Acronyme	**COMPO**		
Titre du projet en français	Connectivité des Populations Marines Application au Lagon Sud de Nouvelle-Calédonie		
Titre du projet en anglais	**C**onnectivity **O**f **M**arine **PO**pulations Application to the South Lagoon of New Caledonia		
Comité d'Evaluation référence (CE)[1]	SVSE 7		
Aide totale demandée		**Durée du projet**	48 mois

SOMMAIRE

[1] Indiquer la référence du CE choisi pour l'évaluation du projet (cf. tableaux page 3 et 4 du texte de l'appel à projets)

1. CONTEXTE ET POSITIONNEMENT DU PROJET / CONTEXT AND POSITIONNING OF THE PROPOSAL

Project overview. In this project, we propose to study larval transport and population connectivity of a fish (damselfish, *Dascyllus aruanus*) and an invertebrate (giant clam, *Tridacna maxima*) species in the South Lagoon of New Caledonia (SLNC) using three emerging and complementary approaches: (1) parentage analysis via genetic fingerprinting, (2) microchemical analysis of trace elements and artificial markers, and (3) biophysical, metapopulation and genetic models of larval transport and its consequences for population dynamics. While these three fields have independently made many significant advances recently, few, if any, studies have integrated these approaches into a single analysis of marine connectivity patterns. In particular, while understanding connectivity is essential for answering many management and scientific questions, such as achieving effective spatial management of marine resources (e.g., marine protected areas -MPAs-) and understanding the spatial structuring of marine ecosystems, there is a significant gap between our ability to experimentally measure connectivity (e.g., through ecological, genetic and microchemical studies) and our ability to model larval transport (e.g., through biophysical models). Here, we propose to bridge this formidable gap by bringing together a group of young researchers with diverse and complementary skills to attack this problem from a variety of angles. The SLNC provides an ideal model system for studying connectivity on a manageable spatial scale, as well as poses a number of pressing management problems, such as assessing MPA effectiveness and conserving threatened marine species and ecosystems. Furthermore, we view this project as the first step needed to build the theoretical, methodological, empirical and computational foundation necessary for applying these techniques in an integrated way to a wide variety of marine connectivity problems in different geographical locations, spatial scales and socio-economic contexts. As such, we feel that this ANR JCJC grant will significantly contribute to building a productive long term collaboration among the participants.

Social, economic and international scientific context. It is widely recognized that the persistence and productivity of marine resources face a number of major challenges from anthropogenic impacts in the coming decades (Lotze *et al*. 2006). A partial list of these challenges includes overfishing (Jackson *et al*. 2001), climate change (Harley *et al*. 2006, Munday *et al*. 2008), pollution (Munday 2004) and habitat degradation (Boesch *et al*. 2001). These impacts have already and will continue to cause social and economic problems through lost productivity of marine systems (Cardinale *et al*. 2006) and displacement of economic activity (Balmford *et al*. 2002), as well as lead to decreased marine biodiversity (Worm *et al*. 2006) and possibly marine extinctions (Davis *et al*. 1998, Cury and Miserey 2008). One of the principal responses to these challenges to marine systems has been an increased focus on spatial management efforts, most notably MPAs. Knowledge of connectivity among marine metapopulations through the exchange of larvae and adults is critical to assessing the

contribution of MPAs to marine populations' biodiversity (Jones *et al*. 2007), persistence (Kaplan 2006) and productivity (Fogarty and Botsford 2007) and has widely been identified as a major science gap (Sale *et al*. 2005, Kaplan *et al*. in press). Nevertheless, connectivity in marine systems, and in particular larval dispersal, has long been viewed as a black-box due to the many difficulties associated with directly observing a multitude of (generally) small individuals in a marine environment. As a result, data needed to accurately parameterise marine metapopulation models is lacking and unjustifiably simplistic assumptions regarding dispersal are often used in place of real knowledge (Gaines *et al*. 2003).

Local context. In the context of increasing demand for accurate information on connectivity patterns, we propose to study larval dispersal and its consequences for dynamics using an integrated approach that includes both experimental and modelling efforts. This cross-disciplinary approach is at the forefront of marine connectivity studies. In particular, the lack of validation of larval dispersal models through accurate experimental studies of connectivity patterns remains *the* major limiting factor preventing the full integration of these models into metapopulation models. The SLNC provides an ideal system for advancing experimental and modelling approaches to dispersal due to its manageable spatial scale, complex spatial distribution of habitats and special marine ecosystems and species. New Caledonia's lagoons and reef ecosystems, including the SNLC, have recently (7 July 2008) been added to the UNESCO's world heritage list in the natural environment category. The SLNC is a coral reef system in which suitable habitats patches for reef associated organisms (i.e., benthic species) are spatially fragmented, which makes the question of connectivity among these habitats particularly relevant. There are also a number of funded regional and national scientific projects that include SLNC as a study area, and that COMPO will benefit from: CORAL REEFS (ANR, 2006–2009), program Bénitiers (ZONECO, 2008–2010) and PAMPA (Liteau III, 2008–2010) (see the Annex at the end of the proposal for more details). Studies addressing MPA effects on reef resources (fish/invertebrates) have a long history in New Caledonia, with a network of 13 MPAs established in the South Lagoon. Recent national programs specifically address MPA issues in New Caledonia (PAMPA). Two species with contrasting biology and ecology are considered in the present project, a fish (the humbug damselfish, *Dascyllus aruanus*) and an invertebrate (the small giant clam, *Tridacna maxima*). These two species are currently model species in two funded projects (CORAL REEFS and ZONECO-Bénitiers), providing background data on larval recruitment, larval behaviour at settlement, and populations densities and genetic structuring. Damselfish are abundant benthic spawners of commercial interest for the ornamental industry, especially *Dascyllus aruanus*. This small sedentary species is strongly associated to live coral and is therefore also of ecological interest as indicators of biodiversity and reef health (Chabanet *et al*. in press). Giant clams constitute emblematic reef species as well as valuable marine resources, whose natural populations are experiencing global decline as a consequence of increasing fishing pressure in most Indo-Pacific countries (Copland and Lucas 1988). Giant clams are now regulated under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

2. DESCRIPTION SCIENTIFIQUE ET TECHNIQUE / SCIENTIFIC AND TECHNICAL DESCRIPTION

2.1. ÉTAT DE L'ART / BACKGROUND, STATE OF ART

A number of authors have recently developed spatial metapopulation models of marine protected areas (MPA) networks that include habitat fragmentation, spatial variability in fishing effort and larval dispersal (Kaplan *et al*. 2006, Walters *et al*. 2007, Kaplan *et al*. 2009). The major limitation to using existing MPA models for making accurate predictions of MPA effects is the considerable uncertainty surrounding larval dispersal and connectivity (Todd 1998, Shanks *et al*. 2003). Assessing marine population larval dispersal and connectivity is a topic of current international interest, as shown by recent special issues (Oceanography, 2007, Vol. 20, No. 3 and Coral Reefs, 2009, Vol. 28, No. 2) and publications in high-impact scientific journals (Jones *et al*. 2005, Almany *et al*. 2007, Hamilton *et al*. 2008, Planes *et al*. 2009) on the subject. Our ability to measure and model larval dispersal has significantly increased recently with the development of genetic, microchemical, ecological and modelling techniques. The challenge is now to integrate these field and modelling studies into a single, coherent approach (Levin 2006, Selkoe *et al*. 2008, Cowen and Sponaugle 2009, Jones *et al*. 2009). This challenge is the core of the COMPO proposal.

Population genetics is widely used to infer connectivity among natural populations. In the marine realm, indirect genetic methods have been primarily used to date (see Hellberg *et al*. 2002 and Hellberg 2007 for reviews), inferring gene flow (related to the absolute number of migrants exchanged each generation) based on simple theoretical models of population structure and the genetic differentiation of allele frequencies (Wright 1931). However, indirect methods estimate connectivity over evolutionary time scales and are incapable to distinguish between contemporary and historical demographic exchanges (Hedgecock *et al*. 2007). Direct genetic methods, on the other hand, excel at estimating connectivity over a single or few generations, either by assigning individuals to populations of origin (Manel *et al*. 2005) or to specific parents (i.e. parentage analysis, Marshall *et al*. 1998). Three recent genetic studies employing parentage analysis in two species of clownfish in Papua New Guinea revealed that more than 30% of larvae are retained within a 2 hectare area in a single generation (Jones *et al*. 2005, Planes *et al*. 2009, Saenz-Agudelo *et al*. 2009). These studies provide the first genetic examples suggesting that larvae may disperse much less than previously thought. Recent work conducted on damselfish (*D. aruanus*) and giant clam (*T. maxima*) in the South Lagoon of New Caledonia (SLNC) using indirect methods suggests restricted larval dispersal in these species despite population connectivity over evolutionary timescales (Fauvelot *et al*. 2007, Buston *et al*. 2009, Fauvelot *et al*. in prep. a, b, Fauvelot and Dumas in prep.). In COMPO, we will build on this existing knowledge using more powerful direct methods, taking advantage of known microsatellite loci for these two species previously developed by COMPO members C. Fauvelot and P. Dumas (Fauvelot *et al*. 2009a, Fauvelot and Dumas in prep.).

