THÈSE

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Assessment of larval connectivity for the management of marine resources

Application to the gastropod *Concholepas concholepas* (loco) in Chile.

Etude de la connectivité larvaire pour la gestion des ressources marines

Application au gastéropode *Concholepas concholepas* (loco) au Chili.

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Résumé étendu

Le long de la côte chilienne, l'une des principales ressources exploitées par les pêcheries artisanales benthiques est le gastéropode marin *Concholepas concholepas*, plus communément appelée « loco ». Dès la fin des années 1980, des signes de surexploitation de cette espèce sont apparus et différents moyens de gestion ont été appliqués en conséquence. Le plan de gestion actuellement appliqué a été initié en 1998 et correspond à la mise en place de droits d'usage territoriaux dans des zones distinctes appelées AMERB (« Areas de Manejo y Explotación de Recursos Bentónicos » ; zones d'exploitation et de gestion pour les ressources benthiques). Cette mesure traduit la volonté d'avoir une gestion spatialisée des stocks de loco au Chili. Depuis la mise en place des AMERB, les captures de loco se sont stabilisées mais elles restent nettement inférieures au rendement du début des années 1980. Des études récentes ont suggéré que l'établissement d'une gestion des stocks de loco à une échelle plus régionale, en considérant les AMERB sous forme de réseaux, pourrait être plus adapté que le mode de gestion local actuel. Afin d'évaluer comment la mise en place de tels réseaux d'AMERB pourrait être possible, je me suis appuyée sur l'exemple des réseaux d'aires marines protégées (AMP). Il a ainsi été montré que pour mieux contribuer à la persistance des populations marines, les AMP doivent être connectées entre elles. Pour les espèces dont les juvéniles et adultes sont relativement sédentaires, comme c'est le cas pour la plupart des espèces benthiques dont le loco, ces connections sont assurées au cours de la phase larvaire planctonique. Pour assurer un fonctionnement en réseau, les échelles spatiales associées à la dispersion des larves et à la distribution des AMP doivent donc coïncider. Or lors de l'établissement des AMERB, aucune étude sur la biologie et l'écologie du loco n'a été mise en place pour évaluer le potentiel de connectivité entre AMERB. Une telle étude est pourtant une étape essentielle vers la mise en place d'un réseau d'AMERB. Dans le cadre de cette thèse, j'ai donc étudié la connectivité larvaire du loco au Chili. La connectivité (larvaire) est définie comme l'échange d'individus (larves) entre des sous-populations géographiquement séparées. La connectivité larvaire est principalement conditionnée par la dispersion larvaire, qui est elle-même la combinaison de différents processus : la ponte, le transport physique, le comportement larvaire, la survie et l'installation.

Afin d'étudier la connectivité du loco, la première étape de mon travail a donc consisté à décrire les principaux éléments de connaissance de ces différents processus pour le loco dans le Chapitre 1. Les locos adultes vivent sur des fonds rocheux, à partir de la zone intertidale et jusqu'à 40 m de profondeur. Après la reproduction, des œufs encapsulés sont relâchés par les femelles et se fixent au fond. Il a été montré que le nombre d'œufs de loco dans une capsule est plus faible au Nord du Chili qu'au Sud. Le pic de ponte a lieu entre l'été et l'automne austral. Après 2 à 3 mois de développement capsulaire, les larves sont relâchées. La durée de dispersion larvaire varie de 2 à 12 mois selon les régions. On suppose que la durée de dispersion dépend de la température de l'eau dans la zone, qui est très variable le long de la côte chilienne. Cependant aucune étude n'a été mise en place pour évaluer directement l'effet de la température sur le développement des larves de loco. Trois stades apparaissent au cours du développement larvaire, deux stades véligères et un stade compétent au cours duquel la larve peut s'installer dans son habitat de vie. Le stade compétent est le seul pour lequel le comportement a été étudié et un comportement de migration verticale en surface pendant la nuit et en profondeur pendant la journée a été mis en évidence pour les larves de ce stade. Après la phase compétente, les larves s'installent sur un substrat. L'installation s'effectue lorsque les larves ont atteint une taille comprise entre 1800 µm et 2000 µm.

Cette synthèse des connaissances biologiques du loco pertinentes pour la connectivité m'a permis de mettre en évidence que plusieurs processus étaient manquants. Tout d'abord, le comportement larvaire a été établi pour le stade compétent mais pas pour les stades véligères. Ensuite, due à la forte variabilité des températures le long de la côte chilienne, on s'attend à ce que la croissance larvaire soit également très variable. J'ai donc mis en place des expériences en laboratoire afin d’évaluer le comportement des larves véligères de stade 1 et la croissance larvaire en fonction de la température. Ces expériences font l'objet du Chapitre 2. J’ai étudié le comportement des larves véligères de stade 1 sous deux photopériodes de 24 heures : une photopériode naturelle avec 10 heures de jour et 14 heures de nuit et une photopériode artificielle consistant en une obscurité constante pendant 24 heures. Pendant la nuit, j'ai observé une augmentation du nombre de larves mobiles. Par ailleurs, les larves étaient situées à une profondeur inférieure pendant la nuit que pendant le jour. Ces résultats ont été obtenus pour les deux photopériodes testées mais ils sont plus marqués avec la photopériode naturelle. Pour la photopériode naturelle, le nombre de larves mobiles dans la colonne diminuait avec la profondeur pendant la nuit tandis que les larves mobiles étaient uniformément distribuées en profondeur pendant le jour. Pour la photopériode d’obscurité constante, le nombre de larves mobiles diminuait avec la profondeur la nuit mais aussi légèrement le jour. Ces résultats suggèrent que les larves véligères de stade 1 ont un comportement de migration verticale nocturne. Ils suggèrent aussi que ce comportement migratoire n’est pas seulement dû à l’absence de lumière et pourrait donc être expliqué par un rythme endogène des larves. Puisqu’un comportement de migration verticale nocturne a aussi été décrit pour les larves compétentes, nous pouvons supposer que les larves de loco suivent probablement un comportement de migration verticale nocturne tout au long de la phase larvaire. Le second processus biologique que j’ai voulu considérer dans ce chapitre est la croissance larvaire. Cependant, les expériences mises en place pour évaluer l’évolution du taux de croissance des larves de loco à différentes températures n’ont pas été concluantes.

L’objectif de ma thèse a ensuite été d’évaluer les échelles de connectivité larvaire du loco afin de proposer la mise en place de modes de gestion mieux adaptés à la biologie et l’écologie de l’espèce. Une des méthodes efficaces pour l’étude de la connectivité est l’utilisation d’un modèle biophysique, *i.e.* de coupler un modèle hydrodynamique simulant les mouvements des masses d’eau à un modèle individu-centré incorporant les principaux processus biologiques de la vie larvaire.

Dans le Chapitre 3, j'ai donc développé un modèle biophysique de dispersion larvaire afin d'évaluer la connectivité du loco le long de la côte chilienne. J'ai d'abord utilisé ce modèle pour évaluer les échelles de connectivité du loco et ensuite pour identifier des sous-populations de loco faiblement connectées, donc relativement indépendantes, en utilisant une méthode récente de partitionnement (clustering) à partir des matrices de connectivité simulées. J'ai testé les effets de différents paramètres du modèle : la résolution du modèle hydrodynamique, la profondeur de la ponte et la durée de dispersion larvaire. De manière générale, le modèle nous a permis de démontrer l'importance des processus physiques sur la connectivité du loco. Les échelles moyennes de connectivité le long de la côte chilienne ont été évaluées entre 170 et 220 kilomètres. Les résultats ont également montré qu'une plus grande durée de dispersion conduit à une augmentation des distances de dispersion mais également à une augmentation des pertes de larves vers le large. Les valeurs simulées de connectivité augmentent généralement avec la profondeur, mettant en évidence l'importance de courants de sub-surface orientés vers la côte et le Sud du Chili pour la rétention larvaire. L'étude de la saisonnalité de la connectivité a montré une période favorable pour l'installation des larves en hiver et au printemps austral. Cette période coïncide avec une faible intensité de l'upwelling le long de la côte chilienne favorisant ainsi la rétention des larves le long de la côte. L'utilisation de modèles hydrodynamiques à différentes résolutions a révélé des patrons de connectivité simulée qualitativement similaires mais avec une diminution des valeurs de connectivité en utilisant le modèle à plus haute résolution. Finalement, la méthode de partitionnement utilisée à partir des matrices de connectivité simulées a permis de déterminer des barrières à la dispersion qui sont principalement expliquées par la géomorphologie de la côte chilienne.

Dans le Chapitre 4, j'ai étudié l'influence de plusieurs processus biologiques et écologique sur les patrons et échelles de connectivité évalués dans le chapitre précédent. Les processus que j'ai successivement implémentés dans le modèle de dispersion larvaire sont la croissance larvaire, l'habitat disponible à la ponte et à l'installation des larves, la fécondité, la migration verticale (telle qu'étudiée dans le Chapitre 2), et la mortalité larvaire. De manière générale, les larves sont principalement transportées vers le Nord dans tout le domaine d'étude. L'implémentation de la migration verticale dans le modèle a conduit à une augmentation des distances de dispersion allant jusqu'à 350 kilomètres pour les larves relâchées dans la région centrale du domaine, mais également à de plus grandes pertes vers le large. L'étude de la saisonnalité de la connectivité du loco a révélé des résultats similaires à ceux du Chapitre 3 et souligne le fait que les processus biologiques implémentés dans le modèle ont peu d'influence sur la saisonnalité. L'analyse des patrons de connectivité a permis de mettre en évidence une diminution des valeurs de connectivité du Nord au Sud fortement dépendante des processus biologiques. En effet, le long de la côte chilienne, les températures diminuant du Nord au Sud, la croissance et la mortalité dépendant de la température expliquent les différences de connectivité obtenues. L'incorporation de l'habitat dans le modèle a également conduit à une diminution des valeurs de connectivité au Sud qui a moins d'habitat favorable au loco qu'au Nord. La fécondité du loco, plus élevée au Sud, a légèrement compensé cette tendance de plus faibles valeurs de connectivité au Sud qu'au Nord. Le partitionnement en différentes sous-populations de loco le long de la côte chilienne suggère des barrières à la dispersion similaires à celles obtenues dans le Chapitre 3 au Nord mais différentes dans la partie Sud du domaine lorsque la migration verticale et la mortalité sont considérées.

Les résultats obtenus dans les Chapitres 3 et 4 suggèrent l'existence de sous-populations de loco relativement indépendantes du point de vue de la connectivité le long de la côte chilienne. Ces sous-populations mises en évidence représentent des entités beaucoup plus grandes que les AMERB, ce qui suggère que les AMERB d'une même sous-population sont fortement connectées entre elles et pourraient être gérées en commun. A partir de données de densité de loco adultes, d'abondance, de taille moyenne, de captures, quotas, taux d'exploitation et localisation des AMERBs, le sous-secrétariat de la pêche au Chili (IFOP) a récemment proposé des « supra

AMERB », *i.e.*, des regroupements régionaux d'AMERB. Dans la section de discussion générale de la thèse, j'ai donc d'abord comparé mes résultats de sous-populations de loco obtenues à partir du modèle de dispersion larvaire au découpage en supra-AMERB proposé par l'IFOP. Comme ce découpage ne couvre pas l'ensemble de la côte chilienne, j'ai ensuite fait une proposition de découpage exhaustif en combinant mes résultats et la proposition de l'IFOP. Ma proposition finale de 7 zones régionales de gestion du loco traduit l'influence de facteurs hydrodynamiques, écologiques et/ou biologiques distincts caractérisant la dynamique de population du loco.

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Voilà ! On y est ! Ecrire les remerciements signifie la fin du manuscrit de thèse, mais aussi la fin de 3 ans de recherche, la fin de 3 ans de jolies rencontres, amicales ou professionnelles sans lesquelles je n'aurai pu finir… Ma thèse étant une cotutelle entre la France et le Chili, mes remerciements seront un mélange de français et espagnol…

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A mes étoiles,

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Chapter 1. General introduction

1.1. The gastropod *Concholepas concholepas* in Chile

1.1.1. History of the fishery

Artisanal benthic fisheries in Chile develop along 4,600 km of oceanic coast from over 100 fishing ports supplying local and international markets. These fisheries add up to 20% of fisheries exports in Chile, being one of the productive activities of longer tradition and largest social impact in the country (Gelcich *et al.*, 2005). Until the end of the 80's, one of the most valuable benthic fisheries in Chile was targeting the marine gastropod *Concholepas concholepas* (Leiva and Castilla, 2002), commonly named 'loco' or 'Chilean abalone' in international markets (Figure 1.1). Marine gastropod resources, including loco, are exclusively exploited by the artisanal fishery sector. For the loco, fishermen extract species by diving from small artisanal boats (Figure 1.2).

Figure 1.1: Pictures of locos extracted after a fishery day (left) and of a can with locos ready to serve (right).

Figure 1.2: Pictures of a fisherman ready to dive from his artisanal boat to extract locos (left) and of "La fiebre del loco", a movie about the loco rush after re-opening the fishery in 1993 (right).

Although this species has been consumed since pre-hispanic times, official systematic records of loco catch and abundance are only available since the 1960's. During the 1960's, loco fishery typically supplied local markets, with annual landings around 5,000 t (Figure 1.3). In 1976, the international market started to be interested in this resource and landings increased steeply reaching a maximum of 25,000 t in 1980. Between 1983 and 1988, fishing effort continued to increase whereas total landings started to decline. At this time, the only fishing regulation applied was a three months closure during the reproductive season. The resource was recognized as overexploited and the tremendous decrease in catch per unit effort led to a complete fishery closure during four years between 1989 and 1992 (Castilla and Fernández, 1998). After re-opening the fishery in 1993, loco landings never recovered the previous levels of extraction despite stringent management regulations.

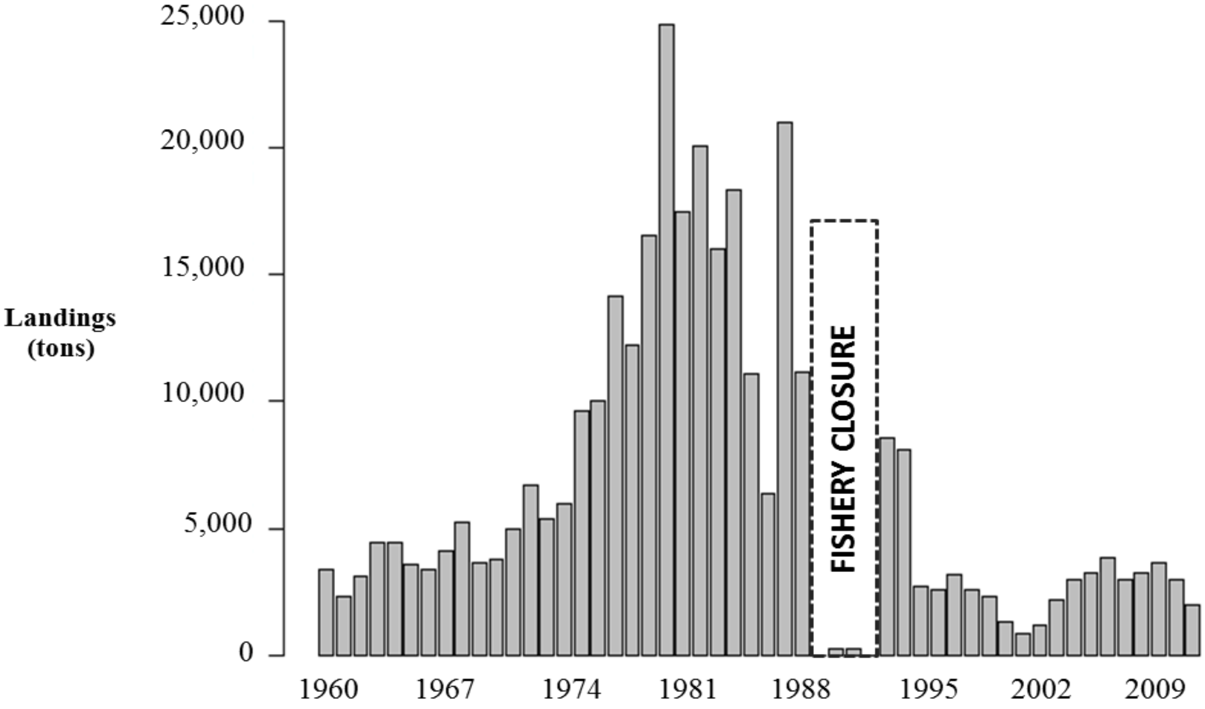


Figure 1.3: Loco landings from 1960 to 2011.

The management instrument known as Benthic Regime of Extraction was designed for and applied to regulate the loco fishery from 1993 to 1997. A total allowable catch quota (TAC) was established for each Chilean administrative Region to be extracted during a short fishing season. The regional TAC was divided by the number of fishermen legally registered in their residence region at that time, and individual catch limits were set. But in the first year, the number of fishermen doubled, which therefore decreased the profits for each fisherman. As the effect of regulation on the loco stock was not as expected, from 1998 onwards a territorial user right type of regulation called Management and Exploitation Areas for Benthic Resources (MEABR) was implemented. Under this exploitation regime, specific subtidal areas are provided by the authority to legally established fishermen organizations that claim for them, following a complex assignment process. The location and limits of each MEABR were defined by fishermen themselves. At the beginning they coincided mostly with spots of high abundance of loco (González *et al*., 2006). No loco fishing is authorized outside MEABR from northern Chile to Region XI. However, illegal catch persist within and out MEABR and would be at least 50% of the total catch in some regions

(González *et al.*, 2006). Fishermen organizations usually congregate fishermen belonging to the same artisanal fishing port named “caleta”, which have a common history of exploitation over the claimed MEABR. Each fisherman belongs to one or more MEABR and cannot go fishing in another one, even in case of a low harvesting year, as it was possible before (González *et al.*, 2006). The regulation established that each MEABR has to be monitored each year, estimating a yearly quota of extraction based on its resource abundance of loco bigger than 10 cm opercular length, which is the minimum legal size of extraction. The direct stock assessment is mostly done by fishermen themselves, supervised by a private consultant. The report and quota estimates are revised and signed by the fishery authority (fishery sub-secretary part of the economy ministry). One of the particularities of MEABR is that each fisherman organization is in charge of its own MEABR resource (Gelcich *et al.*, 2009). Loco is therefore fished and managed within discrete coastal areas where capture quotas are proposed for each area independently of the others. MEABR were first created because of the decline of the loco population but then extended to about thirty different benthic species (gastropods, bivalves, cephalopods, crustaceans, algae, echinoderms) irrespectively of the species price or life history. The resource was extracted from only 25 MEABR all along the Chilean coast in 2000 (Leiva and Castilla, 2002) but this number quickly increased from 185 in 2004 (Fernández and Castilla, 2005) to 535 in 2011, 392 of which include the loco resource (Sernapesca, National service of agriculture and fisheries in Chile, 2012). It was anticipated that the implementation of a local management tool such as MEABR would be more effective than the previous approach based on regional quotas (Bernal *et al.*, 1999). However, although since the beginning of MEABR, legal landings appear to have stabilized, in 2011 the landings of loco in MEABR reached 1,972 t (Figure 1.3), around 9 times lower than in 1981, despite a number of artisanal fishermen registered and allowed to fish loco as high as 14,505 for all Chile (Sernapesca, 2012). Although the delimitation of the MEABR was only based on the fishermen description at the time of their demand and no study has been conducted on the global evolution of the loco abundance, low current catches indicate that the yield of loco fishery reduced.

1.1.2. Towards scaling up loco fishery management

The current spatial-based management, *i.e.*, local spatial assessment of the loco resource abundance and top-down administration of MEABR, did not lead to the expected recovery of the fishery. Now, feedback on this management tool and history of the loco fishery tend to lead towards the collection of information and the implementation of an administration at a regional scale in order to consider networks of MEABR (Gelcich *et al.*, 2008; Tognelli *et al.*, 2009). To date, such networks are poorly developed, mainly due to the late evaluation of priority species and sites to conserve (Gelcich *et al.*, 2009).

In order to assess how the implementation of networks of MEABR could be achieved, recommendations and information available in the literature describing shifts from individual marine protected areas (MPA) to networks of MPAs can be used. The definition of MPA given by Claudet (2011) "a discrete geographic area of the sea established by international, local, territorial, tribal, or local laws designated to enhance the long-term conservation of natural resources therein. This objective is rarely exclusive and often relate to the sustainable use and management of marine resources and to socio-economic development" applies to MEABR likewise. A network of MPAs has been described as a "collection of individual MPAs … operating at various spatial scales … that are designed to meet objectives that a single reserve cannot achieve" (IUCN–WCPA, 2008). The implementation of an MPA network requires scaling up the management coordination of a collection of MPAs. Scaling-up potentially allows enhancing the organization between communities and a larger spatial extension of the management principles (Ban *et al.*, 2011). In the case of the loco management, there would be a need to scale-up from a local management to a regional management. It means adding higher levels in the current organization and spatial distribution of MEABR. However, scaling up to regional actions with a top-down (administrative) implementation requires following planning approaches and recommendations in order to be successful. Several authors advised to establish a multidisciplinary approach including societal, economic, and ecological aims in order to take into account all the processes acting at different scales to have an adaptive management (Pressey and Bottrill, 2008; Ban *et al*., 2011; Christie and Pollnac, 2011; Grorud-Colvert *et al*., 2011).

One of the weaknesses of the current management plan for loco fishery is claimed to be a lack of studies on the biology and ecology of the species at the time MEABR were established (Leiva and Castilla, 2002). Yet, several authors repeatedly advised to study the life cycle of the loco in MEABR (Castilla and Defeo, 2001; Leiva and Castilla, 2002; Fernández and Castilla, 2005; González *et al*., 2006). At the end of the 1980's the Chilean National Fisheries Service already recommended this kind of study (DiSalvo, 1988). In 2000, the lack of knowledge about the planktonic and the recruitment phases of the loco has been mentioned as an obstacle for the evaluation of the adequate extent needed for one particular MEABR and of the spatial distribution of all MEABR along the coast (Leiva and Castilla, 2002). Consequently, most biological and ecological studies of loco started only recently when scientists pointed at the low knowledge of the species in the current MEABR system such as the relevant spatial population processes, their scale and those of the environmental influences on recruitment and production.

Studies of MPA networks have shown that including spawning or nursery areas enhances the probability of recruitment of the species (Gell and Roberts, 2003; Lowry *et al*., 2009). However, these areas have to be connected in order to contribute to population persistence. For this, the scale of larval dispersal, transport patterns, and the distribution of MPAs have to coincide spatially (Kaplan, 2006; Botsford *et al*., 2009). Moreover, to enhance the success of MPA networks, each MPA has to be self-sustaining or in connection to other MPAs via dispersal (Planes, 2011). One of the main goals to consider in the establishment of an MPA network is therefore the connectivity between MPAs (Green *et al*., 2009; Grorud-Colvert *et al*., 2011). A network designed with taking account of connectivity will improve the benefits of conservation and is recommended for its robustness to climate change (Ban *et al*., 2011; Bernhardt and Leslie, 2013).

The current view for the loco is the management of a collection of presumably unlinked individual spatial units, the MEABR. Potential connectivity between MEABR has not been considered yet; and in this case, the management goals may be diminished (Grorud-Colvert *et al*., 2011). Therefore, the assessment of loco connectivity is a crucial step towards the establishment of a successful regional sustainable plan from individual MEABR. In short, the challenge is to establish at which spatial scale, if any, the loco constitutes a metapopulation along the Chilean coast.

1.2. Connectivity in marine metapopulations

1.2.1. Metapopulation dynamics

Sale *et al*. (2006) defined a metapopulation as "a system in which (1) local populations inhabit discrete habitats 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". According to this definition, most marine benthic invertebrate species such as loco can constitute metapopulations because (1) they mostly live in specific suitable (*e.g.*, rocky) patchy habitats surrounded by unsuitable (*e.g.*, sandy) ones and (2) their life cycle is generally characterized by two phases, a pelagic mobile larval phase contributing to significant dispersal between patches and a benthic sessile juvenile and adult phase, leading to a certain independence of local population dynamics on each patch. The transition between these two phases is the critical process of larval recruitment in the adult population. Since the beginning of the 20th century, recruitment is believed to be mainly controlled by environmental factors. Hjort (1914) was the first to propose that larval survival is affected by oceanographic environmental conditions which largely influence recruitment. Thereafter, several hypothesis proposed a link between hydrodynamic and food supply to explain larval recruitment variability (Cury and Roy, 1989; Cushing, 1990; Bakun, 1996). Nowadays, larval recruitment of benthic species is viewed as the result of complex interactions between hydrodynamic that influences larval dispersal and food supply, and geomorphology that determines settlement conditions in the benthic habitat (Pineda *et al*. 2009; Figure 1.4). All these processes (dispersal, food supply, settlement) can be affected by biological characteristics of larvae such as their capacity of migrating in the water column. They are also believed to influence larval recruitment, and therefore metapopulation dynamics, at different spatial and temporal scales. Therefore, an overall study of their effects requires a multiscale complex approach (Pineda *et al*. 2009).

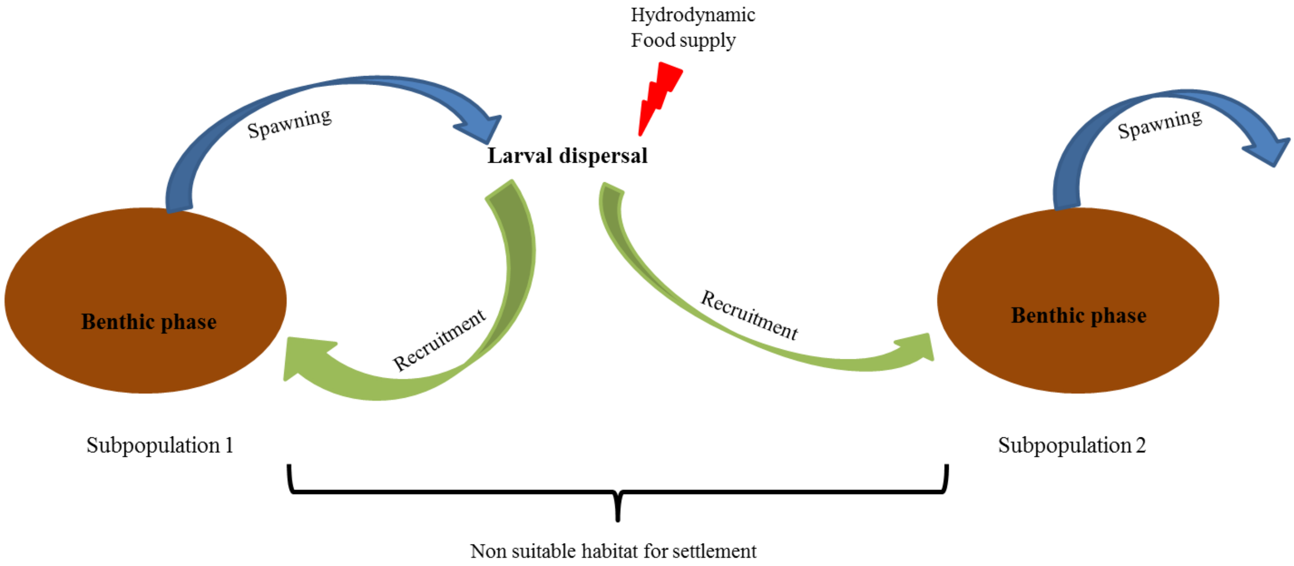


Figure 1.4: Schematic life cycle for benthic species between two subpopulations representing a metapopulation.

Benthic species from shallow waters such as loco move over short distances at the adult stage, and consequently the exchange of individuals between distinct sites only occur during early, pelagic life stages, *i.e.*, population connectivity is limited to larval connectivity. Larval connectivity involves larval transport and larval dispersal (Pineda *et al*., 2007). In the next sections, we used principally Pineda *et al*. (2007) and Ayata (2010) to give a brief summary of larval connectivity.

1.2.2. Larval transport

Larval transport is the combination of physical transport and larval behaviour. Physical transport is described by advection, that induces larval trajectories in a given direction, and diffusion, that adds a random component to trajectories. Due to difficulties to study larvae in the field or in laboratory, larval behaviour is unknown for most species. However, similarities of larval behaviour between different benthic species have been highlighted. Larvae can respond to different stimuli by changing their swimming speed or their position (Kingsford *et al*., 2002). The most frequent larval behaviour observed is vertical migration. Larval vertical migration cycle can be dial, tidal or ontogenetic (Metaxas and Saunders, 2009). Larval behaviour can also be influenced by physical characteristics of the water column such as temperature and salinity or by biological characteristics such as food supply.

1.2.3. Larval dispersal

Larval dispersal refers to the combination of spawning, larval transport (see section before), survival, and settlement. Spawning depends on the number of reproductive adults, their age (or size) and fecundity at age (or size). Spawning may also depend on seasonality. Spawning and settlement locations are highly dependent on suitable habitat. However, before reaching the settlement stage, larvae have to survive during the dispersal phase. Larval mortality during the dispersal phase is generally poorly known, but believed to be very high, around 90% (Rumrill, 1990). Causes of mortality are numerous: predation, starving, lethal temperature, offshore loss due to physical transport, and likely depend on larval stage (Metaxas and Saunders, 2009). Planktonic larval duration (PLD) is variable, between few hours to several days depending on species. The longer PLD is, the smaller is larval survival. Smaller larval survival, is believed to be compensated by larger fecundity (Hedgecock, 1986).

1.2.4. Larval connectivity

Larval connectivity is the "exchange of individuals among geographically separated subpopulations that comprise a metapopulation" (Cowen, 2002; Cowen and Sponaugle, 2009). For benthic species, larval connectivity is the result of larval dispersal (see section before) and post-settlement survival until reproduction. Including reproduction into connectivity is called reproductive connectivity (Pineda *et al.*, 2007). Population persistence and resilience, and genetic diversity are mainly influenced by larval connectivity (Botsford *et al.*, 2001; Hastings and Botsford, 2006; Cowen *et al.*, 2007). The assessment of larval connectivity is therefore essential for the understanding of marine metapopulations dynamics.

1.2.5. Estimating larval connectivity

Larval connectivity can firstly be estimated from field studies by sampling larvae using plankton tows. This method can provide estimates of larval retention (Paris and Cowen, 2004) and of demographic connectivity scale (Lo-Yat *et al.*, 2006). However, this method is not fully satisfactory for larval connectivity studies as it gives a snapshot of the larval distribution at small time scale (Leis *et al.*, 2011). Robust estimates of connectivity patterns are more reliable using methods based on genetics or calcified structure microchemistry (Leis *et al.*, 2011).

The first method for empirical assessment of connectivity is based on studying the chemistry of calcified structure of marine individuals: otoliths for fish and statoliths for invertebrates. These structures contain natural elemental signatures imprinted by the environment of the individual. The method consists in studying biogeochemical markers such as barium, copper or magnesium and provides knowledge of the origin of the collected individuals to evaluate connectivity patterns (Di Franco *et al.*, 2012a; López-Duarte *et al.*, 2012). The markers can also be artificial, *i.e.* individuals are marked through the immersion of the eggs in a fluorescent dye (Jones *et al.*, 1999; 2005) or through the injection of gravid females with barium stable isotope in case of transgenerational isotope labelling (Thorrold *et al.*, 2006).

The other main empirical method to study larval connectivity is to use population genetics. An indirect method consists in using gene flows to distinguish one population into discrete subpopulations and can highlight dispersal barrier (Leis *et al.*, 2011). This method relies on the variance of allele frequencies to differentiate a subpopulation and the total population studied (Weersing and Toonen, 2009). However, the most efficient method to study demographic connectivity using genetics is direct methods like parentage analysis and genetic assignment tests (Leis *et al*., 2011). Parentage analysis allows finding parents of one individual and has been used to assess self-recruitment in larval fish (Berumen *et al*., 2012) and to study larval connectivity patterns (Harrison *et al*., 2012). Genetic assignment tests ensure to link individuals to its parental population and were also used to study connectivity patterns between subpopulations (Hogan *et al*., 2012).

1.2.6. Modelling larval connectivity

As pointed in the previous sections, larval connectivity is a complex process wherein physical and biological factors interact at different temporal and spatial scales. To assess the influence on connectivity of these different factors and estimate connectivity scales, developing a biophysical model, *i.e.* coupling a hydrodynamic model to an individual-based model that incorporates the main biological processes operating during larval life, appears to be an appropriate indirect method (Leis *et al*., 2011).

Hydrodynamic models are based on movement equations representing oceanic circulation at regional to global scales. The horizontal and vertical resolutions of a hydrodynamic model are crucial to determine its ability to resolve physical processes. Only high resolution hydrodynamic models, of the order of kilometre, can resolve oceanic mesoscale processes. Model resolution also depends on forcing data resolution such as wind, temperature, salinity, tide, rainfall, and freshwater input. First generations of coupling between hydrodynamic model and biological model were based on Eulerian equations. Particle concentrations were followed by resolving advection and diffusion. The development of individual-based models (or Lagrangian models; Grimm and Railsback, 2005) allowed representing individual traits. Biophysical models were developed over a wide range of scales, from kilometres to thousands kilometres for spatial scales and from seconds to years for temporal scales. In marine ecology, they are mainly used to simulate larval dispersal of fish or invertebrates but have also recently been used to simulate the trajectories of other organisms like sea turtles (Putman *et al*., 2012). In such models, individuals, representing eggs and larvae, can be "passive", *i.e.* they follow the oceanic circulation as simulated by the hydrodynamic model, or "active" when they are given biological properties such as vertical migration. Such processes can vary with ontogeny and according to environment. For example, larval growth can vary according to seawater temperatures (Domingues *et al.*, 2012).

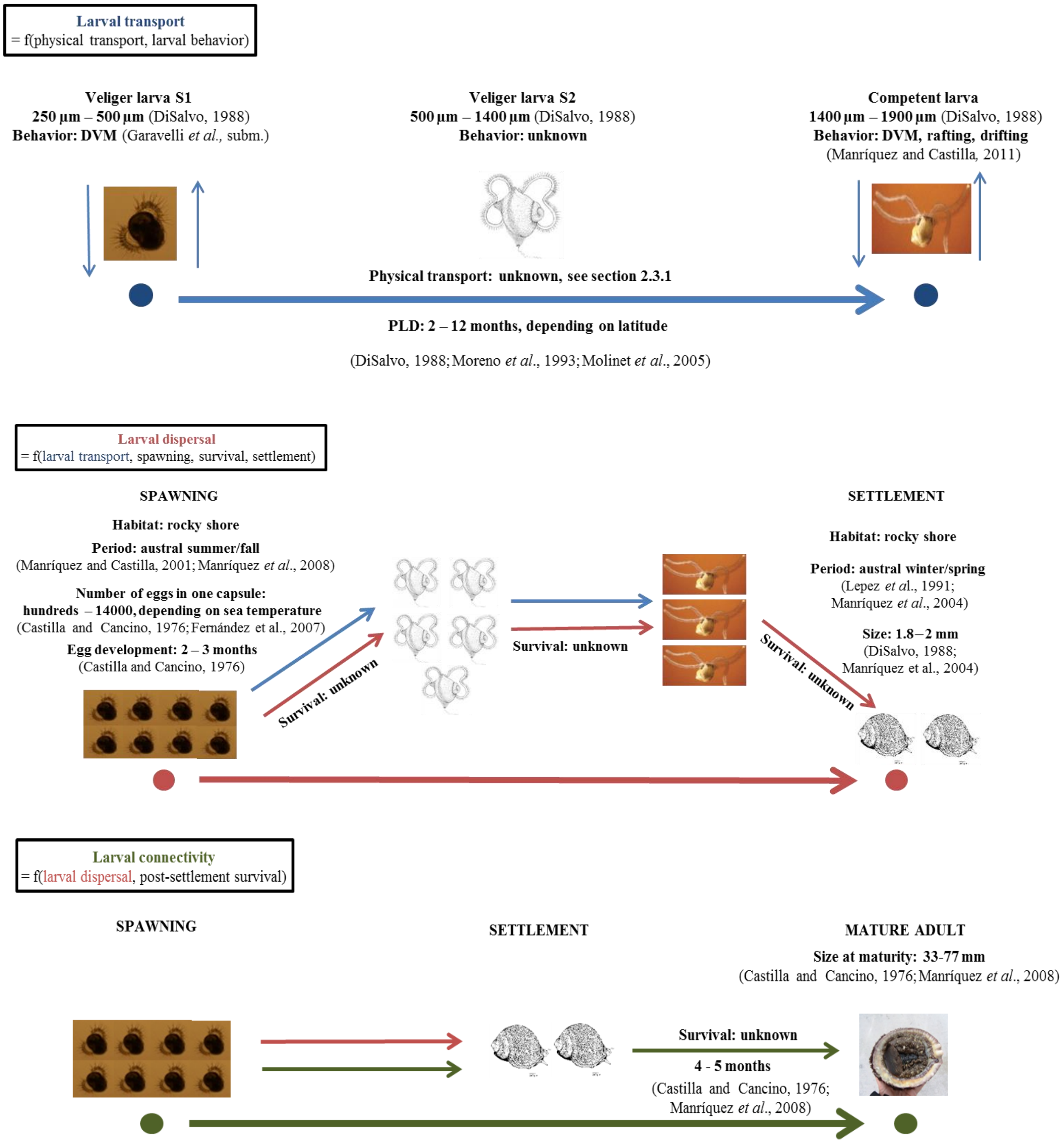
Several studies using biophysical models investigated the effects of biological factors on dispersal and connectivity patterns, such as PLD (Lefebvre *et al.*, 2003; Aiken *et al.*, 2007), egg buoyancy (Garavelli *et al.*, 2012, see Appendix), larval vertical migration (Butler *et al.*, 2011; Yannicelli *et al.*, 2012; Robins *et al.*, 2013), larval mortality (Guizien *et al.*, 2006), and larval growth (Incze and Naimie, 2000). Mullon *et al.* (2002) investigated the influence of environmental constraints on the spatial and temporal spawning patterns of small pelagic fishes. Other studies focused on the evaluation of the dispersal or connectivity spatial scales from MPAs (Di Franco *et al.*, 2012b; Andrello *et al.*, 2013). Finally, biophysical model begin to be used to assess the effect of climate change on larval dispersal and connectivity (Lett *et al.*, 2010; Aiken *et al.*, 2011; Brochier *et al.*, 2013).

In this section, I have defined larval connectivity in the context of marine metapopulations and highlighted the potential influence on dispersal and connectivity of several biological and physical factors. For the assessment of loco connectivity, the next part of this introduction focuses on gathering all information available in the literature about the life history of this species that is relevant to connectivity.

1.3. Loco life history relevant to connectivity

The main elements of loco life history relevant to connectivity are summarized in Figure 1.5 A and detailed in the following sections. Note that survival rates are unknown for all stages. Yearly calendar including the life cycle of loco is represented in Figure 1.5 B.

A.



B.

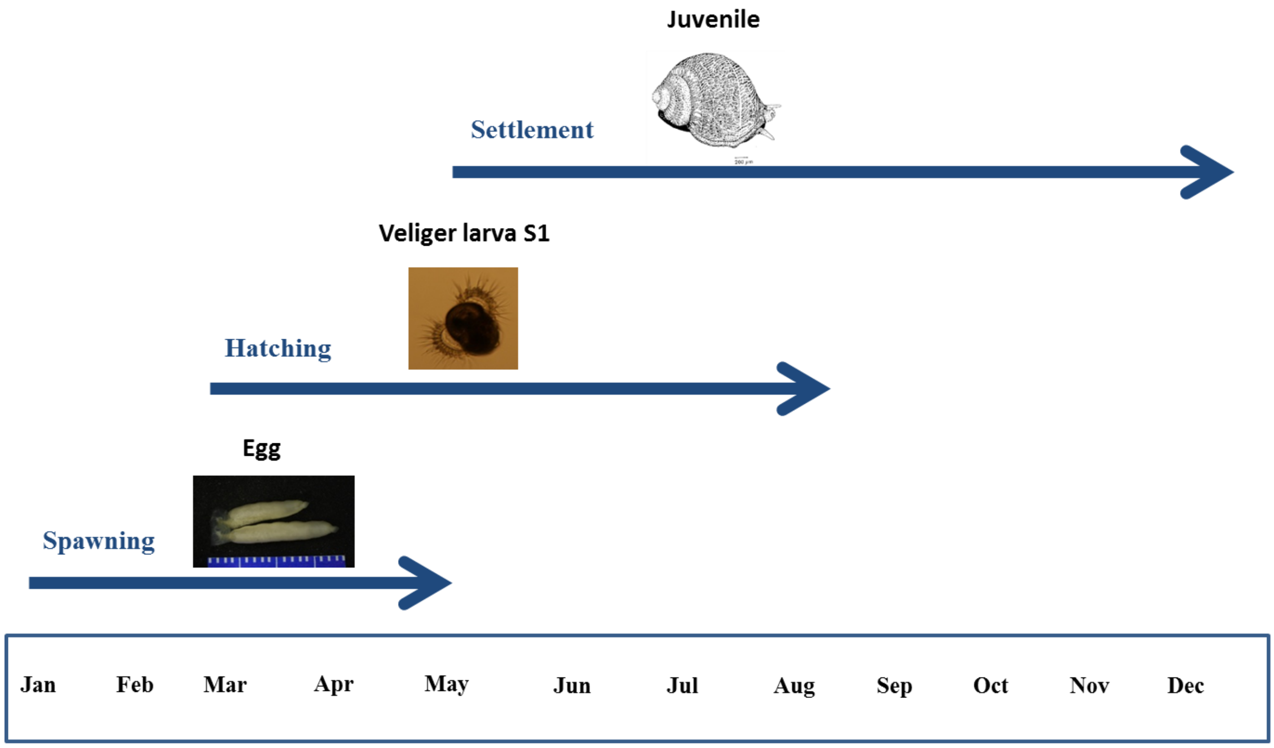


Figure 1.5: Concepts and elements of knowledge involved in larval connectivity for loco. A. Three concepts are represented: larval transport, larval dispersal, and larval connectivity (adapted from Pineda *et al.*, 2007). Each concept is distinguished by a colored arrow with larval transport in blue, larval dispersal in red and larval connectivity in green. PLD = planktonic larval duration; DVM = diel vertical migration. B. Yearly calendar including the life cycle of loco.

