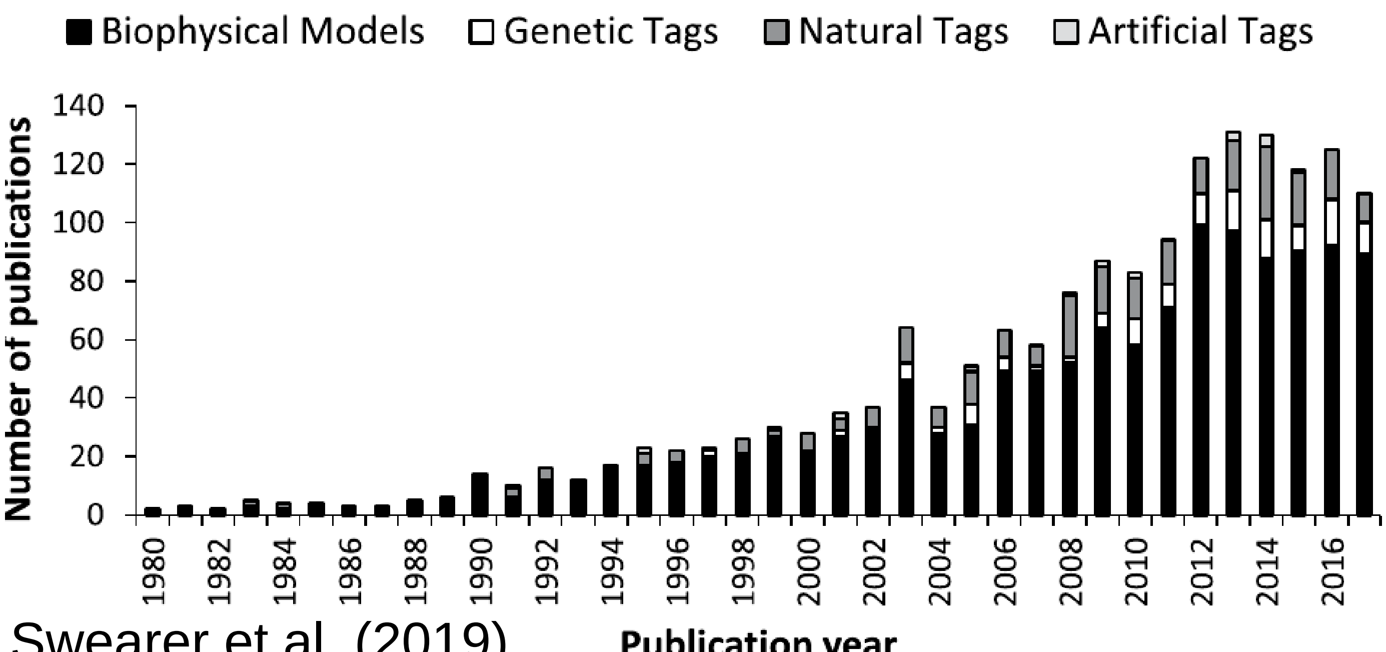
Advection
Diffusion

Advection
Diffusion

Advection
Diffusion

# Larval dispersal models

- Considerable knowledge gained on larval ecology
- Particularly valuable for benthic species
- Complementary to innovative field studies
- Contribute to structure community on connectivity