Microchemical analyses provide an alternative to genetic studies for directly assessing marine populations connectivity over one generation. Calcareous otoliths found in the inner ear of teleost fish are formed at birth and grow daily as new crystal layers are deposited around the existing core. Trace elements from the surrounding waters substitute for calcium in the protein matrix of the otolith, and their concentration may reflect differences in the physical characteristics and elemental composition of the water mass in which they were formed (Elsdon and Gillanders 2003). Thus otoliths formed at the source of larval production potentially carry a natural record of the site of origin. When the natal environment is too homogeneous to provide useful natural fingerprints, the new technique of artificial "transgenerational" marking of embryonic otoliths can be used (e.g., via the exposure of adults to modified concentrations of specific isotopes; Thorrold *et al*. 2006). After their settlement on the reef as juveniles, marked embryos are identified from the microchemical analysis of their otolith core. Almany *et al*. (2007) were the first and only to use this technique in the field for reef fish species, revealing high retention rates of fish larvae around natal reefs. Hamilton *et al*. (2008) used natural fingerprints in Caribbean fish otoliths to demonstrate that planktonic larvae that developed in different environments had different fates once they settled on the reef. This study linked processes of connectivity and natural selection where parental condition and genetic identity have direct consequences on offspring fitness up to three months after settlement (Vigliola and Meekan 2002, Vigliola *et al*. 2007). As it is not yet known if natural fingerprints in fish otoliths are sufficient to differentiate among sites in the SLNC, artificial marking will be used in COMPO. Natural fingerprinting will be examined in a complementary ZONECO program lead by COMPO member L. Vigliola, providing the potential for interesting methodological comparisons between the two techniques in a single geographic area.

Biophysical modelling of marine population dispersal and connectivity (see Miller 2007, Werner *et al*. 2007, Lett *et al*. 2009, Metaxas and Saunders 2009, for recent reviews) provides a complementary approach to empirical genetic and microchemical studies. These numerical models combine hydrodynamic data with larval behavioural characteristics to simulate larval transport patterns. There is currently no biophysical model of larval dispersal applied to any of the species in the SLNC despite the enormous potential for combining models with data in this area. Furthermore, only two biophysical models exist for systems that have similarities (reefs) with the SLNC: one in the Carribean (Paris *et al*. 2005, Baums *et al*. 2006, Cowen *et al*. 2006, Paris *et al*. 2007) and the other in the Great Barrier Reef (James *et al*. 2002, Bode *et al*. 2006), both at quite different spatial scales than those proposed here. Though biophysical modelling is lacking, there has been a considerable effort to develop hydrodynamic simulations in the SLNC using MARS (Douillet *et al*. 2001, Jouon *et al*. 2006), ROMS and ADCIRC (Marchesiello *et al*. 2008) oceanic models (see the Annex at the end of the proposal for more details). This is significant as biophysical models generally use hydrodynamic simulations as the driving mechanism for the model. This is the case for Ichthyop, a generic Lagrangian tool for modelling the dynamics of planktonic larvae developed by COMPO's PI C. Lett, among others (Lett *et al*. 2008). Ichthyop will form the base for the proposed development of a biophysical model applied to damselfish and giant clam in the SLNC.

The importance of biological processes in the mechanisms of larval dispersal is now fully recognised, shifting from the old paradigm of passive entities drifting throughout the ocean under the sole influence of physical processes to a more balanced view in which larvae can orient and actively navigate in their pelagic environment (Levin 2006, Pineda *et al*. 2007). Encompassing species-specific, detailed information about the biological processes affecting transport and recruitment is recognized as a key issue to the success of biophysical models (Werner *et al*. 2007). Yet, our knowledge of these processes is still limited. This is especially true for larval swimming behaviour during the initial pelagic phase, as it is currently recognised that ontogenic and/or periodic changes in vertical position, as well as horizontal active swimming, may constitute evolved strategies that can efficiently reduce dispersal and facilitate self-recruitment in an increasing number of marine species, including fish and invertebrate (Paris and Cowen 2004, Marta-Almeida *et al*. 2006). The two focus species in COMPO are model species in two other projects in the SLNC (CORAL REEFS and ZONECO-Bénitiers). There is therefore significant accumulated knowledge on their early life history that COMPO will benefit from. However, critical information on giant clam larvae swimming abilities, in particular, is still lacking and will be obtained as part of this study.

2.2. OBJECTIFS ET CARACTÈRE AMBITIEUX/NOVATEUR DU PROJET / RATIONALE HIGHLIGHTING THE ORIGINALITY AND NOVELTY OF THE PROPOSAL

Objectives of the project. The objectives of the COMPO proposal are to (i) propose a general framework to study the connectivity of marine populations, based on the assessment and comparison of connectivity patterns obtained from a biophysical model and from empirical (microchemical and genetic) data, and (ii) integrate connectivity patterns into a metapopulation model to evaluate the effects of marine protected areas (MPAs) within the South Lagoon of New Caledonia (SLNC). These two objectives provide a natural balance to the project, including both "pure"-science and applied results and products. We firmly believe that working at this interface between pure and applied science will be productive, ensure swift transfer of knowledge into marine management scenarios and provide a solid base for responding to the increasing number of calls for proposals in this domain.

Novelty and innovation. The ensemble of the work proposed in this project includes a number of innovative aspects with respect to both the global context of marine connectivity studies and marine management, and the local context of marine science in the SLNC. The overall originality of the COMPO proposal clearly comes from the comparison of modelling, microchemical and genetic data to analyse marine population connectivity. There is a limited number of studies on connectivity that compared model results with genetic data, all obtained through indirect methods estimating gene flow (Gilg and Hilbish 2003, Baums *et al*. 2006, Galindo *et al*. 2006, Viard *et al*. 2006, Gerlach *et al*. 2007, Piggott *et al*. 2008, Jolly *et al*. 2009), model results with microchemical data (James *et al*. 2002) or genetic with microchemical data (Jones *et al*. 2005). Combining all these methods is, as far as we know, unique, and represents "a challenge for the future" (Levin 2006) in that it requires integrating information over a variety of spatio-temporal scales and scientific disciplines (Figure 1). The necessity of building integrative studies has been reasserted regularly since Levin's (2006)

review (Selkoe *et al*. 2008, Cowen and Sponaugle 2009, Jones *et al*. 2009), an indication that it is still a challenge today. This integrative work is firmly at the forefront of marine connectivity studies and is widely held to be the path for advancing larval dispersal models into an "operational" phase where they fully participate in the comprehension and management of marine systems.

In the context of coral reef studies, this project represents a significant advance over existing knowledge of connectivity patterns in the region. As underlined in the State of Art Section (2.1), there is currently no biophysical model or MPA model that has been applied to any of the species in the SLNC. To our knowledge, there exists very limited data on reef organisms population connectivity using direct genetic methods in which settlers are assigned to their natal reefs (Jones *et al*. 2005, Planes *et al*. 2009, Saenz-Agudelo *et al*. 2009). Similarly, there is only one example of transgenerational marking of embryonic otoliths in the field for reef fish species (Almany *et al*. 2007). The fact that these studies were published in Current Biology, PNAS, Molecular Ecology, and Science, respectively, underlines the large interest of the international scientific community in these novel methods. Here we propose to investigate population connectivity in the SLNC via larval transport using both transgenerational marking of embryonic otoliths and parentage analysis (Tasks 4 and 5, sections 3.3.4 and 3.3.5), and to enlarge the view of possible connections among reefs at various spatial scales (i.e., not only in terms of local larval retention and self-recruitment, as in previous studies).

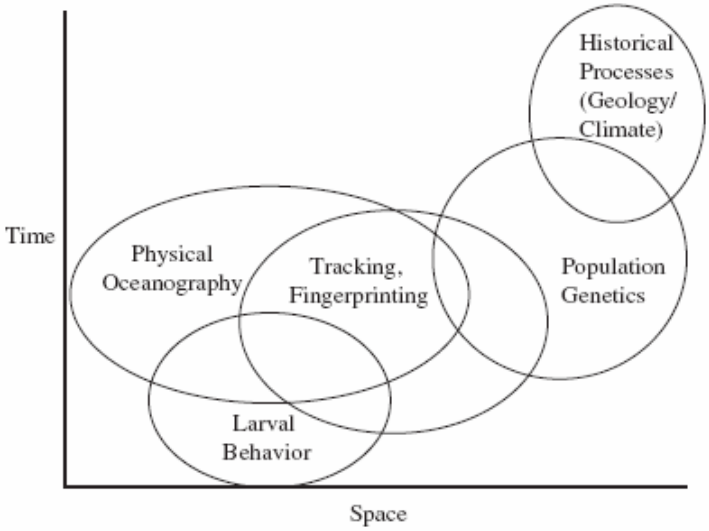


Figure 1: "Time and space scales relevant to different approaches to the study of larval dispersal. A challenge for the future is to integrate these methods." Reproduced from Levin (2006).

Interdisciplinarity. All of the project participants feel strongly that putting together the various disciplines in this project will push each project member to expand his or her scientific horizons, as well as produce an interesting and satisfying collaborative environment. As shown in Figure 1, a global approach to studying marine metapopulations necessarily implies integration across spatio-temporal scales and disciplines. This project will

address the ensemble of the processes and disciplines represented in Figure 1 (except "Historical Processes" as we focus on intermediate scales, though these will hopefully play a role in future research efforts, e.g., as related to predicting the effects of climate change). While the integration of physical oceanography and larval behaviour is customary in biophysical models of larval dispersal (~50% of the models reported in a recent review, Miller 2007), interactions with the other disciplines, microchemistry and genetics, are much less frequent and represent the focus of the project. We feel that the emergence of the techniques we propose to use in this study provides fertile ground for major advances in our understanding of marine connectivity. This project will place the researchers involved at the forefront of these advances.