1.3.1. The oceanographic context

The loco is an endemic species distributed in the Southeastern Pacific coast, from central Peru to Cape Horn including the Juan Fernandez Archipelago (Cárdenas *et al.*, 2008). The distribution range mainly expands over the Humboldt Current System (HCS) north of 45°S. The HCS is one of the four global areas of upwelling in the world. Southern limit of the HCS is represented by the West Wind Drift around 43°S that splits in two large scale currents, a poleward current and the equatorward Humboldt Current (from 40°S) located far from the shore, between 75–85°W (Figure 1.6; Thiel *et al.*, 2007). Two subsurface poleward currents from Peru reach central

Chile: the Peru-Chile Countercurrent (PCCC) located at 100–300 km offshore and the Poleward Under Current (PUC) (Figure 1.6; Parada *et al.*, 2012). The PUC features are linked to the Equatorial SubSurface Water (ESSW) in terms of relatively high salinity, low oxygen concentration and nutrient richness (Schneider *et al.*, 2007). The PUC becomes shallower during the spring-summer season. It also exhibits important variability in seasonal scale, sourced by remote forcing (Hormazábal *et al.*, 2006), although synoptic variability is also prominent. Two equatorward currents are linked with coastal upwelling: the Chile Coastal current (CCC) and the Peru Coastal Current (PCC) (Figure 1.6). Cross-shore circulation along the Chilean coast is represented by an offshore flow in the Ekman layer (Aiken *et al*., 2007). Below, currents velocities get weaker and transport is oriented to the coast. This characteristic describes upwelling events present all along the coast. Coastal upwelling undergoes several mesoscale processes, such as eddies and filaments that advect waters offshore (Figure 1.7; Marín *et al.*, 2001; Hormazábal *et al*., 2004). A region of low eddy kinetic energy is observed north to 30°S whereas it is stronger between 30°S and 38°S (Hormazábal *et al.*, 2004). From northern to southern Chile, seawater temperature is variable, ranging from 13°C to 20°C for latitudes comprised between 18°S and 32°S, and from 11°C to 13°C for latitudes between 32°S and 56°S. (Fernández *et al*., 2000).

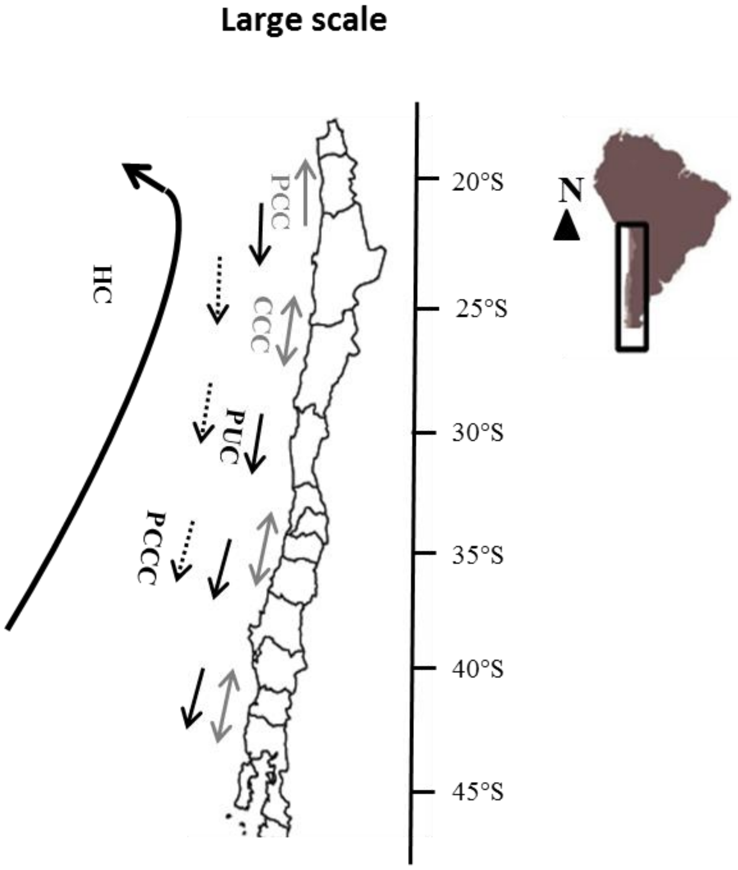


Figure 1.6: Large scale circulation in the Humboldt Current System along the Chilean coast (adapted from Thiel *et al*. 2007): the Peru Coastal Current (PCC; grey solid arrow), the Chile Coastal Current (CCC; grey solid double arrows, CCC is predominantly equatorward but poleward in winter), the Peru-Chile Countercurrent (PCCC; black dashed arrows), the Poleward Under Current (PUC; small black solid arrows), and the Humboldt Current (HC; large black solid arrow).

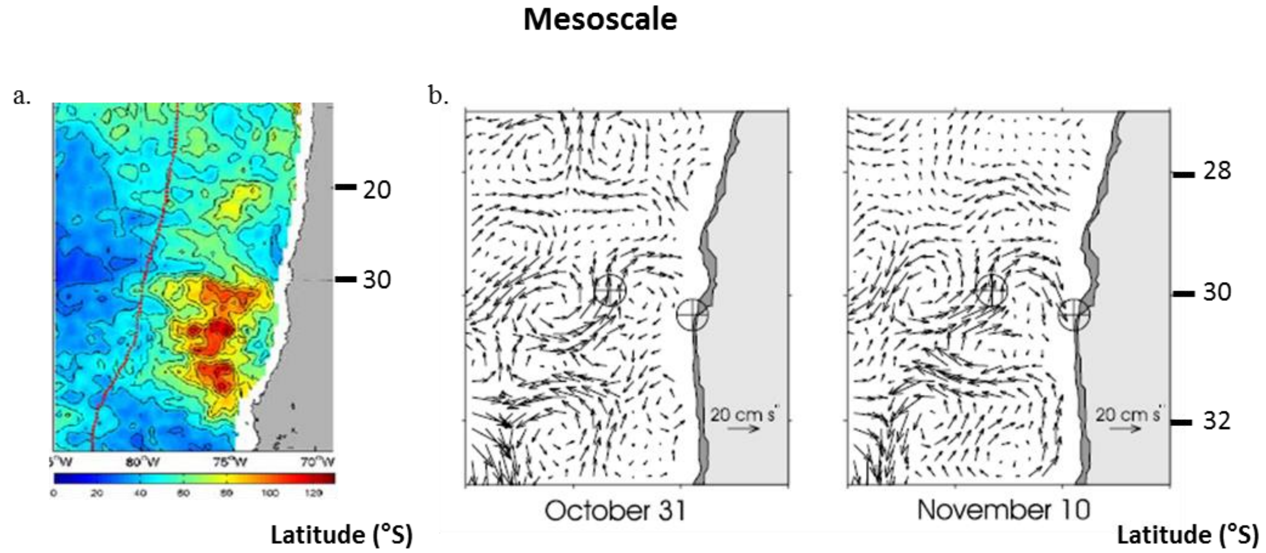


Figure 1.7: Mesoscale circulation in the Humboldt Current System along the Chilean coast. (a.) Time mean eddy kinetic energy ($cm^2.s^{-2}$) calculated from 7.5 years of geostrophic velocity between 500 m and 1000 m depth. Dashed red line represents a 800 km offshore distance (reproduced from Correa-Ramirez *et al.*, 2007). (b.) Surface currents for the 31 October and the 10 November 1996 during passage of a counterclock eddy (reproduced from Hormazábal *et al.*, 2004).

1.3.2. Habitat and spawning patterns

The Chilean coast is defined by sequences of beaches and rocks. Manríquez *et al.* (2004) mentioned that rocky bottom from the intertidal zone down to approximately 40 m depth is the main habitat for loco. Spawning occurs between austral summer and autumn (Manríquez and Castilla, 2001; Manríquez *et al.*, 2008). After mating, encapsulated eggs are produced by females and fixed on rocks until hatching. The number of eggs in a capsule is highly variable between few hundreds to more than 14,000 (Castilla and Cancino, 1976) and depends on sea temperature. Fernández *et al.* (2007) showed that the number of loco embryos in a capsule were fewer in the northern regions than in the southern regions of Chile. This observation was correlated with mean temperatures before egg deposition. Hatching time was experimentally estimated between 69 days and 128 days, at a temperature comprised between 13.5°C and 14.5°C (Castilla and Cancino, 1976).

1.3.3. Larval development, behaviour, and settlement

From hatching, loco larvae are pelagic. Planktonic larval duration (PLD) was assessed in laboratory around 3 months by DiSalvo (1988) and between 3 and 4 months from field studies by Moreno *et al*. (1993) in the southern Chile (39°S). Further south, in fjords and channels (43°S-44°S), it has been shown that the larval dispersal could take longer, between 6 and 12 months (Molinet *et al*., 2005), likely due to the presence of cold seawater in the region leading to slower larval development. PLD of loco is therefore highly variable along the Chilean coast, from two to twelve months. This variability is largely believed to be driven by seawater temperature although the direct effect of temperature on loco larval growth is currently not established.

Hatched larvae are called veliger because of their swimming organ, the velum (Ruppert *et al*., 2003). Larvae are considered early veliger until they reach a size of 1300 µm. Two distinct larval stages have been described for loco; stage 1 between 250 µm and 500 µm, and stage 2 between 500 µm and 1300 µm where changes in morphology appear (DiSalvo, 1988). In southern Chile (43-44°S), the abundance of early veliger (stage 1) larvae has been observed increasing in surface water samples at night compared to day, but no clear daily migratory pattern could be established (Molinet *et al*., 2008). Such observations have never been done for stage 2. Actually, until now, no stage 2 larva has ever been sampled during field studies and larvae in culture never reached this stage either. At the end of the dispersal phase, there is a metamorphosis step and larvae become competent, *i.e.*, ready for settlement. Larval size at this stage is comprised between 1400 µm and 1900 µm (DiSalvo, 1988). Field and laboratory studies on the vertical migration pattern of competent loco larvae have been contradictory. Field sampling in northern and central Chile (Manríquez and Castilla, 2011) indicated that they swam to the surface during the night, whereas other field studies in central Chile suggested the opposite (Poulin *et al*., 2002).

In central Chile, Manríquez *et al*. (2004) observed that the period of higher abundance of settlers was between October and November. In southern Chile, two recruitment periods were observed, in October 1989 and June 1990 (Lepez *et al*., 1991). Recently settled juveniles were observed in northern Chile until 18 m depth (Stotz *et al.*, 1991). Size at settlement has been evaluated between 1800 and 2000 µm (DiSalvo, 1988; Manríquez *et al*., 2004).

1.3.4. Post-larval growth until sexual maturity

Postmetamorphic individuals were observed in the small crevices of the intertidal (Lepez *et al*., 1991) and subtidal rocks (Stotz *et al.*, 1991), and in the low tide pools (Moreno *et al*., 1993). Manríquez *et al*. (2008) observed a postmetamorphic growth rate between 3.69 mm and 3.85 mm per month in the field. Other field studies reported different growth rates, from 1.39 to 2.27 mm per month by Méndez and Cancino (1992), 1.84 mm per month in mean by Lepez *et al*. (1991) in the south of Chile. When juveniles reach a size of 8 mm to 10 mm, they were found migrating to emergent substrata, to the mid and high intertidal zones (Moreno *et al*. 1993). Reproduction has been observed for individuals whom size was comprised between 35 mm and 77 mm (Castilla and Cancino, 1976; Manríquez *et al*., 2008), respectively for individuals of 9 and 20 months after settlement (Stotz, 1997).

1.3.5. Spatial distribution of loco captures

Stotz (1997) showed that at regional scale, there was a good spatial correspondence between areas of high loco captures and upwelling areas (Figure 1.8). Yannicelli *et al*. (unpublished results) studied the spatial patterns of loco capture from 1993 onwards. They found that high/low productivity areas at mesoscale are recurrent over time, regardless of fisheries management regime (Figure 1.9), and that coastal features (topography, shelf width) together with chlorophyll alongshore concentration were significant explanatory variables for the observed patterns. Also within some mesoscale zones, individual MEABR presented similar high/low inter-annual loco landing variability. A recent regional study has shown that high/low captures during the MEABR period coincided with capture areas during the Holocene (Ramírez, 2012). The above results could suggest that coastal features and circulation influence loco larval distribution and determine mesoscale population patterns.

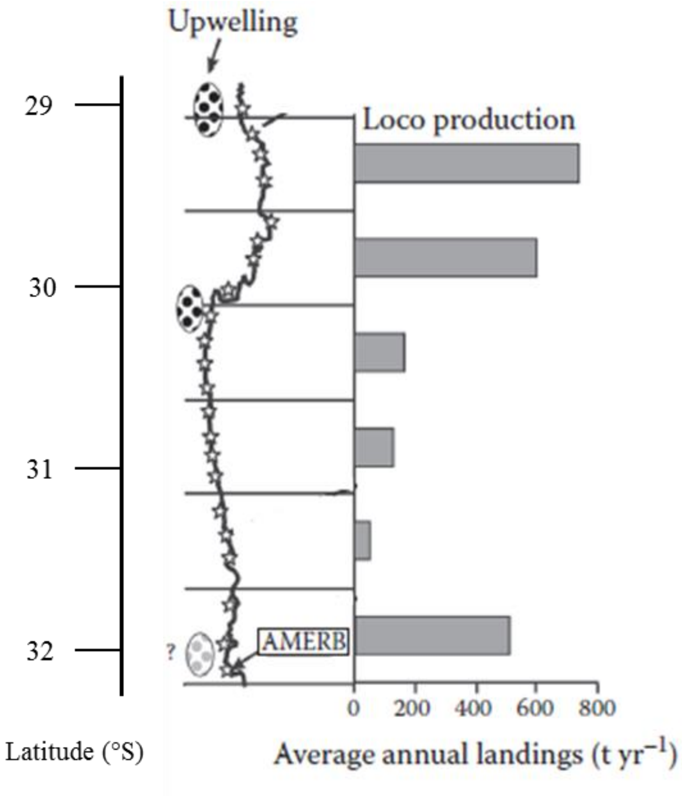


Figure 1.8: Mean annual landings of loco from 1985 to 1995 between 29°S and 32°S with location of upwelling areas and MEABR ("AMERB"). Grey oval represents a supposed upwelling area (from Thiel *et al*., 2007).

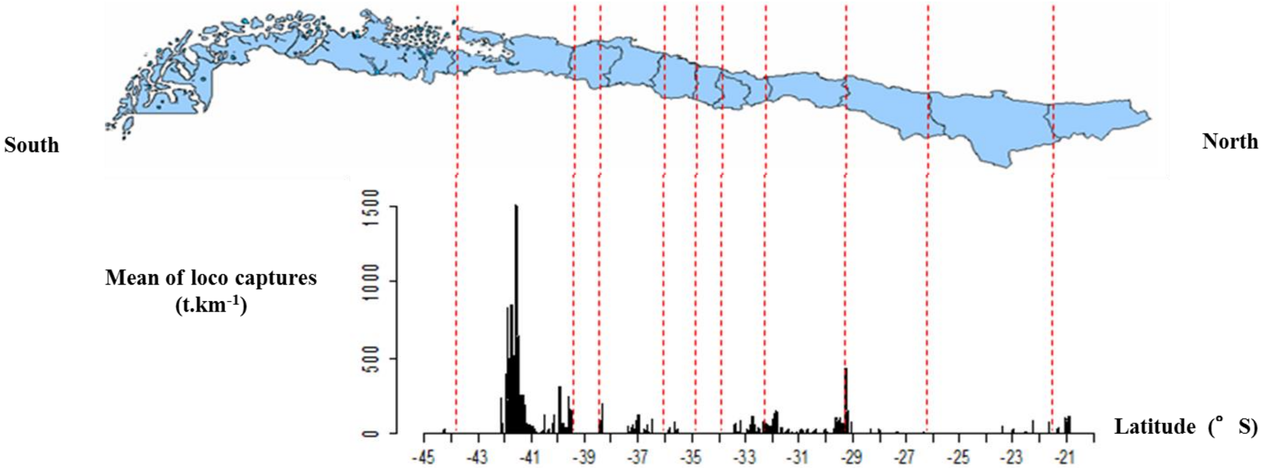


Figure 1.9: Mean captures of loco along the Chilean coast from 1993 onwards (Yannicelli *et al*, unpublished results).

1.4. Objectives of the thesis and contents

The main objective of this thesis is to envision a loco fishery management that is better adapted to the species ecology. For this, I propose to estimate loco connectivity patterns and scales by assessing the influence of several physical, biological, and ecological factors.

In this introduction of the thesis, I described the context and issues of the current loco fishery management and highlighted the need to estimate loco connectivity. Considering the importance of identifying physical and biological factors involved in larval connectivity, I have then identified gaps in established biological knowledge of loco life cycle relevant to connectivity. First, larval behaviour of loco is well established only for the competent stage. Second, as seawater temperature is highly variable along the Chilean coast, larval growth of loco is expected to change largely too. Therefore, in Chapter 2, I describe the results of laboratory experiments conducted to evaluate larval behaviour for early veliger loco larvae and loco larval growth rate depending on temperatures.

In Chapter 3, I propose the first evaluation of loco connectivity scales using an individual-based larval dispersal model. In this biophysical model, I focused on testing the influence on loco connectivity of hydrodynamic model resolution, spawning depth, and planktonic larval duration. The results suggest largely independent subpopulations of loco along the Chilean coast, as far as connectivity is concerned.

In Chapter 4, I evaluate the influence of biological characteristics of loco larvae on loco connectivity scales and subpopulations assessed in Chapter 3. To do this, I implemented loco larval behavior, as assessed in Chapter 2 for early veliger loco larvae, and a larval growth submodel, into the larval dispersal model. I also tested the effects of several other heterogeneous factors along the Chilean coast, available habitat, fecundity, and larval mortality, on the simulated connectivity patterns of loco.

Finally, in the general discussion (Chapter 5), I synthesize the main results obtained along the thesis and propose a new, larger scale, vision for managing loco in Chile.

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Chapter 2. Behavioral and larval growth experiments on veliger *Concholepas concholepas* (loco) larvae

This chapter is an extension of a manuscript entitled "Behavioral experiments on early veliger Concholepas concholepas (loco) larvae" submitted to Plos One by Lysel Garavelli, Claire Saraux, Beatriz Yannicelli, and Christophe Lett.

The abstract of this manuscript is reproduced below.

In laboratory conditions, we investigated the behavior (swimming activity and vertical migration) of early veliger *Concholepas concholepas* (loco) larvae under two 24 hours photoperiods, a natural photoperiod with 10 hours light:14 hours darkness and 24 hours constant darkness. During the night, the number of mobile larvae increased, and those larvae were located shallower than during the day. These results occurred under both photoperiods but most markedly under natural

photoperiod (mean depth = 58.23 cm at day and mean depth = 22.62 cm at night under natural photoperiod). Under natural photoperiod, the number of mobile larvae decreased with depth during the night whereas mobile larvae were evenly distributed with depth during the day. Under constant darkness, the abundance of mobile larvae decreased with depth during night and also (slightly) during day. Measurements of swimming velocities for these larvae did not show significant differences between day and night. Our results suggest that early veliger loco larvae undergo nocturnal vertical migration.

2.1. Behavioral experiments on early veliger loco larvae

2.1.1. Introduction

In marine coastal systems, the distribution and dynamics of invertebrate species is thought to be largely influenced by the larval dispersal phase (Grosberg, 1982; Bradbury and Snelgrove, 2001; Jenkins, 2005). Larval dispersal depends on the interaction of biological and physical factors such as ocean currents and larval behavior (Pineda *et al.*, 2007). Larval vertical migration is poorly known for most invertebrate species. However, modeling results suggest significant effects of larval behavior on larval dispersal of these species (Peliz *et al.*, 2007; Paris *et al.*, 2007; Aiken *et al.*, 2011).

Larval behavior changes with species. In the laboratory, mud crab *Scylla serrata* megalopea were observed swimming upwards in a water column during the day (Webley and Connolly, 2007), whereas the marine gastropod *Kellenia kelletii* larvae migrated upwards during the night (Romero *et al.*, 2012). Larval behavior may also change according to species ontogeny. In the laboratory, *Kellenia kelletii* approaching competency larvae were observed more demersal than younger larvae (Romero *et al.*, 2012). Larvae of the polychaete *Serpula vermicularis* showed positive phototaxis at trochophore stage (1 to 3 weeks post-hatching) and negative phototaxis at metatrochophore stage (4 weeks post-hatching) (Young and Chia, 1982). Such a variability of larval behavioral patterns implies variable effects of this behavior on larval dispersal. Therefore, assessing these effects requires appropriate studies for a given species and its different development stages.

The marine gastropod *Concholepas concholepas (*Bruguière, 1789), commonly called loco, is a highly exploited benthic gastropod species along the Chilean coast. Decreasing captures of loco since the mid 1980's have led to the establishment of spatially-explicit management regulations. However, these regulations have not always resulted in the expected local stocks recovery, partly because of lack in basic knowledge of loco biology and ecology (Leiva and Castilla, 2002), including its early life. Spawning of loco mainly occurs in Chile during austral summer and autumn (from January to May; Manríquez and Castilla, 2001; Manríquez *et al.*, 2008). During these seasons, day length ranges from around 14 hours in January to around 11 hours in May. Along the Chilean coast, temperature is variable, ranging from 13°C to 20°C for latitudes comprised between 18°S and 32°S, and ranging from 11°C to 13°C for latitudes comprised between 32°S and 56°S (Fernández *et al*., 2000). Loco adults spawn intracapsular eggs developing between 1 and 2 months on the rocky shore (Castilla and Cancino (1976) measured egg development times of 69 to 128 days at 13.5°C to 14.5°C in laboratory). Hatched larvae are veliger and develop in two stages distinguished by changes in shell length and morphology. Shell lengths range between 250 µm and 500 µm for the early veliger stage and between 500 µm and 1400 µm for the late veliger stage (DiSalvo, 1988). The late veliger stage begins after 4 to 7 weeks post-hatching (DiSalvo, 1988). During these two stages, veliger larvae disperse in the pelagic ecosystem. Planktonic larval duration varies with latitude, from around 3 months at temperature 16°C (DiSalvo, 1988; laboratory study) to 3–4 months in south-central Chile (39°S; Moreno *et al*., 1993, field study) and 6–12 months further south in fjords and channels (43°S–44°S; Molinet *et al*., 2005, field study). At the end of the larvae development phase, larvae become competent *i.e.* they are ready to settle. Competent larvae have been mainly observed in the neustonic layer, between 20 cm and 30 cm under the water surface (DiSalvo, 1988; Molinet *et al*., 2006). Recently, Manríquez and Castilla (2011) investigated swimming behavior of competent loco larvae. Under experimental conditions with different photoperiods (natural light:darkness cycle, inverted light:night cycle, constant light, and constant darkness), these larvae were observed swimming in the water column during the night. Also, more competent larvae were observed in the sampling water column (20 m depth) during the night than during the day, as suggested by field observations in the same study. However, the swimming behavior of the two stages of veliger loco larvae remains unknown.

The purpose of our study is to investigate the behavior (swimming activity and vertical migration) of early veliger (EV) loco larvae (*i.e.*, the first stage of development). We conducted laboratory experiments to assess the behavior of EV loco larvae in response to natural photoperiod *i.e.* outdoor ambient light cycle (~10 hours light:14 hours darkness, same cycle as the egg collection site) and constant darkness. Finally, we discussed our results regarding a field study lead for EV loco larvae (Molinet *et al*., 2008) and results obtained for competent loco larvae (Manríquez and Castilla, 2011).

2.1.2. Larval culture

The methodology described here was used similarly for the two preliminary (July 2011 and November 2011) and the final (May 2012) trials of experiments that are fully detailed in the following sections. In Herradura Bay (30°S, Chile), capsules containing loco eggs (Figure 2.1) were collected on one occasion from the subtidal by a diver. After collection, they were transported to the aquaculture lab of the Universidad Católica del Norte in Coquimbo (Chile) and kept in a 20 l tank filled with filtered seawater (1 µm + UV treatment) at ambient temperature. Seawater was changed every day until hatching and cultures were continually aerated. Larval cultures were exposed to the outdoor ambient light cycle. Hatching began around 30 days after egg collection. Every day, between 150 and 200 newly hatched larvae were transferred to new 20 l tanks allowing keeping track of birth dates. Larvae were not fed the first day because vitelline material is still present on EV larvae during 24 hours to 48 hours (DiSalvo, 1988). Larvae were fed every morning from the second day until the end of the experiment, with the microalga *Isochrysis galbana* at a final concentration between 20,000 and 30,000 cells.ml^{-1} in each larval tank, following DiSalvo's (1988) protocol.

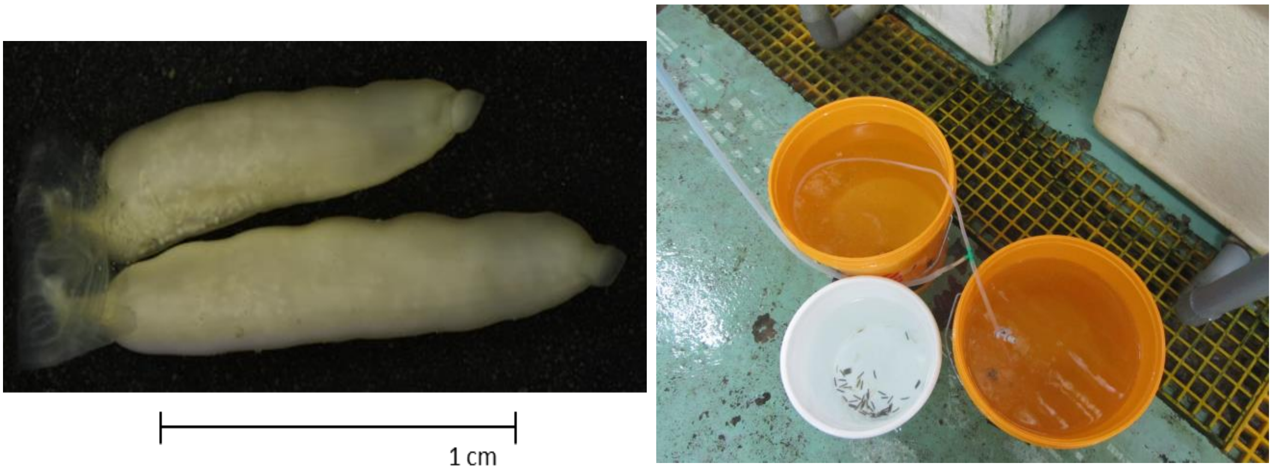

Figure 2.1: Two early stage capsules of loco containing eggs (left). Culture of capsules and early veliger loco larvae (right).

2.1.3. Preliminary trials - June 2011

In order to investigate a circadian rhythm in the vertical distribution and activity of EV loco larvae, we conducted laboratory experiments using plastic columns (10 cm × 30 cm × 4 cm). The columns were filled until 28 cm high with filtered seawater heated at 18°C and placed in an aquarium filled with the same conditions to avoid changes of temperature (Figure 2.2). Columns were marked every 1 cm from 0 (water surface) to 28 (base of the column). In this preliminary trial we wanted to investigate a potential effect of still *vs.* bubbling water with *vs.* without food for loco larvae. Therefore four types of experiments were conducted, all under ambient light cycle (~10:14 hours of light:darkness):

- still water without phytoplankton
- still water and phytoplankton (*I. galbana*)
- water with bubbling regime and without phytoplankton
- water with bubbling regime and phytoplankton (*I. galbana*)

The bubbling regime was achieved from an apparatus and a pipette in the column.

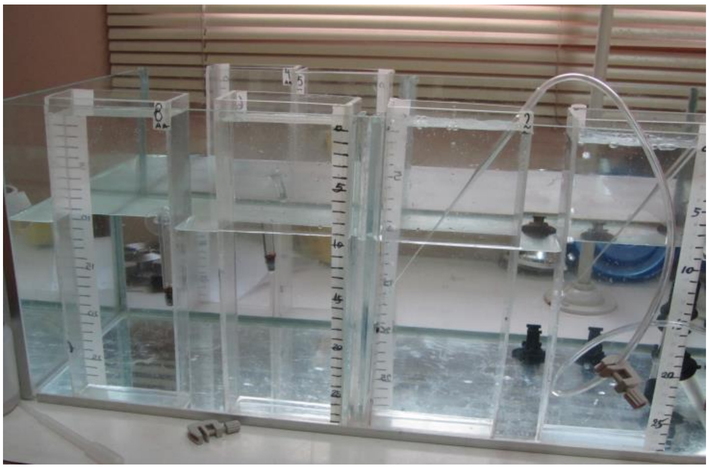

Figure 2.2: Material used for experiments conducted in June 2011 to assess the behavior of 7 days post-hatching early veliger loco larvae.

At the end of the sixth day post-hatching, around 80 larvae were transferred in each column. They spent one night into the column for acclimation. The following morning, the positions of mobile larvae (*i.e.*, those at the bottom of the column were not accounted for) were assessed by taking a series of photos of each column every 3 hours during 24 hours.

As an example, the number of 7 days post-hatching mobile larvae at the surface and at the last level of the column for the experiment with still water and phytoplankton is shown in Figure 2.3. At the surface level of the column, the number of larvae increased during the night. The maximum of larvae observed was 6. By contrast, at the bottom level of the column, the number of larvae decreased during the night.

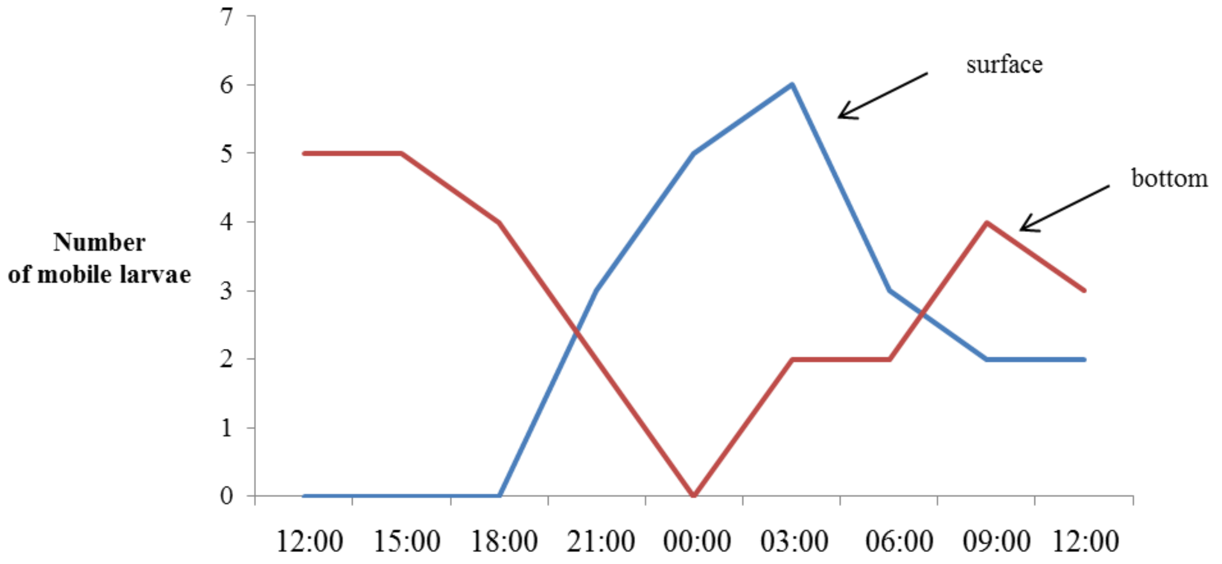

Figure 2.3: Number of 7 days post-hatching mobile early veliger loco larvae per hour at surface (blue line) and bottom (red line) of the column under conditions with still water and phytoplankton.

The second result shown is the number of 7 days post-hatching mobile larvae observed at all depth levels under conditions with bubbling regime and with / without phytoplankton (Figure 2.4). The maximum of activity during 24 hours was observed during the night for the two experimental conditions. Results showed that slightly more larvae were mobile under conditions with bubbling regime and phytoplankton. It seems that the presence of food in the column improved the activity of the loco larvae. The maximum number of mobile larvae was 40 at night. The lowest values of mobile larvae are observed at the beginning and the end of the experiment, during the afternoon (15:00).

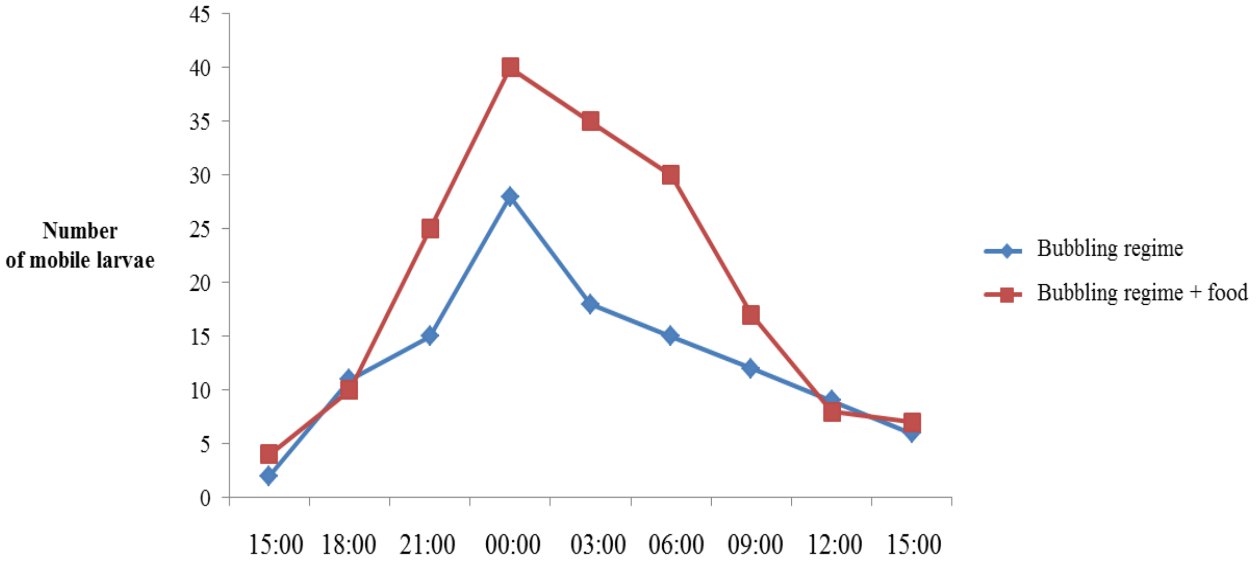

Figure 2.4: Number of 7 days post-hatching mobile early veliger loco larvae per hour in experimental conditions with bubbling regime only (blue line) and with bubbling regime and food (red line).

Although there were promising results in these preliminary experiments conducted to assess larval vertical migration, there were also severe limitations. First there was no replicate, which prevented from using statistical tests to check the significance of the results obtained. Second, the results obtained in the four experimental conditions were inconsistent: a day/night behavioral pattern appeared under some conditions, but not under others. We think that one of the main problems in these first experiments was the too high number of larvae used in each column. This prevented from following larvae individually by eye and forced us to use photos. However, during the processing of these photos, unanticipated difficulties to distinguish larvae from other particles present in the column appeared, which was a problem for a confident assessment of mobile larvae. Therefore, in the second experimental trial, we chose to decrease the number of larvae in the columns to such a level that we were able to assess visually the positions of mobile larvae in the columns.

2.1.4. Preliminary trials - November 2011

In order to investigate a circadian rhythm in vertical distribution and activity of EV loco larvae, we used the same apparatus as in the previous experiment. At the end of the sixth day post-hatching, we transferred 15 larvae in each plastic column filled with filtered seawater (1 µm + UV treatment) at ambient temperature (15°C). They spent one night into the column for acclimation. Two experimental conditions were tested, still water with phytoplankton and bubbling regime with phytoplankton under ambient light cycle (~13:11 hours of light:darkness). Experiments were conducted during 36 hours (from 09:00 to 21:00 the next day). Two replicates were conducted for each experimental condition. The positions of mobile larvae in each column were observed six times by day and four times by night (*i.e.*, about every 4 hours).

The mean depth of mobile 7 days post-hatching larvae is shown in Figure 2.5 as a function of observation time. In the still water treatment, larvae were on average located closer to the surface at night than at day, except for the first observation at 9:00 (Figure 2.5 a.; mean depth was 13.2 cm at night *vs.* 18 cm at day). In turbulent seawater, a peak value was observed at 21:00 but all other values were close to each others (Figure 2.5 b.). The maximum value of mobile larvae in still water was observed at night with a mean of 4 larvae (n=30, 15% of mobile larvae). More mobile larvae were observed with the bubbling regime, also during the night, with a mean of 10 mobile larvae (n=30, 33% of mobile larvae).

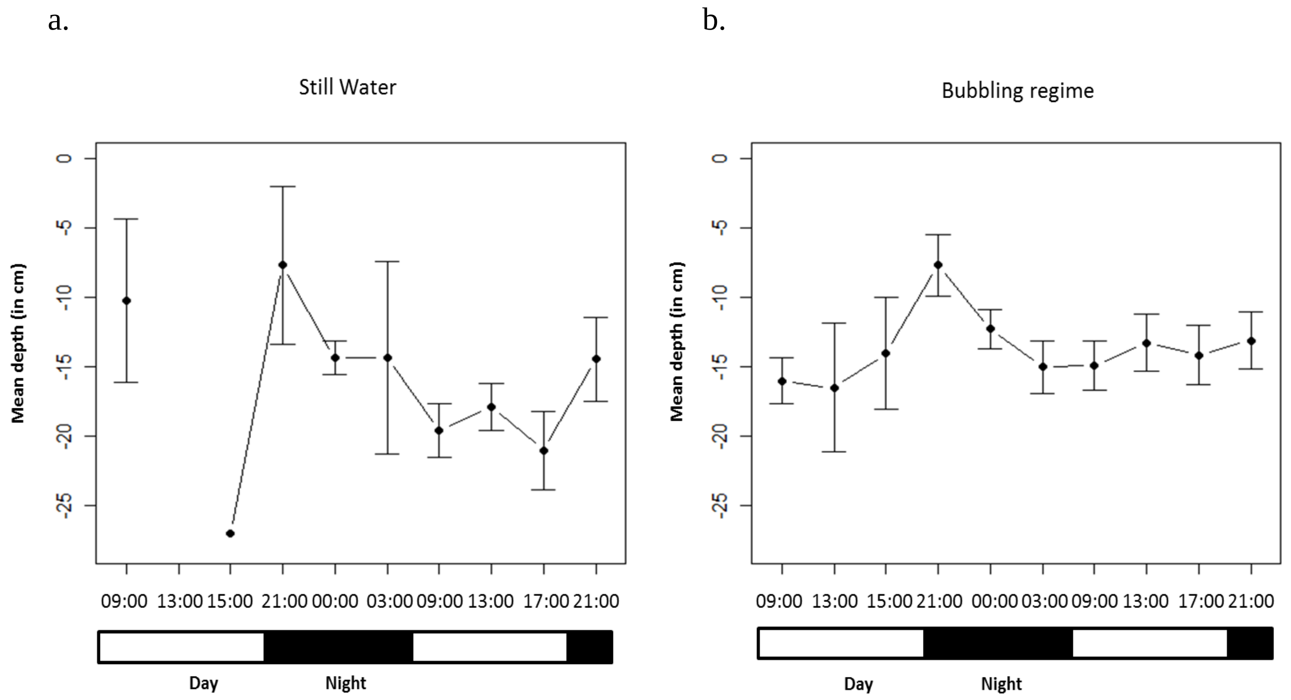

Figure 2.5: Mean depth and standard error of 7 days post-hatching mobile early veliger loco larvae per time of observation under two experimental conditions: still water (a.) and water with bubbling regime (b.). N=30 for each experiment. At 13:00 under still water conditions, there is no data because all larvae were at the bottom of the column.

These new observations of the position of 7 days post-hatching EV larvae in the water column were not concluding. No clear circadian behavioral migration pattern could be established. Furthermore, we did not observe differences in the number of mobile larvae between day and night as suggested by the previous experiment. However, from this second experimental trial, our next point of concern became the size of the columns we used. After the introduction of the larvae in the column, we observed that most of them sank immediately to the bottom. We thought that in such a small (30 cm) column, EV loco larvae could sink at the bottom of the column and tend to stay there, inducing a different behavior than what they do in the ocean.

2.1.5. Final trials - May 2012

A. Material and methods

Larval photoperiodicity

In May 2012, in order to investigate a circadian rhythm in vertical distribution and activity of EV loco larvae, we used two flat-bottom transparent PVC columns that were 120 cm high and 15 cm diameter (Figure 2.6). Columns were filled with filtered sea water until 110 cm of height and they were marked every 10 cm from 0 (water surface) to 110 (base of the column). Therefore, observations on larval abundance and position will be referred to specific vertical sections. Columns were placed indoors where temperature of seawater remained about 13°C +/- 1°C with salinity of 32–33. At the end of the fourth day after hatching, we sampled 70 mobile larvae in the culture tank and introduce them in the column. We found that 70 larvae was a good compromise between allowing visual counting and getting robust migration patterns. Larvae spent one night into the column for acclimation.

Two photoperiods were tested: 10:14 hours of light:darkness (natural light penetrating the surface of the water column through a window) referred along the text as natural photoperiod and constant (24 hours) darkness. Observations were conducted during 24 hours from 09:00 one day to 09:00 the next day. Due to logistical and technical issues, we conducted the experiments on 3 different dates, with two replicates per date. The dates are from 09:00 one day to 09:00 the next day: June 14 and 15 (date 1), June 21 and 22 (date 2) and, June 26 and 27 (date 3). To assess the effect of light level on our results for these 3 dates, solar radiation data were obtained from a weather station located in Coquimbo (30°S, 71°35). The weather station is run by the station network CLIMA directed by el CEAZA (Centro de Estudios Avanzados en Zonas Aridas, www.ceazamet.cl).