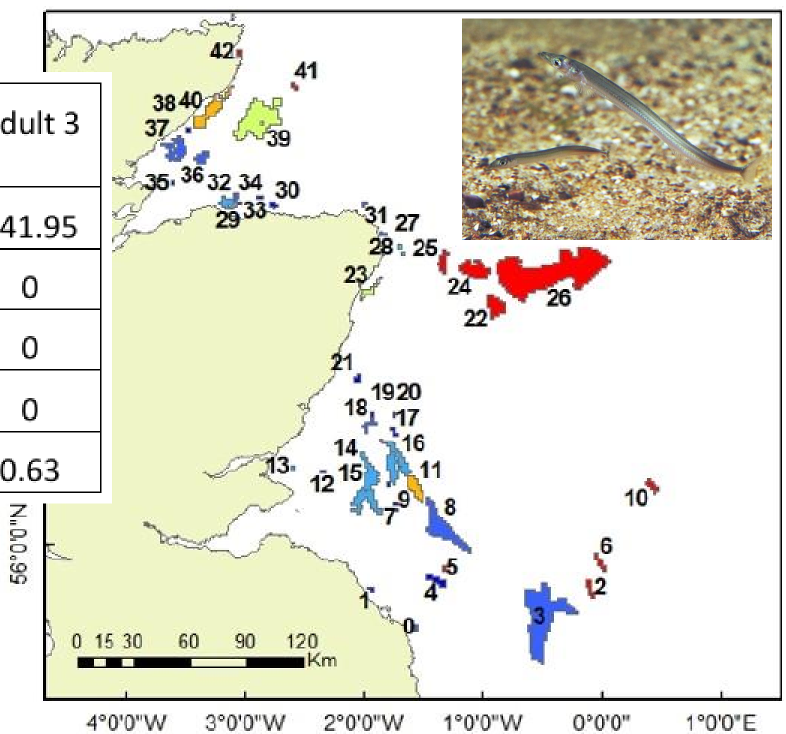

Swearer et al. (2019)

# Larval dispersal models

- Overlook demography and population dynamics
- No particular focus on fisheries / economics

“Assessing spatial patterns of within-stock connectivity provides novel insights for fisheries management” (X et al. subm., sandeel in the North Sea)

| | Stage 0 | Settled juvenile | Adult 1 | Adult 2 | Adult 3 |
|---|---|---|---|---|---|
| Stage 0 | 0 | 0 | 74.31 | 91.08 | 241.95 |
| Settled juvenile | 1 | 0.1323 | 0 | 0 | 0 |
| Adult 1 | 0 | 0.4977 | 0.0126 | 0 | 0 |
| Adult 2 | 0 | 0 | 0.6174 | 0 | 0 |
| Adult 3 | 0 | 0 | 0 | 0.63 | 0.63 |




- Mostly monospecific

# Metacommunity model

- $dp / dt = c\, p\, (h - p) - e\, p$

  $0 < p < 1$ fraction of occupied patches

  $c > 0$ colonisation rate

  $e > 0$ extinction rate

  $0 < h < 1$ fraction of habitable patches

- $dp_i / dt = c_i\, p_i\, (h_i - p_i) - e_i\, p_i$ (Gravel et al. 2011)

  $0 < p_i < 1$ fraction of occupied patches for species i

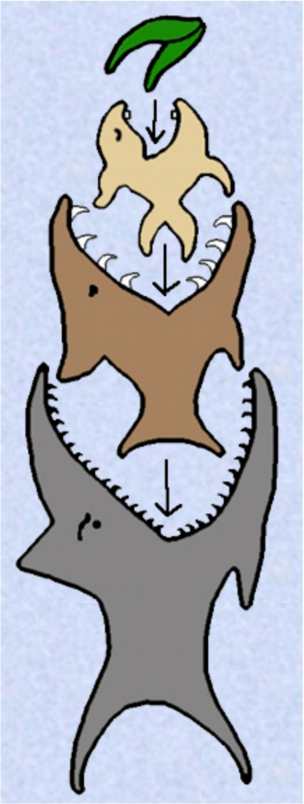
  $c_i > 0$ colonisation rate for species i

  $e_i > 0$ extinction rate for species i

  $0 < h_i < 1$ fraction of habitable patches for species i

# Metacommunity model

- Assume



primary producer is ubiquitous $h_1 = 1$

herbivore feeds on species 1 $h_2 = p_1{}^* = h_1 - e_1 / c_1$

$1^{st}$-level predator feeds on sp. 2 $h_3 = p_2{}^* = h_2 - e_2 / c_2$

$= 1 - e_1 / c_1 - e_2 / c_2$

...