Team. All members of the COMPO proposal belong to the same research institute, the "Institut de Recherche pour le Développement" (IRD), and are young recently-hired research scientists who wish to build a strong and persistent working team. There will be opportunities in the course, and at the end, of the COMPO project, to write common proposals on several aspects connected to COMPO that are outside the scope of this ANR JCJC proposal. The COMPO proposal focuses on intermediate scales (connectivity between reefs), while processes occurring at smaller scales (one reef) or at larger scales (connectivity between the mainland and islands) may also play an important role in the SLNC and in other comparable reef systems. Most of the activities planned in the COMPO proposal will be useful at these different scales as well, providing a basis for future studies. Furthermore, this project will form the foundation for collaborative work using similar techniques in other types of marine ecosystems.

3. PROGRAMME SCIENTIFIQUE ET TECHNIQUE, ORGANISATION DU PROJET / SCIENTIFIC AND TECHNICAL PROGRAMME, PROJECT MANAGEMENT

3.1. PROGRAMME SCIENTIFIQUE ET STRUCTURATION DU PROJET / SCIENTIFIC PROGRAMME, SPECIFIC AIMS OF THE PROPOSAL

To reach the objectives of the COMPO proposal as stated in the previous section (2.2), we propose a scientific programme that emphasizes interdisciplinary work around the central theme of marine connectivity (Figure 2).

Project objective (i) is to "propose a general framework to study the connectivity of marine populations, based on the assessment and comparison of connectivity patterns obtained from a biophysical model and from empirical (microchemical and genetic) data". The development and simulation of the biophysical model constitute COMPO's **Task 3** (section 3.3.3). The biophysical model of larval dispersal will be developed using physical model outputs that are already available and the Ichthyop Lagrangian tool (Lett *et al*. 2008). The evaluation and selection of the physical model outputs that are available at the time of the project start will be performed in **Task 1** (section 3.3.1). The biophysical model will incorporate biological knowledge for the focus species obtained and synthesized from

COMPO's **Task 2** (section 3.3.2). The biophysical model will then be run to simulate connectivity patterns (e.g., a connectivity matrix). In parallel, microchemical and genetic data will be collected and analysed to provide direct estimates of connectivity at various spatial scales. Parentage analysis and elemental fingerprinting will be used to estimate the percentage of self-recruitment in a focal reef and evaluate the effective dispersal of recruits among 10 reefs separated by increasing geographic distances (Figure 3). These works constitute COMPO's **Task 4** and **Task 5** (for the microchemical and genetic data, respectively) detailed in sections 3.3.4 and 3.3.5. The comparison of simulated vs. empirical connectivity patterns is the core of the COMPO proposal and constitutes **Task 6** (detailed in section 3.3.6). We will use an iterative approach to comparing models with data based on gradually building complexity into model simulations (e.g., larval behaviour), allowing us to identify the level of importance of each mechanism for larval dispersal in the region.

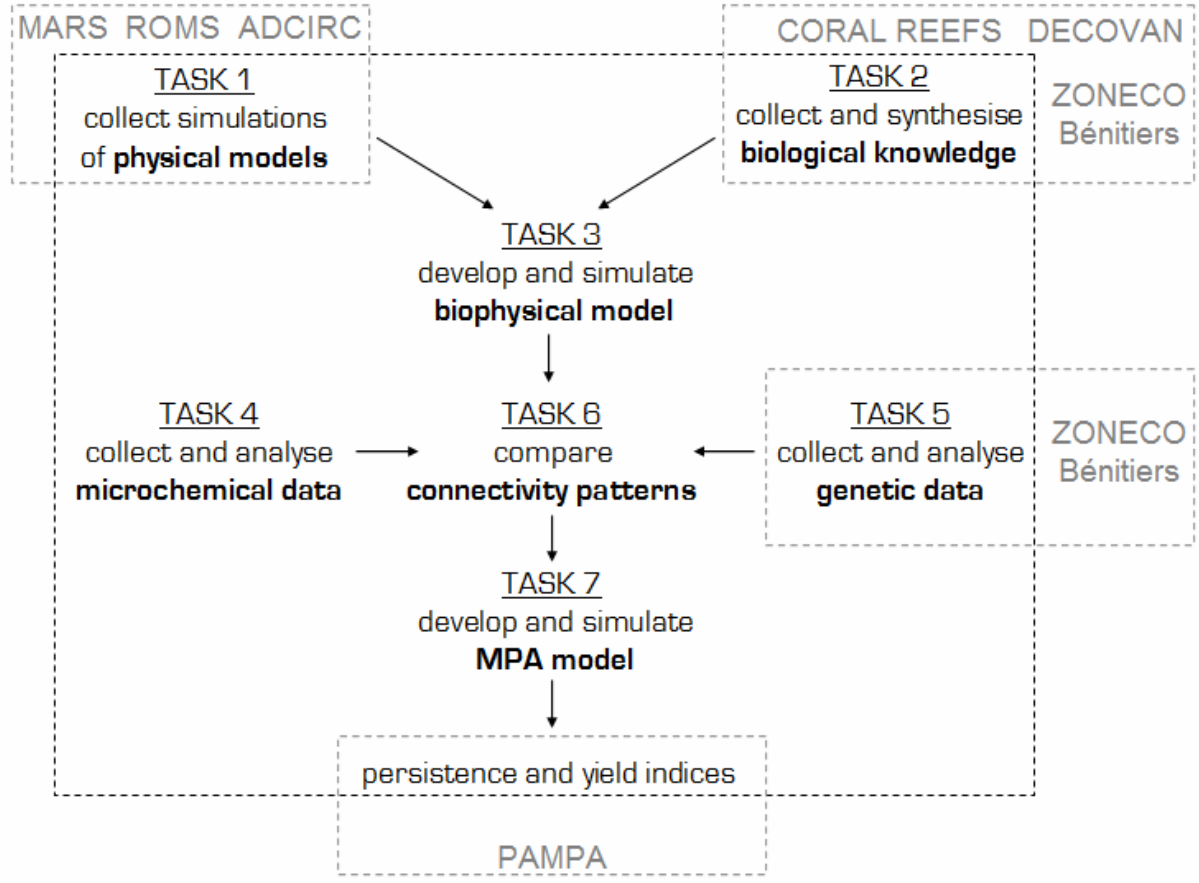
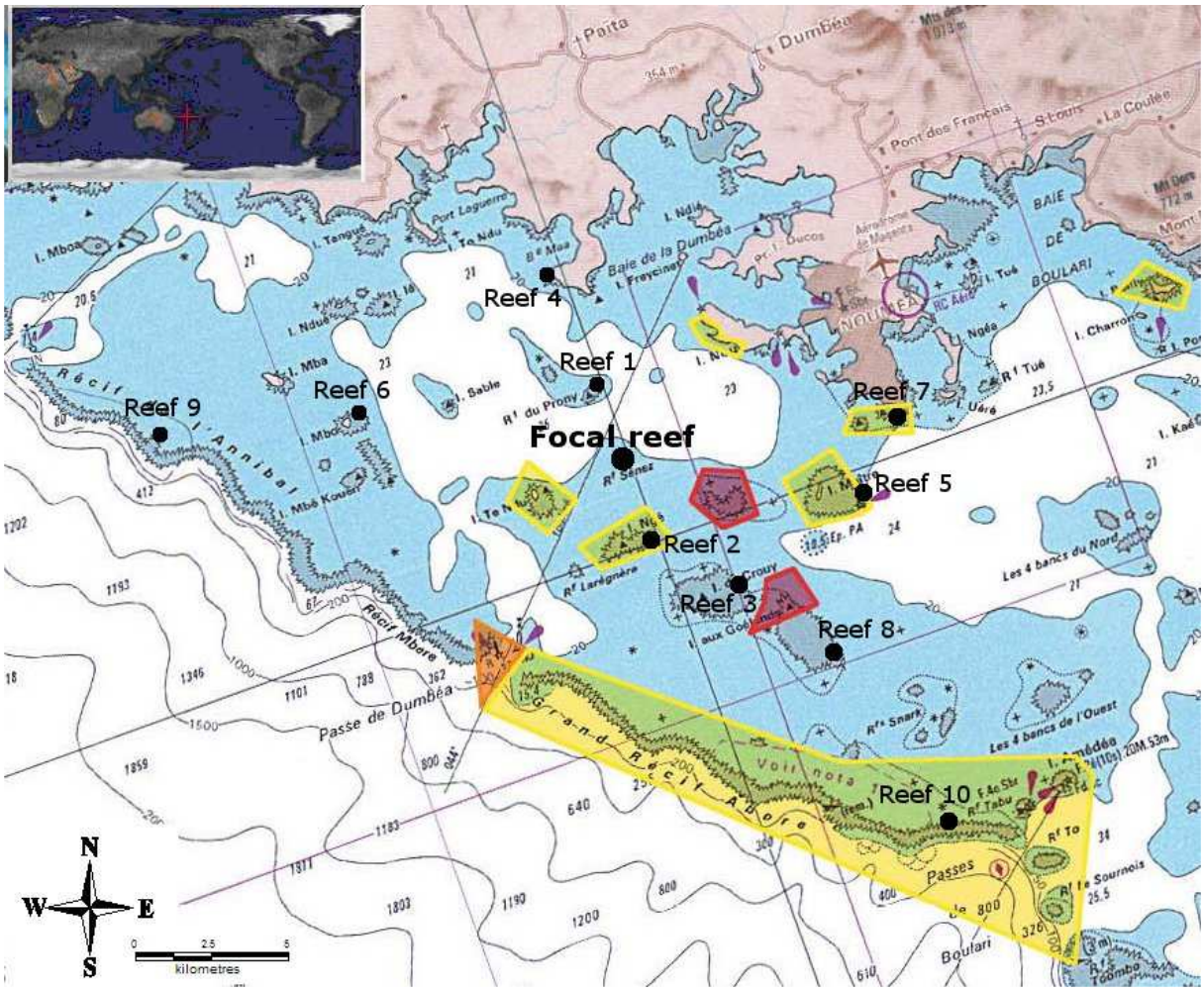


Figure 2: Diagram summarizing the scientific programme of the COMPO proposal. The contour of COMPO is indicated by the black dotted lines, while the grey dotted lines represent the main interactions between COMPO and other funded projects (for more details on these projects, see the Annex at the end of the proposal).