All along the experiment, we considered only the mobile larvae. Larvae at the bottom of the column were not accounted for. The number of mobile larvae in each column section was observed five times at daytime and three times at nighttime (approximately every 3 hours). During the night, larvae were observed using a dim-red light. Experiments were replicated 6 times (2 columns × 3 dates) for each photoperiod, no larvae were reused. We calculated the weighted mean depth (MD) for each observation t and each replicate r for each photoperiod following Miller and Morgan (2013):

$$MD = \frac{\sum_k pk \times Z_k}{\sum_k p_k}$$

where p_k is the number of larvae at section k of the column and Z_k the depth of section k (in cm).

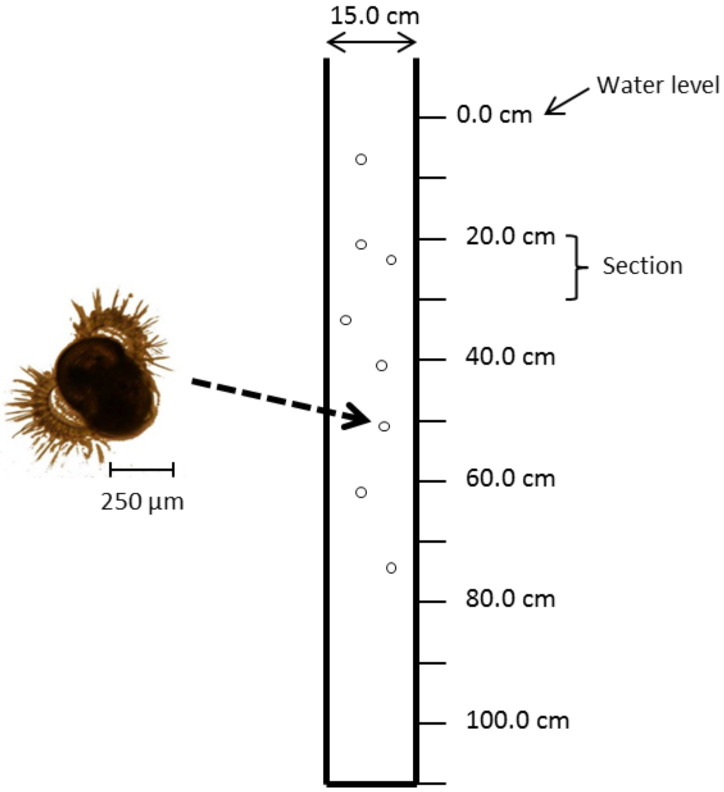

Figure 2.6: Diagram of the transparent PVC column used for investigating the loco larval vertical distribution with a photograph of a 4-days old loco larvae showing the velum. At this stage of development, shell length of early veliger loco larvae measures around 250 µm.

Swimming velocities

From another larval culture, we measured swimming speeds of EV loco larvae. Four days post-hatching, 50 larvae were transferred in Plexiglas columns of 30 cm high and 5 cm in diameter. Columns were filled with filtered sea water until 28 cm of height and were divided in 28 sections of

1 cm. For 24 hours, during 3 minutes each 4 hours of day and night, we filmed movements of 5 days post-hatching larvae in the water column. From these videos, we first identified and described different swimming behaviors. From the larval trajectories that were perpendicular to the bottom (*i.e.* swimming upwards or downwards), we randomly assessed 30 of them (15 during the day, 15 during the night) for swimming velocities calculated using a stopwatch.

The same columns were used to assess the fall velocities of EV larvae. In a petri dish, 30 4-days old larvae were anesthetized following the methodology described in Manríquez and Castilla (2011), *i.e.* submerging larvae in a solution of crystals menthol and seawater. When larvae become immobile, we introduced one larva in the column and we measured its fall velocity between height 10 cm and 20 cm in the water column using a stopwatch. We repeated this method for each of the 30 anesthetized 4-days old larvae.

Statistics

All statistics were computed using R v 2.15.0. The effect of time, day/night, photoperiod, date of experiment, light power, and their interactions on the number of mobile larvae were analyzed using Generalized Linear Models (GLM) fitted with Poisson distribution. Akaike’s Information Criterion (AIC) was used for model selection. To test the light conditions between the three dates of experiments, we used a multifactor analysis of variance (ANOVA). Linear Models (LM) were applied for the mean depth values of mobile larvae in the water column testing the same variables. In order to compare swimming velocities of larvae between day and night, we used a non-parametric test, namely the Wilcoxon signed rank test, as distributions were not normally distributed. Results are given as means ± standard error.

B. Results

Number of mobile larvae

Photoperiods and day/night times explained the number of mobile larvae observed during experiments. The model that included the independent effect of both variables and their interaction was AIC-selected as the best model. On average, fewer mobile larvae were observed under constant darkness (23 ± 1 under constant darkness *vs*. 27 ± 2 under natural photoperiod; Figure 2.7; GLM: z = -3.82, P < 0.001, n = 96). For both photoperiods, the number of mobile 5 days post-hatching larvae was highest during the night (21:00–04:00 period) and lowest during the day (32 ± 1 during the night *vs.* 21 ± 1 during the day; GLM: z = -8.593, P < 0.001, n = 96). However, the effect of the day and night was different in the two photoperiods (GLM: interaction between photoperiod and daytime and nighttime, z = 2.091, P = 0.036, n = 96). The effect of the day and night on the number of mobile larvae was stronger under natural photoperiod, with a mean increase of 61.5% during the night (Mean ± SE: 35 ± 2 mobile larvae during the night *vs.* 22 ± 2 mobile larvae during the day) than under constant darkness, for which the mean increase of mobile larvae at night was of only 35.6% (28 ± 2 larvae during the night *vs.* 21 ± 2 larvae during the day). Similar results were obtained when fitting a model with photoperiod and time as explanative variables. Further, the date at which the experiment was done also significantly affected the difference between day and night periods under natural photoperiod (interaction date*day–night selected in the best AIC model), but not under constant darkness. On the contrary, there was no difference between replicates done in the same date (separate GLMs per date, replicate and the interaction replicate*day–night never selected in the best model and all P > 0.05). For each of the three dates of experiments, the number of mobile larvae was always higher during the night than during the day (all 3 P < 0.003), but the strength of the day–night effect differed. The observed ambient light conditions between these three dates also differed (ANOVA: F = 5.28, P = 0.01). The third date, corresponding to the one with the smallest difference in the number of mobile larvae between day (24 ± 2) and night (31 ± 3), also experienced less light (189 ± 43 W.m^{-2} *vs.* 428 ± 108 W.m^{-2} and 599 ± 102 W.m^{-2} for date 1 and 2 respectively). The light negatively affected the number of mobile larvae (GLM: $z = -7.055$, $P < 0.001$, $n = 48$) under natural photoperiod.

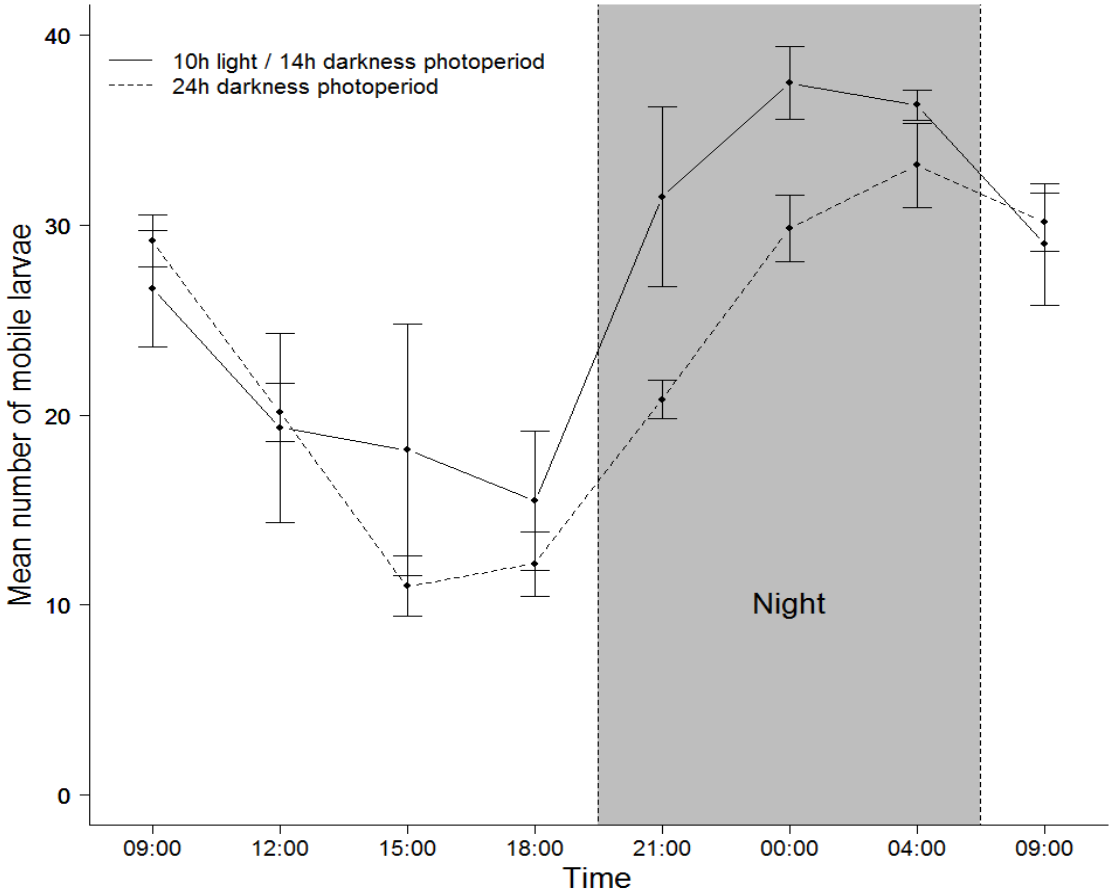

Figure 2.7: Mean and standard error number of mobile early veliger loco larvae per time of observation for the 6 replicates during the two photoperiods tested: 10 h light/14 h darkness photoperiod (plain line) and 24h darkness (dashed line).

Vertical distribution of mobile larvae

The date at which the experiment was done did not have an effect on the mean depth of mobile larvae under natural photoperiod (interaction date*day–night not selected in the best AIC model). The interaction between photoperiod and day and night had a significant effect on the mean depth of mobile larvae, indicating that although larvae were observed closer to the surface during the night than during the day, the relationship between mean depth and day and night times was not the same in both photoperiods. Separate LMs indicated that the mean depth was smaller during the night than during the day in both treatment (LM: a = 35.61 ± 4.71 cm, t = 7.55, P < 0.001, n = 48, LM: a = 17.02 ± 2.74 cm, t = 6.20, P < 0.001, n = 48, for natural photoperiod and constant darkness respectively). The day/night difference in mean depth was about twice higher in the natural photoperiod (58.23 ± 3.36 cm *vs.* 22.62 ± 2.33 cm) than in the constant darkness (47.46 ± 1.67 cm *vs*. 30.44 ± 2.19 cm). The deepest (MD = 82.1 cm) and the shallowest (MD = 16 cm) values of mean depth were obtained at 15:00 and 00:00, respectively, during the natural photoperiod.

The number of larvae present in each depth section of the water column is represented for each time of observation for the natural photoperiod (Figure 2.8 A., B.) and the constant darkness (Figure 2.8 C., D.). Under the natural photoperiod, depth and day and night times and their interaction had a significant effect on the number of larvae in each section of the water column (Figure 2.8 A., B.), meaning that the relationship between the number of larvae and depth was different during night and day (GLM: all P < 0.001, n = 528). Therefore, we fitted separate GLMs on the night and day times. We found that the number of larvae decreased with depth only during the night (GLM: a = -0.42 ± 0.02, z = -22.14, P < 0.001, n = 198), while larvae were uniformly distributed in the water column during the day (GLM: a = 0.01 ± 0.01, z = 0.57, P = 0.57, n = 330).

Under constant darkness, the number of larvae also decreased with depth on average (GLM: a = -0.29 ± 0.02, z = -16.33, P <0.001, n = 528) and was smaller during daytime (GLM: a = -1.03 ± 0.09, z = -11.07, P <0.001, n = 528; Figure 2.8 C., D.). The significant interaction indicates that the relationship with depth was not the same during day and night (GLM: a = 0.22 ± 0.02, z = 9.89, P < 0.001, n = 528). In contrast with the natural photoperiod, we found that the number of larvae decreased with increasing depth during both day (GLM: a = -0.07 ± 0.01, z = -5.489, P < 0.001, n = 330) and night (GLM: a = -0.29 ± 0.02, z = -16.33, P < 0.001, n = 198). This result occurred regardless of the moment considered, but most markedly during the night. Except for the first 09:00 count, the number of larvae significantly decreased with depth at each observation time under the constant darkness photoperiod.

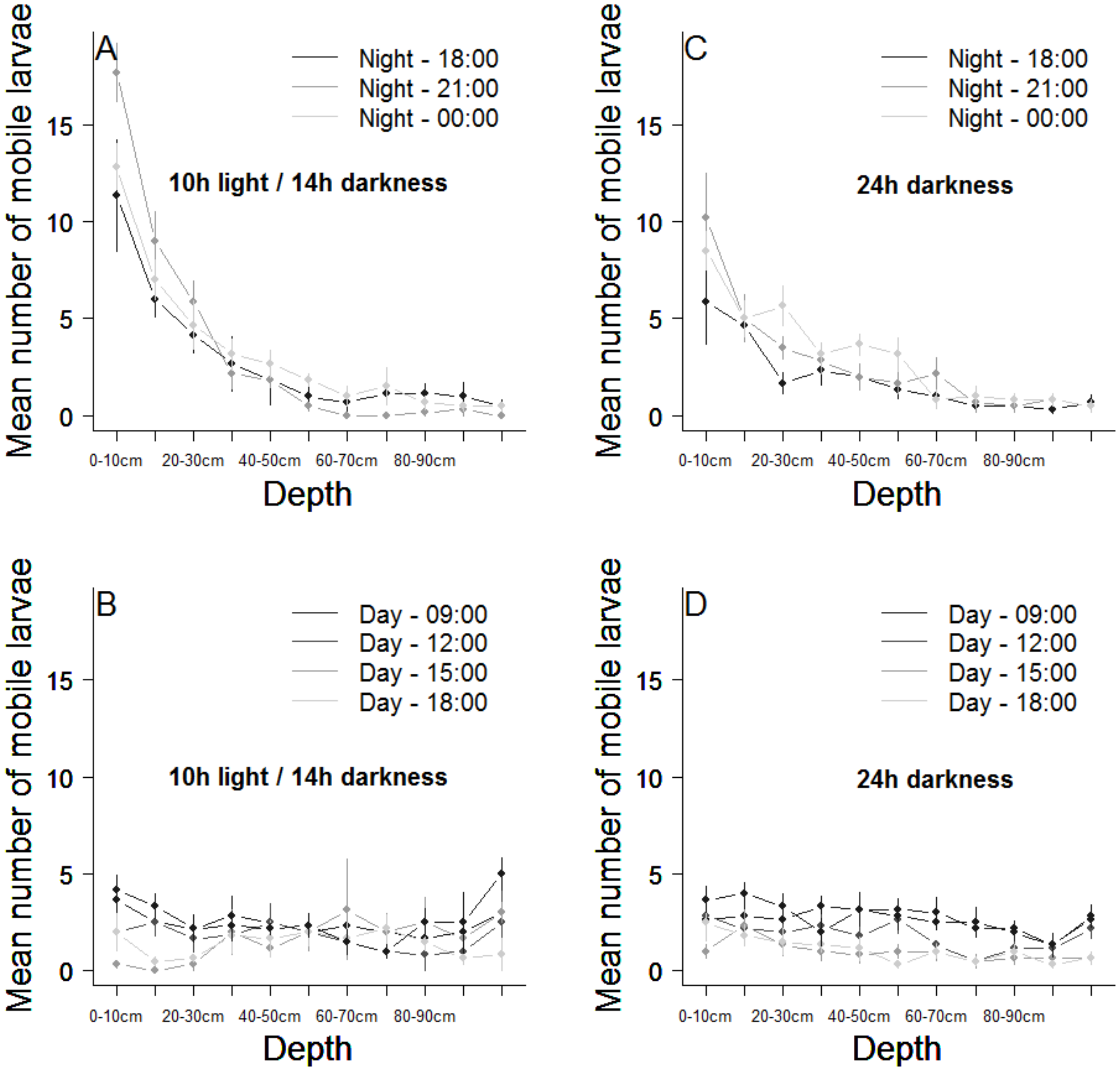

Figure 2.8: Mean and standard error number of mobile early veliger loco larvae present in each depth section of the water column for each time of observation for the 6 replicates under 10 h light/14 h darkness photoperiod during night (A.) and day (B.) and under 24 h darkness photoperiod during night (C.) and day (D.).

Swimming velocities

Swimming velocities were not significantly different between day and night (0.31 ± 0.16 cm.s^{-1} *vs*. 0.32 ± 0.13 cm.s^{-1} for day and night respectively; Wilcoxon test: W = 98.5, P = 0.57). Values ranged from 0.13 cm.s^{-1} to 0.72 cm.s^{-1} during the day and from 0.08 cm.s^{-1} to 0.54 cm.s^{-1} during the night. Using the video images, different swimming behaviors of 5 days post-hatching larvae could be identified. During day and night, they were observed floating displaying the velum or sinking with withdrawing velum. The mean gravitational fall velocities of 5 days post-hatching loco larvae anesthetized and standard error were 0.37 ± 0.06 $cm.s^{-1}$ (range: 0.27–0.51 $cm.s^{-1}$).

2.1.6. Discussion

Our experimental results on early veliger (EV) loco larvae activity and vertical movement in the water column showed that they follow a circadian rhythm. More 5 days post-hatching veliger loco larvae were observed swimming in the water column during the night than during the day regardless of the date at which the experiment was done (Figure 2.7). A 24-hours cycle appeared in the behavior of larvae with a decrease of swimming larvae at the end of the day. Therefore, veliger loco larvae perform the same general behavior as competent larvae (Manríquez and Castilla, 2011). Our results also showed that EV loco larvae were mainly located close to the surface of the experimental water column during the night. Their increased nocturnal swimming activity therefore results on average in an upward vertical migration. The vertical distribution of EV loco larvae has been investigated during one field study (Molinet *et al*., 2008), where the authors sampled more larvae at the surface (0–2 m) during the night than during the day. For competent loco larvae, a similar result was obtained with more larvae sampled during the night (Manríquez and Castilla, 2011).

Results of an enhanced swimming activity and migration towards the surface during the night have been observed under the two photoperiods (natural photoperiod and constant darkness) tested in our experimental study. However, statistical analyses performed on our results showed that the difference between day and night was stronger under the natural photoperiod (Figures 2.7, 2.8). The presence of photoreceptors in EV loco larvae has been observed less of one week after hatching (DiSalvo, 1988). This characteristic could explain that the nocturnal behavior is more pronounced under natural photoperiod experiment. However, our observations that the diurnal larval behavior (less activity, deeper distribution) remained under constant darkness show that this behavior was not only the consequence of the presence of light. Our results show the presence of an endogenous rhythm in the activity of EV loco larvae. An endogenous rhythm has already been observed for the crabs *Carcinus maenas* larvae (Naylor, 1960). The timing of an endogenous rhythm may be influenced by other exogenous cues than light that act as synchronizers. Periodic changes of environmental factors such as hydrostatic pressure and geotaxis have been proposed for causing larval vertical migration (Rudjakov, 1970). Non-opisthobranch gastropod larvae such as loco larvae are known to own visual capacities for orientation in the water column and can detect variability in temperature, salinity, pressure, and gravity (Kingsford *et al.*, 2002). The low diurnal activity of EV loco larvae can also be explained by the avoidance of predators as proposed for competent larvae (Manríquez and Castilla, 2011) or the searching for prey. In our experiments, the presence of phytoplankton could also have influenced the migrating behavior of EV loco larvae as planktonic individuals have been shown to become denser after feeding and sink in the water column in some species (Pearre, 2003).

The patterns we obtained for the vertical distribution of EV loco larvae in the experimental water columns were different between day and night under natural photoperiod (Figure 2.8 A.). Larvae were distributed uniformly in the water column during the day whereas during the night the number of larvae decreased with depth. These observations are not consistent with results from Molinet *et al.* (2008) field study. These authors sampled at surface (0–2 m), middle (8–15 m), and bottom of the sea water column (25–40 m). During both day and night, fewer EV loco larvae were sampled at the surface than at middle and bottom. The study sites are located in southern Chile (44°S) and are characterized by low salinity at the surface. Limited salinity at the surface was a reason for having fewer larvae there (Molinet *et al.*, 2008). However, in the experimental water column we used, such a salinity gradient was not present. Filtered sea water used in our experiments had a high salinity, around 33 PSU. Therefore, the discrepancy between our experimental results and the field results obtained by Molinet *et al.* (2008) may be explained by the effect of salinity on larval vertical distribution suggesting that larvae tend to sink deeper at low salinity.

During day and night, swimming velocities of EV loco larvae were not significantly different. Swimming velocities of EV loco larvae during the night (average = 0.32 $cm.s^{-1}$) were lower than those observed for competent larvae (average between upward and downward swimming velocities = 0.44 $cm.s^{-1}$; Manríquez and Castilla, 2011). Such a difference can be explained by change in the morphology of loco larvae during the dispersal phase. At the EV stage, larvae have a velum that is represented by two round lobes while the velum is defined by four elongated lobes that allow better displacement in the water column at the competent stage (DiSalvo, 1988). Fall velocities of EV loco larvae were also lower (average = 0.37 $cm.s^{-1}$) than those observed for competent larvae (average = 2.08 $cm.s^{-1}$; Manríquez and Castilla, 2011). Competent larvae measure around 1,700 µm (DiSalvo, 1988) that is 7 times higher than EV larvae shell length. Competent larvae are therefore bigger and denser than EV larvae, explaining higher fall velocities.

Our study on EV loco larvae revealed behavioral similarities and differences between this stage and the competent larval stage (Manríquez and Castilla, 2011). Loco larvae undergo nocturnal vertical migration at both stages but the influence of the photoperiod tested on the vertical distribution of EV loco larvae has not been observed for competent loco larvae. These contrasting results suggest that competent loco larvae have experienced the natural photoperiod sufficiently to have a well-established circadian rhythm that can hardly be influenced by a different artificial photoperiod. A larger difference in swimming activity between day and night was also observed for competent larvae (Manríquez and Castilla, 2011) than for EV loco larvae (Figure 2.7). These results are likely explained by more swimming abilities developed at competent stage. Taken together, these results suggest that nocturnal vertical migration predominates loco larval behavior all along the larval life, and that the extent of this migration is increasing with larval development. However, this statement needs to be confirmed by field or experimental studies for the late veliger loco larvae.

Benthic invertebrate species such as loco move over short distances at the adult stage, and consequently the exchange of individuals between distinct sites only occurs at larval stages. This exchange of individuals is a fundamental process for ensuring marine population connectivity (Cowen and Sponaugle 2009). Connectivity for loco may be influenced by the nocturnal vertical migration described for loco larvae. Indeed, in Eastern boundary upwelling systems like in Chile, current velocities and directions usually vary widely with depth. Vertical migration can be incorporated in coupled physical-biological models (Miller *et al.*, 2007; Metaxas and Saunders,

2009) to test its effect on larval dispersal and connectivity, as it has been recently investigated for other benthic species in Chile (Aiken *et al*., 2011; Yannicelli *et al*., 2012).

2.2. Larval growth experiments on veliger loco larvae

2.2.1. Introduction

In marine species with a pelagic larval stage, the growth during this stage can be influenced by biotic (food supply) and abiotic factors. One of the main abiotic factors affecting larval growth is seawater temperature. Several experimental studies on invertebrate species showed that decreasing temperatures slow down larval development and are associated with higher larval mortality rates, and increasing temperatures accelerate larval development (Katsanevakis and Verriopoulos, 2006; for the marine gastropod *Crepidula fornicata*: Pechenik and Lima, 1984; Rigal, 2010). Fast larval development induces short planktonic larval duration (PLD) (O'Connor *et al*., 2007) and therefore higher survival to the dispersal phase. However, depending on the sensitivity of the species, high temperatures can also induce larval mortality (Rumrill, 1990). From biophysical models of larval dispersal, it has been shown that increased mortality rate induces less local retention (Guizien *et al*., 2006) and that increased PLD increases dispersal distance and connectivity size (Ayata *et al*., 2010).

In this thesis, we wish to incorporate a larval growth model for loco in a biophysical larval dispersal model to assess the influence of this biological characteristic on the connectivity patterns of the species. Indeed, along the Chilean coast, loco larvae face a wide range of seawater temperatures, from 20°C to 11°C from North to South (Fernández *et al*., 2000). Moreover, seawater temperatures also vary with depth and season (Shaffer *et al*., 1999), and so is larval growth. As far as we know, there is no study of the influence of seawater temperature on loco larval growth. Therefore, we decided to conduct laboratory experiments to assess the influence of the temperature on the growth rate and the pelagic larval duration of loco larvae.

2.2.2. Material and methods

In July 2011, encapsulated eggs of loco were collected by a diver in Herradura Bay (30°S, Chile). They were transported to the aquaculture sector of the Universidad Católica del Norte in Coquimbo (Chile) and were transferred in a 20 l tank filled with filtered sea water (1 µm + UV treatment) at ambient temperature (13°C). Seawater was changed every day until hatching and cultures were continually aerated. Hatching occurred around one month after egg collection. EV larvae were transferred in three 20 l seawater tanks maintained at different temperatures: 13°C, 15°C, and 18°C. These values were chosen to encompass most of the range of seawater temperatures faced by loco larvae along the Chilean coast (Fernández *et al.*, 2000). The tank filled with seawater temperature at 13°C +/- 1°C was preserved in the aquaculture sector. The two other tanks were transferred in a room where temperature was controlled to 15°C +/- 1°C. In one of the two tanks, seawater was heated to 18°C +/- 1°C using a thermostat. Larvae were fed from the second day with the microalga *Isochrysis galbana* added to the tanks at a concentration between 20,000 and 30,000 cells.ml$^{-1,}$ following DiSalvo's (1988) protocol.

In order to investigate the effect of temperature on larval growth, the evolution of loco larvae shell length was observed. 30 larvae were sampled weekly from each larval culture tank and killed with formaldehyde. Each larva was photographed using a camera integrated in a microscope (Figure 2.9). The length of the shell for each larva was scaled using the software ImageJ. Due to a high rate of larval mortality in the tanks, these measures could only be done during 24 days. No data is available for the first week due to a problem with the camera.

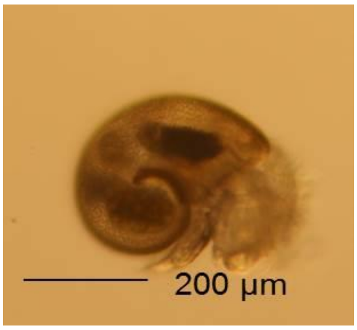

Figure 2.9: Photograph of a 10 days post-hatching early veliger loco larva using a camera integrated in a microscope.

2.2.3. Results and Discussion

Between 10 and 24 days after hatching, the length of veliger larvae shell increased for each temperature of culture (Figure 2.10). The higher increase is observed at 18°C, with a mean length increasing from 244 µm to 297 µm. The mean growth rates observed over the 2-weeks period were 1.51 $\mu m.d^{-1}$, 1.55 $\mu m.d^{-1}$, and 3.8 $\mu m.d^{-1}$ for 13°C, 15°C, and 18°C respectively. From these first results, it appeared that the growth rate of loco larvae increased with increasing temperature.

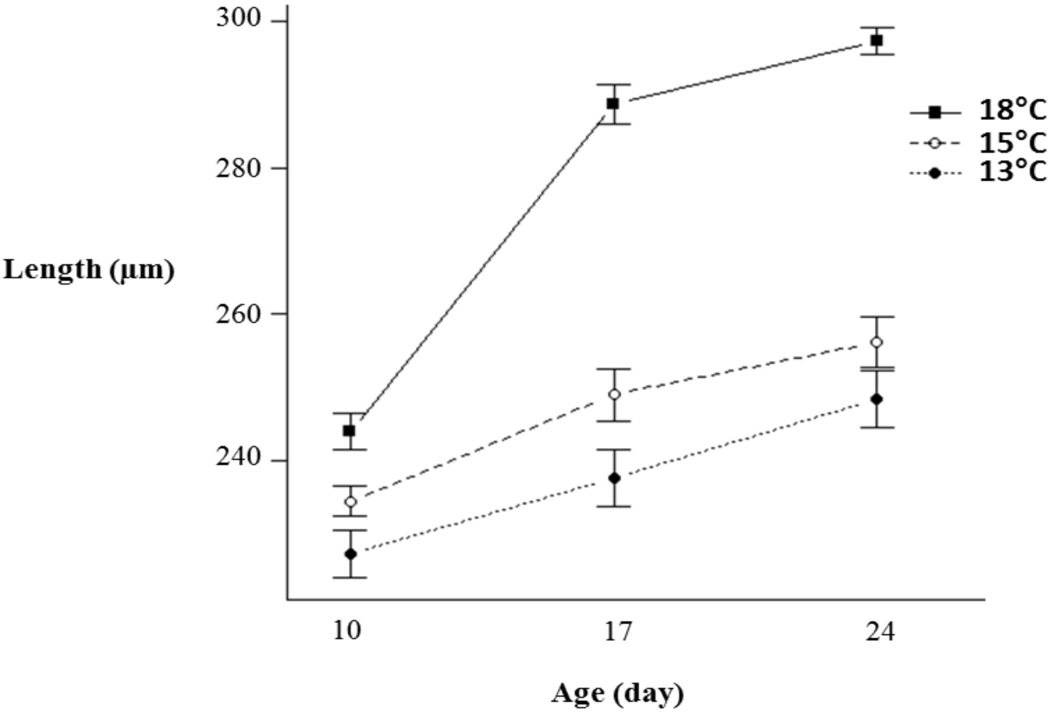

Figure 2.10: Shell length of veliger loco larvae in relation with day and temperature (13°C, 15°C, and 18°C).

However, from these estimates of growth rates, and assuming that they would remain similar along larval development, it would take from 437 days at 18°C to 1,100 days (3 years) at 13°C for our ~240 µm larvae to reach 1900 µm, the mean size they have at settlement (Disalvo, 1988; Manríquez *et al.*, 2004). Larval duration of loco is long (2 to 12 months), but clearly not that long. Our estimates are wrong, likely due to a problem of larval culture. Indeed, cyanobacteria were observed in the larvae that could have disturbed their growth and also lead to high mortality.

These experimental results were not conclusive, and due to logistic issues, we were not able to repeat this experiment. To achieve our objective of including larval growth dependence to temperature into our dispersal model, we chose to use an alternative, theoretical approach. This approach is fully detailed in Chapter 4.

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Chapter 3. Identifying appropriate spatial scales for marine conservation and management using a larval dispersal model: the case of *Concholepas concholepas* (loco) in Chile

This chapter is submitted as such to Progress in Oceanography by Lysel Garavelli, David Michael Kaplan, François Colas, Wolfgang Stotz, Beatriz Yannicelli, and Christophe Lett.

The abstract of the submitted manuscript is reproduced below.

Along the coast of Chile, fisheries targeting the marine gastropod *Concholepas concholepas*, commonly named "loco", were highly valuable until the end of 80's when catches declined significantly. Since the late 90's, a management plan based on territorial-users-rights areas has been established, with limited effect on the stock recovery. More effective loco conservation and management is impeded by lack of information regarding connectivity via larval dispersal between these individually-managed areas. To develop a global view of loco connectivity, we integrate loco life history information into a biophysical, individual-based larval dispersal model. This model is

used to evaluate the scales of loco connectivity and to partition the coast into largely independent subpopulations using a recently developed connectivity-matrix clustering algorithm. We find mean dispersal distances ranging from 170–220 km depending on release depth of larvae and planktonic larval duration. The identified subpopulations reveal barriers to connectivity related to headlands and embayments of the Chilean coast. Settlement success levels depend quantitatively on the physical and biological processes included in the model, but connectivity patterns remain qualitatively similar, an indication of the robustness of the identified subpopulations. Model estimates of settlement success peak for larval release dates in late austral autumn characterized by weak upwelling, in agreement with experimental results. Our analysis divides the a priori relatively homogeneous Chilean coast into a set of subpopulations with minimal connectivity between them. Using different model spatial resolutions and larval life-history parameters, robustness of results was confirmed, providing a solid basis for their use in management decisions.

3.1. Introduction

Heterogeneous spatial distributions of benthic populations, as well as of anthropogenic pressures on these populations, have significant consequences for conservation and management (Brazeiro and Defeo, 1999; Martone and Micheli, 2012). Identifying adequate spatial scales to set regulations, conduct monitoring and assess conservation efforts involves integrating multidisciplinary and multi-scale biophysical and social information (Orensanz *et al*., 2005). Biologically relevant scales, such as those of population connectivity and underlying mechanisms driving connectivity, are thought to be of major interest (Green *et al*., 2009; Ban *et al*., 2011). Despite its relevance, the scale of population connectivity is an unresolved topic for majority of marine species. Here we evaluate the spatial structure of population connectivity via larval dispersal of *Concholepas concholepas*, commonly known as “loco”, an ecologically-important benthic carnivore that is highly exploited along the Chilean coast (Castilla, 1999).

Loco populations along the coast of Chile currently suffer from historical problems of overexploitation and ineffective management. Although loco has been consumed since pre-hispanic times, systematic records of loco catch and abundance are only available since 1960’s. During the 80’s, loco began to be exported, becoming one of the most valuable benthic fisheries in Chile (Leiva and Castilla, 2002). As a result, fishing effort and landings increased very steeply during this period. Total catch fluctuated and then declined at the end of 80’s. A three-year fishery closure was implemented, followed by stringent management regulations, to mitigate overexploitation. Despite these efforts, catch levels have never recovered and are currently approximately 12% of the peak level from the 80’s (Sernapesca, National service of agriculture and fisheries in Chile, 2012).

Current approach for management of loco populations relies heavily on individual-managed, territorial-user-rights areas referred to as “Management and Exploitation Areas for Benthic Resources” (MEABR). Since the implementation of the first MEABR in 1998, there has been hope that territorial user rights would be more effective than previous loco management based on regional quotas (Bernal *et al*., 1999). Location and limits of each MEABR are defined by fishers, and initially coincided primarily with locations of high loco abundance (González *et al*., 2006). Annual monitoring of each MEABR is used to fix a yearly quota of extraction based on abundance estimates of loco bigger than 10 cm opercular length, the minimum legal size of extraction. Stock assessments are performed primarily by fishers themselves, in conjunction with private consultants and the national fishery authority. In 2011, there were 535 MEABR along the Chilean coast, 392 of which included loco as a target resource (Sernapesca, 2012).

In line with institutional proposals in Chile to scale up marine conservation by implementing networks of marine protected areas (MPAs), Gelcich *et al*. (2008) advised considering MEABR in networks to enhance the conservation of marine species, including loco. A central consideration for the establishment of MPA networks is spatial connectivity between subpopulations (Kaplan, 2006; White and Costello, 2011). Ensuring network connectivity increases population persistence (Botsford *et al*., 2003) and robustness to climate change (McCook *et al*., 2009). Therefore, the assessment of potential connectivity between MEABR is a crucial step towards the establishment of a successful regional sustainable management plan integrating individual MEABR.

The life cycle of loco is characterised by a long pelagic larval phase (2 to 12 months, DiSalvo, 1988; Moreno *et al*., 1993; Molinet *et al*., 2005) and an adult benthic phase of low mobility. Population connectivity of loco is therefore limited to larval phase, but little information is available regarding scales of loco larval dispersal. This lack of information has been highlighted as an impediment to effective management and conservation (Fernández and Castilla, 2005; González *et al*., 2006).

To assess larval dispersal in marine populations, three main approaches are currently being used: population genetics, micro-chemistry of calcifying structures (*e.g.*, otoliths and statoliths) and individual-based larval dispersal models (Leis *et al*., 2011). The first two of these approaches have previously been applied to study loco connectivity. Using a molecular approach, Cárdenas *et al*. (2008) concluded that loco correspond to a single taxonomic unit from Peru to southern Chile. This study was followed by a phylogeographical evaluation of genetic differentiation of loco between the three main biogeographical provinces in the Humboldt Current System (HCS) (Cárdenas *et al*., 2009). Significant differences in population genetic structure associated with biogeographical barriers were not observed, an indication of gene flow in the whole HCS. Manríquez *et al*. (2012) used differences in trace element composition of statoliths of pre-hatch loco larvae and recruits to assess connectivity between three areas in distinct regions of Chile. At the kilometer scale of individual sampling sites, recruits were not found to have been retained in the area of sampling. At regional scale of order 100 km (between sites), differences in concentrations of elemental signals were observed for sampled pre-hatch larvae and recruits. Although authors could not define the exact origin of recruits, they concluded that there was a strong indication of a lack of dispersal among sampling areas.

While these two studies provide significant information regarding connectivity in loco populations over large and small spatio-temporal scales, they do not measure connectivity over intermediate spatial scales most relevant for management and loco ecology. Biophysical models applied to marine benthic invertebrate species have been widely used to study the influence of larval biology on larval dispersal (Metaxas and Saunders, 2009). In this study, we integrate loco life history information into a biophysical, individual-based larval dispersal model to develop a global view of loco population connectivity and its consequences for management. We first detail biological and ecological processes involved in early life stages of loco that are relevant for the study of connectivity. We then integrate some of those processes into our larval dispersal model and use it to evaluate the scales of loco population connectivity. We finally discuss the implications of our results for management and conservation.

3.2. Material and Methods

3.2.1. Regional ocean dynamics pertinent for loco dispersal

Loco are distributed along the coasts of the Southeastern Pacific, from central Peru (6°S) to Cape Horn (55.8°S), including the Juan Fernandez Archipelago (Cárdenas *et al*., 2008). Coasts within loco distribution range are under the influence of two different systems: the Humboldt Current System (HCS) north of ~42–45°S, and the Cape-Horn Current and Interior Chilean Sea to the South. In the coastal HCS, Strub *et al.* (1998) observed two currents associated with coastal upwelling: a predominantly equatorward surface current (Chile Coastal Current; CCC) and a subsurface poleward current (Poleward Under Current; PUC at 100–300 m depth) (Figure 3.1). On time scales of weeks to months, alternating upwelling-downwelling events associated with surface current reversals are driven by coastal wind variability (Rutllant *et al*., 2004). Although Chilean coast is rather straight, coastal upwelling varies conspicuously in strength and frequency along the coast, with upwelling centers and upwelling shadows generally being found at and equatorward of headlands, respectively (Figueroa and Moffat, 2000). Mesoscale features, such as offshore spreading filaments, are recurrent near coastal headlands (Marín *et al*., 2001), whereas cyclonic and anticyclonic eddies develop near the coast due to surface and subsurface topographic features (Yannicelli *et al*., 2012). While filaments and eddies potentially transport coastal organic material beyond upwelling or shelf break fronts into open ocean (Letelier *et al*., 2009), other smaller scale eddies and recirculating features also associated with coastal topography may facilitate coastal retention (Yannicelli *et al*., 2012).

3.2.2. Hydrodynamic model

To simulate oceanic circulation of the HCS, we used the Regional Oceanic Modeling System (in its ROMS «UCLA» version; Shchepetkin and McWilliams 2005, 2009). ROMS is a free-surface split-explicit model solving the hydrostatic primitive equations using terrain-following curvilinear vertical coordinates. We followed a quasi-equilibrium approach, *i.e.*, the model is forced by monthly climatological means both for atmospheric forcing and open-ocean model boundaries. This approach has been successfully used in previous studies to simulate the mean circulation and the mesoscale dynamics of eastern boundary upwelling systems (*e.g.* Marchesiello *et al*., 2003; Penven *et al.*, 2005; Veitch *et al*., 2010; Mason *et al.*, 2010). The model was initially implemented over a large domain covering the South-East Pacific (from 15°N to 41°S and from 100°W to the South American coast) with a horizontal resolution of 7.5 km. Surface forcing is from mean-monthly climatologies: heat and freshwater fluxes are taken from the Comprehensive Ocean-Atmosphere Dataset (Da Silva *et al.*, 1994), and wind stress is from the NASA Quick Scatterometer-based climatology SCOW (Scatterometer Climatology of Ocean Winds; Risien and Chelton, 2008). Open-boundary forcing is a monthly climatology taken from SODA (Simple Ocean Data Assimilation; Carton and Giese, 2008) over the period 2000-2006. Integration is made for 13 years, the first 3 years being the spin-up. Time series of current velocities were averaged and stored every 3 days. We refer the reader to Colas *et al*. (2012, 2013) for more details on this simulation and its validation against observations. In order to reach a higher spatial resolution over the northern Chile coastal region we used an offline-nesting approach (Mason *et al*., 2010), where the 7.5 km resolution, large domain solution (described above) is used to supply lateral boundary information to force a 3 km resolution, smaller domain solution. This smaller domain is embedded within the large regional domain, and extends from 21°S to 35°S and from 78°W to the Chilean coast. This approach allows the regional and mesoscale structures (eddies) resolved by the 7.5 km solution to be transmitted through the open boundaries of the smaller 3 km resolution domain. The surface atmospheric forcing of the 3 km solution is identical to that of the 7.5 km solution. An integration of this nested domain is made for 6 years, the first 2 years being considered as spin-up. Time series of current velocities were averaged and stored every 2 days.

3.2.3. Loco life history

To build the individual-based larval dispersal model for loco, we reviewed adult and larval loco life history. Adult loco have been observed on rocky substrates from intertidal zone down to approximately 40 m depth (Manríquez *et al.*, 2004). Individuals become reproductively mature at between 3.5 cm and 7.7 cm opercular length (Castilla and Cancino, 1976; Manríquez *et al.*, 2008), corresponding to approximately 9 and 20 months after settlement, respectively (Stotz, 1997). Spawning of loco occurs in Chile principally in austral summer and autumn (Manríquez and Castilla, 2001; Manríquez *et al.*, 2008). After mating, females produce encapsulated eggs that are fixed on rocks until hatching. Eggs hatch after a period of several months (Castilla and Cancino (1976) measured incubation times of 69 to 128 days at 13.5°C to 14.5°C), emerging as planktonic larvae that are dispersed before settling into the coastal adult habitat.