$N^{th}$ species feeds on $N - 1^{th}$

$$h_N = p^*_{N-1} = 1 - \sum_{j=1}^{N-1} e_j / c_j$$

# Metacommunity model

- Assume

  all e and all c are equal

  $$p_N^* = 1 - \sum_{j=1}^{N} e_j / c_j = 1 - N\, e/c$$

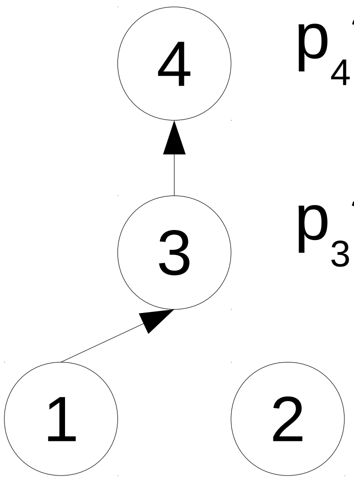
  persistence of N species if $p_N^* > 0 \Leftrightarrow N < c/e$

  e.g. $e / c = 0.3$ $c / e = 3.33$

  $p_1^* = 0.7$ $p_2^* = 0.4$ $p_3^* = 0.1$ 3 species can persist not 4

- Long linear food chains are less persistent than short ones

# Metacommunity model

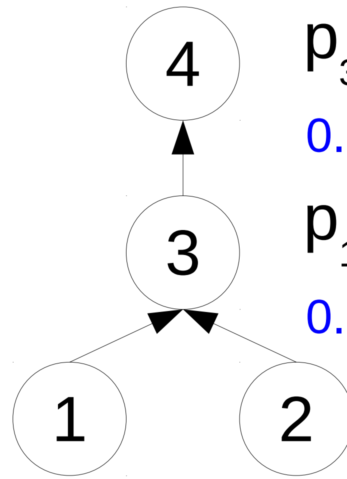



$p_4{}^* = p_3{}^* - e_4 / c_4$

0.4 – 0.3 = 0.1

$p_3{}^* = p_1{}^* - e_3 / c_3$

0.7 – 0.3 = 0.4

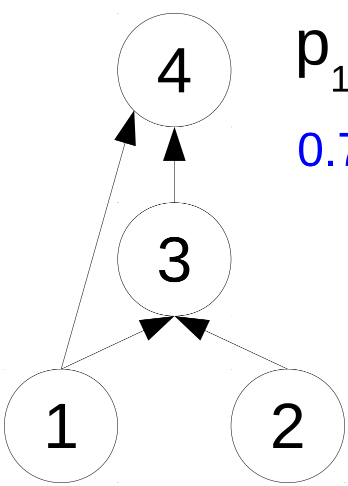



$p_3{}^* - e_4 / c_4$

0.61 – 0.3 = 0.31

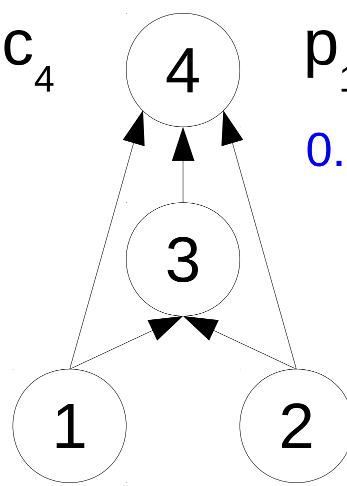
$p_1{}^* + p_2{}^* (1 - p_1{}^*) - e_3 / c_3$