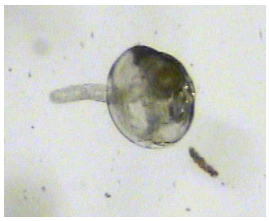


(a)

(b)

(c)

(d)



(e)

Figure 3 : (a) Location of the eleven reefs of the South Lagoon of New Caledonia sampled in COMPO's Tasks 4 and 5. The distance from the focal reef to reef 10 is 22 km. Yellow polygons indicate normal MPAs where fishing is prohibited but access authorised, whereas red/orange polygons indicate special MPAs where access is forbidden. (b–e) The two focus species in COMPO. *Dascyllus aruanus* (b) adult and (c) settler; *Tridacna maxima* (d) adult and (e) pediveliger larva.

We will apply this general framework for two species of the South Lagoon of New Caledonia (SLNC) exhibiting highly contrasted biology/ecology and therefore dispersal abilities: a finfish (the humbug damselfish, *Dascyllus aruanus*, Figure 3) and a bivalve (the small giant clam, *Tridacna maxima*, Figure 3). The percentage of self-recruitment will be estimated for

these two species in the focal reef, as well as larval dispersal from this focal reef to 10 surrounding reefs. Four of the sampled reefs are located within marine protected areas (MPAs, reefs 2, 5, 7, 10, Figure 3) and can be sampled providing authorizations granted to IRD scientists from the Southern Province of New Caledonia.

Project objective (ii) is then to "integrate connectivity patterns into a metapopulation model to evaluate the effects of Marine Protected Areas (MPAs) within the South Lagoon of New Caledonia (SLNC)". This work constitutes COMPO's **Task 7** and is detailed in section 3.3.7. One particularly central element of this objective will be to test the hypothesis that dispersal modelled as a uniform advection-diffusion process is adequate to represent the effects of MPAs. This assumption is often used in the MPA literature, but is generally believed to be a weakness in current model-based MPA assessments. Addressing this question in the SLNC system will not only improve estimates of the effects of the SNLC MPA network, but also provide insight into the importance of making similar improvements in other analogous systems. This objective will also have applied benefits, providing concrete evaluations of persistence and yield in the existing MPA network, as well as indications of benefits of extending or modifying that network.

3.2. COORDINATION DU PROJET / PROJECT MANAGEMENT

TÂCHE 0 / TASK 0

Objective: Project management
Leader: Christophe Lett

The main element of the COMPO project management will be one-week annual workshops. Three workshops are planned for the end of years 2011, 2012 and 2013, and will be held in Nouméa, New Caledonia. Regular web-based conference calls will also be used (and have already been quite successful in organising this proposal), starting with the kick-off meeting at the beginning of 2011, and followed by others between the annual workshops to ensure continuous advancement of the project.

In the course of the last year of the COMPO project (2014), we plan on presenting project results as a group at an internationally-recognized conference (e.g., AGU Ocean Sciences Conference, the DIVERSITAS Open Science Conference, the International Coral Reefs Symposium, the Annual Larval Fish Conference, etc.). This should serve as a perfect opportunity to increase project impact and visibility through the proposal of a special session on integrative approaches to marine population connectivity.

COMPO's PI and project manager will be principally based in Sète, France, during the course of the project, but will request "Missions Longue Durée" (MLD) to Nouméa, New Caledonia, to ensure the connection between France-based and New Caledonia-based members and activities of the project. MLD are special exchanges available to IRD researchers that enable scientists to benefit from long-term (3 to 9 months) missions in another institution or country. MLD are funded by IRD at no cost to the ANR.

NB: This task is numbered Task 8 in the online proposal submission system which did not allow a task to have number 0.

3.3. DESCRIPTION DES TRAVAUX PAR TÂCHE / DETAILED DESCRIPTION OF THE WORK ORGANISED BY TASKS

3.3.1 TACHE 1 / TASK 1

Objective: Collect and evaluate simulations of physical models
Deliverable: A set of relevant physical simulations to use in the biophysical model (Task 3)
See: Figure 2 (page 12) for the position of Task 1 within COMPO scientific programme
Leader: Christophe Lett
Involved: David Kaplan

Oceanic modelling activities have been performed in New Caledonia using three different models: MARS (Model for Applications at Regional Scale, Lazure and Dumas 2008), ROMS (Regional Ocean Modeling System, Shchepetkin and McWilliams 2005) and ADCIRC (ADvanced CIRCulation model). MARS was the first model used with a configuration covering the South Lagoon of New Caledonia (SLNC) (Douillet *et al*. 2001, Jouon *et al*. 2006, Figure 4). This configuration has been both extended and refined and the horizontal resolution of the current MARS configuration is 540 m with 23 sigma (terrain following) layers in the vertical dimension (R. Le Gendre, IRD, pers. com.). ROMS was the second model used, mainly at the larger scale of all ofNew Caledonia (Marchesiello *et al*. 2008), although a configuration at the scale of the SLNC could become available in a near future (J. Lefèvre, IRD, pers. com.). Both MARS and ROMS are finite-difference models. In an effort to accurately model and forecast for the whole Lagoon of New Caledonia, physical oceanographers have turned to a finite element model, ADCIRC (Marchesiello *et al*. 2008). The advantage of finite element models over finite-difference models is that they use an unstructured grid mesh, which allows for much finer resolution around specific reefs of interest, for example. Finer resolution is also possible, although less flexible, with finite-difference models, using embedding procedures that allow nesting a high-resolution small-scale grid within a lower-resolution larger-scale one (Penven *et al*., 2006). The disadvantage of finite element models is that they have not yet proven totally reliable to handle three-dimensional oceanic dynamics. Consequently, the ADCIRC model applied to the Lagoon of New Caledonia is currently two-dimensional (J. Lefèvre, IRD, pers. com.) while the MARS and ROMS models are three-dimensional.

At the time of writing this proposal, the most suitable oceanic model simulations to use in COMPO are the ones from MARS as they are at the relevant (lagoon) scale and they incorporate the vertical dimension (which is important as larvae can actively move in the water column). Furthermore, because MARS is the model historically used in New Caledonia, there is strong local expertise in this model. But as the development of new models, configurations, and tools, is an active research field, an evaluation of the different products available at the time of the project start will be performed in order to choose the

best options for COMPO (e.g., best resolution of complex SLNC topography and best representation of flow patterns).

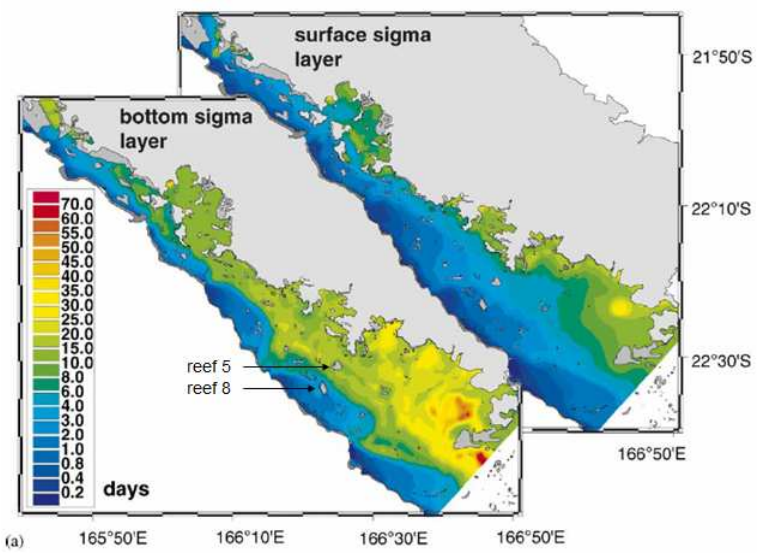


Figure 4 : Time needed for a water parcel, initially located at the point considered, to leave the South Lagoon of New Caledonia in the MARS physical model. Reproduced from Jouon *et al*. (2006) with the addition of reefs 5 and 8 locations, two of the sampling sites in the COMPO proposal (see Tasks 4–5 and Figure 3).

3.3.2 TACHE 2 / TASK 2

Objective: Collect and synthesize biological knowledge on damselfish and giant clam
Deliverable: Synthesis of biological knowledge to be included in biophysical model (Task 3)
See: Figure 2 (page 12) for the position of Task 2 within COMPO scientific programme
Leader: Pascal Dumas
Involved: Cécile Fauvelot, Laurent Vigliola, Master student

The main objective of this task is to provide biological and ecological knowledge on the early life stages of the humbug damselfish *Dascyllus aruanus* and of the small giant clam *Tridacna maxima* (Figure 3) required for the biophysical model (Task 3). Available data on adult density, habitat preferences, recruitment patterns, larval behaviour and settler survival of both species will be collected from literature, existing databases and ongoing projects. To fill the gap between existing knowledge and modelling requirements, additional experimental data on larval behaviour will be obtained using hatchery-reared larvae. This will be particularly important for giant clam for which little data exist as compared to damselfish.