There are at least two North–South gradients in reproduction and dispersal that are likely important for connectivity in loco populations. The number of eggs in a capsule is highly variable, ranging from few hundred to more than 14,000 (Castilla and Cancino, 1976). Fernández *et al.* (2007) showed that the number of loco embryos in a capsule was lower in northern regions than in southern regions of Chile. This observation was correlated with mean water temperature before egg deposition. Similarly, planktonic larval duration (PLD) has been found to vary depending on latitude. PLD was assessed at around 2 to 3 months from laboratory studies (DiSalvo, 1988) and between 3 and 4 months from field studies in south-central Chile (39°S) (Moreno *et al.*, 1993). Further south, in fjords and channels (43°S–44°S), it has been shown that the larval phase may be longer, between 6 and 12 months (Molinet *et al.*, 2005), likely due to lower water temperatures in the region.

Vertical position in the water column may play an important role in dispersal of loco larvae. Larvae possess a specialized swimming organ, known as vellum, which can be used for vertical migration (Ruppert *et al.*, 2003). In southern Chile (43–44°S), the abundance of small loco larvae (stage 1, size between 250 µm and 500 µm, DiSalvo, 1988) was observed to increase in surface water samples at night (Molinet *et al*., 2008). Similar results have been found in laboratory experiments (Chapter 2). Diurnal migration has also been observed in competent larvae (1400 µm and 1900 µm, DiSalvo, 1988), though the direction of migration has not been consistent between studies. Field studies in central Chile suggested that they swim to the surface during the day (Poulin *et al*., 2002), whereas other recent field studies in northern and central Chile coupled with laboratory observations indicated the opposite (Manríquez and Castilla, 2011).

Loco early life history is summarized in Figure 3.1.

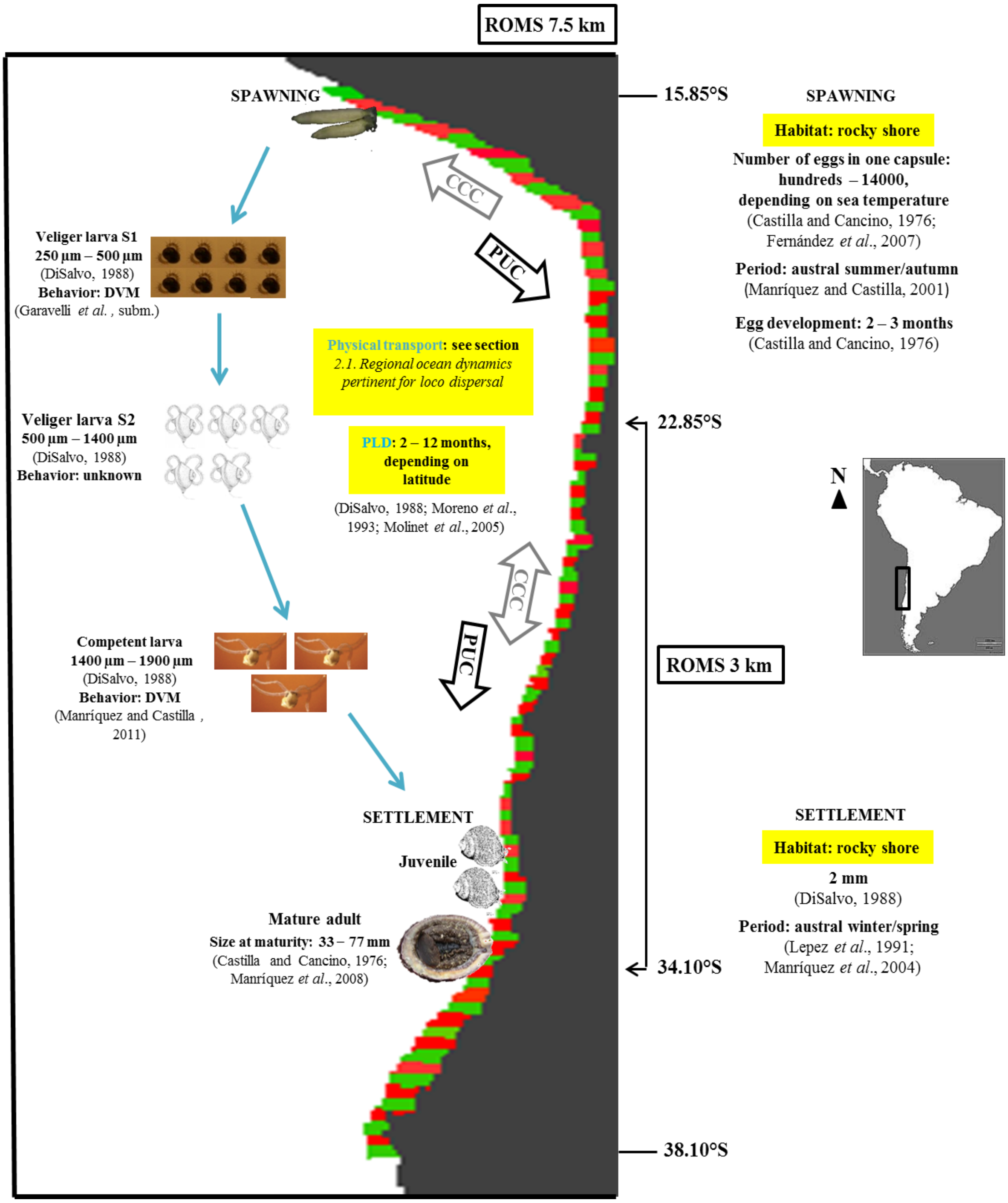

Figure 3.1: Schematic representation of loco life history from spawning to mature adult mapped on our study area. The three larval stages are pelagic. The areas used in our larval dispersal model for release and settlement of loco larvae along the coast are shown in red and green. The two hydrodynamic model (ROMS) configurations that we used as inputs to our larval model differ in horizontal resolution (7.5 km and 3 km) and spatial extent. Highlighted elements are those used in the larval dispersal model. PLD = planktonic larval duration; DVM = diel vertical migration; CCC = Chile Coastal Current; PUC = Poleward Under Current.

3.2.4. Larval dispersal model

The individual-based offline Lagrangian tool Ichthyop 3.1 (Lett *et al.*, 2008) was used to model loco larval dispersal. Virtual loco larvae are advected passively by velocity fields derived from the ROMS configurations. Locations of each virtual larva (latitude, longitude and depth) are tracked every hour in three dimensions using a forward-Euler advection scheme. Horizontal diffusion was added following Peliz *et al.* (2007). At the beginning of each month, 100,000 individuals were randomly released from habitat areas. These areas were defined as sections of 0.25° of latitude all along the Chilean coast stretching from the coast to the 500 m isobaths, a compromise between knowledge of loco spawning areas and their representation in the model. For the 7.5 km and 3 km ROMS configurations, locations of habitat areas ranged from 15.85°S to 38.10°S and from 22.85°S to 34.10°S, respectively (Figure 3.1). Two release depths that encompass the spawning depth ranges of loco were tested: 0–20 m and 40–60 m. After spawning, individuals were tracked for a maximum time period of either 80 days (the minimum value of PLD for loco in the area) or 140 days (the maximum value). Settlement success was defined as being located in a habitat area at any time during the competency period, here the last 20 days of the PLD. Simulations were repeated from January to December during 4 years of ROMS simulations.

Outputs of simulations are represented as connectivity matrices for each spawning depth and PLD. Values of the connectivity matrix C_{ij} are calculated as the percentage of particles released from area *j* that are transported to area *i*.

To assess the effect on connectivity of loco habitat limitation for both spawning and settlement, the percentage of rocky shore within each latitudinal band of 0.25° was estimated. First, the length of the coast was calculated from digitized Chilean Military Geographic Institute (IGM) charts 1:250,000. Then, we substracted the length of unsuitable habitat defined as sandy beaches longer than 4 km without any obvious rocky subtidal shelf within each band. Sandy shores were geo-referenced using GoogleEarth 7.1.1.1580. The result was expressed as a percentage of total coastal length per band. For each connectivity matrix, we multiplied the values of each column and each row by the proportion of rocky shore to adjust for limited habitat area for larval production and larval recruitment, respectively.

Connectivity matrices were used to (i) evaluate the compatibility between our results and those of Manríquez *et al*. (2012) indicating absence of larval dispersal between their northern (23–24°S) and central (33–34°S) sampling areas; and (ii) identify highly independent subpopulations using the methodology developed by Jacobi *et al*. (2012). This latter method calculates a set of contiguous subpopulations that minimize connectivity between subpopulations for a given desired level of aggregation, controlled by a single tunable parameter, here referred to as the connectivity threshold. Subpopulations were identified for connectivity matrices obtained for a spawning depth 0–20 m, with and without available habitat for loco. This method was applied to connectivity matrices from the 7.5 km resolution ROMS model covering the full area relevant for management. Jacobi *et al*.'s (2012) algorithm first transforms the connectivity matrices into symmetric matrices, *i.e.* the connectivity between an area *i* and an area *j* is set as the average connectivity between these areas $\frac{c_{ij}+c_{ji}}{2}$. The algorithm also allows for an optional normalization of all connectivity matrix rows, which was not used as this would eliminate the effect of habitat area limitation. In a limited number of cases the algorithm identified a single, isolated area as a subpopulation; in this situation, we regrouped the area with the closest subpopulation.

3.3. Results

3.3.1. Distribution of loco habitat

Available loco habitat (rocky shores) is highest in the center of the study domain, dropping along northern and southern edges (Figure 3.2). From 19°S to 33°S, sandy shores larger than 4 km are scarce and concentrated in a few embayments, leading to long rocky coastal continuums that are highly favorable for loco populations. By contrast, north and south of this central area, the percentage of available loco habitat varies significantly, with typical values around 60–80%.

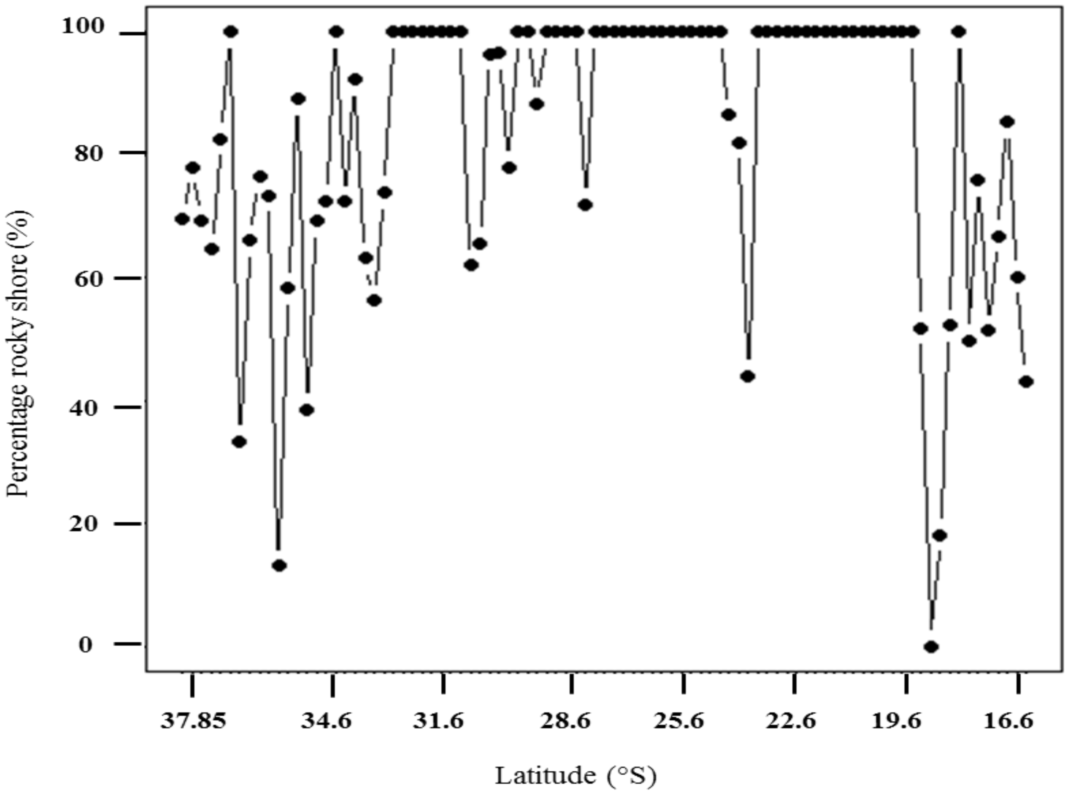

Figure 3.2: Percentage of rocky shore representing available habitat for loco every 24 km along the Chilean coast, from 15.85°S to 38.1°S.

3.3.2. Larval dispersal distance

The distribution of distances traveled by loco larvae from spawning to settlement are represented from the larval dispersal model outputs for spawning depth 0–20 m (Figure 3.3). For both ROMS configurations, the mean dispersal distance of larval settlers is about 170 km after 80 days of PLD (Figures 3.3 a., b.), whereas it is about 220 km after 140 days of PLD (Figures 3.3 c., d.). The overall probability of successful settlement is around 2 times greater for the shorter PLD than for the longer PLD. For both PLD values, the number of settling larvae obtained after running the dispersal model over the 7.5 km ROMS configuration was approximately twice that obtained using the 3 km ROMS configuration. Similar patterns are obtained for spawning depth 40–60 m (results not shown).

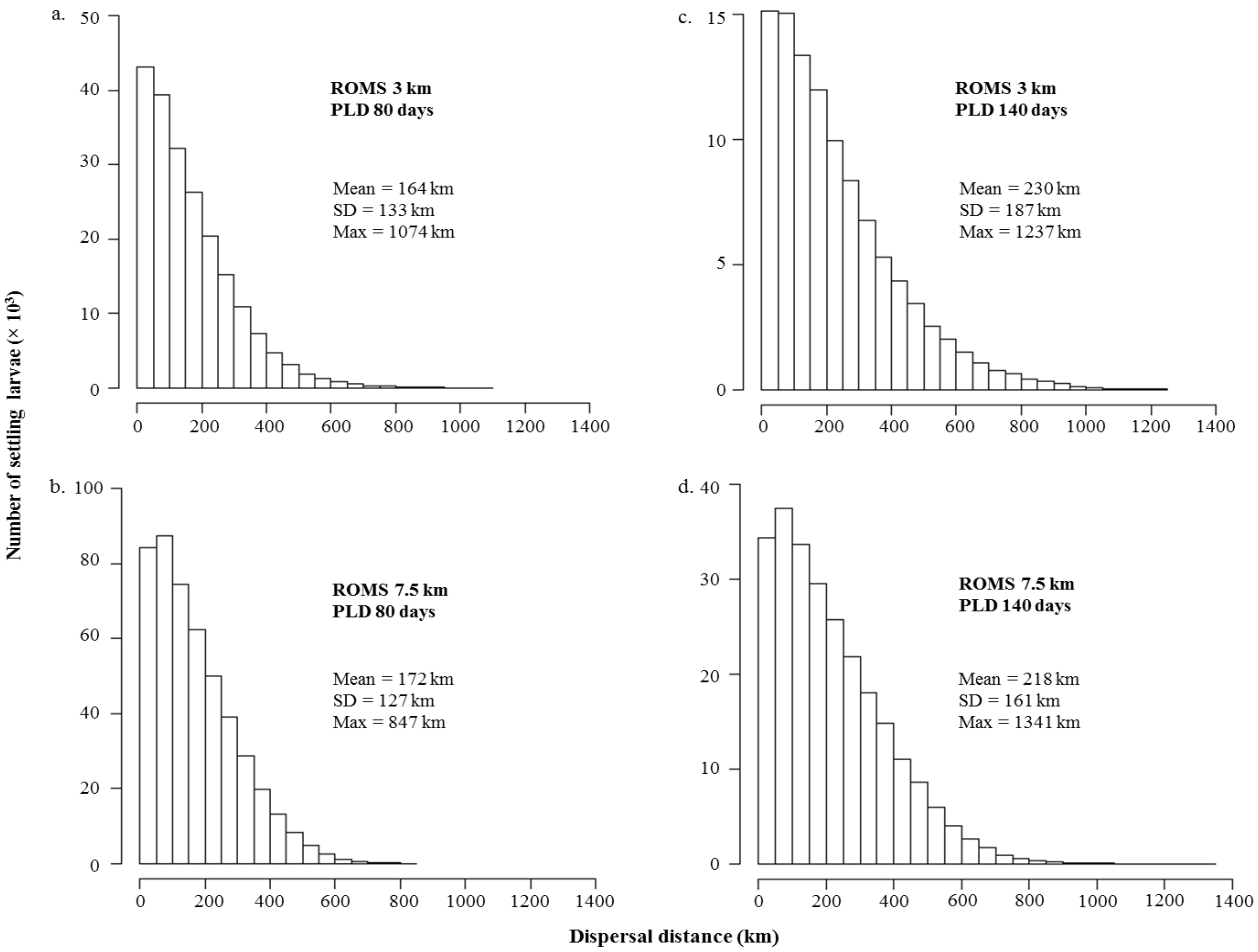

Figure 3.3: Distributions of dispersal distances for settled loco larvae for spawning depth 0–20 m after 80 days and 140 days of planktonic larval duration for ROMS 3 km (a. and c. respectively) and ROMS 7.5 km (b. and d. respectively). Mean, standard deviation (SD) and maximum distance (Max) are indicated.

3.3.3. Connectivity matrices

Connectivity matrices obtained using the 7.5 km ROMS configuration are shown in Figure 3.4. Connectivity values are highest on, or close to, the matrix diagonal, indicating that settlement within an area is generally higher than transport among distant areas. At the northern edge of the domain, higher connectivity values are obtained above the matrix diagonal, indicating that virtual larvae are mainly transported to the North, for the two spawning depth levels and PLDs tested. In contrast, in the central part of the domain there is a slight larval transport to the South for spawning depth level 40–60 m (Figures 3.4 c., d.). For both values of PLD, connectivity values are around 2 times higher for spawning depth level 40–60 m (Figures 3.4 c., d.) than for level 0–20 m (Figures 3.4 a., b.). When limited available habitat for loco is considered, the connectivity values decrease in the northern (to 19°S) and southern (from 33°S) parts of the study area (Figure 3.5). Though connectivity patterns from the 3 km ROMS configuration are largely consistent with those from the lower resolution model, two hotspots of high connectivity at 26°S and 29°S are more clearly visible with the 3 km ROMS configuration (Figure 3.6).

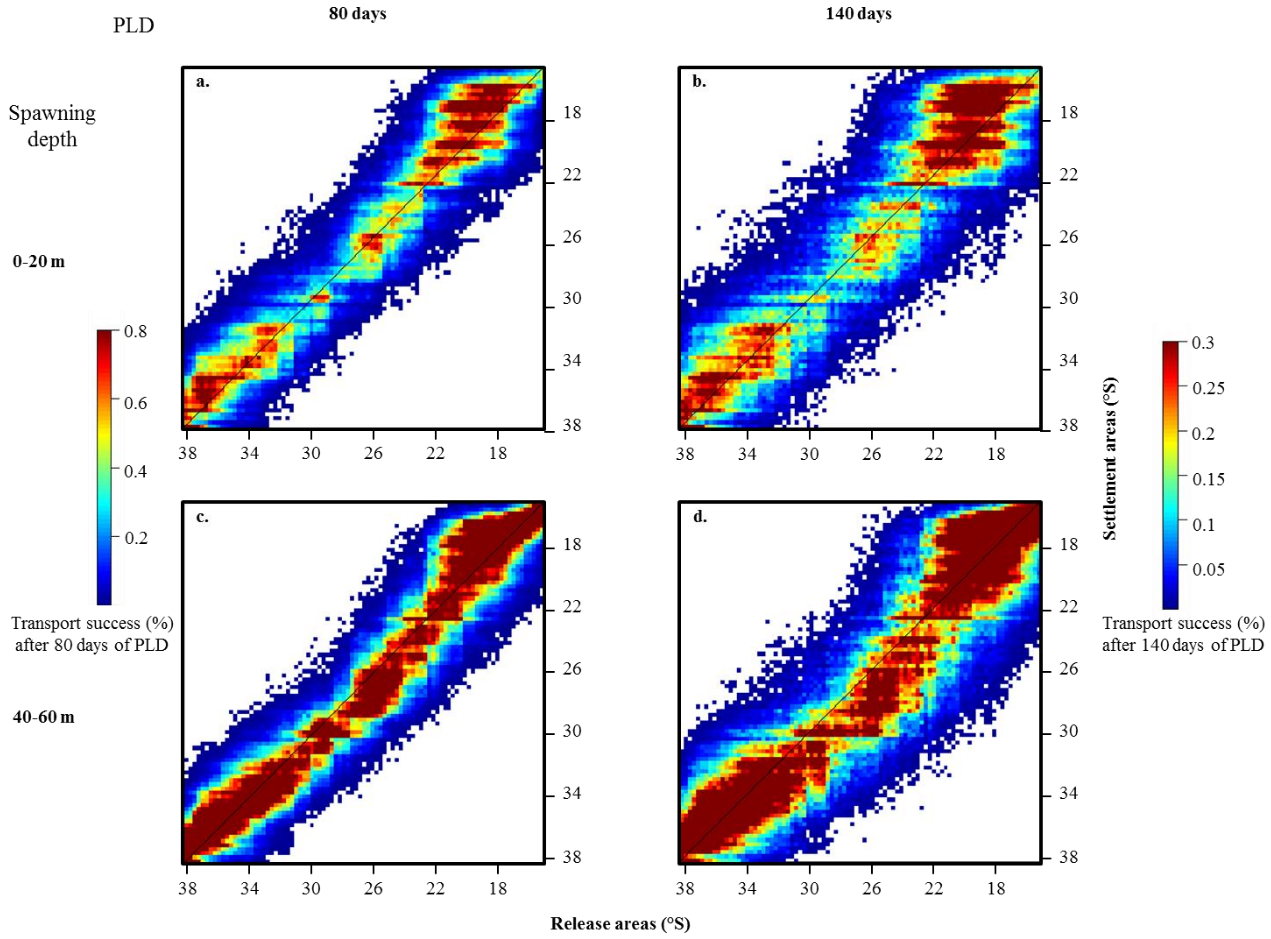

Figure 3.4: Connectivity matrices obtained with the 7.5 km resolution ROMS configuration for PLD (planktonic larval duration) =80 days and spawning depth 0–20 m (a.) 40–60 m (c.); for PLD= 140 days and spawning depth 0–20 m (b.) 40–60 m (d.). Note that colour bars are different for PLD=80 days (maximum value of transport success set to 0.8%) and PLD=140 days (maximum 0.3%).

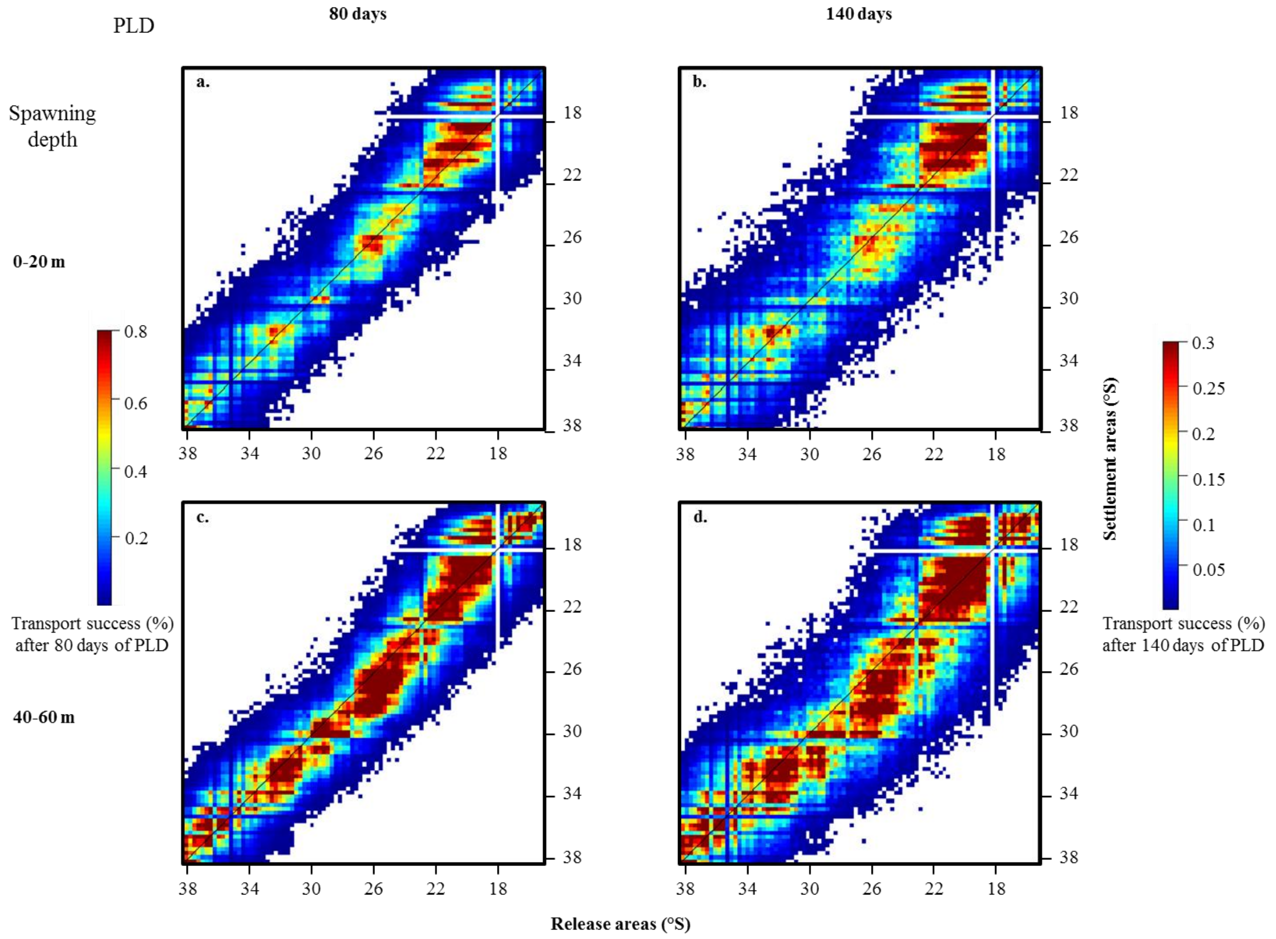

Figure 3.5: Same as Figure 3.4 but taking into account the limited habitat availability of loco for both release (columns) and settlement (rows).

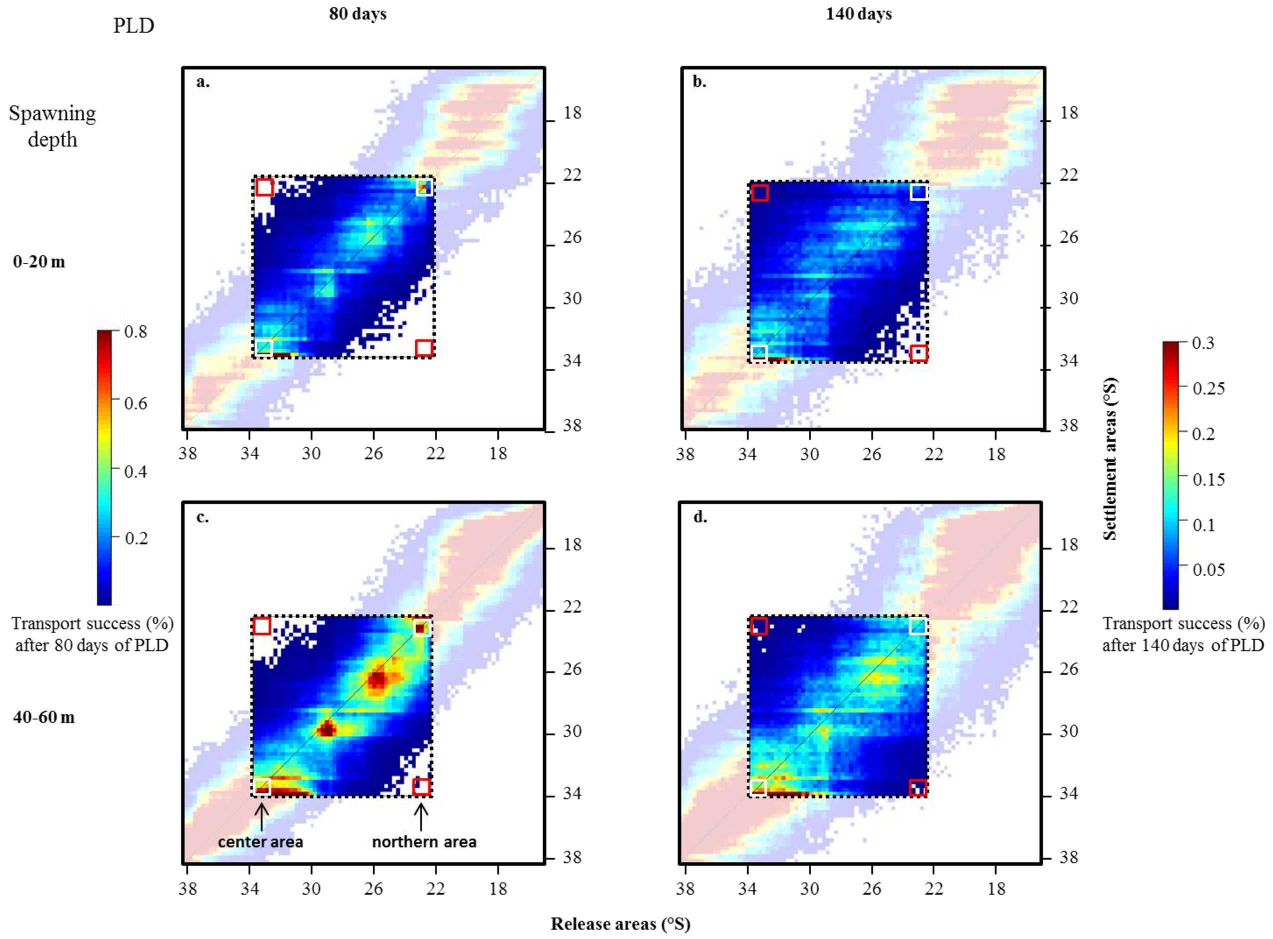

Figure 3.6: Same as Figure 3.4 with the results obtained using the 3 km resolution ROMS configuration superimposed to those obtained using the 7.5 km configuration. White squares represent retention within the central (33–34°S) and northern (23–24°S) areas sampled by Manríquez *et al*. (2012) and red squares represent transport from one area to the other.

The northern (23–24°S) and central (33–34°S) areas examined by Manríquez *et al*. (2012) are represented by squares in Figure 3.6. Transport between the two areas was essentially null for PLD=80 days regardless of the spawning depth. For PLD=140 days, ~1 individual in 100,000 was transported on average from the northern area to the central area when spawned at the 40–60 m depth level. In the opposite direction, ~2–3 individuals in 100,000 were transported for the two spawning depth levels.

3.3.4. Connected clusters

Partitioning of the loco population into subpopulations is shown in Figure 3.7 for spawning depth 0–20 m and PLD=80 days without and with considering available habitat for loco (Figures 3.7 a. and 3.7 b., respectively). The number of subpopulations varies from 2 to 6 along the Chilean coast. Without available habitat (Figure 3.7 a.), for both PLD values, the first separation into two subpopulations is identified at ~29°S, followed by a separation at ~23°S. The next separation occurs at ~31°S and the last two separations occur at ~16°S and ~28°S. At 6 subpopulations, self-recruitment (number of recruited larvae in a subpopulation *i* coming from the subpopulation *i*) is weak for the 2 smaller subpopulations (20% and 19%) compared to the others. Also, percentages of larvae exchanged between 2 subpopulations increase significantly. When habitat is considered (Figure 3.7 b.), for both PLD values a similar partitioning is observed with separations at ~29°S from 2 subpopulations, ~16°S from 3 subpopulations and at ~23°S from 4 subpopulations. Southern part of the domain is divided into 2 subpopulations with a separation at ~35°S from 6 subpopulations. From 3 subpopulations, self-recruitment for the northern subpopulation is weak (<20%). From 6 subpopulations, percentages of larvae exchanged between subpopulations increase from 28°S. The percentage of all larvae exchanged between subpopulations reaching 20%. For spawning depth 40–60 m, similar partitioning into subpopulations is observed (results not shown).

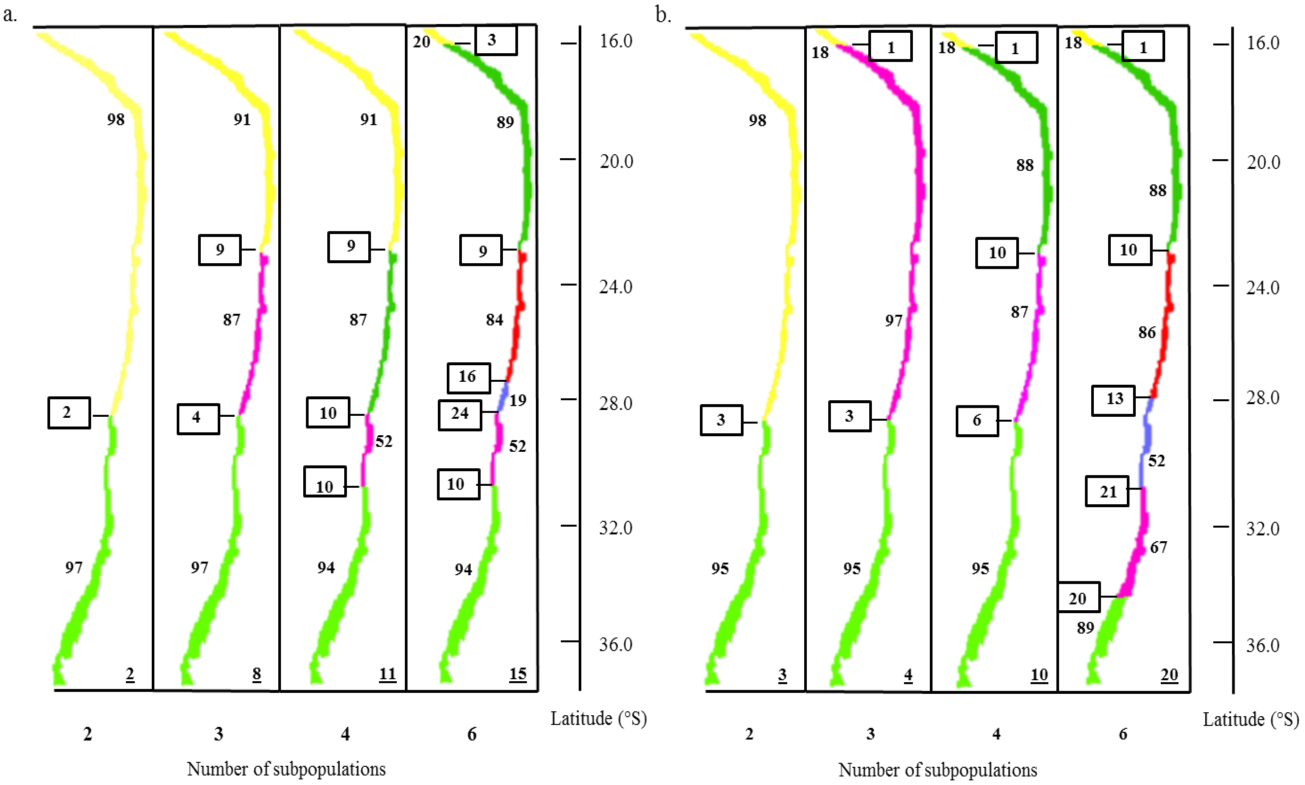

Figure 3.7: Partitioning of the loco population into subpopulations successively identified by the method of Jacobi *et al.* (2012) from the connectivity matrices of (a.) Figure 3.4 a. (spawning depth 0–20 m, planktonic larval duration = 80 days) and (b.) Figure 3.5 a. (spawning depth 0–20 m and planktonic larval duration = 80 days with loco habitat availability). We calculated the percentage of larvae exchanged between two adjacent subpopulations (relative to total recruitment originating in the two subpopulations, numbers in box), the percentage of all larvae exchanged between subpopulations (underscored numbers), and the percentage of self-recruitment for each subpopulation (fraction of settlers originating in the same subpopulation).

3.3.5. Seasonality in connectivity

Favorable release areas for loco larvae settlement globally along the coast are mainly located in the North of the study area (17–26°S), and in the South (32–38°S, Figure 3.8), regardless of PLD or release depth. There are less settling larvae originating from the center of the study area. Most favorable release months are in austral autumn and winter (March–August, Figure 3.8). The seasonal pattern is stronger in the South than in the North, and for the surface (0–20 m) than for the subsurface (40–60 m) depth level, which results in a small effect of seasonality in the North at depth. The seasonal patterns are similar for the two values of PLD tested.

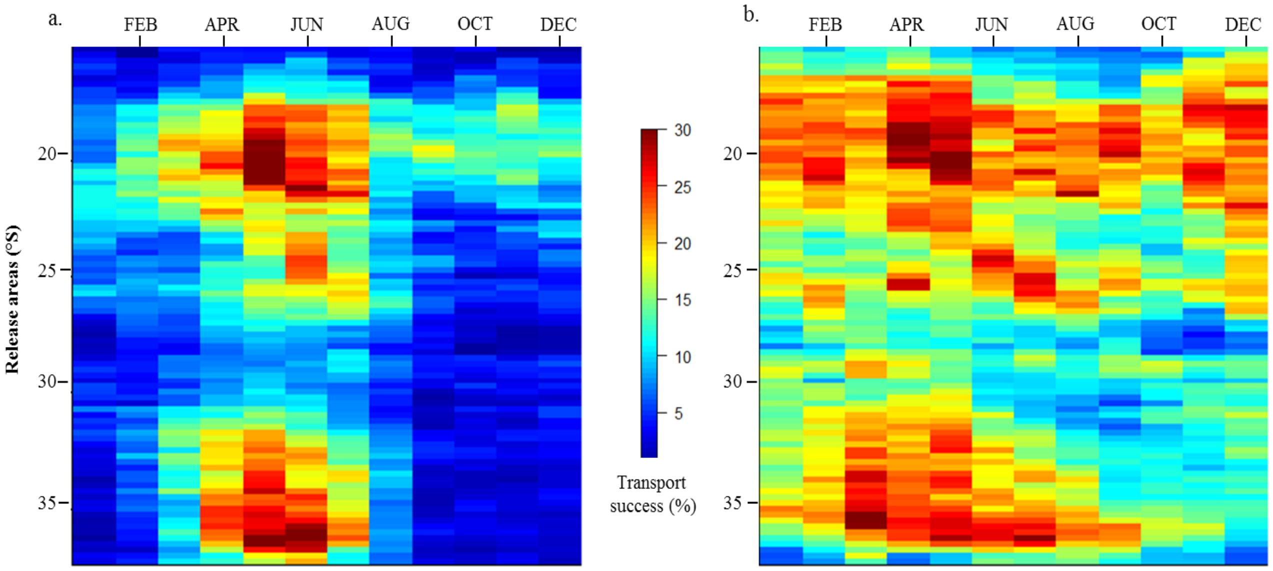

Figure 3.8: Transport success of loco larvae in relation to area and month of release for planktonic larval duration = 80 days and spawning depth (a.) 0–20 m and (b.) 40–60 m.

3.4. Discussion

Our results are globally consistent with previous studies on loco (*Concholepas concholepas*) population connectivity, but also provide significant new information at regional spatial scales. We found low levels of dispersal between sites separated by several 100 km (Figure 3.6), consistent with Manríquez *et al*. (2012). Nevertheless, non-negligible dispersal was observed all along the coast, with mean dispersal distances ranging from 170–220 km (Figure 3.3) depending on PLD. These simulated levels of dispersal are consistent with little indication of significant larval retention at the scale of kilometers (Manríquez *et al*., 2012) and low levels of (long-term) genetic differentiation among widely separated loco individuals (Cárdenas *et al*., 2009).

The clustering analysis to identify highly-independent subpopulations revealed generally consistent patterns across model configurations and parameter choices (Figure 3.7). In all cases, a major split occurs at approximately 29°S, and the northern part of the domain is more highly structured than the southern part. The split at 29°S coincides with a zone characterized by an extensive bay system (Coquimbo, Guanaqueros, and Tongoy bays) and an offshore-oriented current divergence (Hormazabal *et al*., 2004). Coquimbo bay and areas immediately to the south (~29–31°S) form a subpopulation. This zone has already been described as a particularly high larval retention area (IFOP, INFORME 2002). The separation at Mejillones peninsula (23.06°S) coincides with an abrupt change in the orientation of the coastal shelf that likely influences connectivity patterns. Separation at 16°S appears from 6 subpopulations when habitat availability is not considered (Figure 3.7 a.) and from 3 subpopulations when it is considered (Figure 3.7 b.). At 16°S, connectivity values (Figures 3.4 a., b.) and percentage of loco available habitat (Figure 3.2) are low which explains the observation of this separation at the beginning of the partitioning. When habitat availability is considered (Figure 3.7 b.), separation at ~35°S appears, likely driven by lower levels of rocky-bottom habitat south of these points (Figure 3.2). Adding habitat along the coast increases percentage of larvae exchanged between subpopulations in the southern part of the study domain. Surprisingly, subpopulations identified are largely independent of PLD and change only slightly with spawning depth. This, in combination with the fact that some of the identified major barriers to connectivity correspond to known features (like capes and bays) of the Chilean coast, suggest that these results are fairly robust, generic features of coastal circulation in the area. From 6 subpopulations, percentages of exchanged larvae between subpopulations increased significantly and self-recruitment decreased.

Whereas connectivity patterns are globally consistent across model configurations and parameter choices, absolute levels of recruitment success are sensitive to these factors. Recruitment success using the higher spatial resolution ocean model was roughly a third of that obtained with the lower resolution model. Coastal oceanographic observation in Chile highlight the importance of mesoscale processes like eddies, filaments, and meandering currents (Hormazabal *et al*., 2004) that could cause offshore losses of larvae (Parada *et al*., 2012). The model configuration at 3 km reproduces more accurately coastal bathymetry and, therefore, coastal mesoscale processes are expected to be better resolved than in the configuration at 7.5 km, likely driving reduced recruitment success. However, as relative patterns of recruitment are generally more useful than absolute values for assessing connectivity differences, the coherence between connectivity patterns across model resolutions lends support to using the larger, lower-resolution domain more appropriate for management issues.