0.7 + 0.7 * 0.3 – 0.3 = 0.61




$p_1{}^* + p_3{}^* (1 - p_1{}^*) - e_4 / c_4$

0.7 + 0.61 * 0.3 – 0.3 = 0.583

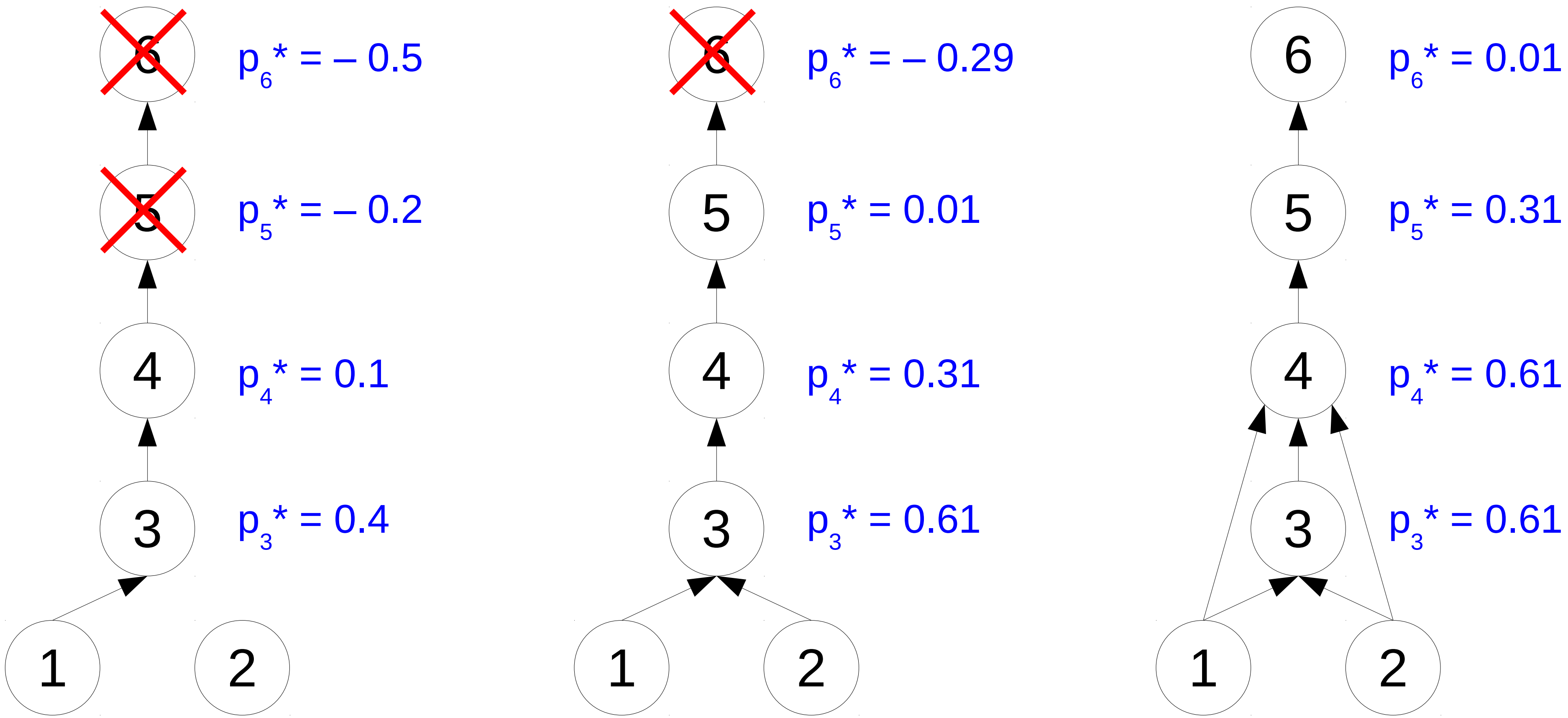



$p_1{}^* + p_2{}^* (1 - p_1{}^*) - e_4 / c_4$

0.7 + 0.7 * 0.3 – 0.3 = 0.61

# Metacommunity model

- Persistence increases with connectance

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Ifremer