Dascyllus aruanus is an abundant, well-studied tropical reef fish species of the tropical Indo-Pacific (Allen 1991) that lives in small groups of less than 10 individuals in well defined lagoon micro-habitats (branching coral colonies, Holbrook *et al*. 2000). It is a benthic spawner that breeds on a lunar cycle and each female can spawn several times at 13-59 days interval during the summer season (Mizushima *et al*. 2000). Eggs remain in benthic nests for 3-5 days after which hatchlings are released in the plankton where they disperse for 16-24 days

(Wellington and Victor 1989) prior to settling on adult reef habitats. Swimming speed and vertical migration patterns of pelagic larvae in the water column, habitat preference of settlers, recruitment patterns and somatic growth are well known for this species (e.g. Sweatman 1985, Leis and Carson-Ewart 1997, Kingsford 2001). Furthermore, embryos, settlers, juveniles and adults are easy to identify, collect and manipulate. Thus, this species is particularly well suited for field tagging studies, e.g. transgenerational marking of embryos, and a review of existing literature will be sufficient to collate most biological information required for the biophysical model (Task 3). However, it has been shown that recruitment intensity of *D. aruanus* is mediated by habitat quality and the presence of conspecifics ("recruitment facilitation", Sweatman 1985). Population size of *D. aruanus* and quality of settlement habitat will therefore be estimated by underwater visual censuses (see Task 4). Reading otoliths of collected settlers and juveniles (see Task 4) will also provide estimates of planktonic larval duration, which is a very sensitive parameter in biophysical models.

The second focus species is the small giant clam *Tridacna maxima*. Giant clams are emblematic species throughout the Indo-Pacific, and are particularly vulnerable to human pressure (Lucas 1994). As a result of the generalized depletion of natural populations (sometimes to the point of extinction) in many countries, they have become one of the most comprehensively studied groups of tropical marine organisms and are listed under Annex II of CITES / IUCN Red List of threatened species. *T. maxima* is the geographically most widespread giant clam species, extending from the Red Sea and Western Indian Ocean to the central Pacific (Raymakers *et al*. 2004). Adults are generally deeply encrusted in the coral substrate of shallow reefs habitats and spawn one or several times per year during the summer season. In contrast with *D. aruanus*, they exhibit very limited dispersive phase: at day 1, embryos rapidly emerge from their egg membrane as swimming, filter-feeding trocophore larvae that will settle on hard substrate for metamorphosis after only 4-10 days (Jameson 1976, Munro 1993). This short planktonic larval duration (PLD) is mediated by local, environmental conditions, in particular temperature, food and habitat availability (Lucas 1994). Several authors highlighted considerable regional variation of all biological parameters of giant clams across the Pacific (Hart *et al*. 1998, Hean and Cacho 2003). Since no data is available in New Caledonia regarding the biology of *T. maxima*, the influence of the seasonal water temperature patterns on PLD will be assessed under controlled laboratory conditions. There is also a serious need to investigate undocumented behavioural processes (in particular swimming behaviour) that may strongly influence larval transport. For example, vertical migration in the water column punctually occurs for hatchery-reared larvae of *T. maxima* (personal observation from the task leader). Swimming behaviour, including horizontal displacement and vertical migration patterns of giant clams larvae in response to light, food and ontogeny, will thus be assessed in COMPO using laboratory experiments.

While collecting early *T. maxima* larvae directly from the water column would be extremely hazardous, nursery techniques including spawning induction and larval rearing are well mastered in New Caledonia (e.g. 4.10^6 larvae of *T. maxima* were produced in 2009 for the DECOVAN project, project leader P. Dumas). The experiments planned in COMPO will be

conducted similarly using hatchery-reared trocophore larvae, i.e. during the initial phase before settlement. Influence of temperature on PLD will be assessed using controlled larvae densities reared in 150 l replicate water tanks (1.0–1.5 10^6 larvae per tank) submitted to contrasted temperatures corresponding to the range of summer variations generally observed for lagoon water temperature in New Caledonia (27–31°C). Vertical movement patterns will be investigated by recording the individual positions of larvae released in sets of vertical 1m glass towers using complementary observation techniques (visual/automated photographic techniques). Towers will be subjected to 2 experimental treatments referring to light cycle (day vs. night) and food availability (zooplankton vs. no food). We will also estimate the swimming abilities of *T. maxima* larvae by estimating average horizontal displacement speeds in horizontal (180 x 50 x 40 cm) raceways, under contrasted current speed reflecting natural current conditions encountered in the lagoon.

D. aruanus and *T. maxima* are currently the model species in several projects in which COMPO participants are involved (often as leaders) and from which results will feed COMPO. For *D. aruanus*, these include projects on larval recruitment and settlers survival (the CORAL REEFS project, Fauvelot *et al*. in prep. a), reproductive behaviour (Buston *et al*. 2009) and population structure in systems with contrasted levels of fragmentation (Fauvelot *et al*. in prep. b), including in New Caledonia. In addition, adult density of *D. aruanus* and habitat quality on the eleven sampling sites will be estimated during the field survey detailed in Task 4 (using underwater transects), to be completed with a larger local dataset already available from IRD-UR227-CoRéUs team database, Fisheye (data from M. Kulbicki, IRD-UR227). For giant clams, ongoing research programs led by IRD in New Caledonia and Vanuatu will provide additional data on recruitment patterns, population dynamics, ecology, and population genetics (programmes ZONECO-Bénitiers 2008–2010, CRISP-Fonds Pacifique "DECOVAN" 2009–2011, projects leader P. Dumas). For example, results of a recent genetic analysis of *T. maxima* samples from New Caledonia using indirect methods suggested that local reefs may be composed of genetically differentiated gene pools, further suggesting limited dispersal of larvae (Fauvelot and Dumas in prep.).

Pascal Dumas is the leader of this task. He will be in charge of the giant clam synthesis and laboratory experiments, while Cécile Fauvelot and Laurent Vigliola will assist him for the damselfish synthesis. The Master student will help conducting laboratory experiments on giant clam larvae. There is virtually no risk that this task cannot be completed. The literature exists, rearing small giant clam is a well mastered technology in New Caledonia, and IRD lab is perfectly suited to conduct experiments in controlled conditions.

3.3.3 TACHE 3 / TASK 3

Objective: Develop a biophysical model to simulate connectivity patterns
Deliverables: Simulated connectivity patterns to use in model/data comparison (Task 6)
See: Figure 2 (page 12) for the position of Task 3 within COMPO scientific programme
Leader: Christophe Lett
Involved: Pascal Dumas, Cécile Fauvelot, Laurent Vigliola, PhD student

The biophysical model of damselfish and giant clam dispersal will be developed using the Ichthyop tool (Lett *et al*. 2008). Ichthyop is a free Java tool distributed on the web (http://www.previmer.org/ichthyop/) that was developed by COMPO's PI, among others. It is a generic version of a series of modelling experiments performed by the IRD and its partners in South Africa (Mullon *et al*. 2002, 2003, Huggett *et al*. 2002, Parada *et al*. 2003, Lett *et al*., 2006, 2007b, Miller *et al*. 2006), Peru (Lett *et al*. 2007a, Brochier *et al*. 2008a) and Morocco (Brochier *et al*. 2008b).

The biophysical model will be based on an "offline forcing" of a biological model by a physical model (Figure 5). The physical model will provide three-dimensional dynamic fields of current velocities ($\vec{u}$ in Figure 5) and potentially other variables (e.g., temperature T) to the biological model that tracks the location ($\vec{x}$ in Figure 5) and potentially other variables of interest (e.g., length L of individual larvae) of a collection of individuals i over time t.

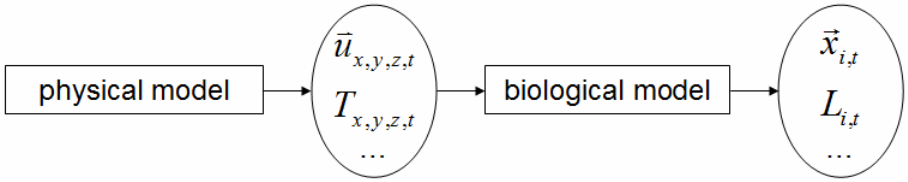


Figure 5 : A schematic view of the approach used for implementing the biophysical model in COMPO.

As seen in the description of Task 1, configurations from three different physical models (MARS, ROMS and ADCIRC) have been developed by physical oceanographers in New Caledonia. In addition to physical model outputs, Ichthyop requires the definition of release (spawning) and destination (settlement) areas. These areas will be defined according to available data on reef habitats for both species. Other important biological processes (e.g., larval behaviour, see below), as synthesised in Task 2, will be incorporated in the model step by step.

The biophysical model will first be run using passive entities to represent eggs and larvae. They will be transported solely by the water movements as simulated by the physical model, during ~1 week or during ~2–3 weeks, the approximate planktonic larval duration of giant clam and damselfish, respectively (see Task 2).

From this run we will calculate a connectivity matrix for both species:

$$M = \begin{pmatrix} m_{11} & m_{21} & \dots & m_{n1} \\ m_{12} & m_{22} & \dots & m_{n2} \\ \vdots & & \ddots & \vdots \\ m_{1n} & \dots & \dots & m_{nn} \end{pmatrix}$$

with m_{ij}, $i, j \in \{1,2,3,\ldots,n\}$, the proportion of virtual larvae transported from site i to site j, and n the number of sites (for simplicity we assume that all sites are release -spawning- and destination -settlement- areas).