We examine the influence of two larval biological processes on connectivity: spawning depth and PLD. Spawning depth influences retention due to opposing surface and subsurface currents. At depth, currents are generally weaker and oriented toward the coast, explaining increased recruitment rates for larvae released at 40–60 m depth than for 0–20 m depth (Figures 3.4, 3.6), a result consistent with other modeling works in upwelling systems (Brochier *et al*., 2008a; Brochier *et al*., 2008b). The increase in southward larval transport for 40–60 m spawning depth coincides with subsurface southward currents (see Appendix Figure 3.A). Northward larval transport was expected due to the net northward coastal currents, but this was not observed for the 0–20 m spawning level (Figure 3.4). The bulk of released individuals were indeed transported north, but these same “northward” individuals were often transported offshore, *i.e.* outside our coastal settlement areas, by offshore Ekman flow along the Chilean coast (Aiken *et al*., 2011) and by mesoscale features, such as eddies and filaments, that are intensified by coastal upwelling (Marín *et al*., 2001). Our results therefore highlight the importance of onshore subsurface currents and (relatively rare) poleward currents produced by wind relaxation events for loco recruitment.

Increasing PLD produced an increase in mean larval dispersal distance (Figure 3.3) and a decrease in retention, connectivity (Figures 3.4, 3.6), and global settlement (Figure 3.3) like in other modeling studies (Lefebvre *et al*., 2003; Lett *et al*., 2010; Aiken *et al*., 2011). In our model, we used a constant PLD value all along the coast, whereas in reality PLD depends on sea temperature (O’Connor *et al*., 2007). Given the latitudinal extension of the Chilean coast, temperature is one of the characteristics of the marine environment that is particularly variable. From 18°S to 32°S, temperatures in surface waters close to the coast range from 13°C to 20°C. Temperature variability is less pronounced in the South of Chile, ranging from 11°C to 13°C for latitudes comprised between 32°S and 56°S (Fernández *et al*., 2000). Experimental data support loco PLD increasing from around 60 days in the northern part of the study area to 120 days to the South, consistent with temperature changes (DiSalvo, 1988; Moreno *et al*., 1993). This gradient should increase offshore larval losses as one goes from northern to southern Chile.

One important biological process that has not been implemented in our model is larval mortality. Long PLDs such as those described for loco imply high total mortality rates during transport. Data on larval mortality is not available for loco, but a mortality rate of 0.12 d^{-1} has been estimated for the veliger larvae of *Mytilus edulis* (Rumrill, 1990). Assuming such a rate for loco would imply that one larva is 2,000 times more likely to survive 60 days than 120 days, which means that loco larvae spawned in southern Chile could be much more exposed to mortality than those spawned in the North. This effect, combined with increased offshore transport for longer PLDs and reduced loco habitat in the southern part of the domain, suggest that real recruitment success may be significantly lower in the southern part of the study area than in the North. This provides a reasonable explanation for increased reproductive investment by adult locos via higher numbers of loco embryos per capsule towards the South (Fernández *et al*., 2007), as increased larval production could counterbalance these larval losses.

Spawning for loco in Chile occurs principally in austral summer and autumn (January–May, Manríquez and Castilla, 2001; Manríquez *et al*., 2008). Loco eggs are attached to rocky bottom during 2 to 3 months (Castilla and Cancino, 1976). Hatching of larvae therefore occurs mainly in austral autumn and winter (March–August), the period identified as the most favorable for larval settlement in our simulations (Figure 3.8). As PLD for loco larvae is between 2 and 4 months in the study domain (DiSalvo, 1988; Moreno *et al*., 1993), settlement occurs principally in austral winter and spring in the study area. Aiken *et al*. (2011) also observed maximum settlement in austral winter in South Chile from their modeling study. Overall, loco larvae are transported between austral autumn and spring, and not in summer, the period when intensity of upwelling along the Chilean coast is generally maximal (Thiel *et al*., 2007) and therefore unfavorable to larval coastal retention.

The partitioning of the study domain into subpopulations provides a template for defining regional management units for coordinating MEABR management efforts. Despite its relatively simple coastal geometry, connectivity along the Chilean coast north of 42°S is heterogeneous enough to define rather independent subpopulations (Figure 3.7). We identified a partitioning into 4 subpopulations having low levels of inter-connectivity and high levels of self-recruitment, suggesting that MEABR within each subpopulation are largely connected, whereas MEABR between subpopulations are rather independent. From a management perspective, the identification of those spatial sub-units imply that: i) in order to evaluate the performance of the system and state of the fishery, data of individual MEABR need to be integrated over each subpopulation; ii) identification of productivity hotspots and conservation efforts should be organized at the level of subpopulations; and iii) environmental and population monitoring should be conducted in at least one location within each zone. Using this partitioning to organize such regional management efforts would provide a compromise between previous large-scale quotas and current small scale user-rights management that is better tuned to loco biology and dispersal. Clearly, considerations other than biology, in particular societal and economical concerns, also determine a number of manageable fishery units. However, our results provide an initial, biologically-optimal partitioning that can then be adapted to societal constraints, highlighting the utility of such a tool for decision support for management of marine resources.

Acknowledgments

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Appendix A

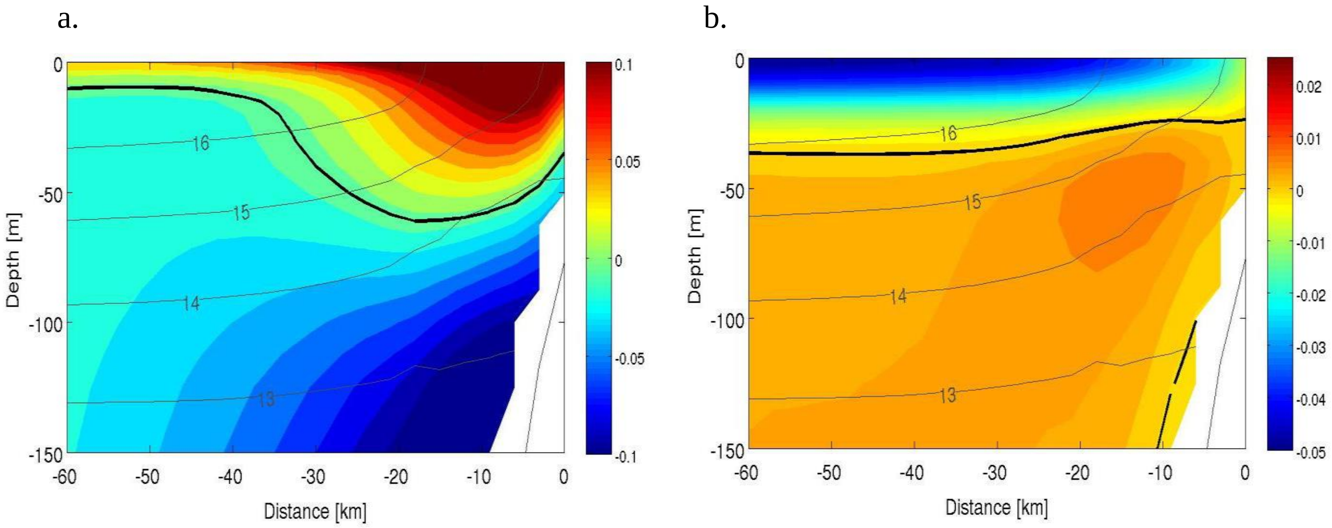


Figure 3.A: Vertical sections of annual mean of (a.) alongshore and (b.) cross-shore velocity components (m/s) averaged between 22°S and 34°S for the 3 km ROMS model. Black contours represent velocity = 0 m/s.

Chapter 4. Influence of biological factors on connectivity patterns for *Concholepas concholepas* (loco) in Chile

4.1. Introduction

In coastal waters, benthic invertebrate populations are spatially distributed in a patchy habitat. Persistence and distribution of such populations is largely influenced by the capacity and scales of exchange of individuals between patches, *i.e.* the connectivity (Hastings and Botsford, 2006). In most marine benthic species, two phases predominate the life cycle: a pelagic larval phase and a benthic adult phase. For these species, connectivity is generated by the success of dispersal of early life individuals between origin (spawning) and destination (nursery, settlement) areas (Cowen and Sponaugle, 2009). Spawning occurs in specific areas where habitat is available and larval production is linked to the fecundity of adults. Larval dispersal depends on physical transport, larval behavior, survival and the availability of suitable habitat (Pineda *et al.*, 2007). The implication of physical transport for connectivity has been largely demonstrated (Siegel *et al.*, 2003; Aiken *et al.*, 2007). Though biological factors have been relatively less well studied due to their inherent complexity and difficulty of field and experimental observations, biophysical individual-based models have highlighted the importance of different factors, such as larval behavior, larval mortality, and larval growth, for dispersal and connectivity (Metaxas and Saunders, 2009). Here we use an individual-based biophysical model to study the cumulative and separate effects of larval diel vertical migration, temperature-dependent larval growth, larval mortality, spatial gradients in adult egg production and spatial heterogeneity in habitat availability on larval transport and settlement of the marine gastropod *Concholepas concholepas* (commonly named loco) in Chile.

Larval behavior has been most frequently included in biophysical models in the form of vertical migration (Peliz *et al.*, 2007; Butler *et al.*, 2011). Larvae of many species are able to respond to physical (salinity, temperature) or biological (food availability) constraints by migrating in the water column. Generally, including a diel vertical migration (DVM) scheme in a larval dispersal model for benthic species increases larval settlement and decreases offshore losses (in Irish Sea, Robins *et al.*, 2013; in Chile, Aiken *et al.*, 2011). In the case of organisms that inhabit coastal upwelling areas, improved settlement success with DVM could be due to larvae being located below the Ekman layer, thereby avoiding offshore transport or even be transported onshore. Nevertheless, the robustness of increased settlement due to DVM has rarely been tested in a comparative framework including other mechanisms affecting larval transport and different hypotheses regarding the nature of DVM (Paris *et al*., 2007; Parada *et al*., 2008).

Another biological factor that influences recruitment is larval survival. Mortality of larvae is supposed to be high during this period, between 1.6 and 35.7% d^{-1} for marine invertebrate larvae (Rumrill, 1990). In a study focusing on several marine invertebrate species between the North Sea and the Baltic Sea, larval mortality rate has been evaluated close to 90% over the larval dispersal phase (Pedersen *et al*., 2008). Including daily mortality rate in biophysical models for benthic species can change larval destination positions (Guizien *et al*., 2006) and induce equivalent larval losses as do hydrodynamic processes (Ellien *et al*., 2004). It is therefore important not to ignore the potential consequences of larval survival for spatial patterns of connectivity.

Finally, larval growth is thought to be one of the main factors affecting the planktonic larval duration (PLD) and ultimately larval survival and recruitment. Temperature is believed to be one of the most influent factors on larval growth (Metaxas and Saunders, 2009). It has been demonstrated to strongly influence larval growth in a wide variety of species (Pechenik and Lima, 1984; O'Connor *et al*., 2007). Therefore, temperature is often used as a proxy for larval growth rates in biophysical models (Incze and Naimie, 2000; Domingues *et al*., 2012; Nolasco *et al*., 2013).

To our knowledge, few comparative studies exist examining the impacts of these diverse factors on connectivity of marine benthic invertebrates. We therefore propose to use a biophysical model integrating these factors to study dispersal of loco in Chile. Loco was a highly valuable benthic fishery until the end of the 80's (Leiva and Castilla, 2002). Then the resource became over-exploited and different management plans were applied to ensure the sustainability of the fishery. The current management plan is the establishment of spatially-explicit management regulations named "Management and Exploitation Areas for Benthic Resources" (MEABR). Previous biophysical modeling studies developed for this species have considered passive larval dispersal, no mortality and a fixed PLD for all individuals (see Chapter 3). For loco, the end of larval dispersal, *i.e.* settlement, occurs when competent larvae metamorphose (DiSalvo, 1988). Therefore, loco larval settlement occurs within a restricted final size range rather than after a constant duration of larval dispersal, as was implemented in Chapter 3. Yet, given the DVM pattern established at early (see Chapter 2) and later (Manríquez and Castilla, 2011) larval stages of loco, the long larval dispersal phase (2–4 months from laboratory and field studies in south-central Chile to 12 months further south in the fjords; DiSalvo, 1988; Moreno *et al*., 1993; Molinet *et al*., 2005), and the wide range of temperatures along the Chilean coast (from 13°C to 20°C for latitudes comprised between 18°S and 32°S, and from 11°C to 13°C for latitudes between 32°S and 56°S; Fernández *et al*., 2000), larval behavior, growth, and mortality are all expected to have significant effects on loco connectivity patterns and may therefore influence loco population dynamics. Finally, a latitudinal gradient in loco adult fecundity has been observed with less fecundity in the northern regions than in the southern regions of Chile (Fernández *et al*., 2007). It has been hypothesized that this gradient in part compensates for temperature- and transport-driven differences in larval mortality (see Chapter 3).

In this study, we propose to investigate numerically the influence on loco connectivity scales and patterns of several biological factors: DVM, a temperature-dependent larval growth model, regional fecundity capacity of loco adults, available habitat for spawning and settlement areas, and larval mortality. We begin this study with a detailed discussion of our modeling approach and the different model configurations that were carried out. From outputs model, we then discuss the influence of each biological factor on loco connectivity and investigate loco subpopulations along the Chilean coast.

4.2. Material and methods

4.2.1. Dispersal model

We refer to the third chapter of this manuscript for details on the ROMS (Regional Oceanic Modeling System) hydrodynamic model 7.5 km resolution configuration used. Modelling loco larval dispersal was performed using the individual-based offline Lagrangian tool Ichthyop v. 3.1 (Lett *et al.*, 2008). Using a forward-Euler advection scheme with velocity fields derived from ROMS, locations of each virtual larva (latitude, longitude and depth) was tracked every hour in three dimensions. Horizontal diffusion was added following Peliz *et al*. (2007). Release areas were designed as sections of 0.25° of latitude all along the Chilean coast from 15.85°S to 38.10°S stretching from the coast to the 500 m isobaths, a compromise between knowledge of loco spawning areas and their representation in the model. In these areas, 100,000 individuals were randomly released each month from January to December during 4 years. For model configurations without growth included, the criterion used for settlement was for larvae to be in settlement areas (chosen as being the same as release areas) anytime in the last 20 days of a fixed PLD. For model configurations with growth included, the criterion was for larvae to be in settlement areas and have the minimal size to settle. Results are represented as connectivity matrices. Values of the connectivity matrix C_{ij} are calculated as the percentage of particles released from area *j* that are transported to area *i*. We also calculated mean dispersal distances of settled larvae in relation to their release area. Dispersal distance is the difference in kilometers between the location of settlement (latitude and longitude) and the location of release for each larva.

4.2.2. Model configurations

Six model configurations were performed referred to as M1–M6 (Table 4.1).

Model configuration M1 was designed to study the effect of larval DVM on loco connectivity patterns. Three DVM amplitudes were chosen to encompass the loco larval vertical distribution: 0–20 m (M1a), 0–40 m (M1b), and 0–60 m (M1c). In M1, individuals were located at the surface at night (from 19:00) and at depth during the day (from 07:00). The DVM behavior implemented was applied every day along the whole PLD (see Chapter 2; Figure 4.1; Manríquez and Castilla, 2011). PLD was set to 80 days (the minimum value of PLD for loco in the area) or 140 days (the maximum value).

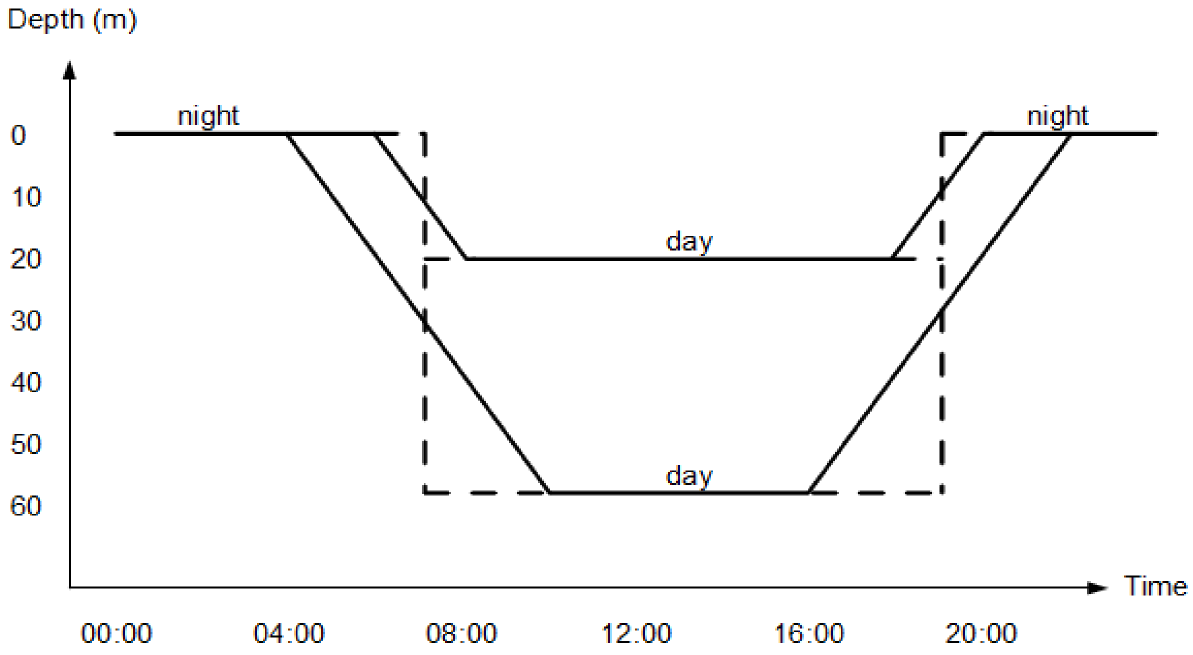


Figure 4.1: Diel vertical migration scheme as implemented in the larval dispersal model between 0-20 m and 0-60 m (dashed lines). These two schemes are caricatures of a putative vertical migration of larvae of 2 hours or 6 hours, respectively, at the constant velocity of 10 $m.s^{-1}$ estimated from Chapter 2 (plain lines).

Model configuration M2 aimed at investigating the effect of larval growth in relation to temperature on the connectivity patterns. To develop a growth model for loco larvae in relation to temperature, we used the relation established by O'Connor *et al.* (2007) from a meta-analysis of the relationship between PLD and temperature:

$$\ln(PLD) = \beta - 1.34 \times \ln(T/15) - 0.28 \times (\ln(T/15))^2 \qquad (1)$$

where T is temperature in °C, β is a species-specific parameter, and PLD is in days.

For loco larvae, under laboratory conditions at T=16°C, PLD has been evaluated around 3 months (DiSalvo, 1988). Therefore, from equation (1), we found $\beta = 4.587$. For the range of temperatures between 10 °C and 22°C experienced by loco larvae in the HCS (Fernández *et al*., 2000; Thiel *et al*., 2007), equation (1) gives PLD ranging from 161,5 days to 56,4 days (Figure 4.2).

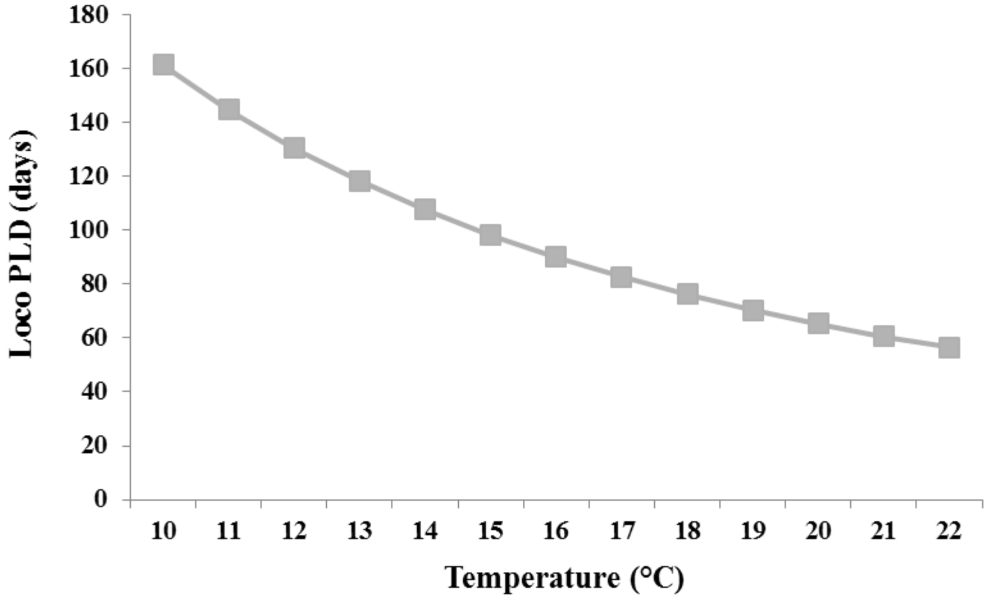


Figure 4.2: Relation between loco planktonic larval duration (PLD) and temperature adapted from O'Connor *et al*.'s (2007) meta-analysis.

To transform these PLD values into growth rates (GR in $\mu m.day^{-1}$), we assumed a linear growth from size at hatching (250 µm; DiSalvo, 1988) to size at settlement (1900 µm; DiSalvo, 1988; Manríquez *et al*., 2004):

$$GR(T) = (1900-250)/PLD(T) \quad (2)$$

In the loco larval dispersal model, for every time step $\Delta t=1/24$ day, we calculated GR(T) based on temperature at the virtual larva location obtained from the hydrodynamic model, and then updated the larva length (L in µm) using:

$$L_{t+\Delta t} = L_t + GR(T)*\Delta t \quad (3)$$

In M2, individuals were released between 0 and 20 m depth and were tracked for 140 days (the maximum value of PLD for loco in the area).

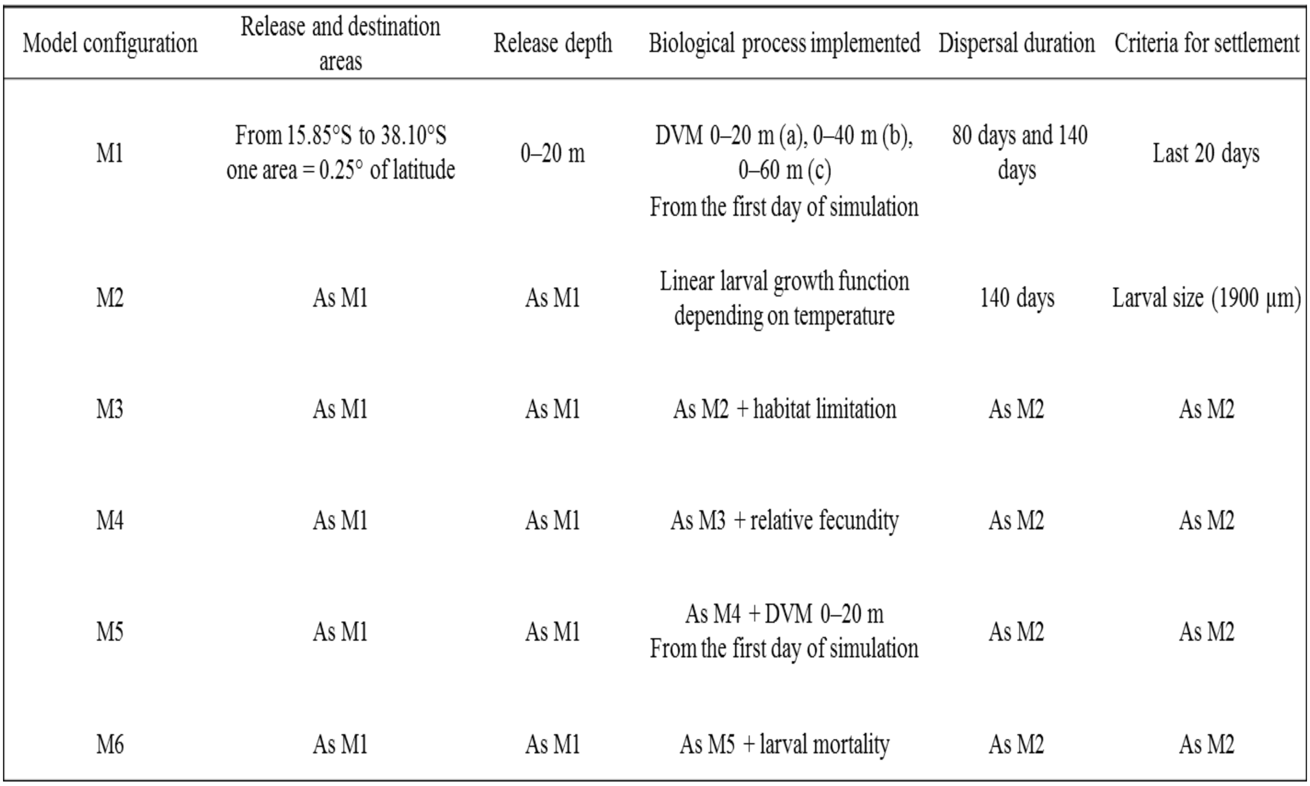
With the connectivity matrix resulting from M2, we assessed the additional potential effects on connectivity of spatial heterogeneity along the Chilean coast of loco habitat limitation (M3) and relative fecundity (M4). For loco habitat, we evaluated the proportion of rocky shore within each latitudinal band of 0.25° as explained in Chapter 3. We then multiplied the connectivity values of each column and each row by the corresponding proportion of available habitat to adjust for limited habitat area for larval production and larval settlement, respectively. The effect of loco fecundity was estimated using Fernández *et al*. (2007) study on loco embryos packing in egg capsules. They observed fewer loco embryos per unit area of capsule in northern regions than in southern regions of Chile with a break in the number of embryos observed around 29−30°S. Moreover, there was no difference in the number of loco embryos per unit area of capsule among the sampling sites north of this break, nor among the southern sampling sites. From their results, we calculated the mean number of embryos per unit area of capsule in the northern and southern regions of the break and assessed the ration between the two values. Ratio of the mean number of loco embryos per unit area of capsule was 1.68 between the northern and southern regions. From 29.35°S to the southern limit of our study domain, we multiplied the values of each column (representing release areas in the connectivity matrix) by this ratio to adjust our connectivity values for loco relative fecundity.

We then added the effect on connectivity of DVM (M5) by including a larval DVM scheme between 0 and 20 m into the larval dispersal model as described for M1. We chose this DVM range due to similar qualitative patterns observed between model configurations using DVM.

Finally, to assess the effect of larval mortality on loco larvae connectivity (M6), we used a mortality rate of 0.12 d^{-1} estimated for veliger larvae of *Mytilus edulis* by Rumrill (1990), in the absence of corresponding estimates for loco larvae. The connectivity matrix with mortality was constructed by first weighting each larvae by $(1-0.12)^{age}$ where age is the age at settlement in days, and then calculating the connectivity matrix as the weighted sum over larvae as a function of release and settlement locations divided by the number of larvae released from the site of origin.

Results obtained from all model configurations are compared to those obtained in Chapter 3 with spawning depth 0–20 m and PLD = 140 days. This model configuration is called M0.

Table 4.1: Summary of processes and parameters used in the different model configurations performed. DVM = diel vertical migration.



Model configuration	Release and destination areas	Release depth	Biological process implemented	Dispersal duration	Criteria for settlement
M1	From 15.85°S to 38.10°S one area = 0.25° of latitude	0–20 m	DVM 0–20 m (a), 0–40 m (b), 0–60 m (c) From the first day of simulation	80 days and 140 days	Last 20 days
M2	As M1	As M1	Linear larval growth function depending on temperature	140 days	Larval size (1900 µm)
M3	As M1	As M1	As M2 + habitat limitation	As M2	As M2
M4	As M1	As M1	As M3 + relative fecundity	As M2	As M2
M5	As M1	As M1	As M4 + DVM 0–20 m From the first day of simulation	As M2	As M2
M6	As M1	As M1	As M5 + larval mortality	As M2	As M2

4.2.3. Identification of subpopulations

Like in Chapter 3, we used the methodology of subpopulations identification developed by Jacobi *et al*. (2012) to identify independent subpopulations from the obtained connectivity matrices. The method used allows calculation of a set of contiguous subpopulations that minimize connectivity between subpopulations for a given desired level of aggregation. Subpopulations were identified for connectivity matrices obtained for each model configuration (M1 to M6). In Jacobi *et al*.'s (2012) method, the connectivity between an area *i* and an area *j* is calculated as the average connectivity between these areas $\frac{c_{ij}+c_{ji}}{2}$. In a limited number of cases the algorithm identified a single, isolated area as a subpopulation; in this situation, we regrouped the area with the closest subpopulation.

4.2.4. Statistics

In M1 and M2, we performed a sensitivity analysis to test the effect of release area and release month on the simulated values of recruited larvae using a multifactor analysis of variance (ANOVA). For M1, the effect of the PLD on the proportion of recruited larvae was analyzed using Generalized Linear Models (GLM) fitted with binomial distribution. In all cases, p values < 0.05 were taken to indicate significant results.

4.3. Results

4.3.1. Mean alongshore velocity currents

Near-surface mean alongshore velocity currents derived from the hydrodynamic model used in this study are represented in Figure 4.3 between 16°S and 38°S. Mean positive values indicate that near-surface currents are mostly oriented northwards along the domain. Current velocities are higher at the southern and northern limits of the domain. Minimum values of velocity are observed between 25°S and 29°S. Around this minimum, two peaks of higher velocities are particularly visible at 24°S and between 29.5°S and 30−31°S.

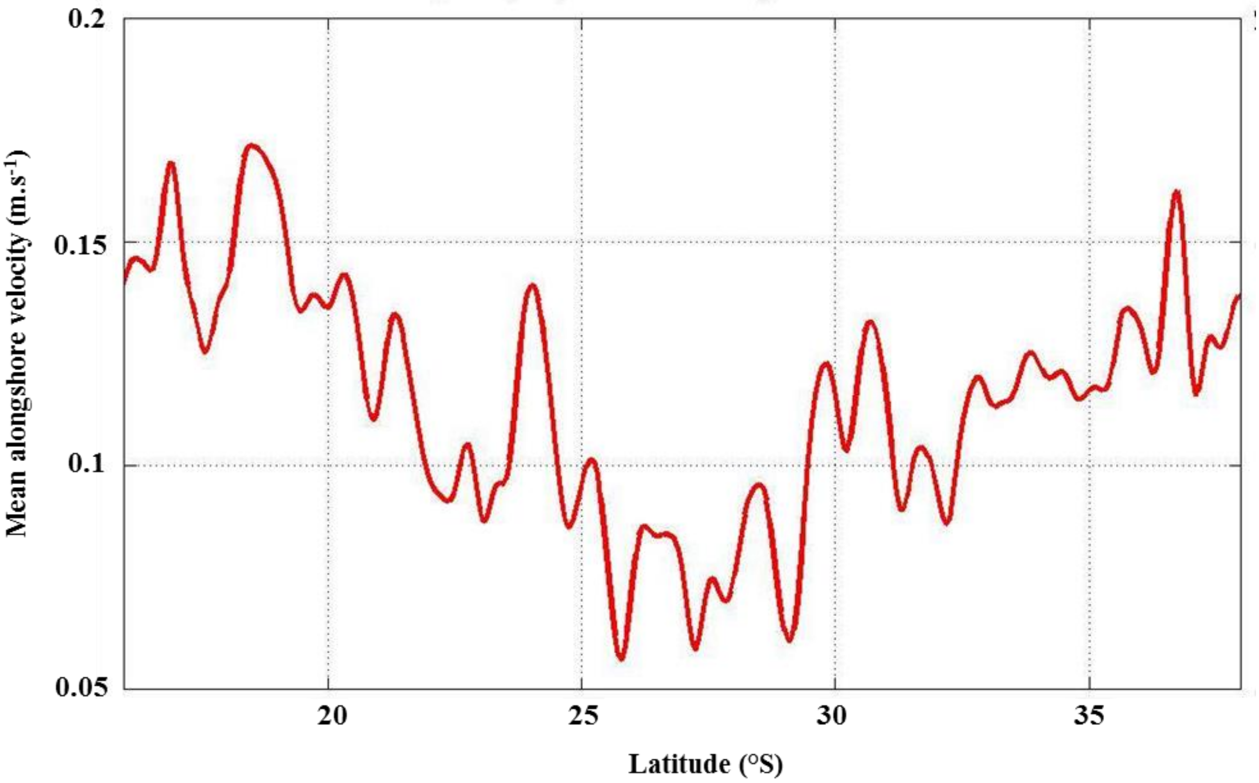


Figure 4.3: Mean annual velocities of near-surface (0−5 m depth) alongshore currents between 16°S and 38°S derived from hydrodynamic model (averaged over 30 km from the coast).

4.3.2. Effect of larval DVM on loco connectivity

Results of mean dispersal distances of settled larvae in relation to their release area are showed for M0 (*i.e.* from Chapter 3 with spawning depth 0−20 m) and M1a (*i.e.* including DVM depth range between 0 and 20 m) after 140 days of PLD (Figure 4.4). Mean dispersal distances along the study domain are 220 km and 262 km for M0 and M1a, respectively. However, dispersal distances for M0 are higher than for M1a in the northern limit of the domain. For M1a, mean dispersal distances traveled by larvae are highest for release zones between 23°S and 25°S and between 29°S and 31°S (Figure 4.4). Maximum mean dispersal distance is observed for larvae released at 30°S with 398 km. Minimum is for larvae released at 18°S with 176 km traveled. Similar patterns of dispersal are observed for M1b (DVM = 0−40 m), and M1c (DVM = 0−60 m) (Table 4.4).

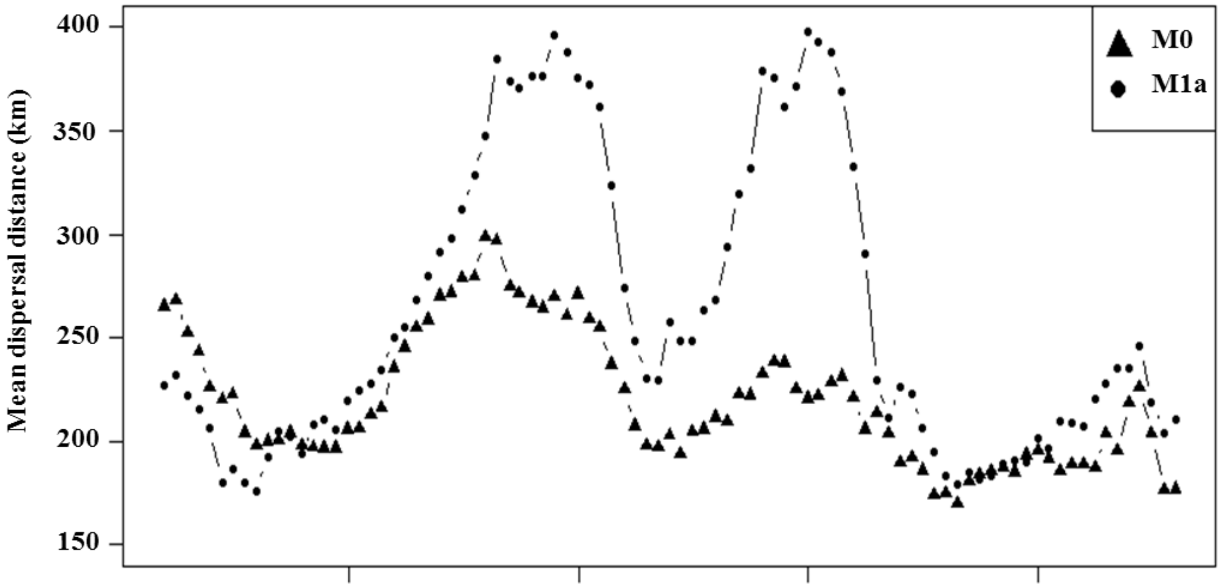


Figure 4.4: Model configurations M0 (from Chapter 3 with spawning depth 0−20 m) and M1a (diel vertical migration = 0−20 m): Mean dispersal distances traveled by settled loco larvae in relation to their release area for planktonic larval duration = 140 days.

In model configurations M1a, M1b, and M1c, release month is the factor explaining most variance in the proportion of settled larvae for both PLD values (Table 4.2). Percentage of variance explained by release month generally increases with the increase of DVM range. Figure 4.5 shows the seasonality in connectivity for M1a (DVM range 0−20 m) after 80 days (a.) and 140 days of PLD (b.). Favorable release areas for loco larvae settlement are located between 17°S and 27°S and between 32°S and 38°S for both PLD values. Similar patterns are observed for M1b and M1c with increased transport success values obtained with increased DVM range (results not shown). Favorable release period for loco settlement is between March and July (austral autumn and winter) for PLD = 80 days and between January and June (austral summer and autumn) for PLD = 140 days.

Table 4.2: Model configurations M1a (diel vertical migration DVM = 0−20 m), M1b (DVM = 0−40 m), and M1c (DVM = 0−60 m): sensitivity analysis (ANOVA) on proportion of recruited larvae with release area and release month factors. Analysis is performed for planktonic larval durations (PLD) 80 days and 140 days.

Factor	Freedom Degree	Model configuration	Percentage variance explained	p value	Model configuration	Percentage variance explained	p value
Release area	88	M1a PLD 80 days	21.47	$< 2.2 \times 10^{-16}$	M1 a PLD 140 days	24.91	$< 2.2 \times 10^{-16}$
Release month	11		36.46	$< 2.2 \times 10^{-16}$		30.01	$< 2.2 \times 10^{-16}$
Release area * release month	968		20.76	$< 2.2 \times 10^{-16}$		17.47	$< 2.2 \times 10^{-16}$
Residuals	3204		21.29			27.6	
Release area	88	M1b PLD 80 days	20.57	$< 2.2 \times 10^{-16}$	M1b PLD 140 days	19.11	$< 2.2 \times 10^{-16}$
Release month	11		35.8	$< 2.2 \times 10^{-16}$		38.22	$< 2.2 \times 10^{-16}$
Release area * release month	968		19.89	$< 2.2 \times 10^{-16}$		16.42	$< 2.2 \times 10^{-16}$
Residuals	3204		23.71			26.22	
Release area	88	M1c PLD 80 days	16.45	$< 2.2 \times 10^{-16}$	M1c PLD 140 days	15.66	$< 2.2 \times 10^{-16}$
Release month	11		42.83	$< 2.2 \times 10^{-16}$		46	$< 2.2 \times 10^{-16}$
Release area * release month	968		17.75	$< 2.2 \times 10^{-16}$		14.59	$< 2.2 \times 10^{-16}$
Residuals	3204		22.96			23.74	

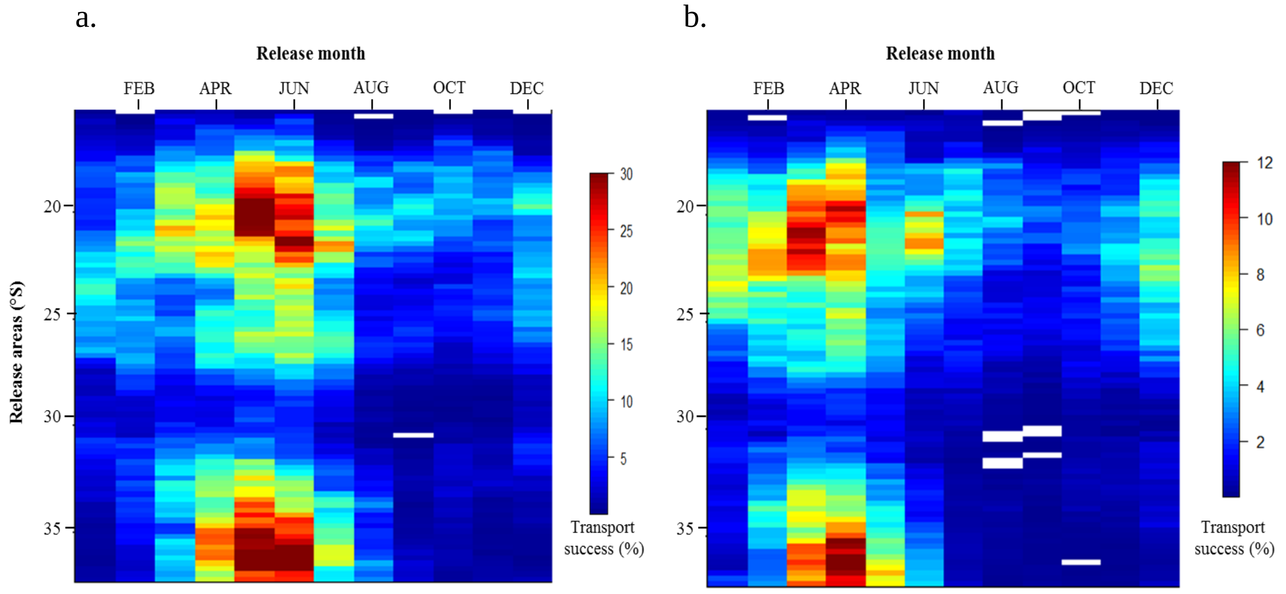


Figure 4.5: Transport success of loco larvae in relation to area and month of release for M1a (diel vertical migration = 0−20 m) after 80 days of planktonic larval duration (a.) and 140 days (b.).