Because m_{ij} are proportions, and under the assumption that mortality is not significantly different between the different sites, there is no need to include mortality in the biophysical model at this stage. One step further is to include a constant mortality rate, which might change the simulated connectivity patterns because larvae transported from distant sites would face longer periods of increased mortality than those transported from close sites.

According to the estimation of the time needed for a water parcel (i.e., a passive larva) to leave the SLNC in MARS simulations (mainly < 6 days at the surface, Jouon *et al*. 2006, Figure 4), we expect very low simulated connectivity values that will not compare well with the data. The inclusion of larval behaviour into the biophysical model will therefore be necessary. For example, vertical movements of larvae within the water column are expected to greatly change connectivity levels, as suggested by the contrasting residence times obtained in Figure 4 for bottom and surface layers. All behavioural processes included in the model will be based on the synthesis and laboratory experiments performed in Task 2. By analogy with landscape ecology (Kindlmann and Burel 2008), we will call "structural" and "functional" connectivity, respectively, the patterns obtained using passive entities or entities that have some degree of interactions with their marine environment (like differential mortality or behaviour).

Christophe Lett is the leader of this task. He will be mainly in charge of the biophysical model development. Pascal Dumas, Cécile Fauvelot and Laurent Vigliola will provide the ecological expertise for the inclusion of giant clam and damselfish larval behaviour into the model. The PhD student will be in charge of running the simulations and deriving the connectivity matrices. There is virtually no risk that this task cannot be fulfilled because the development of the biophysical model will be based on an existing tool, Ichthyop. The only potential problem is that the current version of Ichthyop is compatible with MARS and ROMS outputs but not with ADCIRC. We will most likely use MARS simulations (see Task 1), but if we also decide to use ADCIRC simulations as a complement, we will adapt Ichthyop to ADCIRC. This will be relatively easy with Ichthyop version 3.0, which is due by April 2010 (P. Verley, PREVIMER, pers. com.), because one of the objectives of this new version is to make the compatibility to any physical model easy to handle.

3.3.4 TACHE 4 / TASK 4

Objective: Collect and analyse microchemical data to provide empirical connectivity patterns
Deliverable: Empirical connectivity patterns to use in model/data comparison (Task 6)
See: Figure 2 (page 12) for the position of Task 4 within COMPO scientific programme
Leader: Laurent Vigliola
Involved: Cécile Fauvelot, PhD student

The main objectives of this task are to: (i) Determine at which spatial scale reef fish populations are effectively connected; (ii) Assess the rate at which local populations are self-replenished; (iii) Estimate the variability of self-recruitment within a local population; (iv) Evaluate if connectivity rates are modified by post-settlement mortality. To achieve these objectives we will use the technique of transgenerational marking of embryonic otoliths in a small focal reef population of a damselfish, *Dascyllus aruanus* (see Task 2 for details about this species), and follow over time the fate of self-recruits in this focal reef (i.e. where embryos will be marked) and the ability of embryos hatched on the focal reef to colonize neighboring patches as a function of distance to the focal patch (Figure 3).

The following sampling protocol is common to Tasks 4 and 5. Eleven study reefs have been selected in the South Lagoon of New Caledonia (SLNC) in an area covered by the biophysical model (Figure 3). The focal reef in which self recruitment rates will be estimated is surrounded by 10 other study reefs (Figure 3). Population size of *D. aruanus* and quality of settlement habitat will be estimated by underwater visual censuses (UVC) in each of the 11 reefs. Ten UVC transects will be surveyed at each reef following Clua *et al*. (2006). At time T1 of the study, the entire or a large fraction of the focal reef adult population will be injected with an enriched ^{137}Ba isotope solution in order to mark embryonic otoliths. A few days later, a few nests will be collected by divers and embryo otoliths extracted to evaluate tagging success. *D. aruanus* have a 3–5 day egg development phase and a 16–24 day larval duration, so that it will take approximately one month for eggs to hatch, metamorphose, and settle on a reef. Therefore, at T1+1 month and T1+2 months, settlers (corresponding to the embryos that have been marked one month earlier) and 1-month post-settlement juveniles will be collected by divers using hand nets and anaesthetic solution (clove oil). This entire procedure (tagging and collection of settlers and one-month post-settlement juveniles) will be repeated three times so that self-recruitment rates will be estimated for three monthly cohorts (Nov. 2011, Dec. 2011, and Jan. 2012 cohorts) at two different times (e.g., T1+1 month and T1+2 months for cohort 1) (Table 1). In addition, juveniles of the three tagged cohorts (i.e. 1, 2, and 3-month post-settlement juveniles from cohorts 3, 2, and 1, respectively) will be collected at T1+4 months in the 11 selected reefs to determine the number of migrants from the focal reef and thus determine at which spatial scale *D. aruanus* populations are effectively connected.

	T1 Nov.	T1+1 month Dec. 2011	T1+2 months Jan. 2012	T1+3 months Feb.	T1+4 months Mar.
Focal reef - cohort 1	Tag	Settlers	Juveniles 1		
Focal reef - cohort 2		Tag	Settlers	Juveniles 1	
Focal reef - cohort 3			Tag	Settlers	Juveniles 1
All reefs & cohorts					Juveniles 1–3

Table 1. Calendar for sampling the sites in Tasks 4 and 5. Juveniles 1 (resp. 2, 3) are one-month (resp. two- and three-month) post-settlement juveniles.

A shift in the rate of self-recruitment estimated from settlers and from one-month post-settlement juveniles will indicate natural selection based on juveniles origins and a

modification of connectivity rates by post-settlement mortality (i.e., "realised connectivity"). The sampling design used here follows that already employed by the task leader for another damselfish (Vigliola and Meekan 2002, Vigliola *et al*. 2007). In the tropical South Pacific, reef fish settlement follows summer temperatures and peaks in summer from October to January (Doherty and Williams 1988). Thus, field work is expected to start in November 2011 (T1) and end in March 2012 (T1+4 months).

Otolith will be extracted from embryos using a new technique developed in Darwin by Vigliola, Meekan & Parry in October 2008 for embryos of another benthic spawner damselfish, *Stegastes nigricans*, (unpublished but see Chittaro *et al*. 2006). Embryos will be dissolved in bleach, centrifuged, rinsed in ultra pure water and centrifuged 5 times, grouped at the center of a petri dish by applying a rotating movement under a dissecting microscope, let dried in clean HEPA conditions and then collected with a double side tape for LA-ICPMS analysis. Otoliths of settlers and juveniles will be extracted and sectioned using conventional techniques (Vigliola *et al*. 2007) but under clean conditions that are appropriate for micro-chemistry. Ba (138 and 137) and Ca will be measured at the core of sectioned otoliths for settlers and juveniles and for the whole otolith for embryos (which is just a core) using LA-ICPMS. Otolith data will also provide the age of all collected individuals and their planktonic larval duration (a key parameter in biophysical models), using the methods described by Vigliola *et al*. (2000). Analyses will be performed at the Charles Darwin University (CDU, Darwin, Australia) where Laurent Vigliola has long standing collaborations with Dr. Mark Meekan (Australian Institute of Marine Science, Darwin office) and Pr. David Parry (CDU). The LA-ICPMS in Darwin is an Agilent 7500 ce octopole reaction system fitted with an UP-213 laser (New Wave Research).

Laurent Vigliola is the leader of this Task. The PhD student will contribute to all aspects of the task, including field work, otolith preparation, LA-ICPMS, data analysis and publications. Cécile Fauvelot will contribute to the field work (see Task 5). Task 4 is relatively risky since transgenerational tagging is a new technique and there is no guarantee that tagged embryos will return to natal reefs in sufficient numbers. However, the task leader will benefit from advices from the team that developed the technique (Thorrold *et al*. 2006, Almany *et al*. 2007) and recent studies indicate about 60% self-recruitment for coral reef fishes. Furthermore, if no tagged individuals are collected, data on adult densities and results from the genetics (Task 5) can still be used in the model/data comparison (Task 6), and reporting no self-recruitment will remain publishable at the highest level.

3.3.5 TACHE 5 / TASK 5

Objective: Collect and analyse genetic data to provide empirical connectivity patterns
Deliverable: Empirical connectivity patterns to use in model/data comparison (Task 6)
See: Figure 2 (page 12) for the position of Task 5 within COMPO scientific programme
Leader: Cécile Fauvelot
Involved: Laurent Vigliola, PhD student

The objective of this task is to investigate the effective number of migrants exchanged among reefs as well as the effective number of recruits returning to their natal reef (i.e. self-recruitment rates) for both damselfish and giant clam. We will focus on two species in this task: the coral reef damselfish *Dascyllus aruanus* and the giant clam *Tridacna maxima* (see Task 2, section 3.3.2, for details about these species).

D. aruanus genetic structuring has been investigated by the task leader through indirect population genetics in French Polynesia (Fauvelot and Planes 2002, Fauvelot *et al*. 2003, Fauvelot *et al*. 2007), and in New Caledonia (Fauvelot *et al*. in prep. b) using recently developed genetic markers (Fauvelot *et al*. 2009a). Results of these genetic studies showed evolutionary connectivity of *D. aruanus* populations over large spatial scales (up to 450 km, Fauvelot *et al*. 2007, Fauvelot *et al*. in prep. b), but a closer look at relatedness patterns of recently settled juveniles showed that *D. aruanus* larvae may disperse in clouds in which close relatives remain together, and likely not far from parental colonies (Buston *et al*. 2009), suggesting possible self-recruitment.

T. maxima genetic structuring has also been investigated by the task leader through indirect population genetics on four reefs sampled in New Caledonia, using recently developed markers (Fauvelot and Dumas in prep.), showing that observed departure from equilibrium conditions in sampled populations may be due to a Wahlund effect (i.e. a mixture of several differentiated gene pools), and therefore to restricted larvae dispersal, as found within the Indo-Malay archipelago (Nuryanto and Kochzius 2009).

In COMPO, additional genetic data will be obtained with direct genetic methods using the paternity approach, analyzing recently settled juveniles and putative parents. The same calendar (Table 1) and sampling sites (Figure 3) as for the microchemical data (Task 4) will be followed. It is important to note that all fish sampled in this project will be commonly analyzed using the two complementary genetic and microchemical analyses. At time T1, all potential adults from the focal reef will be genetically characterized, and recruits collected at T1+1 month, +2 months and +3 months on the focal reef will be genetically analyzed and assigned to their potential parents. If there are too many adults to sample and analyze all individuals, adult densities will be estimated in order to estimate the number of potential parents as compared to the number of adults sub-sampled. At T1+4 months, recruits of less than four months old will be collected from the 10 surrounding reefs and genetically analyzed in order to determine if their parents were located on the focal reef and thus evaluate the effective dispersal distances reached by the recruits from the focal reef (Table 1, Figure 3).

Fin clipping for the damselfish and mantel biopsies for the giant clam will be conducted under water on adults and tissues will be conserved in 80% ethanol. Fish recruits will be kept entire and preserved directly in individual 80% ethanol containing tubes. Fish juveniles (i.e. newly recruited fishes of one, two and three months) will be collected in branching coral colonies using an anesthetic (clove oil) solution injected under a transparent plastic bag covering the coral colony and hand nets (Fauvelot *et al*. in prep. b). For the giant clams, since

newly settled juveniles are almost impossible to be located because of their small size, the smallest individuals (i.e., individuals of one year old that have a mean shell length of ~ 60 mm) will have a mantel biopsy performed and these will be genetically compared against adults of ~ 25 cm shell length, corresponding to mature adults of approximately 4 years old (Nash *et al*. 1988).

Eleven and eight microsatellite loci for *D. aruanus* (Fauvelot *et al*. 2009a) and *T. maxima* (Fauvelot and Dumas in prep.), respectively, will be analyzed for all sampled adults and collected recruits. All molecular analyses will be conducted at the newly settled "Plate Forme du Vivant" (PFV) located in the IRD center in Nouméa, New Caledonia. Microsatellites containing PCR products will be analyzed on a 3130Xl ABI (Applied Biosystem) in order to score multilocus genotypes for each individual. Parentage analyses will be assessed with a likelihood approach (Meager 1986). We will use the software FAMOZ (Gerber *et al*. 2003) to compute log-likelihood-based paternity. FAMOZ provides log of the odds ratio (LOD) scores that are estimated for assigning parentage. This program uses simulations based on a comparison of offspring assignment with allelic frequencies and genotype frequencies to build a statistical test for the parentage assignment.

Cécile Fauvelot is the leader of this task. She will be in charge of the genetic analysis conducted on both damselfish and giant clam for which she has ample experience. The PhD student will contribute mainly to the genetic data analysis. The field work will be conducted together with Laurent Vigliola and the PhD student (see Task 4). Task 5 is relatively risky as we currently have no guarantee that 100% of larvae originating from the focal reef will not disperse away from all studied reefs (i.e further than 22 km). However, based on recent reproductive behavior results (Buston *et al*. 2009) and genetic data obtained using indirect methods (Fauvelot *et al*. 2007, Fauvelot *et al*. in prep. b), we have no reason to believe so. Moreover, even if all analyzed settlers from the eleven sampled sites are found not to originate from the focal reef, this is still a publishable result. Genetic data obtained from the analysis of settlers from the 11 focal reefs will also be processed with 'classical' population genetic models to infer gene flow among sampled reefs (see Task 6).

3.3.6 TACHE 6 / TASK 6

Objective: Use empirical connectivity patterns from Tasks 4 and 5 to validate simulated connectivity patterns from Task 3
Deliverable: Validated simulated connectivity patterns to use in MPA model (Task 7)
See: Figure 2 (page 12) for the position of Task 6 within COMPO scientific programme
Leader: Christophe Lett
Involved: Team effort

From the connectivity matrix M calculated from the biophysical model (see Task 3), we will compute the number of larvae that have settled at any site $i \in \{1,2,3,\ldots,n\}$ as MN, where $N = (N_1, N_2, N_3, \ldots, N_n)$ is a vector with N_i the number of eggs released at site i, that can be estimated from existing data of population density and fecundity.

For analysis of the microchemical and genetic data (Tasks 4 and 5), we assume for simplicity that the focus site, where adults are caught for tagging and genetic characterisation, is site 1; that the vast majority of adults were caught, and that sites 1 to k, $k < n$, were sampled, i.e., settlers were caught to study if they came from the focus site. For every sampled site $l \in \{1,2,3,\ldots,k\}$, we will calculate the proportion p_l of the settlers caught that came from the focus site.

The observed values of p_l can be compared to the values $\tilde{p}_l$ of p_l estimated from the model: $\tilde{p}_l = m_{1l}N_1 / \sum_{i=1}^{n} m_{il}N_i$. We will calculate an index that evaluates the differences between the values observed in the data and obtained in the model, e.g., $\sqrt{\sum_{l=1}^{k}(p_l - \tilde{p}_l)^2 / k}$.

This comparison concerns model vs. microchemical and model vs. genetic data, but the same approach can also be used to compare microchemical vs. genetic data. One way to estimate that the model/data comparison is satisfactory is when there is not a larger difference between model and genetic data on the one hand, model and microchemical data on the other, than there is between microchemical and genetic data. As long as the model/data comparison is not satisfactory, we will come back to the biophysical model and include additional biological knowledge (see Tasks 2 and 3).

In the approach described above, at least as a first approximation, mortality would not have to be included in the model (because we would compare proportions and use the assumption that mortality is not significantly different between the different sites). We may however never reach the situation of a satisfactory model/data comparison for a number of reasons, among which the sensibility of the model results to the number of eggs released (the N vector). As such, an alternative analysis focusing on dispersal from site 1 only will also be performed. For every sampled site $l \in \{1,2,3,\ldots,k\}$, we will calculate a relative settlement proportion, i.e., the number of settlers caught on site l that came from the focus site divided by the total number of settlers collected at all sampling sites that came from the focus site. This value is $\tilde{p}_l^{\,*} = m_{1l}N_1 / \sum_{i=1}^{k} m_{1i}N_1 = m_{1l} / \sum_{i=1}^{k} m_{1i}$ in the model and it can also be estimated from the data. As before, because the $\tilde{p}_l^{\,*}$ values are proportions, we would not have to include mortality in the model. The advantage of this approach over the approach described above is that the estimation of the N vector is not needed. However, the $\tilde{p}_l^{\,*}$ values provide a less comprehensive representation of connectivity than the $\tilde{p}_l$ values (because only k elements - m_{1i} for $i \in \{1,2,3,\ldots,k\}$- of the connectivity matrix M are needed to calculate the $\tilde{p}_l^{\,*}$ values whereas $k \times n$ elements - m_{il} for $i \in \{1,2,3,\ldots,n\}$ and $l \in \{1,2,3,\ldots,k\}$- are used to calculate the $\tilde{p}_l$ values).

To compare the connectivity patterns simulated for giant clam with those assessed using a classical (indirect) genetic approach within the ZONECO-Bénitiers project, we will follow the methodology proposed by Galindo *et al*. (2006). This requires the development of a genetic model that simulates the effects of both larval dispersal and genetic drift. The genetic model will use as input the connectivity patterns simulated by the biophysical model, and will simulate genetic drift on a one-locus, two-allele neutral marker without mutation. Genetic differences among populations (F_{ST}) will be calculated from both the genetic data and model, and compared.

We will not be able to estimate the uncertainty associated with empirical connectivity values because sampling of all sites will be performed only once (at T1+4 months, Table 1). This is a limitation of the approach but doing replications of all sites sampling would simply be too costly. However, the assessment of self-recruitment will be performed for three cohorts in the focal reef (at T1+1, T1+2 and T1+3 months for settlers and at T1+2, T1+3 and T1+4 months for one-month post-settlement juveniles, Table 2), which is an improvement compared to recent studies using microchemical (Almany *et al*. 2007) and genetic (Planes *et al*. 2009) techniques. On the modelling side, uncertainty in the above-mentioned $\tilde{p}_l$ and $\tilde{p}_l^*$ values will come from four principal factors. The first one is the uncertainty associated with the N vector (the number of eggs released at the different sites), which can be estimated from the data. The other three principal factors of uncertainty will affect the M connectivity matrix. The first of these factors concerns the value used for planktonic larval duration (PLD) in the biophysical model (Task 3). It is likely the most sensitive parameter in biophysical modelling and for this reason a confidence interval of PLD will be carefully determined for both species in Task 2. The second factor concerns larval behavior, i.e., vertical movement pattern and horizontal swimming speed, which will also be estimated in Task 2. The last factor of uncertainty resides in the physical simulations (Task 1). Physical simulations used in biophysical models are only valid "statistically". This means that even when physical models are forced by a repeated climatology, there are differences in the simulation outputs between individual years due to intrinsic mesoscale activity. The resulting uncertainty in the values of matrix M elements can be estimated by using a set of physical simulations; a series of 5–10 years of simulations is usually enough in practice.