Connectivity matrices obtained for M1 are shown for both values of PLD (80 days and 140 days; Figure 4.6). Compared to the connectivity matrix obtained in Chapter 3 with spawning depth 0−20 m and PLD = 140 days (Figure 4.9 a.), DVM scheme included in the dispersal model lead to a decrease of the connectivity values, especially from 23°S to the southern limit of the domain (M1a; Figure 4.6 b.). Three hotspots of released larvae that successfully settled are observed at 16–22°S, 24–27°S, and 32–38°S, and values of connectivity increase with the increase of DVM range (M1b, Figure 4.6 c., d. for DVM = 0−40 m; M1c, Figure 4.6 e., f. for DVM = 0−60 m). Globally, similar qualitative patterns are observed between model configurations using DVM scheme. For all DVM schemes, all along the study domain, connectivity values are lowest in the southern part of the domain and higher values of connectivity are above the diagonal, indicating that virtual larvae are mainly transported to the North. Finally, particularly for PLD values = 140 days, a gap in the connectivity matrix is clearly visible between 28 and 31°S with near-zero values (Figure 4.6 b., d., f.). For all DVM schemes, smaller values of connectivity are obtained for PLD = 140 days than for PLD = 80 days (GLM: $z = -94.57$, $p < 2.2 \times 10^{-16}$, $n = 8544$; mean 2.63% *vs*. 7.44% for M1a; GLM: $z = -108.3$, $p < 2.2 \times 10^{-16}$, $n = 8544$; mean 4.09% *vs*. 10.14% for M1b; GLM: $z = -105.9$, $p < 2.2 \times 10^{-16}$, $n = 8544$; mean 4.81% *vs*. 10.95% for M1c).

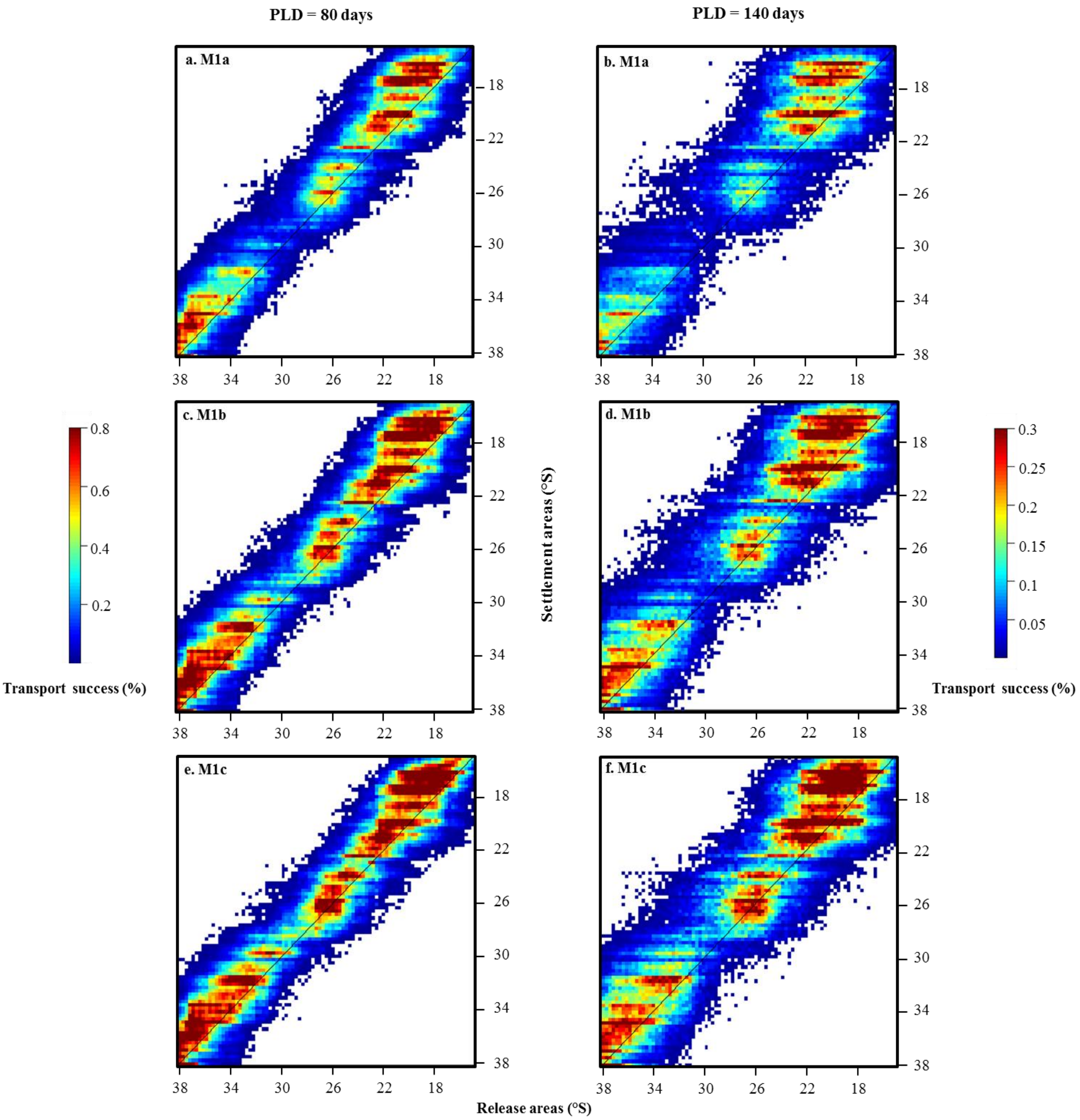


Figure 4.6: Connectivity matrices obtained for M1a (diel vertical migration DVM = 0–20 m) and PLD (planktonic larval duration) = 80 days (a.), 140 days (b.); for M1b (DVM = 0–40 m) and PLD = 80 days (c.), 140 days (d.); for M1c (DVM = 0–60 m) and PLD = 80 days (e.), 140 days (f.). Note that color bars are different for PLD = 80 days (maximum value of transport success set to 0.8%) and PLD = 140 days (maximum 0.3%).

4.3.3. Effect of larval growth, available habitat, relative fecundity, DVM, and larval mortality on loco connectivity

Distribution of the length of virtual loco larvae at settlement after 140 days of PLD is shown in Figure 4.7 for M2 (model configuration including growth process only). Most larvae settled at 1.9 mm, the minimum length set for settlement criterion. The mean length at settlement is 2.31 mm ± 0.47 mm. Maximum length at settlement for loco larvae is 4.8 mm.

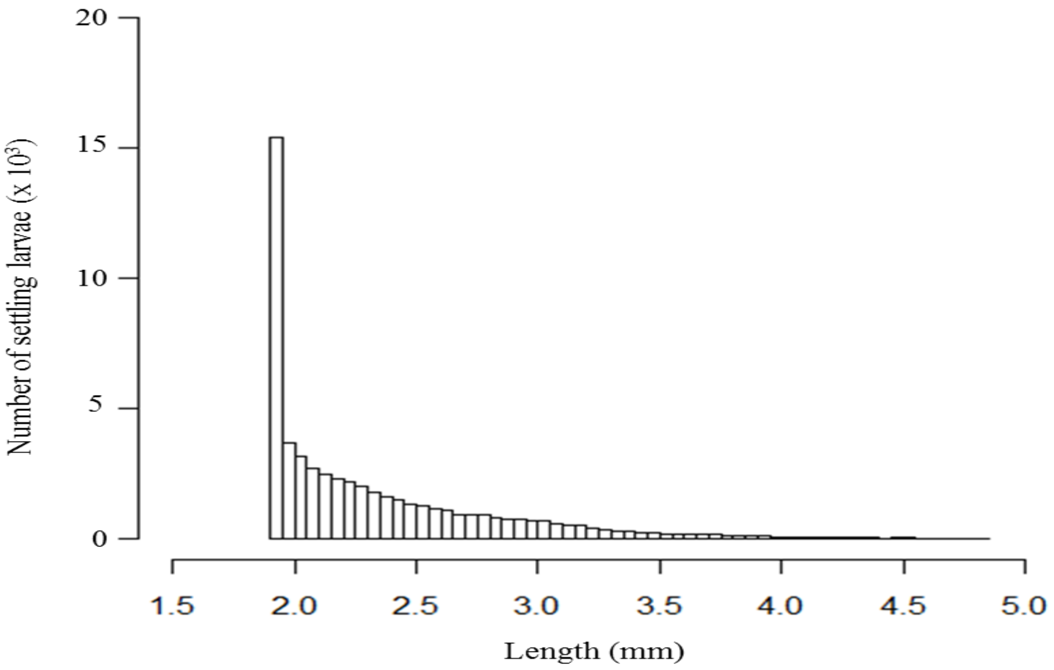


Figure 4.7: Distribution of length at settlement for loco larvae after 140 days of planktonic larval duration for model configuration M2 (with growth model only).

Contrarily to M1 (Table 4.2), in M2, the factor explaining most variance in the proportion of settled larvae is release area (Table 4.3). Mean dispersal distances are represented in Figure 4.8. Since similar patterns were observed between M2, M3, and M4 (Table 4.4); results for M4, M5, and M6 were only represented. The mean dispersal distance for M4 shows little variability around 200 km for all release zones (Figure 4.8). Adding DVM scheme in the model configuration (M5) notably increases dispersal distances (Table 4.4) mainly between 22°S and 32°S and at 36−37°S. Larvae were transported 100 km to 150 km further than in M4 when they were released in this region. Dispersal distances decrease at the northern limit. Maximum dispersal distances are observed for settled larvae released around 30°S. Particularly, around this zone, when larval mortality is included in the model (M6), distances decrease.

Table 4.3: Model configuration M2 (with growth model only): sensitivity analysis (ANOVA) on proportion of recruited larvae with release area and release month factors.

Factor	Freedom Degree	Percentage variance explained M2	p value M2
Release area	88	48.88	$< 2.2 \times 10^{-16}$
Release month	11	20.44	$< 2.2 \times 10^{-16}$
Release area * release month	968	8.05	6.5×10^{-4}
Residuals	3204	22.6	

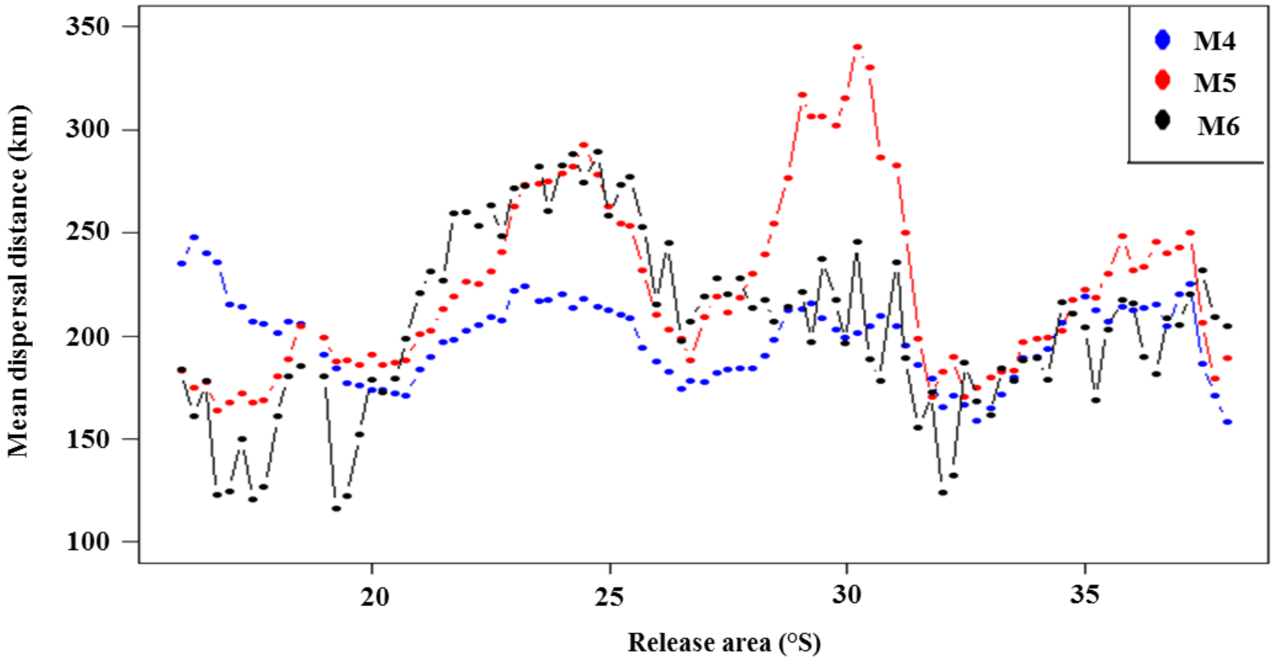


Figure 4.8: Model configurations M4, M5, and M6 (see Table 4.1 for model configurations details): Mean dispersal distances of settled larvae in relation to their release areas.

Compared to the connectivity matrix obtained in Chapter 3 with spawning depth 0−20 m and PLD = 140 days (M0; Figure 4.9 a.), adding growth in the dispersal model and a settlement criterion based on minimal length (model configuration M2; Figure 4.9 b.) lead to an increase of the mean settlement success (Table 4.4). However, in M2 compared to M0, a decrease of the loco larval transport success is observed in the southern part of the domain, particularly from 29°S to 38°S (Figure 4.9 a., b.). From connectivity matrix obtained for M2, we successively included available habitat (M3), relative loco fecundity (M4), DVM (M5), and larval mortality (M6). When limited available habitat for loco is considered (M3), there is a decrease in connectivity values in the northern (to 19°S) and southern (from 33°S) areas of the study area (Figure 4.9 c.). Between 18°S and 22°S, connectivity values on the columns of the connectivity matrix are high, *i.e.* there is a strong larval transport success from this zone. Moreover, between 17°S and 23°S, connectivity values on the rows of the connectivity matrix are high, *i.e.* there is a strong larval transport success to this zone. Including fecundity ratio notably increases connectivity values in the southern areas (M4; from 32°S to 38°S, Figure 4.9 d.). When DVM behavior is integrated (M5; Figure 4.9 e.), connectivity values in the southern part of the study domain (from 28°S) decreased again compared to previous connectivity matrices. The northward transport is marked all along the study domain and very low connectivity values are obtained for larvae released around 29−30°S. High connectivity values are still observed between 17°S and 23°S. Finally, when larval mortality is included (M6; Figure 4.9 f.), connectivity values of loco larvae dramatically decreased and were around 120,000 times smaller than values obtained without mortality. Qualitatively, there was a gradual decrease in connectivity from 23°S to the southern limit of the domain. From 29°S to the South, settlement of larvae is nearly null.

For all model configurations, higher values of connectivity were observed in the northern part of the domain, between 17°S and 22°S (Figure 4.9 b., c., d., e., f.). Spots of higher connectivity are also obtained between 23°S and 27°S and at (or south of) 33°S, except when larval mortality is included in the model (M6).

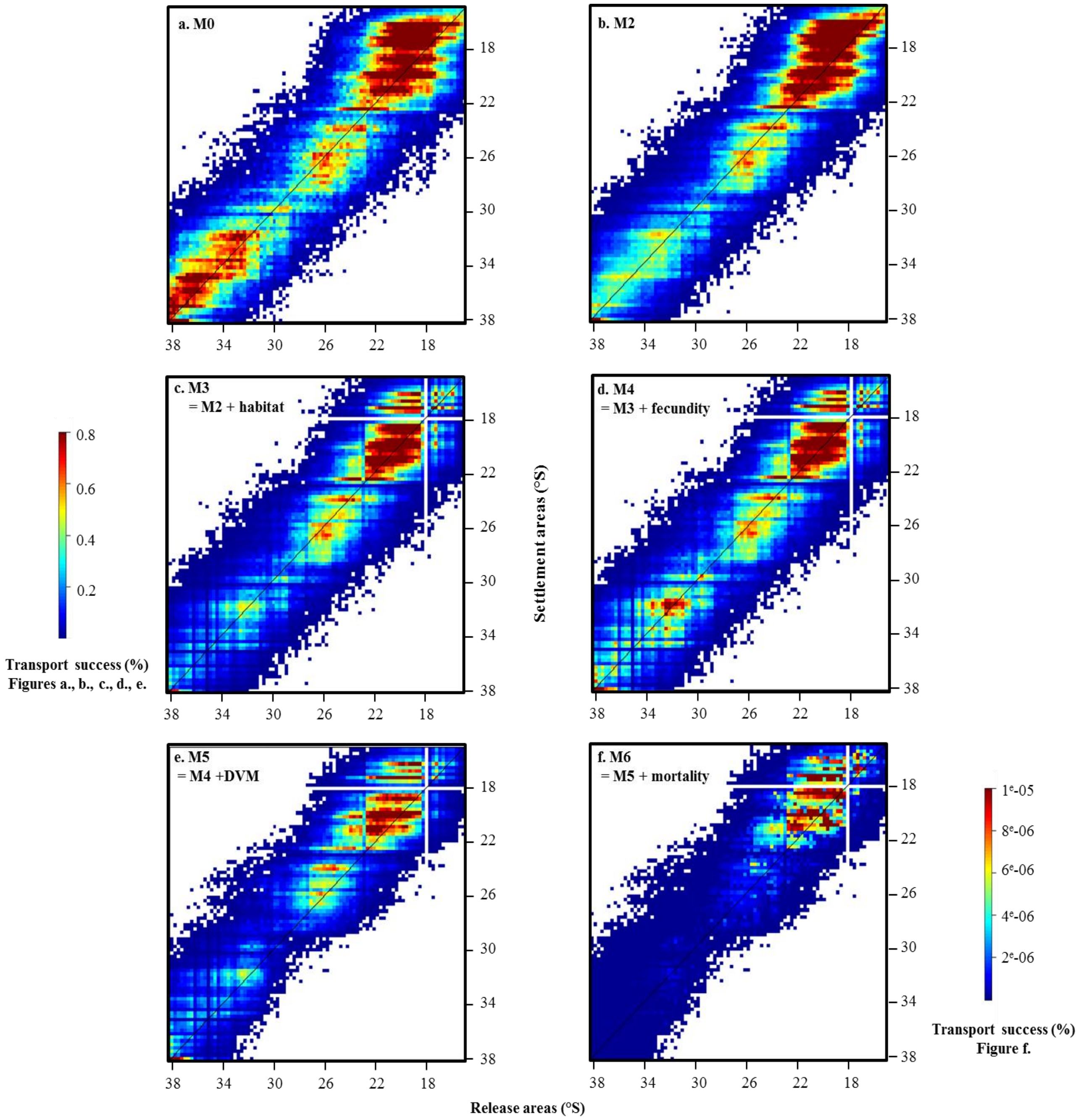
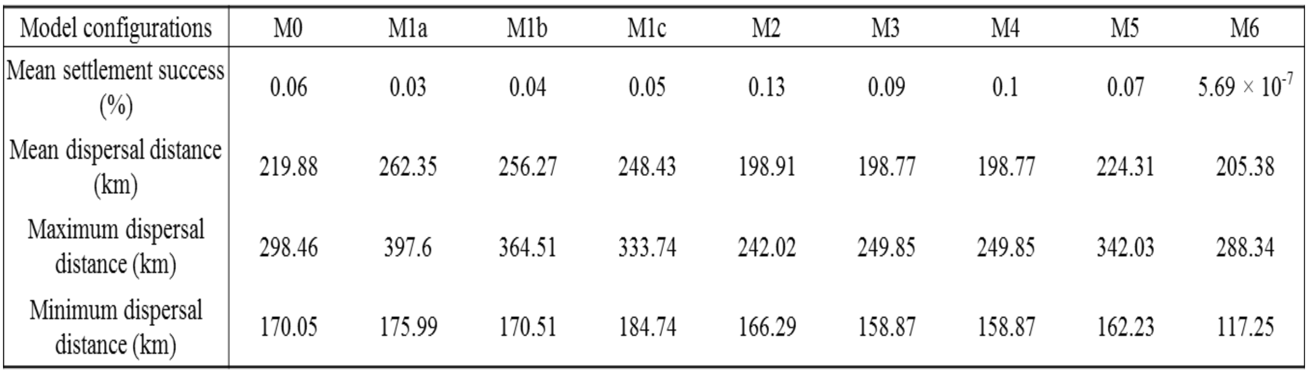


Figure 4.9: Connectivity matrices obtained for model configurations M2 (with growth model only, b.), M3 (c.), M4 (d.), M5 (e.), and M6 (f.). Figure a. is reproduced from Chapter 3 with spawning depth 0−20 m and planktonic larval duration = 140 days (model configuration M0). Note that the colour bar is different for panel f.

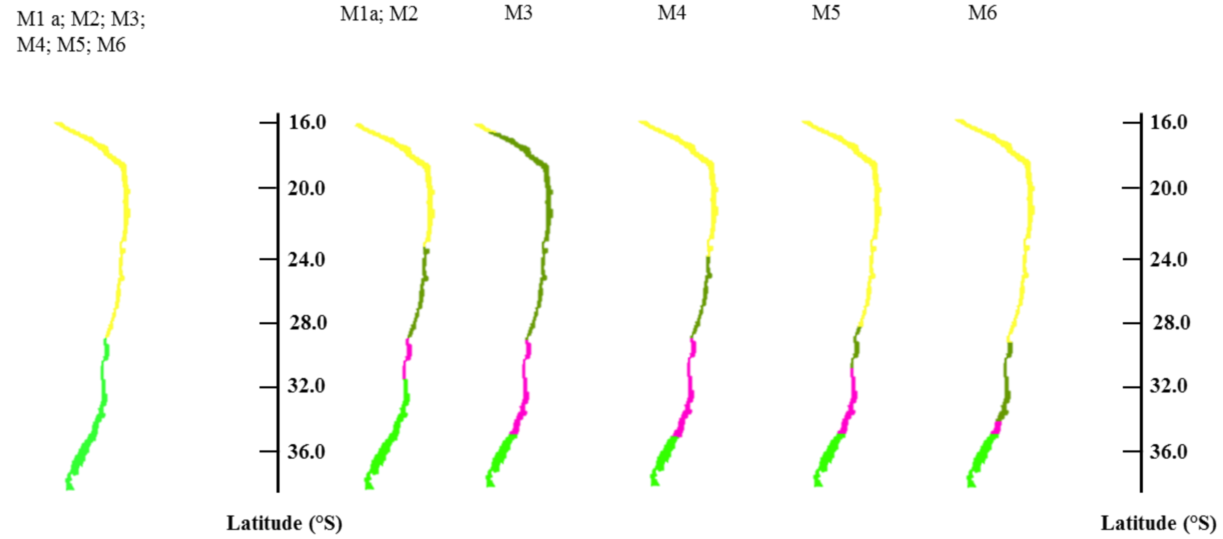
Table 4.4: Summary of results obtained for all model configurations: M0, M1a, M1b, M1c, M2, M3, M4, M5, and M6 (see Table 4.1 for model configurations details).



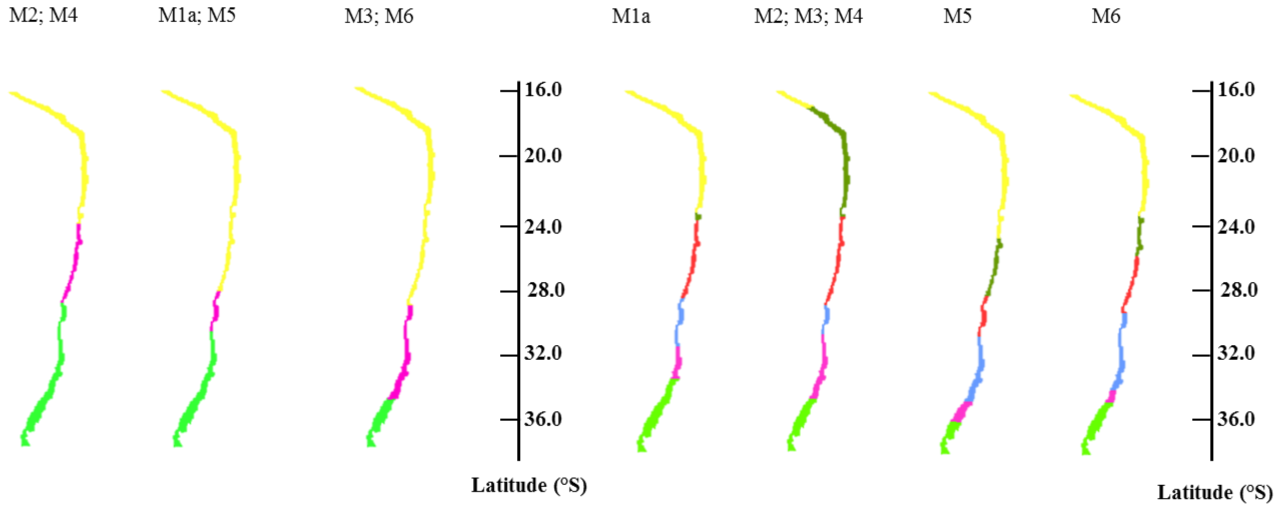
Model configurations	M0	M1a	M1b	M1c	M2	M3	M4	M5	M6
Mean settlement success (%)	0.06	0.03	0.04	0.05	0.13	0.09	0.1	0.07	5.69×10^{-7}
Mean dispersal distance (km)	219.88	262.35	256.27	248.43	198.91	198.77	198.77	224.31	205.38
Maximum dispersal distance (km)	298.46	397.6	364.51	333.74	242.02	249.85	249.85	342.03	288.34
Minimum dispersal distance (km)	170.05	175.99	170.51	184.74	166.29	158.87	158.87	162.23	117.25

4.3.4. Loco subpopulations

From connectivity results obtained for each model configuration, we obtained partitioning into 2 to 6 loco subpopulations along the Chilean coast (Figure 4.10). The first separation is obtained above or below the region around 29−30°S for all model configurations. A separation is observed at ~17°S for M2, M3, and M4, *i.e.* when DVM and mortality are not considered. A recurrent separation appears around 24°S (except for M5). From 31°S to the southern limit, a separation is also observed around 35°S (except for M1a). When DVM is included, the southern part of the domain (from 30°S) is divided into 3 subpopulations instead of 2 when it is not.



2 subpopulations **4 subpopulations**



3 subpopulations **6 subpopulations**

Figure 4.10: Partitioning of the loco population into subpopulations successively identified by the method of Jacobi *et al*. (2012) from the connectivity matrices obtained with model configurations M1a, M2, M3, M4, M5, and M6 (see Table 4.1 for model configurations details). Note that clustering obtained with M1a with PLD (planktonic larval duration) = 80 days and PLD = 140 days are similar.

4.4. Discussion

The main objective of our study was to assess the influence of several biological characteristics important for larval transport and settlement on simulated connectivity patterns for loco in Chile. Our results show consistent relative spatial patterns of connectivity for all model configurations, with relatively well-defined areas of high connectivity and an overall decrease in settlement rates from North to South. Nevertheless, absolute connectivity levels change significantly between model configurations and the contrast between North and South is accentuated (in all cases, particularly when larval mortality is added). Dispersal distances and connectivity patterns vary depending on the biological factors considered in our larval dispersal model, with a rigid surface/at-depth DVM scheme leading to decreased settlement success and increased dispersal distances (Table 4.4). Recurrent loco subpopulations separations around 17°S, 24°S, 29−30°S, and 35°S suggests that these areas represent real dispersal barriers for loco (Figure 4.10).

Mean dispersal distances traveled by simulated loco larvae range between 100 km and 360 km, depending on release area and biological processes implemented in the model (Table 4.4). Globally, a net northward transport was observed along the study domain, as expected from net equatorward surface currents along most of the Chilean coast (Figure 4.3; Thiel *et al*., 2007). The step-by-step inclusion of each biological process illustrates the different effects of each on dispersal distances. Between model configurations M2, M3 and M4, spatial patterns of mean dispersal distances did not significantly vary due to the successive inclusion of habitat limitation and fecundity (Table 4.4). Among all the model configurations examined in this study, DVM and larval mortality were the biological processes that most heavily influenced simulated dispersal distances of loco larvae (Figures 4.4; 4.8). In both simulations M1 and M5, adding a DVM increased the mean dispersal distances and net northward transport compared to a similar model configuration without a DVM (Figures 4.6; 4.9). In our larval dispersal model, DVM process forces larvae to stay at surface during the night. Near-surface alongshore current velocities (Figure 4.3) showed a particular region between 23°S and 32°S with successive high and low values of mean current velocities, consistent with differences in dispersal distances observed in this region (Figures 4.4, 4.8). Large near-surface current velocities correspond to areas with large dispersal distances when DVM is implemented in the model. The inclusion of larval mortality counterbalances this effect in the southern portion of the study domain (around 30°S) where dispersal distances are noticeably lower than those without larval mortality (Figure 4.8). This is presumably because larval dispersing long distances have considerably longer dispersal times in the relatively cold waters of southern Chile, leading to higher mortality rates for these long distance dispersers.

Loco connectivity patterns vary spatially from North to South and are dependent on biological factors implemented in the model. Higher connectivity values are generally obtained for the northern part of the study domain than for the southern part (Figure 4.9). Differences between North and South intensified with the inclusion of larval growth (M2; Figure 4.9 b.), diel vertical migration (M5; Figure 4.9 e.) and mortality (M6; Figure 4.9 f.). For all model configurations, larvae released between 18°S and 22°S have high settlement rates to areas between 17°S and 23°S (Figure 4.9). This region of high connectivity values along the Chilean coast is therefore likely to be favorable to the maintenance of loco populations. Indeed, high densities of loco adults and loco catches have been described in this region, mainly between 20 and 22°S (IFOP INFORME, 2010−2011). A secondary hotspot of connectivity is obtained between 23°S and 27°S. There are few loco fishermen in this zone and loco catches are low (IFOP INFORME, 2010−2011). Finally, higher connectivity is also observed at (or south of) 33°S, except when mortality is included in the model. These results are also consistent with high values of loco density observed in this area (IFOP INFORME, 2010−2011).

Temperature variability along the Chilean coast (Fernández *et al.*, 2000) has predictable impacts on connectivity contrasts between North and South. Larvae in warmer northern waters have faster growth, and hence shorter dispersal times to settlement, leading to lower mortality rates compared to those of larvae experiencing colder, southern waters. The inclusion in the model of habitat availability (M3) decreases connectivity south of 33°S due to low levels of available habitat for loco in this zone (Figure 4.9 c.). By contrast, including relative fecundity (M4) leads to a slight relative increase in connectivity south of 32°S (Figure 4.9 d.) due to higher reproductive outputs in this region (Fernández *et al*., 2007). Globally, our results do not support the hypothesis that fecundity compensates temperature effects.

Adding DVM to the model produces two unexpected results: (1) settlement rates are globally reduced (Table 4.4), and (2) reductions in settlement rates are more significant in the South of the study domain than in the North (Figures 4.6, 4.9 e.). In general, the model with DVM has lower loco larval settlement rates than does the model without DVM. Increasing the DVM vertical range does improve settlement rates, but values do not exceed those for the model without DVM for the set of DVM vertical ranges assessed in this study (Figure 4.6; Table 4.4). These results contrast with several other studies that found increased recruitment with DVM (Armsworth, 2001; Cowen *et al*., 2006; Paris *et al*., 2007). Nevertheless, our results are consistent with a modeling study from the upwelling region of California that also found that DVM behavior decreased recruitment (Carr *et al*., 2008). Carr *et al*. (2008) concluded that this was because increased nighttime dispersal due to exposure to the fast moving Ekman layer is not compensated by decreased transport velocities during the day while at depth. Similarly, the rigid DVM scheme used in our model forced all larvae into the upper part of the water column half the time, in contrast to model configurations without DVM for which larvae spawned at depth do not necessarily come to the surface during transport. This evidently results in considerably lower recruitment rates and higher dispersal distances with DVM. However, it is important to note that the daily ocean circulation model outputs used in our study to estimate dispersal do not resolve the effects of the diurnal sea breeze that may be important for onshore transport in the region (Kaplan *et al*., 2003).

Enhanced differences in connectivity between North and South with DVM included in our larval transport model may be explained by the greater intensity of offshore surface currents in southern Chile. In the hydrodynamic model, offshore currents are dominant in surface waters, particularly in the southern part of Chile, where positive offshore transport is stronger and over a wider range of depths than in the North (see appendix, Figure 4.A). Furthermore, from 29°S, eddy kinetic energy is stronger, linked to favorable upwelling wind stress (Correa-Ramirez *et al.*, 2007). Around 30°S (Coquimbo bay), connectivity values are very low, particularly when DVM is implemented (Figures 4.6, 4.9 e.). This zone has been described as an area of intense upwelling (Colas *et al.*, 2012). However, this region has also been described as an intensive recruitment zone for loco (IFOP, INFORME 2002). In our hydrodynamic model, wind stress forcing is from satellite data and, close to the coast, wind data are extrapolated and higher than expected (see appendix, Figure 4.B). Consequently, mixed layer depth is deeper than 20 m, as observed in Figure 4.B. With a DVM scheme between 0 and 20 m, larvae are likely to stay in the mixed layer *i.e.* they are mostly transported offshore. With a deeper DVM scheme as tested in model configurations M1b and M1c, our results showed higher connectivity values around this zone meaning that shallower DVM behavior is not advantageous in this zone using our model.

Seasonality in connectivity indicates that the most favorable larval release period for settlement of loco is austral autumn and winter for a 80 days PLD and austral summer and spring for a 140 days PLD (Figure 4.5 for DVM model configuration). In all cases, settlement mainly occurs in austral winter and spring in our larval dispersal model (Results not shown), as also found in Chapter 3 for the base larval dispersal model without DVM, growth and other larval behavior processes. During this period, upwelling is weak, which is favorable for larval retention along the coast (Thiel *et al.*, 2007). The consistency of results across model configurations indicates that seasonality in connectivity for loco is mainly affected by hydrodynamic factors, not larval behavior.

The identification of loco subpopulations from the connectivity matrix highlighted several robust patterns in the partitioning along the coast (Figure 4.10), which are also consistent with those obtained in Chapter 3. In all simulations, a common major separation between subpopulations was obtained around 29−30°S. This zone has already been described as a biogeographical barrier for invertebrate recruitment (Navarrete *et al.*, 2002). A second robust separation was observed at

~24°S. This location near Antofagasta consists of a significant cape that likely impacts offshore transport and larval dispersal. Other separations occurred in some model configurations, but not all, at around ~17°S and ~35°S. Globally, robust separations observed in all cases are explained by geomorphological features along the Chilean coast. Biological processes, such as DVM and mortality, split the southern part of the domain in more subpopulations due to low connectivity values in this region, but did not affect major separations linked to geomorphological features.

Globally, biological factors successively included in our larval dispersal model to describe loco connectivity allow representing general patterns of loco distribution along the Chilean coast. Loco connectivity is significantly more important in the northern part than in the southern part of Chile due to the combination of currents direction, seawater temperatures influencing growth and mortality processes, and high levels of available habitat. Moreover, inclusion of both larval DVM and mortality mitigates the positive effect of loco fecundity observed in the South. The general tendency of contrasting connectivity between northern and southern parts of Chile and the description of different subpopulations suggest that management should be appropriately adapted for each of these zones. Using a higher-resolution hydrodynamic model would be an important improvement that may help understand why the central part of Chile, around 30°S, has low connectivity in our model, but is associated with significant local catches. Another limit of our model is the use of larval mortality dependent on seawater temperature only. Larval mortality is also believed to be highly dependent on food availability, which may be included in our model by coupling it with estimates of primary and secondary productivity and implementing a bioenergetic model of larval growth and mortality.

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Appendix

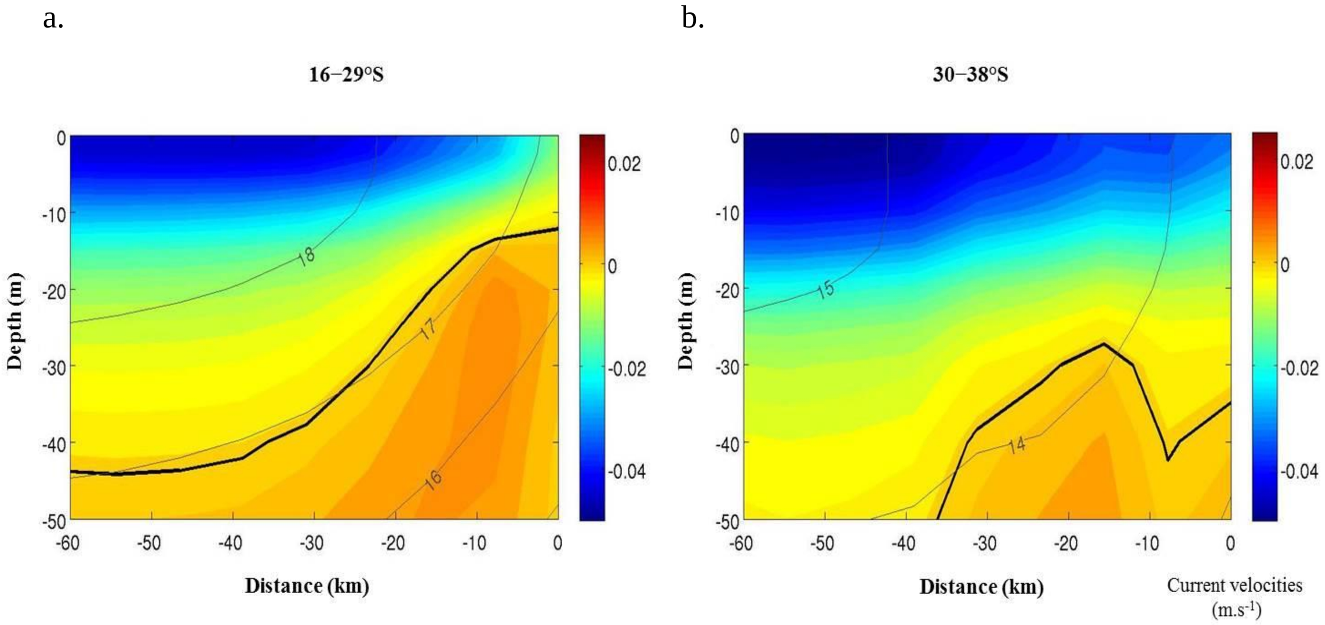
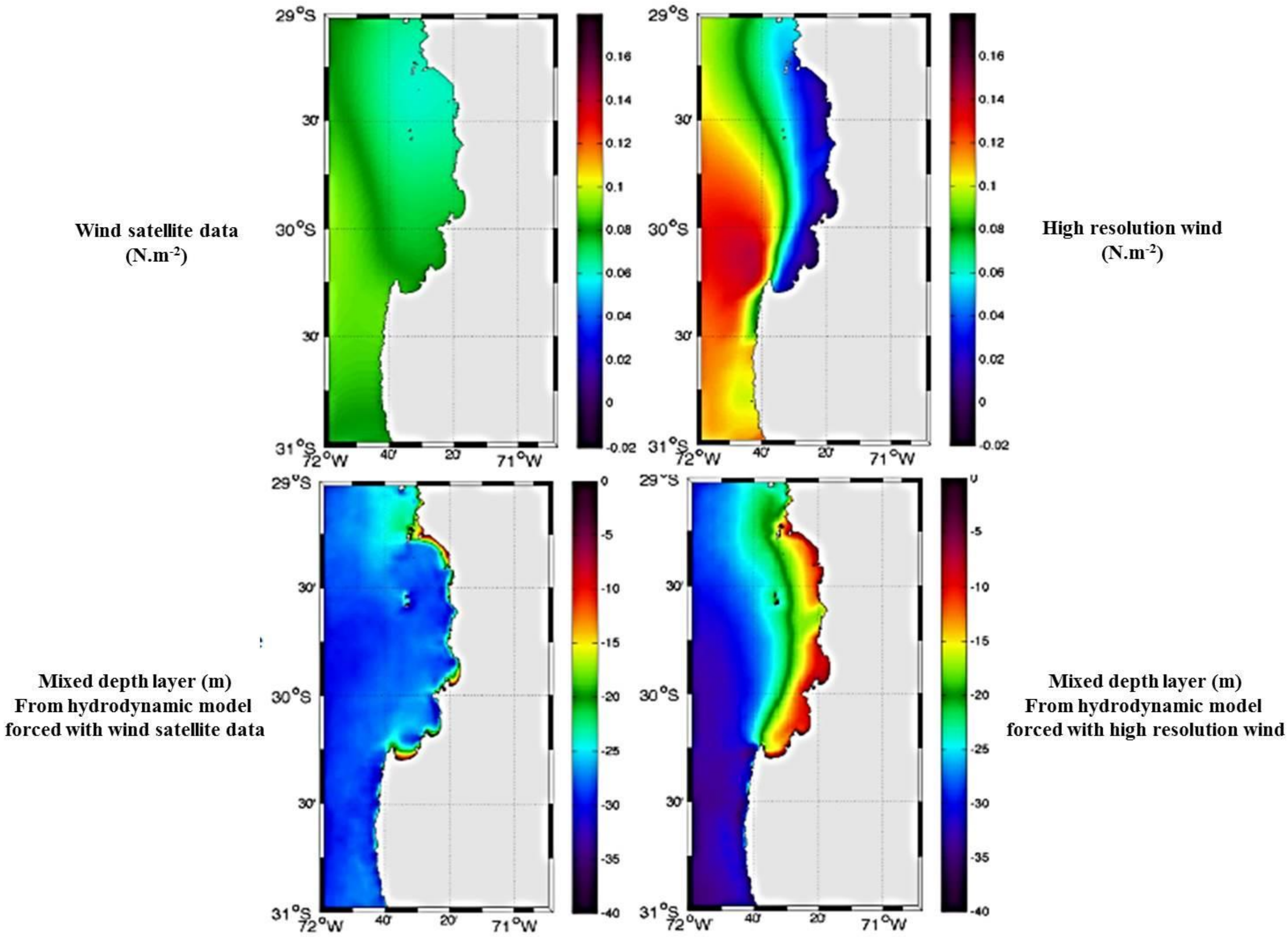


Figure 4.A: Vertical sections of the annual mean of the cross-shore component of current velocity (m.s^{-1}) averaged between 16°S and 29°S (a.) and 30°S and 38°S (b.) for the hydrodynamic model used. Positive values indicate onshore transport. Black contours represent onshore speed = 0 m.s^{-1}. Gray contours indicate temperature isotherms.


Wind satellite data ($N.m^{-2}$)

High resolution wind ($N.m^{-2}$)

Mixed depth layer (m) From hydrodynamic model forced with wind satellite data

Mixed depth layer (m) From hydrodynamic model forced with high resolution wind

Figure 4.B: Annual mean of wind stress magnitude ($N.m^{-2}$) from satellite data (top left) and from high resolution model (top right) between 29°S and 31°S. Mixed depth layer (m) from satellite data (bottom left) and from high resolution model (bottom right) between 29°S and 30°S.

Chapter 5. General discussion

In Chile, loco fishery was the most valuable benthic fisheries until the end of the 80’s (Leiva and Castilla, 2002). Loco local management system applied since 1998, *i.e.* MEABR, did not lead to the expected recovery of the fishery. Consequently, recent studies have proposed to scale-up the management of the species by incorporating networks of MEABR (Gelcich *et al*., 2008). The main objective of this thesis was to evaluate loco connectivity scales in order to establish the most adapted management to the species. In the introduction of the thesis (Chapter 1), I highlighted gaps in the knowledge of loco early life history that impede the assessment of connectivity. In the thesis, I used two main approaches, an empirical study to evaluate loco larval biological processes in the first stage of its life cycle (Chapter 2), and a theoretical biophysical model of larval dispersal to evaluate loco connectivity scales, patterns, and subpopulations along the Chilean coast (Chapters 3 and 4). The larval dispersal model for loco was first developed to study the influence of physical factors on loco connectivity (Chapter 3). Thereafter, I successively incorporated a series of biological processes in the larval dispersal model to assess their effect on loco connectivity patterns (Chapter 4). In this general discussion, I synthesize the main results of the thesis and propose a new vision for the management of loco based on our results and loco field studies.

5.1. Biological characteristics of loco larvae

In the description of loco connectivity in the introduction, I highlighted two important biological processes: the behavior of early veliger larvae and the growth of loco larvae. By establishing laboratory experiments, we attempted to evaluate these two processes in Chapter 2. Firstly, our results showed that under both photoperiods early veliger loco larvae behavior was determined by a nocturnal vertical migration. More larvae were swimming at night, and they were located shallower at night in the experimental columns. This migratory behavior is not only due to the absence of light during the night and could be explained by endogenous rhythm influenced by other exogenous cues such as pressure or salinity. Such a behavior has also been described for competent loco larvae (Manríquez and Castilla, 2011). From this study, we could postulate that loco larvae likely undergo nocturnal vertical migration all along their pelagic life. In the Chapter 4 of the thesis, we used this result to incorporate a diel vertical migration (DVM) scheme in the larval dispersal model developed. The second biological process of loco connectivity we wanted to consider in Chapter 2 was larval growth. Unfortunately, our experimental study did not lead to successful results. In order to incorporate loco larval growth into our larval dispersal model, we chose to use a theoretical approach developed in Chapter 4.

5.2. Influence of hydrodynamic factors on loco connectivity

In Chapter 3, results from our biophysical larval dispersal model showed the importance of the hydrodynamic of the study area for loco connectivity. Globally, mean scales of connectivity along the Chilean coast ranged between 170 kilometers and 220 kilometers. We observed weak retention along the coast and exchanges of larvae on several hundreds of kilometers. Higher pelagic larval duration increased dispersal distances but also offshore larval losses. By implementing different spawning depth, our results showed an increase of the connectivity values along the coast with depth. This result highlighted the implication of onshore and southward currents for loco recruitment when larvae were released deeper. The study of the seasonality of loco connectivity underlined favorable period of loco larval hatching in austral autumn and winter leading to a favorable settlement period in austral winter and spring coinciding with weak intensity of upwelling. In Chapter 3, we also tested the influence of the resolution of the hydrodynamic model on loco connectivity. Our results showed similar qualitative connectivity patterns but a decrease of the connectivity values using the high resolution model. Finally, the clustering methodology (Jacobi *et al*., 2012) used from our results of connectivity matrices described different loco subpopulations along the coast indicating robust larval dispersal barriers for loco, mainly linked to the geomorphology of the Chilean coast.

5.3. Influence of biological factors on loco connectivity

In Chapter 4, we implemented in our larval dispersal model several biological factors characterizing loco larval biology and ecology such as growth, habitat, fecundity, DVM as assessed in Chapter 2, and mortality. Results obtained from different model configurations showed dispersal distances of loco larvae dependent on release zone and biological factor. Globally the study domain was dominated by net simulated northward transport of loco larvae. When DVM was considered, larval dispersal highly increased until 350 km for larvae released in the central part of the study domain. Results of seasonality showed similar patterns as in Chapter 3 and underlined little influence of biological factors on seasonality in connectivity. Analysis of the connectivity patterns showed a zone of high connectivity in the northern part of the domain (17−23°S) from all the model configurations. Also, results highlighted a decrease of the connectivity values from North to South highly dependent of the biological factor used. Indeed, along the Chilean coast, temperatures decrease from North to South and in our model, larval growth and mortality are dependent on temperatures, explaining the observed differences of connectivity levels observed. The inclusion of habitat lead to a decrease of the connectivity values in the South due to low level of available habitat there. Loco fecundity being higher in the South, a slight relative increase of connectivity occurred when it was implemented. The implementation of larval DVM and mortality increased the contrast of connectivity for loco between North and South. We showed in the discussion of Chapter 4 that more larvae were transported offshore when they are forced to perform DVM up to the surface. Net decrease of connectivity observed in the southern part of the study domain when DVM and mortality were implemented lead to a different separation into subpopulations in this region. Other separations observed were similar to those observed in Chapter 3 and explained by geomorphological related coastal oceanographic processes.

5.4. Consequences for loco management

I used a clustering algorithm recently developed by Jacobi *et al*. (2012) to identify putative independent loco subpopulations along the Chilean coast from the connectivity matrices obtained in Chapters 3 and 4. To our knowledge, this is the first time that this methodology is used in the perspective of management applications of marine species. The method relies on a partitioning of a population into several subpopulations which, in our study, allowed identifying geomorphologic and biological characteristics acting as larval dispersal barriers for loco. As previously mentioned, a number of robust patterns in the identification of subpopulations from connectivity matrices have been identified. In our results, a subpopulation corresponds to a much larger entity than most MEARB. Consequently, one of our subpopulations generally corresponds to a large number of (connected) MEABR, which suggests the need to reevaluate the scales at which loco is managed, as proposed by Gelcich *et al*. (2008). This result is also coherent with the concept of supra MEARB recently proposed by the fishery sub-secretary in Chile (IFOP). Since 2006, IFOP has proposed each year a report where data of density of loco adults, abundance, mean size, captures, captures per suitable habitat, quotas, exploitation rate, and MEABR location are recorded. All this data was analyzed with the objective of identifying different regional groups of MEABR, named supra MEABR. At the beginning, only 34 MEARB were monitored and 7 supra MEABR were identified. In one given supra MEABR, the different MEABR had similar patterns of loco density, size or captures. Same methodology has been used during the other years with a greater number of monitored MEABR (163 MEABR monitored in 2010). This lead to changes in the description and location of supra MEABR. In 2011, from 20°S to 45°S, 10 supra MEABR have been proposed, 2 in the northern part, 4 in the central part and 4 in the southern part (Figure 5.1).

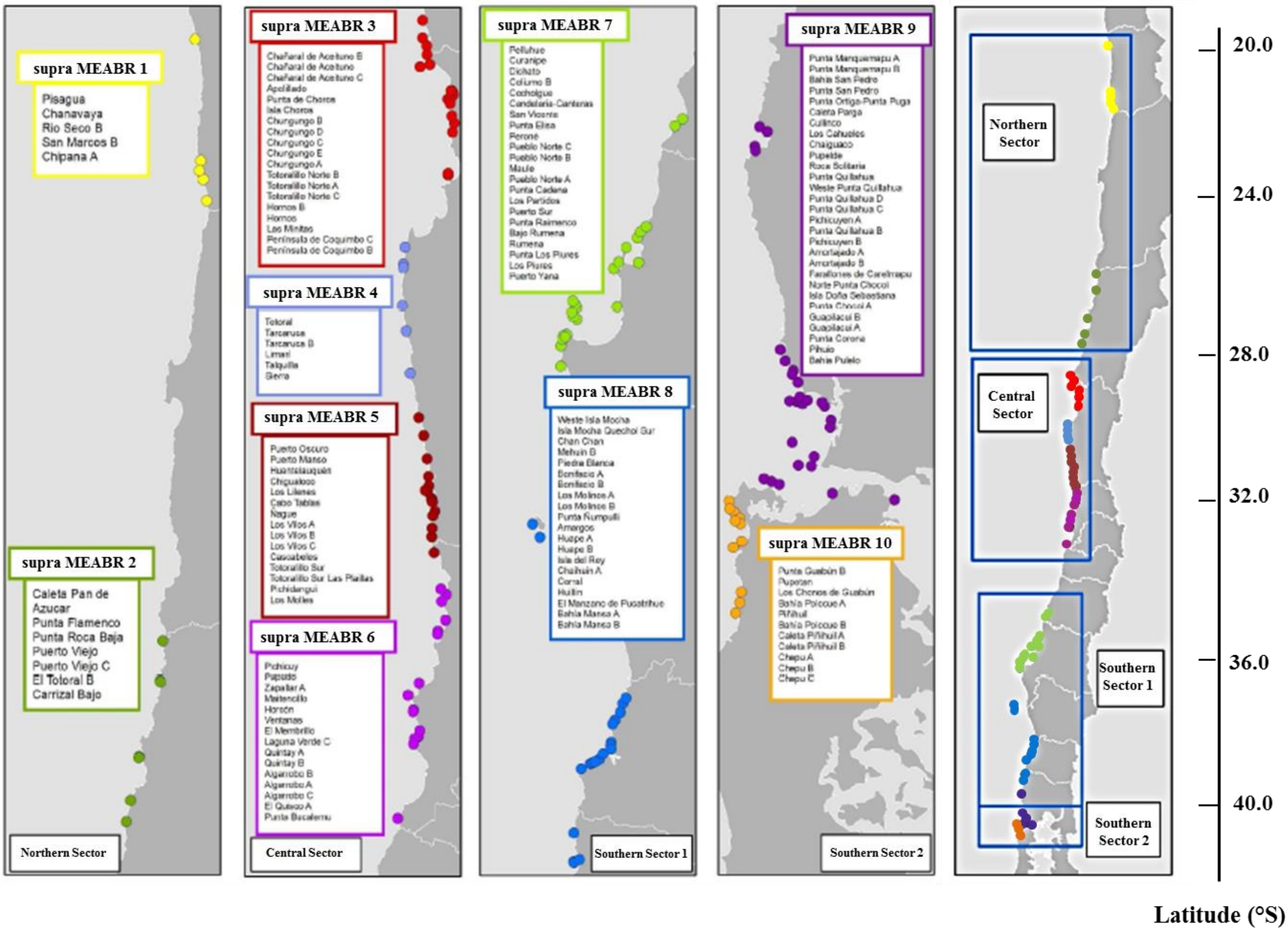


Figure 5.1: Geographic distribution of supra MEABR identified by the fishery sub-secretary of Chile (IFOP). Reproduced and modified with the authors' permission from IFOP report 2010−2011.

I used our results of loco subpopulations identified from simulated connectivity and the supra MEABR identified by IFOP to propose a new vision of loco management at a regional scale. Doing so, I consider that our connectivity study and the IFOP study are complementary. Indeed, in IFOP study, only about half of the MEABR has been studied along the Chilean coast, which explains gaps in the supra MEABR map (Figure 5.1). The larval dispersal model developed in this thesis allows representing all potential zones of loco distribution in the study domain. In order to only consider the subdomain where our and IFOP studies overlap, I did a new clustering analysis of simulated connectivity matrices between 20°S and 36°S, from model configurations M0, M5, and M6. M0 corresponds to the model configuration from Chapter 3 with spawning depth 0−20 m and PLD of 140 days; M5 corresponds to the model configuration from Chapter 4 with growth, habitat, fecundity and DVM included. Additionally, mortality is included in M6. M0 is therefore the simplest model configuration to represent loco connectivity whereas M6 is the more complex, and M5 in between.

Loco subpopulations identified from our connectivity matrices and supra MEABR from IFOP study between 20°S and 36°S are represented in Figure 5.2. I chose to represent 7 subpopulations in order to compare with the 7 supra MEARB proposed. I also consider that this number represents a compromise between local and regional management. In the northern part of the domain, between 20°S and 29°S, 2 to 4 supra MEABR can be described considering the potential separations. From our model, 3 to 5 subpopulations have been identified depending on the model configuration. Globally, a similar separation is observed around 24°S and combining our results with supra MEABR, we can postulate a probable separation there. Between 28°S and 29°S, no supra MEABR is defined and one subpopulation is observed only for M0. Most results therefore lead to propose 2 regional management areas for loco in the northern part of the study domain: 20–24°S and 24–29°S. The two similar separations between our subpopulations and supra MEABR are located at 29°S (potential separation between two supra MEABR) and 31°S (exact separation). However, a single subpopulation is defined from 29°S to 31°S in all our results (Figure 5.2 a., b., c.)

whereas 2 supra MEABR are located in this zone. From our contested results obtained around 30°S and discussed in Chapter 4, it seems favorable to establish two regional management areas within this zone as proposed by IFOP study. In the southern part of the study domain, from 31°S, 3 to 4 supra MEABR can be described (Figure 5.2 d.). Limit at 32°S between 2 supra MEABR is “exact” but such a separation is not observed between our subpopulations. Further south, around 34°S, a separation is observed for M5 and M6 (Figures 5.2 b. and c. respectively) corresponding to a gap between 2 supra MEABR. Combining our results and those from IFOP study, we can propose 3 regional management areas in the southern part of the domain: 31–32°S, 32–34°S and 34–36°S.

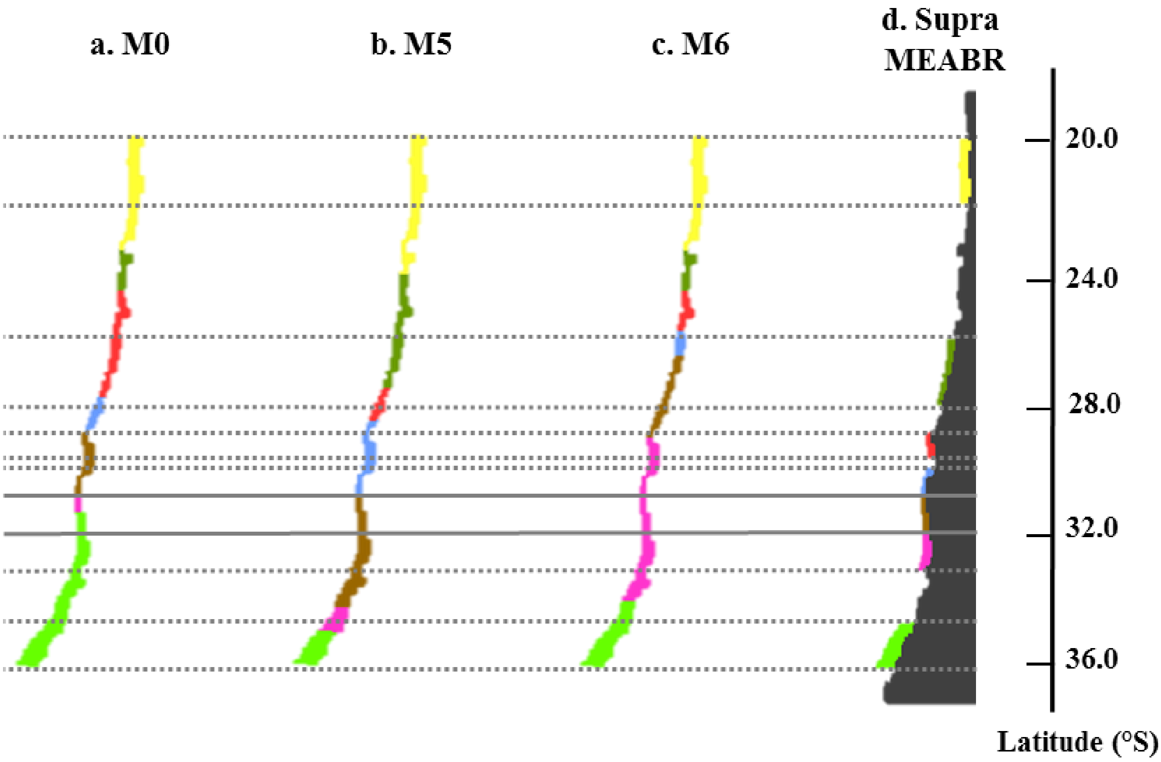


Figure 5.2: Partitioning of the loco metapopulation into 7 subpopulations identified by the method of Jacobi *et al*. (2012) from the connectivity matrices obtained between 20°S and 36°S with model configurations M0 (a.), M5 (b.), and M6 (c.), and supra MEABR identified by IFOP (d.). Grey dashed lines represent potential separation between two supra MEABR and grey solid lines represent exact separation between two supra MEABR.

The general scheme of regional management areas wherein consider networks of MEABR that I propose for loco follows in Figure 5.3. From the northern limit of the domain to 29°S, separations between regional areas correspond to rough changes in the orientation of the coast with the Antofagasta Cape at 24°S and the beginning of Coquimbo Bay at 29°S. We showed in Chapters 3 and 4 that those geomorphological characteristics represent larval dispersal barriers for loco. Between 29°S and 31°S, in the Coquimbo Bay, two smallest management areas are proposed representing areas of high loco abundance and catches observed from IFOP field studies. From 31°S, regional management areas are also smaller than northern management areas and represent both weak connectivity observed in Chapter 4 and weak loco catches and abundance observed from IFOP field studies. Distinct spatial scales management between northern and southern part of Chile had been suggested in Chapter 4. Regional management of loco therefore relies on hydrodynamic, biological and ecological factors characterizing loco population dynamics.

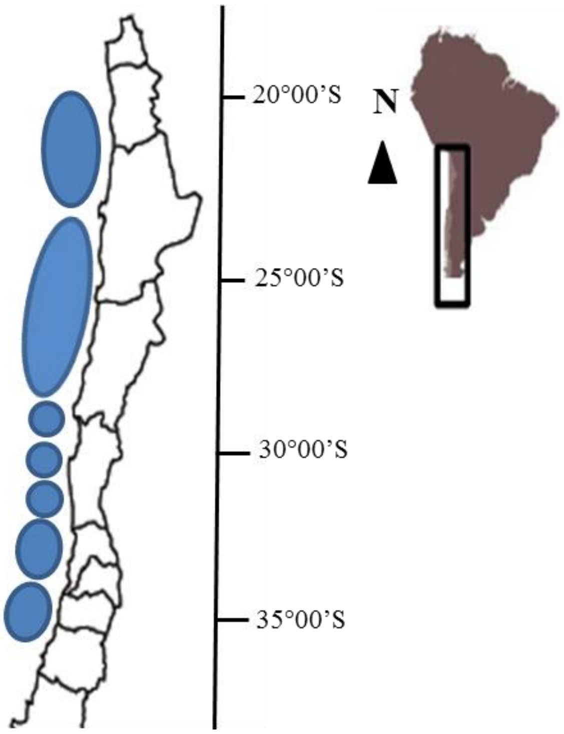


Figure 5.3: Regional areas proposed for loco management wherein consider networks of MEABR between 20°S and 36°S.

5.5. Conclusion and perspectives

In this thesis, I have highlighted the need to study the biology and ecology of loco in order to overcome current issues in the management of this species in Chile. The method I used, based on modeling larval dispersal and clustering simulated connectivity matrices, lead to the identification of robust patterns of larval connectivity along the Chilean coast that can be used, in combination with other information, to set relatively independent management entities of loco at a regional scale. However, I showed that simulated loco connectivity depends on hydrodynamic and biological factors implemented in the larval dispersal model. Therefore, a number of limitations in the current modeling approach have to be considered before fully concluding on the usefulness of the present results for decision support of loco management.

Although outputs of the hydrodynamic models used in the thesis were validated using observed data (Colas *et al*., 2012), the representation of the circulation remains limited, particularly close to the coast. For example, I showed that resolving coastal features that are potentially important for larval retention in central Chile around the Coquimbo Bay likely requires higher resolution than used in the present work. By comparing our connectivity results using two different model resolutions, I showed that the simulated patterns were qualitatively similar but quantitatively different. Although a qualitative approach is sufficient to define areas that are more/less connected to others, quantitative results are required to determine if, for example, these areas are self-persistent (Burgess *et al*., 2013).

The individual-based model used in the present thesis allows the incorporation of various biological factors as I did for loco, but some of them need to be better defined. For example, the growth submodel and larval mortality are currently only dependent on temperature. However, such processes are also affected by food supply (Metaxas and Saunders, 2009). Coupled physical-biogeochemical models have been run to simulate phytoplankton and zooplankton concentration fields used as prey fields for larvae in dispersal models (*e.g.*, in upwelling areas, Brochier *et al*., 2013; Koné *et al.*, 2013). A way to integrate the combined effects of food supply and temperature on growth is using a bioenergetic model for growth based for example on the DEB theory (Dynamic Energy Budget; Kooijman, 2010). For example, a DEB model has been used to test the influence of environmental variability on the growth of European anchovy (Pethybridge *et al.*, 2013). Another biological factor that I implemented in the model is DVM. This factor is potentially critical because simulated loco connectivity patterns differed significantly with/without DVM. Vertical migration is a mechanism that usually changes with ontogeny as shown for larvae of several benthic species (Pfeiffer-Herbert *et al.*, 2007; Butler *et al.*, 2011). Comparing the results of DVM obtained for early veliger larvae (Chapter 2) with those for competent larvae (Manríquez and Castilla, 2011) suggest that the extent of DVM increases with larval development. Implementing an ontogenic DVM scheme could be the next step in the development of our larval dispersal model for loco.

A northward transport all along the study domain has been simulated for settled loco larvae (although we also showed that larvae released deeper were mainly transported southwards). However, our study domain does not cover the entire distribution range of loco. In Chile, loco are distributed until Cape Horn including the Juan Fernandez Archipelago (Cárdenas *et al.*, 2008). South of 40°S, the circulation is dominated by the poleward Cape Horn current and the offshore West Wind Drift mainly oriented northwards (Thiel *et al.*, 2007). Our domain study is therefore embedded into a larger domain where loco live and the dynamics of the whole loco population should be assessed over this entire domain.

Our larval connectivity model is a demographic model representing life cycle of loco from spawning to settlement. Several post-recruitment processes can also explain loco spatial distribution along the Chilean coast such as mortality and growth of juveniles and adults. Another factor is obviously the fishing effort. To take these processes into account, the perspective after this work is to develop a population model of loco dynamics based on realised connectivity patterns in order to improve the representation of loco distribution and its management. Moreover, it is important to keep in mind that not only the physical, biological, and ecological knowledge are required for management of marine resources but also economic, social, and institutional aspects (Charles and Wilson, 2009).

Finally, and perhaps more importantly, even if the use of models is an adapted method to study marine population connectivity (Leis *et al*., 2011), it is necessary to compare the model results with direct empirical methods such as statoliths chemistry (in the case of invertebrate species) or population genetic structure (Jones *et al*., 2009). For loco, both methods have been applied to assess the scales of connectivity. In a phylogeographical study of genetic differentiation of loco, Cárdenas *et al*. (2009) showed that there was no significant genetic structure in the loco population, indicating gene flow along the Chilean coast. However, the method used gives a historical perspective (*i.e.*, evolutionary connectivity) that does not provide direct information on population connectivity at demographic time scales (*i.e.*, demographic connectivity, Leis *et al*., 2011). Indeed, a limited gene flow can maintain genetic homogeneity while having little impact on the population demography. Only recently, molecular markers of loco have been identified (Cárdenas *et al*., 2011), which are a necessary first step for future genetic studies of population connectivity such as genetic assignment tests. Manríquez *et al*. (2012) assessed connectivity between three areas in distinct regions of Chile by evaluating the concentrations of trace elements in loco statoliths of pre-hatch larvae and recruits. Their study suggested discrete adult loco populations at the scale of kilometers and little larval exchange between regions. However, they could not directly conclude about loco connectivity due to the sparse sampling areas in their study. Therefore, empirical assessment of loco population connectivity is still needed. In the future, I recommend that studies of loco connectivity for management decisions integrate empirical efforts with modelling works as I developed in this thesis.

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Appendix

Modeling the dispersal of Cape hake ichthyoplankton

Lysel Garavelli, Arnaud Grüss, Britta Grote, Nicolette Chang, Melanie Smith, Philippe Verley, Erling Kåre Stenevik, David Michael Kaplan, Christophe Lett. (2012) Journal of Plankton Research 34, 665-669.

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Modeling the dispersal of Cape hake ichthyoplankton

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The two Cape hake species of the southern Benguela ecosystem, the shallow-water and deep-water hakes *Merluccius capensis* and *M. paradoxus*, are economically the most important marine resources in South Africa. Recruitment is a key process in the dynamics of marine organisms, yet very little is known about the early life history of Cape hakes, especially the location of spawning grounds and transport of eggs and larvae. For each species, ichthyoplankton dispersal off South Africa is simulated by coupling oceanographic simulations to an individual-based model in order to track virtual individuals. Results indicate that the most favorable spawning areas for transport to nursery areas are located off the south-western coast and the eastern Agulhas Bank, and highlight partly different drift routes followed by the two ichthyoplankton species off Cape Columbine. Transport from spawning to nursery areas is the highest in austral winter for a spawning depth ranging between 0 and 100 m. These modeling results are in broad agreement with available knowledge on the ecology of Cape hakes. The present work on Cape hakes complements previous modeling studies on anchovy and sardine in the same area. Taken together, these studies underline the correspondence between cross-shore (for hakes) or alongshore (for anchovy and sardine) transport mechanisms and the spawning strategies used by these key species of the southern Benguela ecosystem.

KEYWORDS: *Merluccius* spp.; Southern Benguela; larval dispersal; modeling

INTRODUCTION

Fish recruitment depends largely on environmental conditions (Sinclair, 1988; Cushing, 1990; Bakun, 1996), particularly those experienced by early ichthyoplanktonic life stages. Ichthyoplankton transport is a dynamic and complex process central to ichthyoplankton survival and recruitment, particularly in highly variable upwelling areas (Hutchings, 1992). In such environments, species are evolutionary adapted through their spawning strategies to environmental conditions so as to maximize recruitment success, avoiding potential limiting factors such as variability in larval food supply and loss of larvae due to strong seasonal surface offshore transport. Although we are only beginning to understand the complexity and variety of spawning strategies, potential approaches for responding to environmental constraints include spawning during periods of sufficient food availability (Sherman *et al.*, 1984), or spawning in

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areas with environmental conditions to which the species are adapted (Sakurai *et al*., 2000). Many theories have attempted to explain the recruitment success of species (Cole and McGlade, 1998) and there is currently wide agreement that several factors simultaneously influence recruitment (Cury and Roy, 1989; Bakun, 1996).

The upwelling system of the Southern Benguela experiences significant seasonal and short-term variability in currents, temperature and primary productivity (Hutchings *et al*., 2009), conditions which likely play a significant role in larval transport and recruitment success. Fish recruitment in the region has been experimentally studied over the past three decades for small pelagic species, such as anchovy and sardine (Boyd and Hewitson, 1983; Painting *et al*., 1998; van der Lingen and Huggett, 2003). Furthermore, a number of simulation studies have addressed the abiotic and biotic conditions experienced by small pelagic ichthyoplankton during their dispersal phase using individual-based biophysical models (Mullon *et al*., 2003; Koné 2006; Miller *et al*., 2006; Parada *et al*., 2008). In contrast, recruitment of demersal fish species, such as Cape hakes, has been poorly documented. Given significant differences in habitat preferences, longevity and other life-history parameters between small pelagic and demersal species, it is reasonable to assume that larval transport and recruitment also differ, and, therefore, these processes merit additional attention for demersal populations. In this paper, we address this knowledge gap by examining spatial and temporal patterns of larval transport and recruitment of demersal hake species found along the South African coast using an individual-based biophysical model.

There are two hake species living in the southern Benguela ecosystem, the shallow-water hake, *Merluccius capensis* (Castelnau, 1851) and the deep-water hake *Merluccius paradoxus* (Franca, 1960). Both species live in continental waters off South Africa and Namibia (Payne and Punt, 1995). *Merluccius capensis* is mainly found in shallow waters, <300 m depth, whereas *M. paradoxus* predominantly inhabits deeper waters, between 150 and 500 m depth (Botha, 1971). Cape hakes are economically the most important marine resource in South Africa. They are targeted by demersal trawl and long-line fisheries. Annual catches of hakes declined in the 1970s and have remained relatively stable since (Payne and Punt, 1995; van der Westhuizen, 2001). Since the 1990s, the demand for large hake individuals has encouraged fishers to explore rocky grounds and to fish deeper waters. Concerns have been raised that exploration of these new fishing grounds could have detrimental effects on the recruitment success of hakes and their long-term productivity (especially for *M. paradoxus*) because of the important contribution of large individuals to reproduction (Hutton and Sumaila, 2002; Field *et al*., 2008). Due to the socioeconomic significance of hake fisheries in South Africa, management and sustainability measures have been proposed for these species. One of them is the establishment of offshore marine protected areas (MPAs) for the conservation of pelagic and demersal species (Sink and Attwood, 2008). A detailed understanding of larval dispersal and transport patterns has been regularly identified in the MPA literature as essential to evaluating marine reserve effects (Kaplan, 2006; Botsford *et al*., 2009), and, therefore, improving our understanding of Cape hake larval dispersal is an important part of this offshore MPA implementation effort.

Cape hakes in the southern Benguela ecosystem appear to have spatially distinct spawning and nursery areas. The areas offshore the south coast and the Cape Peninsula (34.15°S, 18.29°E) have been identified as important centers for Cape hake spawning (Assorov and Berenbeim, 1983; Crawford *et al*., 1987; Hutchings *et al*., 2002; Burmeister, 2005; Grote *et al*., 2007). Using species-specific genetic markers (von der Heyden *et al*., 2007), Stenevik *et al*. (Stenevik *et al*., 2008) compared the spatial distributions of the ichthyoplankton for the two Cape hake species, and found that eggs and larvae of *M. paradoxus* are found further offshore than those of *M. capensis* along the west coast of South Africa. From these observations, they suggested that eggs and larvae of each species follow partly distinct drifting routes, with those of *M. capensis* following a more inshore route than those of *M. paradoxus*. The authors concluded that these species may therefore have different nursery areas. Additional support for different nursery areas is provided by abundance distribution maps for *M. paradoxus* (Le Clus *et al*., 2005a) and *M. capensis* (Le Clus *et al*., 2005b). *Merluccius paradoxus* juveniles (i.e. individuals smaller than 20 cm) are usually found further offshore than *M. capensis* juveniles (Fig. 1). In order to investigate temporal patterns of spawning, Grote *et al*. (Grote *et al*., 2007) sampled Cape hake ichthyoplankton along a cross-shore transect off the Cape Peninsula as part of the Sardine and Anchovy Recruitment Program (SARP). The SARP line is located in a transition zone for several small pelagic fish species separating their spawning and nursery areas. Peak abundances of hake eggs and larvae were found from June to October, and the authors therefore concluded that this period represented the main peak spawning period for Cape hakes.

Transport of larval fish between spatially distinct spawning and nursery areas, as must occur for Cape hake larvae, is believed to be primarily influenced by one physical and two biological processes: advection by

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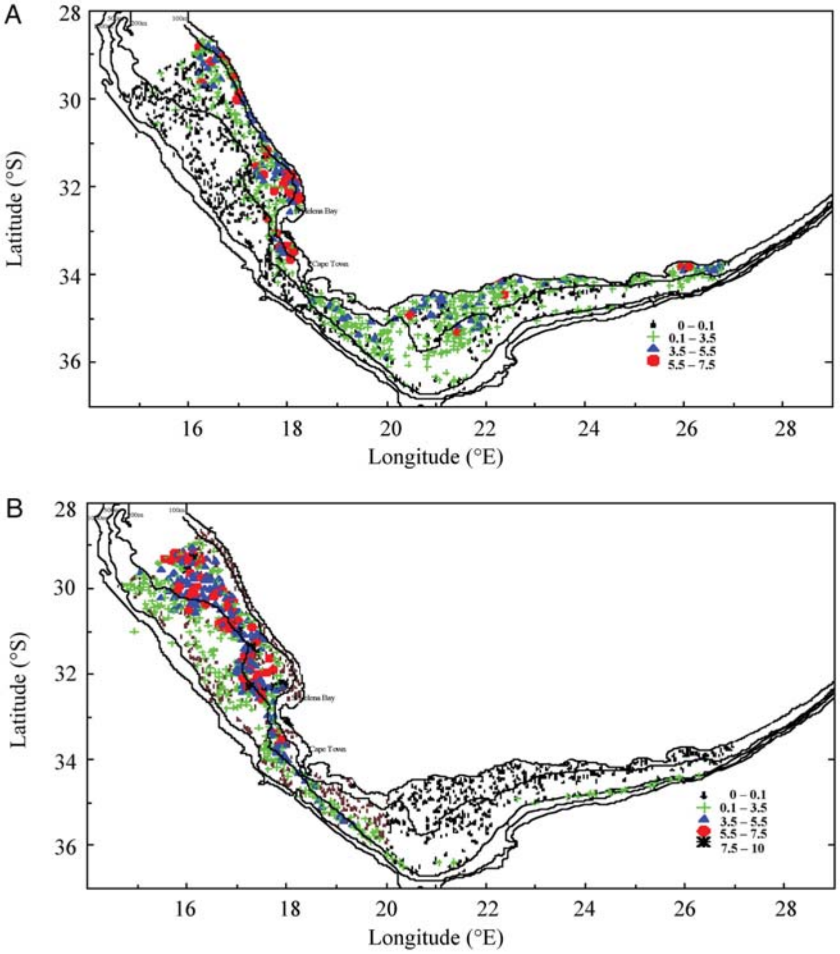

Fig. 1. Abundance distribution of *M. capensis* juveniles (<20 cm; **A**) and *M. paradoxus* juveniles (<20 cm; **B**) derived from western and southern coast surveys in the period 1990–2003. The number per 30-min trawl was root–root transformed and averaged by grid-block. Reproduced with the authors' permission from Le Clus *et al.* (Le Clus *et al.*, 2005a, b).

currents, egg buoyancy and larval vertical migration. Advection due to currents in the southern Benguela can be simulated using data from hydrodynamic models (Chang, 2009), which have been shown to compare favorably with regional hydrographic data at multiple depths and offshore distances. For Cape hake egg buoyancy and larval migration in the southern Benguela ecosystem, there are currently little data. Sundby *et al.* (Sundby *et al.*, 2001) measured buoyancy of *M. capensis* eggs in the northern Benguela and estimated that an average egg ascends about 100 m from spawning to hatching due to buoyancy, with the lightest and heaviest eggs ascending 175 and 50 m, respectively. Assuming these results are also representative of hake in the Southern Benguela, egg buoyancy potentially significantly alters larval depth and, therefore, may be quite important for Cape hake larval dispersal. Existing studies of other hake species have not found direct evidence for significant larval vertical migration, although the spatial and temporal resolution of these studies are not sufficient to exclude the possibility of vertical migratory behavior in hakes (*M. merluccius*, Sabatés, 2004; *M. productus*, Sakuma *et al.*, 2007). Given this weak evidence for the importance of vertical migration of Cape hake larvae, we focus in this study on the effects of egg buoyancy, although the potential consequences of vertical migration are addressed in the Discussion.

The objectives of this study are to investigate transport of eggs and larvae, as well as connectivity between spawning and nursery areas, for Cape hake species. In particular, we examine the consequences of a spawning seasonality on larval transport, and determine relative transport success for several different potential spawning areas. We begin by briefly describing the biophysical larval-dispersal model used and the various simulations performed. Then, we compare the results of our

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simulations to the results of previous studies, i.e. to Stenevik *et al.*'s (Stenevik *et al.*, 2008) hypothesis of distinct trajectories for larvae of the two Cape hake species, and to Grote *et al.*'s (Grote *et al.*, 2007) analysis of the seasonality of hake spawning patterns. In the Discussion, we highlight a number of strengths and weaknesses of our approach and consider the results obtained for Cape hake in light of those previously obtained for anchovy and sardine from similar biophysical simulations.

METHOD

Study area

The Benguela ecosystem is one of the four major eastern boundary upwelling systems (the others being the California, Canary and Humboldt currents systems). It is located off the southwestern coast of Africa and is divided into two sub-systems, the northern and the southern Benguela ecosystem. The southern Benguela ecosystem extends from Lüderitz in Namibia southwards along the South African west coast and eastwards to 28°E (Shannon *et al.*, 2003). Two currents are dominant in this area, the cold Benguela current flowing equatorward along the west coast of South Africa and the warm Agulhas current along the south coast of South Africa (Hutchings *et al.*, 2002). The Agulhas current bounds the Agulhas Bank from Cape Peninsula (34°20′S, 18°40′E) to Algoa Bay (33°50′S, 25°50′E). Off the Cape Peninsula, water masses merge into the fast coastal jet current that flows along the shelf break along the west coast (Hutchings *et al.*, 2002). The present study area is located between Oranjemund on the border of Namibia (28°33′S, 16°25′E) and Algoa Bay along the southern coast of South Africa (Fig. 2).

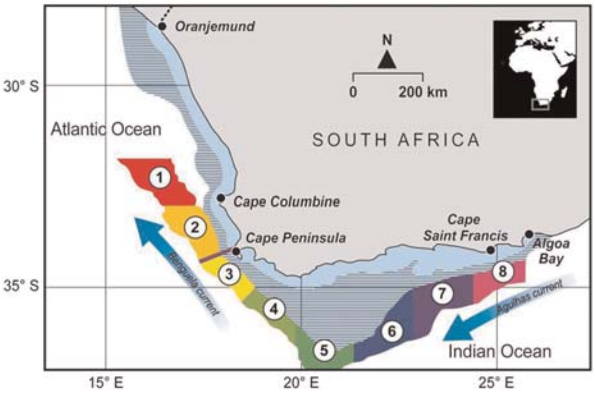

Fig. 2. Map of the study area, spawning areas (1–8), the SARP line (line off Cape Peninsula between areas 2 and 3) and the coastal nursery areas (continuously shaded area for *Merluccius capensis* and stripped area for *Merluccius paradoxus*) used in simulations S3 and S4.

Hydrodynamic model

The hydrodynamic model used is the regional ocean modeling system (ROMS) (Shchepetkin and Mc Williams, 2005) in a configuration covering the southern Benguela from 28 to 39°S and 11 to 27°E (Chang, 2009). The area is discretized at 8 km resolution in the horizontal dimension. In the vertical, the model has 32 vertical terrain-following levels, with a resolution from 1 to 4.7 m at the surface and from 3.2 to 1030 m in the bottom layers, depending on the local water column depth. The model resolution is sufficiently high to allow the main mesoscale features influencing hake egg and larval dispersal to be reproduced. The open boundary conditions for this configuration are obtained from SAfE (Southern Africa Experiment), a larger climatological model designed specifically to model the southern African oceanic region at 25 km horizontal resolution (Penven *et al.*, 2006). Atmospheric forcing is derived from a monthly mean climatology such that direct intraseasonal and interannual forcing is absent. Nevertheless, mesoscale dynamics intrinsic to the model solution introduce additional variability. The model reaches a statistical equilibrium in three climatological years. Time series of current velocities in three dimensions are averaged and stored every 2 days from years 4–9 for use in the dispersal model. The model climatology reproduces the dominant water column and current structure over the Agulhas Bank, in good agreement with observations and literature (Chang, 2009), although a coherent *in situ* three-dimensional data set for the region is not available. The model represents the large seasonal signal over the shelf, with surface temperatures generally consistent with the monthly satellite-derived climatology of SST over the Agulhas Bank from Demarcq *et al.* (Demarcq *et al.*, 2003).

Dispersal model

We developed a dispersal model using Ichthyop (version 3.1). Ichthyop (Lett *et al.*, 2008) is an offline Lagrangian model, distributed as a free Java tool, which relies on an individual-based approach (Grimm and Railsback, 2005). Individuals here represent Cape hake eggs and larvae and are characterized by their latitude (°S), longitude (°E) and depth (m). Locations of individuals are updated every hour (time-step of the Lagrangian model) in three dimensions using the velocity fields

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from the hydrodynamic model outputs interpolated in space and time and the forward-Euler integration scheme.

Simulations track individuals from release to destination areas, here corresponding to spawning and nursery areas. The horizontal extent of release and destination areas consisted of all areas inside the model domain between a pair of isobaths (m). The vertical extent of the area was defined by specifying a thickness (upper and lower spawning depths for spawning areas). A fixed number of individuals were homogeneously distributed over the release areas in all simulations. A total of 10 000 individuals were released at the beginning of each month from January to December, and from climatology years 4–9 (this number of individuals was selected as being high enough to provide robust simulated patterns). The presumed duration of eggs and larval drift for hakes in the southern Benguela ecosystem is based on estimations gathered for several hake species. Duration of the egg stage for hake species was estimated to be 4 days (for *M. capensis*, Sundby *et al.*, 2001; for *M. merluccius*, Bjelland and Skiftesvik, 2006). For *M. merluccius* in the laboratory, metamorphosis into the juvenile begins when unpaired fins appear, around 30 days post-hatching (Bjelland and Skiftesvik, 2006). At that time, individuals are considered to have swimming capacity, an indication of the end of the larval stage. Steves and Cowen (Steves and Cowen, 2000) found a larval dispersal duration of 34.5 days post-hatching at temperatures between 8.7 and 11.4°C (*M. bilinearis*, New York Bight continental shelf). Arneri and Morales-Nin (Arneri and Morales-Nin, 2000) estimated it to be 40 days post-hatching at 12°C (*M. merluccius*, central Adriatic Sea). For the same species, Bjelland and Skiftesvik (Bjelland and Skiftesvik, 2006) estimated it to be around 30 days post-hatching at 10–12°C. Sea surface temperatures generally lie between 13 and 15°C all year round off the west coast of South Africa, as well as from June to October off the entire coast of South Africa (Demarcq *et al.*, 2003) during the putative Cape hake spawning season. Combining this information, dispersal duration of about 30 days from egg fertilization to metamorphosis is a reasonable approximation for Cape hake species in the southern Benguela. Other parameters varied between simulations and are detailed below.