Task 6 is the core of the COMPO proposal and all members will contribute. The PhD student will provide the simulated connectivity patterns from Task 3. Cécile Fauvelot, Laurent Vigliola and the PhD student will provide the empirical connectivity patterns from Tasks 4 and 5. Pascal Dumas, Cécile Fauvelot and Laurent Vigliola will bring the expertise for the inclusion of giant clam and damselfish biological knowledge into the model from Task 2. The genetic model will be developed by Tri Nguyen-Huu. The model vs. data comparisons will be performed by Christophe Lett, who will also lead the task. The simulated connectivity patterns will be integrated by David Kaplan for use in Task 7. Task 6 is relatively risky, as the comparison of model with biological data usually is. As we reported above alternative ways of performing the model/data comparison, we are confident that we will produce interesting comparisons despite these risks.

The beginning and ending of Task 6 constitute the two milestones identified for the accomplishment of the project. These milestones are discussed further in section 3.4.

3.3.7 TACHE 7 / TASK 7

Objective: Develop an MPA model that integrates validated simulated connectivity patterns from Task 6 to assess the MPA network in the SLNC
Deliverable: Simulated indices of MPA effects
See: Figure 2 (page 12) for the position of Task 7 within COMPO scientific programme
Leader: David Kaplan
Involved: Pascal Dumas, Laurent Vigliola

Understanding and predicting the functioning of the existing MPA network in the SLNC remains an important management objective, goal of this project and step towards advancing our understanding of the general effects of connectivity on MPA networks. Here we propose to integrate habitat maps and spatial estimates of anthropogenic impacts on marine species in the SLNC developed by New Caledonia project participants and their research group into the spatially-explicit MPA model developed in Kaplan *et al*. (2006, 2009). This is an equilibrium model that describes a species with dispersing larvae and sedentary adults, and is suitable for assessing MPA impacts on persistence and fisheries yield for the two target species and, more generally, for a wide variety of reef species in the SLNC. The model has already been used to assess the effects of coastal MPA implementation on the persistence of populations as part of the California (USA) MPA implementation process (Kaplan *et al*. 2009), and, therefore, we feel confident it can be applied to the SLNC MPA network. The major advancement proposed in this study will be the integration of the realistic, validated dispersal patterns developed in Task 6 into the model.

There are two critical questions that we wish to address with this modelling effort: (i) as determined via comparisons between the model with idealised larval dispersal patterns, as used in previous work (Kaplan *et al*. 2009), and the model with realistic dispersal patterns, in what way and where spatially does population dynamics differ when more accurate dispersal patterns are used in the model; and (ii) in what way and under what conditions does the existing MPA network contributes to persistence and fisheries yield in the SLNC. The first of these questions will be assessed by testing the model with the connectivity pattern developed in Task 6 against the null hypothesis that dispersal can be accurately approximated as an advection-diffusion process (Kaplan 2006). This examination goes directly towards assessing the value of more idealised or simplistic approaches to designing and assessing MPA networks that are widely used elsewhere (Ball and Possingham 2000, Possingham *et al*. 2000, Walters et al. 2007, Kaplan *et al*. 2009). Furthermore, while the validation of the dispersal patterns in Task 6 will undoubtedly provide insight into the importance of realistic dispersal estimates for this system, this modelling effort will provide tangible evidence in terms of predicted changes in equilibrium population densities of how connectivity affects to population and ecosystem functioning in this system. Additional validation of these connectivity patterns and the modelling approach itself should in turn be

possible through comparisons between predicted patterns of adult density and observed patterns obtained as part of other MPA studies in the area (particularly PAMPA for both fish and invertebrates).

Addressing the second of these questions, namely identifying how the MPA network contributes to persistence and fisheries yield in the SLNC, will be achieved by building on the MPA assessments developed for the California MPA network (Kaplan *et al*. 2009). For commercial mollusc species in New Caledonia, historical data on adult densities inside vs. outside reserves provide relevant baselines for assessing MPA effects. In addition, our work will be carried out in the overall context of the PAMPA project, whose goal is to develop a board of indicators of MPA functioning and management. MPA modelling results will be summarized in terms of appropriate statistical measures of their contribution to persistence and yield, as compared both to the system in the absence of MPAs and to alternative/improved MPA network designs. One particular advance over prior work that we will explore in the context of this project is the potential of using randomised MPA designs to assess the relative value of the existing MPA network with respect to alternatives and to identify optimal MPA configurations (similar to approaches that assess the contribution of different habitats to a MPA network -Ball and Possingham 2000, Possingham *et al*. 2000- but using a full population model to provide more realistic estimates of MPA effects).

David Kaplan is the leader of this task. He will be in charge of the development of the MPA model. Pascal Dumas and Laurent Vigliola will provide the indicators from the PAMPA project, and relevant habitat, anthropogenic pressure and adult density data needed for model parameterization. Given the existing track record of using this model for MPA assessment and the availability of relevant historical data on both target species in the area, we are confident that this task involves relatively little risk provided that connectivity patterns are successfully developed in Task 6.

3.4. CALENDRIER DES TACHES, LIVRABLES ET JALONS / PLANNING OF TASKS, DELIVERABLES AND MILESTONES

Figure 6 shows the planning of tasks and milestones in the COMPO proposal. There are two milestones. The first one concerns beginning of Task 6, the comparison of connectivity patterns, which depends on the accomplishment of Tasks 1–5. As we expect data from different methods (microchemistry and genetics) in the different tasks, and for two species (giant clam and damselfish), there is little or no chance that comparisons between model and data will not be possible. In the worst case, we count on data from Task 4 or 5, for one species. As indicated in the scientific programme (section 3.1), as long as model and data connectivity patterns do not compare well, the model will be improved (therefore Task 3 continues in parallel of Task 6 in Figure 6). Once there is an agreement that the comparison is satisfactory (see Task 6), Task 7 begins. This is the second milestone.

In Table 2 is reported, for each task of the COMPO proposal, a synthesis of years, topic, leader and deliverables. Only the minimum deliverables to consider a task as successful, i.e.,

contributing to the project, are reported. But we expect additional deliverables, in particular publications in international journals and talks in regional (New Caledonia), national and international conferences (see Section 4). There will also be annual progress reports, as well as a report at the end of each task.

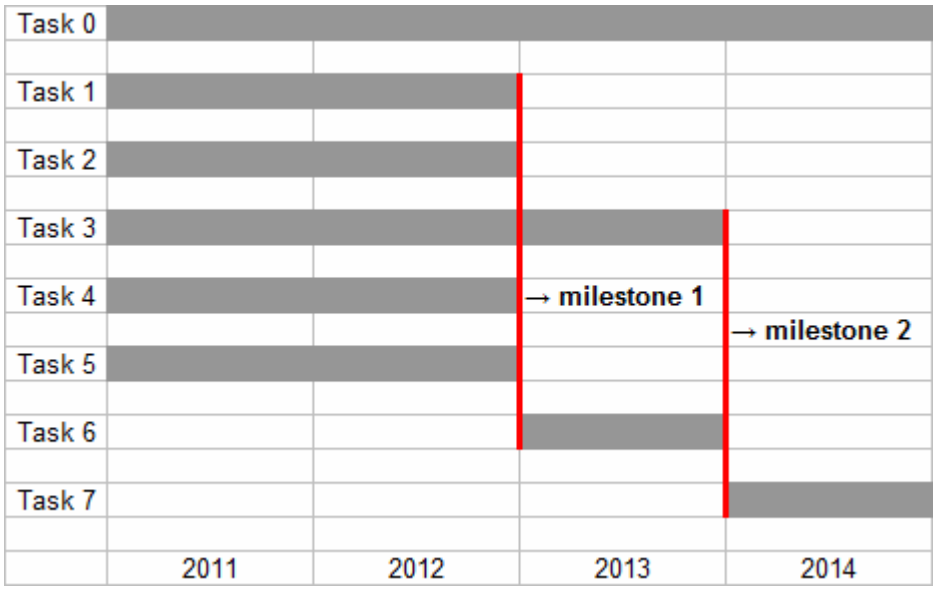


Figure 6: Diagram summarizing the planning of tasks and milestones in the COMPO proposal.

Task	Years	Topic	Leader	Deliverables
1	2011–2012	Evaluation of physical models simulations	Christophe Lett	Physical simulations
2	2011–2012	Larval ecology	Pascal Dumas	Synthesis of biological knowledge
3	2011–2013	Biophysical modelling	Christophe Lett	Simulated connectivity patterns
4	2011–2012	Microchemistry	Laurent Vigliola	Empirical connectivity data
5	2011–2012	Population genetics	Cécile Fauvelot	Empirical connectivity data
6	2013	Comparison of connectivity patterns	Christophe Lett	Validated simulated connectivity patterns
7	2014	MPA modelling	David Kaplan	Simulated indices of MPA effects

Table 2: A synthesis of years, topic, leader and minimum deliverables associated with each task of the COMPO proposal.

In addition to the six COMPO team members, a PhD student is expected to contribute to the first (2011–2013) part of the project, and a Master student to 6 months in 2011.

Hatchery production of giant clam larvae including subcontracting (1 technician * 1 month) and rental of larval production unit and equipment
Estimated cost: 6 000 €
Laboratory experiments (aquariums & equipment)
Estimated cost: 3 000 €
Total estimated cost for giant clam larvae experiments: 9 000 €

Total estimated cost: 47760 €

7. ANNEXES

7.1. REFERENCES BIBLIOGRAPHIQUES / REFERENCES

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7.2. BIOGRAPHIES / CV, RESUME