Four sets of simulations were performed, referred to as S1–S4 (Table I). Simulations S1 and S2 were

Table I: Overview of conditions and objectives of the different simulations performed

Simulation	Release area	Release depth	Destination zone	Dispersal duration	Egg buoyancy	Objectives
S1	Inshore release zone, 100–300 m isobaths (*M. capensis*) Offshore release zone, 300-1500 m isobaths (*M. paradoxus*)	50-100 m	No	30 days forward	No	Distinct drift routes for eggs and larvae of the two Cape hake species described by Stenevik *et al.* (2008)
S2	As S1	As S1	No	30 days backward	No	
S3	8 spawning areas, from Saint Helena Bay on the west coast to Cape Saint Francis on the south coast area 1, 300–2000 m isobaths areas 2 to 8, 200–2000 m isobaths	0–100m, 100–300 m, 300–500 m	SARP line, 0–2000 m isobaths	20 days forward	No	Seasonnality of spawning patterns described by Grote *et al.* (2007)
S4a, S4b	As S3	As S3	S4a: nursery area, 0–99 m isobaths (*M. capensis*) S4b: nursery area, 99–200 m isobaths (*M. paradoxus*)	40 days forward 40 days forward	No	Spawning patterns for the two Cape hake species
S4c, S4d	As S3	As S3	S4c: nursery area, 0–99 m isobaths (*M. capensis*) S4d: nursery area, 99–200 m isobaths (*M. paradoxus*)	40 days forward 40 days forward	Yes with egg densities 1.024, 1.025, 1.026 g · cm^{-3}	Spawning patterns for the two Cape hake species

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designed to study Stenevik *et al.*'s (Stenevik *et al.*, 2008) hypothesis of distinct drift routes for eggs and larvae of the two Cape hake species. For both S1 and S2, two release areas were chosen off the west coast, between the Cape Peninsula and Cape Columbine. The first release zone was located inshore and delimited by the 100 and 300 m isobaths (Fig. 3B), whereas the second one was located further offshore, from 300 m to the 1500 m isobaths (Fig. 3A). The inshore and offshore areas were defined based on eggs and larval bottom depth distribution in Stenevik *et al.* (Stenevik *et al.*, 2008) for *M. capensis* and *M. paradoxus*, respectively. Release depth was set to 50–100 m, the depth range at which most eggs and larvae were found by Stenevik *et al.* (Stenevik *et al.*, 2008). Individuals released were tracked for 30 days (dispersal duration) forwards in time (S1) to estimate the putative destination of the youngest individuals (eggs) sampled by Stenevik *et al.* (Stenevik *et al.*, 2008). Individuals were also tracked backward in time (S2) for 30 days to estimate the putative origin of the oldest individuals (1-month-old larvae) sampled by Stenevik *et al.* (Stenevik *et al.*, 2008).

Simulation S3 aimed at investigating the seasonality of spawning patterns described by Grote *et al.* (Grote *et al.*, 2007). We used eight release (spawning) areas from Saint Helena Bay on the west coast to Cape Saint Francis on the south coast, stretching from the 200 to the 2000 m isobaths for areas 2–8 (Fig. 2). Area 1 stretches from the 300 m to the 2000 m isobaths as the 200 m isobath is near the coast in this zone. Bathymetric lines were based on the information found in Assorov and Berenbeim (Assorov and Berenbeim, 1983), Hutchings *et al.* (Hutchings *et al.*, 2002), Burmeister (Burmeister, 2005) and Grote *et al.* (Grote *et al.*, 2007). Three spawning depth ranges were considered to represent the entire spawning habitat of Cape hakes according to mean egg depth concentrations reported by Stenevik *et al.* (Stenevik *et al.*, 2008) in the southern Benguela (0–200 m) and by Sundby *et al.* (Sundby *et al.*, 2001) in the northern Benguela (100–400 m): 0–100, 100–300 and 300–500 m. The drift period duration was set to 20 days, the age of the oldest larvae sampled by Grote *et al.* (Grote *et al.*, 2007). The destination zone in S3 was the SARP line (Fig. 2), from the coast to the 2000 m isobath, so as to compare simulation results to the observations of Grote *et al.* (Grote *et al.*, 2007). Transport success was computed as the percentage of released individuals reaching the SARP line between 0 and 20 days.

Simulations S4 were run in order to further investigate Cape hake spawning seasonality and more specifically to study whether transport of Cape hake ichthyoplankton between spawning and nursery areas could explain the spawning seasonality observed by Grote *et al.* (Grote *et al.*, 2007). We used the same spawning areas and depths as in S3. The destination area in S4 was the nursery area. To determine the extent of the nursery area, we used distribution maps of juveniles derived by Le Clus *et al.* (Le Clus *et al.*, 2005a,b) for the two species (Fig. 1). Between metamorphosis and juvenile stage, active movement of individuals may occur and juvenile distribution from surveys may generally not overlap the nursery areas. However, Cape hakes are believed to undertake their first ontogenic migration when they reach approximately 20 cm (Botha, 1971; Crawford *et al.*, 1987), thus we considered that the areas where juvenile ($<$ 20 cm) distribution is high (i.e. $>$3.5 per 30-min trawl over the period 1990–2003, Fig. 1) represents a proxy for the main nursery areas for hakes. We found that the area between 0 and 99 m isobaths all along the coast was a good approximation of the nursery area for *M. capensis* (Fig. 1A). Similarly, the area between the 99 and 200 m isobaths effectively represents the nursery area for *M. paradoxus* on the west coast (Fig. 1B). As there is evidence that *M. paradoxus* also recruits on the south coast (Crawford *et al.*, 1987; Hutchings *et al.*, 2002), and to be able to compare the simulation results for the two species more directly, we decided to extend the nursery area for *M. paradoxus* along the south coast in the simulations (Fig. 2). Transport success was computed as the percentage of released individuals reaching the nursery area between 20 and 40 days (a time window centered on the 30-day approximate dispersal duration). Simulations S4a and S4b were run for *M. capensis* (nursery area from 0 to 99 m isobaths) and *M. paradoxus* (nursery area from 99 to 200 m isobaths), respectively. We finally re-ran these simulations including egg buoyancy (S4c for *M. capensis* and S4d for *M. paradoxus*). The egg buoyancy scheme was included in the model following Parada *et al.* (Parada *et al.*, 2003), during the first 4 days of each individual's life, which corresponds to the duration of the egg stage for *M. capensis* (Sundby *et al.*, 2001). Egg densities were estimated using data from the same study (Sundby *et al.*, 2001). Based on their results, three values of egg density were tested: 1.024, 1.025 and 1.026 g cm^{-3}.

In both S3 and S4, a sensitivity analysis was performed on the simulated values of transport success, using a multifactor analysis of variance (ANOVA). The percentage of variance explained by different factors and their interactions were calculated for results on the simulated transport success to the destination areas (independent variables being spawning area, spawning month, spawning depth and egg density in S4c and S4d). Normality (using a Kolmogorov–Smirnov test) was tested prior to conducting ANOVA.

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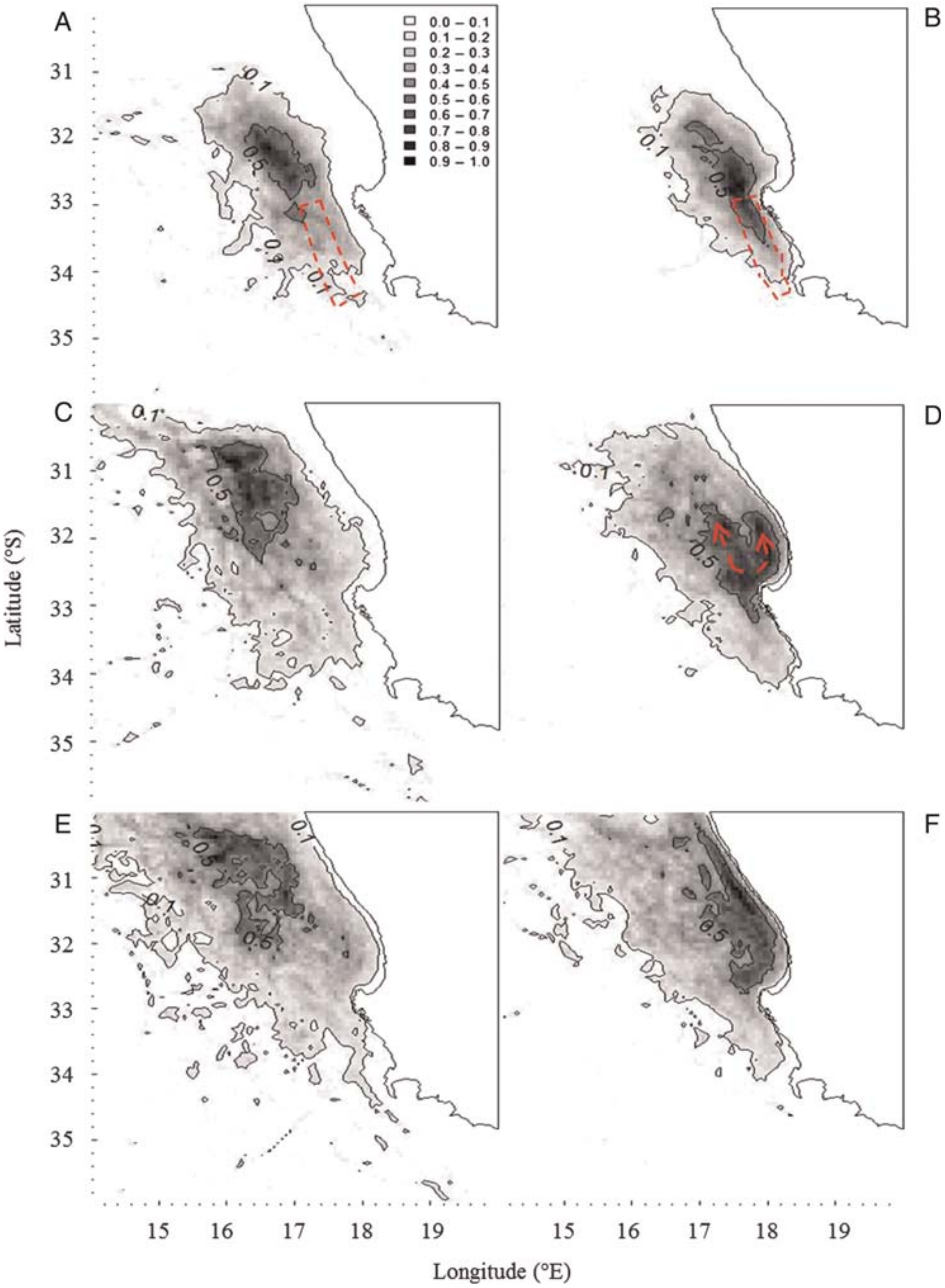

Fig. 3. Simulation S1: average dispersal patterns for *Merluccius paradoxus* (left column) and *Merluccius capensis* (right column) virtual ichthyoplankton are shown after 10 (**A** and **B**), 20 (**C** and **D**) and 30 (**E** and **F**) days of forward passive drift. Values shown are relative to the maximum value for each panel and two contour lines (0.1 and 0.5) have been added. The release areas are marked as a dotted line in A and B. The arrows in D show the two drift routes followed by individuals.

RESULTS

Ichthyoplankton drift routes

For simulations S1 and S2, results are presented as distribution maps, on which two contour lines are added for clarity (Figs 3 and 4). We drew these maps at times 10, 20 and 30 days by dividing the represented area into 100*100 cells, summing the number of virtual larvae in each cell over depth, averaging these values over all months and years of simulation, and then dividing them by the maximum number at the corresponding time. Results for passive drift forward in time after

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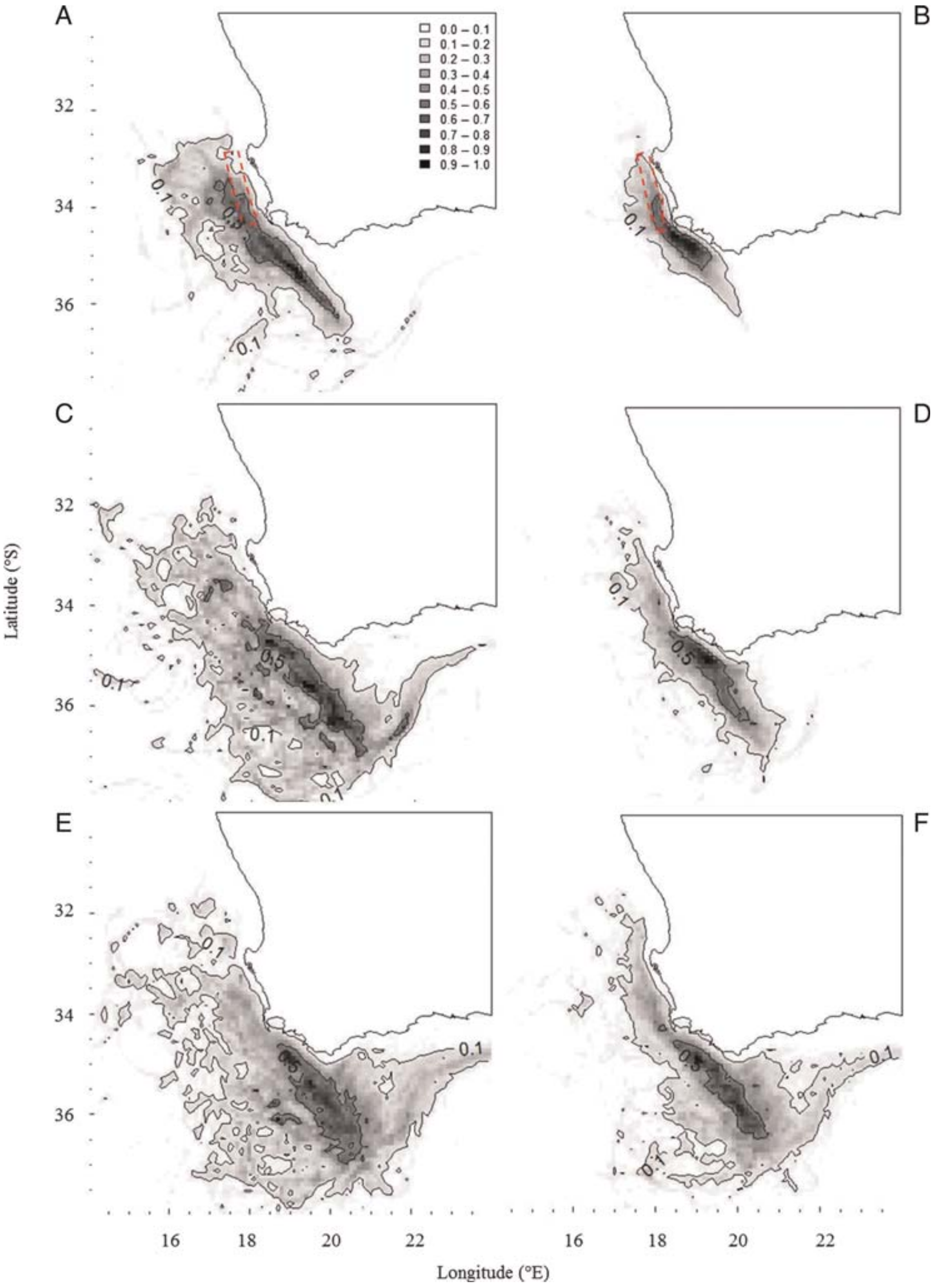

Fig. 4. Simulation S2: average dispersal patterns for *Merluccius paradoxus* (left column) and *Merluccius capensis* (right column) virtual ichthyoplankton are shown after 10 (**A** and **B**), 20 (**C** and **D**) and 30 (**E** and **F**) days of backward passive drift. Values shown are relative to the maximum value for each panel and two contour lines (0.1 and 0.5) have been added. The release areas are marked as a dotted line in A and B.

10 days show that individuals representing *M. paradoxus* ichthyoplantkon are located further north and offshore than *M. capensis* (S1; Fig. 3A and B). After 20 days, most *M. paradoxus* virtual larvae are still located offshore (Fig. 3C), whereas a significant number of *M. capensis* virtual larvae drift inshore along the western coast in the St Helena Bay area (32°S, 18°E) (Fig. 3D). Two main drift routes can be distinguished for *M. capensis* immediately off Cape Columbine, between 32 and 33°S (arrows in Fig. 3D). After 30 days of passive drift, most individuals for *M. paradoxus* remain offshore the western coast (Fig. 3E), whereas most individuals for *M. capensis* are located along the western coast (Fig. 3F). Results for passive drift 10, 20 and 30 days backward

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in time show that virtual larvae originating from the two release areas have similar distributions, although those representing *M. paradoxus* are more widespread than those representing *M. capensis* (S2; Fig. 4). The 30-day backward simulations show that the oldest virtual larvae could have originated mainly from the western Agulhas Bank, but also from the Cape Peninsula area or the offshore edge of central Agulhas Bank (Fig. 4E and F).

Ichthyoplankton transport to the SARP line

Simulation S3 shows that the spawning area is the factor explaining most of the variance in simulated values of transport success (56.21%) (Table II). Transport success to the SARP line is represented for the eight spawning areas in Fig. 5. It is highest for spawning areas 3 and 4, which are located directly south of the SARP line (Fig. 2). However, significant transport to the SARP line also occurs from spawning area 2, which is located north of the line, and from areas 5 and 6 which are located far south-east. Spawning depth is the next most important single factor explaining the variance (but only 2.61%, Table II). Successful transport to the SARP line decreases significantly with increasing spawning depth, from ~15% on average for 0–100 m to ~8% for 300–500 m. The interaction between spawning area and spawning depth contributes to 8.2% of the variance. In contrast, spawning month only explains 0.48% of the variance, which suggests that there is almost no seasonality in the simulated values of transport success to the SARP line.

Table II: Simulation S3: results of the sensitivity analysis (ANOVA) for factors used in simulated transport of individuals to the SARP line

Factor	Percentage variance explained	df	*P*-value
Spawning area	56.21	7	$<2.2 \times 10^{-16}$
Spawning month	0.48	11	1.92×10^{-3}
Spawning depth	2.61	2	$<2.2 \times 10^{-16}$
Spawning area*spawning month	3.43	77	9.72×10^{-11}
Spawning area*spawning depth	8.2	14	$<2.2 \times 10^{-16}$
Spawning month*spawning depth	0.27	22	0.85
Residuals	28.78	1594	

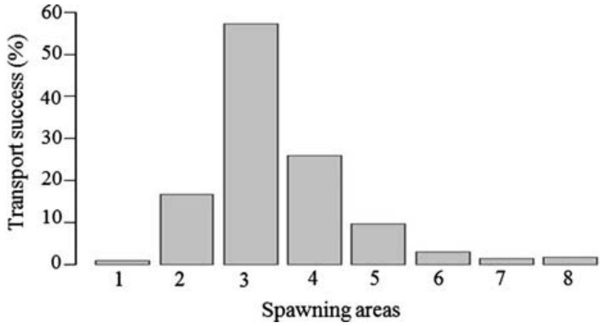

Fig. 5. Simulation S3: individuals transport success to the SARP line (%) in relation to spawning areas (see Fig. 2).

Ichthyoplankton transport to the nursery area

On average, a much lower percentage of individuals is transported to the nursery area (simulation S4) than to the SARP line (S3). In simulations for each species (S4a for *M. capensis*, S4b for *M. paradoxus*), the factors explaining most variance in simulated transport success are the same as in S3, i.e. spawning area, spawning depth and the interactions between these two factors (Table III). Transport success to the nursery area from the eight spawning areas is shown for both species in Fig. 6. Transport success to the nursery area for *M. capensis* (S4a) is low for all spawning areas with the highest percentage for area 8 (3.4%) located off the eastern Agulhas Bank. The lowest values of transport success are obtained for spawning areas 1 and 6, which are far from the nursery area; although a higher percentage of individuals spawned even further in area 5 make it to the nursery area. Transport success to the nursery area is higher for *M. paradoxus* than for *M. capensis* from the eight spawning areas especially from areas 5 (12.4%) and 8 (12.1%), which are located off the central and eastern Agulhas Bank, respectively (Fig. 6, S4b). As in S3, transport success to the nursery area decreases with spawning depth, and spawning month explains <1.5% of the variance for both species. However, for *M. capensis*, the interaction between spawning month and depth explains 7% of the variance (Table III). A strong seasonal pattern of transport success to the nursery area, with a peak from April to August, is obtained when spawning depth ranges between 0 and 100 m (Fig. 7A). An opposite seasonal pattern is observed for the depth level 100–300 m. The interaction between spawning month and depth explains little variance for *M. paradoxus* since the same seasonal pattern is observed for the three spawning depth levels with a slight peak between July and September (Fig. 7B). Another peak is present in

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Table III: Simulation S4: results of the sensitivity analysis (ANOVA) for factors used in simulated transport of individuals to the nursery area for M. capensis *(S4a) and* M. paradoxus *(S4b)*

Factor	Percentage variance explained S4a	p S4a	Percentage variance explained S4b	p S4b	df
Spawning area	11.74	$<2.2 \times 10^{-16}$	12.2	$<2.2 \times 10^{-16}$	7
Spawning month	1.07	6.82×10^{-3}	1.47	3.9×10^{-5}	11
Spawning depth	5.04	$<2.2 \times 10^{-16}$	14.61	$<2.2 \times 10^{-16}$	2
Spawning area*spawning month	4.29	0.02	3.96	0.01	77
Spawning area*spawning depth	5.00	$<2.2 \times 10^{-16}$	8.25	$<2.2 \times 10^{-16}$	14
Spawning month*spawning depth	7.00	$<2.2 \times 10^{-16}$	0.96	0.23	22
Residuals	65.82		58.5		1594

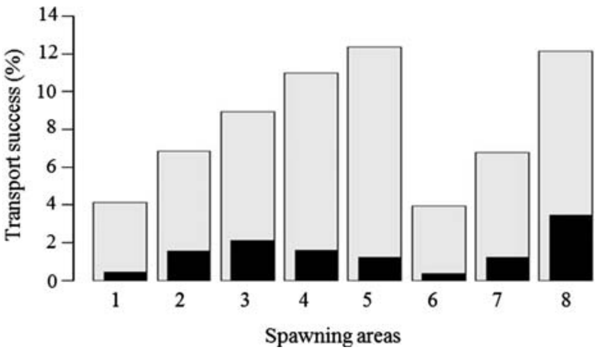

Fig. 6. Simulations S4a and S4b: individuals transport success to the nursery area (%) in relation to spawning areas (see Fig. 2) for *Merluccius capensis* (S4a, black bars) and *Merluccius paradoxus* (S4b, grey bars).

December for spawning depth levels 100–300 m and 300–500 m for both species.

When egg buoyancy is considered in the dispersal model (simulations S4c and S4d), results of the ANOVA show the same general trends as before, although more factors and their interactions explain a significant amount of the variance, particularly for *M. capensis* (Table IV). However, for both species, the lowest percentages of variance explained by single and interacting factors are obtained for the egg density factor. Yet, egg buoyancy has a significant effect on simulated mean egg depth, at least for some values of egg density and spawning depth (Fig. 8). Indeed, for spawning depth ranges 100–300 m and 300–500 m, the mean virtual egg ascent after 4 days is around 100 and 150 m, respectively, for the lowest and intermediate values of egg density (1.024 and 1.025 g cm^{-3}). In contrast, simulated egg depth decreases for individuals released from 0 to 100 m with the highest value of density (1.026). When buoyancy is ignored (simulations S4a and S4b), the mean virtual egg depth varies very slightly, around 15 m of descent for individuals released at 100–300 and 300–500 m and with almost no change when spawning depth ranges between 0 and 100 m (Fig. 8).

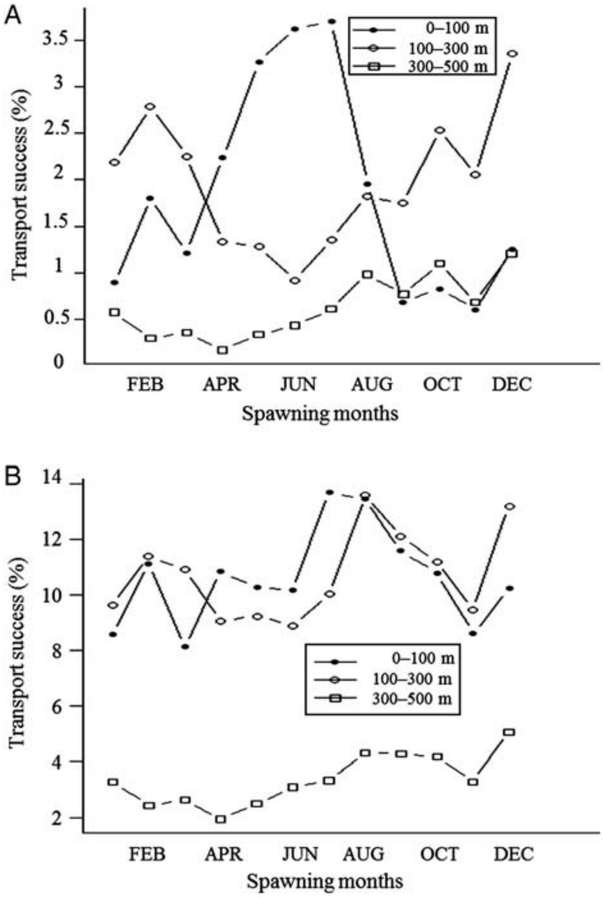

Fig. 7. Simulations S4a and S4b: individuals transport success to the nursery area (%) in relation to spawning months and spawning depth ranges (0–100 m, 100–300 m, 300–500 m) for *Merluccius capensis* (S4a, **A**) and *Merluccius paradoxus* (S4b, **B**).

DISCUSSION

A coastal jet current is known to transport water from the south coast of South Africa, particularly from the western Agulhas Bank, to the west coast (Shannon and Nelson, 1996; Hutchings *et al.*, 2002). This current has been identified both from hydrographic data and

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Table IV: Simulation S4: results of the sensitivity analysis (ANOVA) for factors used in simulated transport of individuals to the nursery area with egg buoyancy for M. capensis *(S4c) and* M. paradoxus *(S4d)*

Factor	Percentage variance explained S4c	p S4c	Percentage variance explained S4d	p S4d	df
Spawning area	4.14	$<2.2 \times 10^{-16}$	14.31	$<2.2 \times 10^{-16}$	7
Spawning month	4.06	$<2.2 \times 10^{-16}$	1.91	$<2.2 \times 10^{-16}$	11
Spawning depth	4.53	$<2.2 \times 10^{-16}$	5.48	$<2.2 \times 10^{-16}$	2
Egg density	2.15	$<2.2 \times 10^{-16}$	0.15	2.88×10^{-5}	2
Spawning area*spawning month	5.09	$<2.2 \times 10^{-16}$	5.14	$<2.2 \times 10^{-16}$	77
Spawning area*spawning depth	4.25	$<2.2 \times 10^{-16}$	3.02	$<2.2 \times 10^{-16}$	14
Spawning month*spawning depth	6.12	$<2.2 \times 10^{-16}$	2.08	$<2.2 \times 10^{-16}$	22
Spawning area*egg density	2.55	$<2.2 \times 10^{-16}$	0.56	5.68×10^{-5}	14
Spawning depth * egg density	3.13	$<2.2 \times 10^{-16}$	1.59	$<2.2 \times 10^{-16}$	4
Spawning month * egg density	4.03	$<2.2 \times 10^{-16}$	1.35	9.53×10^{-13}	22
Residuals	59.89		64.34		5008

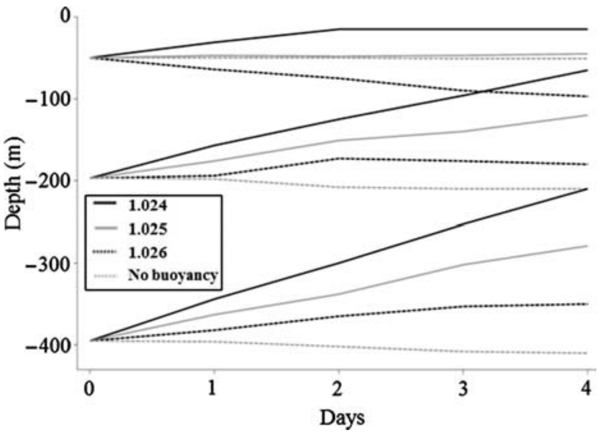

Fig. 8. Simulations S4c and S4d: time evolution of mean virtual egg depth with/without buoyancy included in the model, for three spawning depth ranges (0–100 m, 100–300 m, 300–500 m), and three egg densities (1.024, 1.025, 1.026 g cm^{-3}).

hydrodynamic simulations (Penven, 2000; Penven *et al.*, 2000; Chang, 2009; Veitch *et al.*, 2009). The role of this jet current in the transport of eggs and larvae of small pelagic fish from spawning areas on the Agulhas Bank to nursery grounds on the west coast of South Africa has also been well documented (Hutchings, 1992; Huggett *et al.*, 1998; 2003; Miller *et al.*, 2006). Our results suggest that this coastal current is also an important feature for the dispersal of Cape hake ichthyoplankton.

After 10 days of simulated passive transport, ichthyoplankton distributions are different for the two Cape hake species. After 20 days, results reveal two likely drift routes followed by *M. capensis* ichthyoplankton (simulation S1, Fig. 3D). These two main drift routes correspond to the jet current dividing into two branches, as identified by Boyd *et al.* (Boyd *et al.*, 1992), Penven (Penven, 2000) and Stenevik *et al.* (Stenevik *et al.*, 2008). Penven (Penven, 2000) showed that this division is due to the presence of Cape Columbine and studied the two branch features. The offshore route is coupled to a strong north western current and the inshore route to a weak current directed towards the coast. The patterns we obtained in our simulations suggest that ichthyoplankton of the two species follow partly distinct drift routes. *Merluccius paradoxus* is mostly transported offshore, whereas *M. capensis* follows mainly an inshore route (Fig. 3). The two species may therefore have different nursery areas, as proposed by Stenevik *et al.* (Stenevik *et al.*, 2008). These potentially different nursery areas are also consistent with the results of Le Clus *et al.* (Le Clus *et al.*, 2005a,b) that *M. paradoxus* juveniles are usually found further offshore than *M. capensis* juveniles (Fig. 1). Results from S2 likely highlight the spawning areas of Cape hake eggs and larvae sampled by Stenevik *et al.* (Stenevik *et al.*, 2008). The possible spawning areas derived from the simulations are the western Agulhas Bank (Fig. 4), as proposed by Stenevik *et al.* (Stenevik *et al.*, 2008), and to a lesser extent the Cape Peninsula area and the central Agulhas Bank (Hutchings *et al.*, 2002).

Simulations S3 and S4 were firstly designed to investigate possible reasons for the seasonality in Cape hake ichthyoplankton abundance observed by Grote *et al.* (Grote *et al.*, 2007), with a peak from June to October. Our results for S3 (transport from spawning areas to the SARP line, Table II) showed that spawning month explained very little of the variance in the simulated transport success. This result suggests that the seasonal pattern described by Grote *et al.* (Grote *et al.*, 2007) cannot be explained by seasonality in the conditions for transport of Cape hake ichthyoplankton to the SARP line, and is therefore likely a pattern of spawning

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seasonality, as the authors suggested. Our results for S4 (transport from spawning areas to the nursery areas, Table III) showed that spawning month again explained very little of the variance in the simulated transport success. However, a large effect of the interaction between spawning month and depth was revealed for *M. capensis*. For the spawning depth level 0–100 m, we obtained a seasonal pattern of transport success to the nursery areas with a peak from April to August (Fig. 7A). For the 0–100 m depth level, we also obtained a slight peak from July to September for *M. paradoxus* (Fig. 7B) that coincides with that observed by Grote *et al.* (Grote *et al.*, 2007). It is at 0–100 m depth level that Stenevik *et al.* (Stenevik *et al.*, 2008) also found most Cape hake eggs and larvae (0–50 m for *M. capensis* larvae, 50–100 m for *M. capensis* eggs and *M. paradoxus* eggs and larvae). Therefore, achieving more favorable conditions for transport to the coastal nursery areas could be a reason for Cape hakes to spawn in winter to early spring, at a time of the year where offshore transport by currents off Cape Columbine weakens (Stenevik *et al.*, 2008).

In both simulations S3 and S4, spawning area was the factor explaining most of the variance in simulated transport success (Tables II and III). In S3, we decided not to distinguish between the two Cape hake species as data in Grote *et al.* (Grote *et al.*, 2007) were presented for both. Results indicate that egg and larval sampling at the SARP line is likely dominated by spawning areas in the immediate vicinity of the line off the western Agulhas Bank, although more distant areas off the central and eastern Agulhas Bank also make a significant contribution to ichthyoplankton densities in the area (Fig. 5). In S4, we focused on transport to the nursery areas and therefore distinguished between the two Cape hake species that are believed to have different nursery areas (Figs 1 and 2). Like in S3, we found that the western edge of the Agulhas Bank was a favorable release area for transport to the coastal nursery areas, but also off eastern Agulhas Bank and off central Agulhas Bank (for *M. paradoxus*, in particular) (Fig. 6). From our simulations S2, S3 and S4, different favorable spawning areas can be described, which have already been identified for both species, off the western Agulhas Bank (Crawford *et al.*, 1987; Grote *et al.*, 2007), the central Agulhas Bank (Hutchings *et al.*, 2002) and the eastern Agulhas Bank (Assorov and Berenbeim, 1983; Burmeister, 2005).

Ichthyoplankton mortality due to starvation, predation and lethal temperatures, which are not considered in the model, is known to affect the transport success to the nursery areas (Bayley and Houde, 1989; Hutchings, 1992; Hutchings and Boyd, 1992). For Cape hakes, peak spawning coincides with a time of weak to moderate upwelling (Hutchings *et al.*, 2002; Grote *et al.*, 2007). This could be explained by a spawning strategy in line with the 'optimal environmental window' (Cury and Roy, 1989). Weak upwelling will decrease offshore loss and likely increase growth rates due to higher surface temperatures (although this is winter), but potentially increase starvation through a lack of phytoplankton food. Early life stages also have biological characteristics which could affect their transport success to the nursery areas. However, the consideration of egg buoyancy in our simulations of transport to the nursery areas (S4c and S4d) showed that despite having a significant effect on simulated mean egg depth (Fig. 8), egg buoyancy plays a negligible role in transport to the nursery area. In contrast, Parada *et al.* (Parada *et al.*, 2003) showed that for anchovy in the southern Benguela ecosystem, egg buoyancy had a major influence on ichthyoplankton transport. Whereas egg density explained the least variance in simulated transport success to nursery areas in our ANOVA (Table IV), egg density explained the most variance in Parada *et al.*'s (Parada *et al.*, 2003). Two main factors explain these contrasting results. First, the range of egg densities used in our simulations (1.024–1.026 g cm^{-3}), estimated from Sundby *et al.*'s (Sundby *et al.*, 2001) data, was narrow compared to that used in Parada *et al.* (Parada *et al.*, 2003) (1.021–1.027 g cm^{-3}). Conversely, the range of spawning depths we used (0–500 m for Cape hake spawning) was large compared to that used in Parada *et al.* (Parada *et al.*, 2003) (0–75 m for anchovy spawning). These two factors combine to produce a much smaller effect of egg buoyancy for Cape hake than for anchovy. Differences in spawning areas between the two species, and therefore in the routes they follow from spawning to nursery areas, may also partly explain the observed differences in the influence of egg buoyancy.

In our larval dispersal model, we decided to not include larval vertical migration behavior or constraints on the vertical distribution of larvae. The vertical movements of Cape hake larvae remain unknown as to date no study has specifically focused on their vertical distribution over sufficiently small temporal scales. Sakuma *et al.* (Sakuma *et al.*, 2007) found no significant day–night difference in the vertical distribution of *M. productus* larvae, but did observe a positive correlation between the temperature of the mixed layer and the abundance of *M. productus* larvae caught. They suggested that hydrographic conditions influence the passive transport of larvae and that the correlations obtained can be explained by movement of water masses in the study area. These results would suggest that water movements are responsible for the observed

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depth distribution of larvae rather than active vertical behavior. Water movements like those described by Sakuma *et al.* (Sakuma *et al.*, 2007) are represented in the oceanographic model that underlies our larval transport simulations. Nevertheless, this and other similar studies (Sabatés, 2004) cannot eliminate the possibility of vertical migratory behavior for Cape hakes. Although the effects of such movements have not been examined here, we can hypothesize that they would be most important for hake larvae residing in the upper ~100 m of the water column due to the presence of distinct surface and sub-surface water masses with different and often opposing current velocities. In the Benguela ecosystem, simulation studies on small pelagic ichthyoplankton have indicated that forcing larvae to remain below the Ekman layer increased retention within coastal nursery areas (Mullon *et al.*, 2003; Stenevik *et al.*, 2003), and that including diurnal vertical migration increased transport of larvae to coastal nursery areas (Parada *et al.*, 2008).

Results from our biophysical model can also be discussed with respect to the limitations of the physical model. The solution of the hydrodynamic model was forced with monthly mean climatology which includes neither interannual nor intra-month (day to week) variability. Although interannual and intra-month variability are not directly forced by the atmosphere in this configuration (Chang, 2009), intrinsic oceanic variability is allowed to develop in the model, producing temporal variations in oceanic fields on all time scales. This, along with intense seasonal upwelling in the system, contributed to the significant variability obtained in our results. The use of this climatologically forced ocean model is further justified by the fact that spawning regions of Cape hakes are located offshore where the effects of large-scale currents, such as the Agulhas and Benguela Currents, are dominant. Nevertheless, future studies should use forcing fields including interannual and intra-month variability to more accurately represent long-term current fluctuations.

Shallow regions, within the 50 m isobath, close to the coast and within the many bays along the south coast, are known to experience rapid reversals in wind direction (over the period of hours to days). The average influence of these small events may be to increase nearshore retention, an effect that is not well represented in our oceanographic model due to the 8 km spatial resolution. This potential source of bias is partially compensated for by the relatively wide offshore extent of Cape hake recruitment zones (out to 100 or 200 m depth). Furthermore, accurately representing these fluctuations is quite difficult, requiring nested oceanographic simulations at finer spatial resolutions.

The offline method used for running our individual-based model is also an approximation as it filters some high-frequency signals in the circulation. The model does not include vertical diffusion, which would increase the variance of larval depths in the results and potentially modify horizontal transport patterns. This limitation should be addressed in future studies via the integration of the vertical diffusivity coefficient from the hydrographic model in the larval transport model. Distribution patterns could also be modified by horizontal diffusion. However, there is still little information for the parameterization of this process in the region.

Biophysical models were previously used in the southern Benguela to study eggs and larval dynamics of anchovy (Huggett *et al.*, 2003; Mullon *et al.*, 2003; Parada *et al.*, 2003, 2008) and sardine (Miller *et al.*, 2006). The results from our study linked with the results observed for anchovy and sardine provide general conclusions regarding the early life history of these species in the southern Benguela. Spawning areas for anchovy are located on the south coast of South Africa, from the shore to the 200 m isobath, and the nursery area is located along the west coast, out to the 500 m isobath (Huggett *et al.*, 2003). Therefore, transport success to nursery areas of anchovy in the southern Benguela relies on an alongshore transport mechanism from the south coast to the west coast. Spawning and nursery areas for sardines are located, respectively, all along the southern Benguela ecosystem coast and on the upper west coast, from the shore to the 500 m isobath (Miller *et al.*, 2006). Therefore, the transport success to the nursery areas for sardine relies on an alongshore transport mechanism, similar to that for anchovy, and on a retention mechanism within the west coast. Cape hake spawning areas are located off the continental shelf (from the 200 to the 2000 m isobaths) and nursery areas are located along the coast. Larval transport success for Cape hakes in the southern Benguela therefore relies on a cross-shore transport mechanism between offshore spawning areas and onshore nursery grounds. Some of the major differences observed in the ecology of anchovy, sardine and hake in the southern Benguela ecosystem, especially differences in spawning seasonality, probably reflect the favored environmental conditions for alongshore versus cross-shore transport.

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Lysel GARAVELLI

Etude de la connectivité larvaire pour la gestion des ressources marines.
Application au gastéropode *Concholepas concholepas* (loco) au Chili.

Assessment of larval connectivity for the management of marine resources.
Application to the gastropod *Concholepas concholepas* (loco) in Chile.

Résumé

Au Chili, l'une des principales ressources exploitées par les pêcheries artisanales benthiques est le gastéropode marin *Concholepas concholepas*, plus communément appelé « loco ». Des signes de surexploitation de cette espèce sont apparus à la fin des années 1980 et différents modes de gestion ont été appliqués. Le plan de gestion actuel correspond à la mise en place de droits d'usage territoriaux pour une multitude de petites zones distinctes gérées de manière indépendante. L'un des points clés permettant d'étudier l'efficacité de ce mode de gestion est d'estimer les échelles auxquelles ces zones sont connectées par la dispersion larvaire. L'objectif de cette thèse est d'évaluer ces échelles et les patrons de connectivité du loco le long du Chili. J'ai d'abord mis en évidence des manques dans la connaissance des facteurs influençant potentiellement la connectivité larvaire du loco. J'ai participé à combler ces manques par des expériences en laboratoire montrant un comportement migratoire vertical nocturne des larves de premier stade du loco. Par la suite, j'ai développé un modèle biophysique de dispersion larvaire appliqué au loco en intégrant les effets de plusieurs facteurs hétérogènes le long de la côte chilienne : habitat disponible, fécondité, transport, croissance, migration verticale, et mortalité larvaires. J'ai utilisé ce modèle pour établir des matrices de connectivité entre zones le long du Chili. A partir de ces matrices, j'ai utilisé un algorithme de partitionnement pour définir des sous-populations de loco indépendantes afin d'orienter le mode de gestion actuel du loco vers une échelle plus régionale, en meilleure adéquation avec l'écologie de l'espèce.

Mots-clés : pêcherie, gestion, loco, connectivité, biologie, écologie, dispersion larvaire, expériences en laboratoire, modélisation biophysique

Abstract

In Chile, one of the commercial species targeted by benthic fisheries is *Concholepas concholepas*, commonly named "loco". It was a highly valuable benthic fishery until the end of the 80's. Then the resource became over-exploited and different management plans were applied to ensure the sustainability of the fishery. The current management plan is the establishment of territorial users' rights in distinct areas managed independently. One of the main challenges to ensure the efficiency of this management plan is to estimate the scales at which these areas are connected by larval dispersal. The main objective of the thesis is to evaluate loco connectivity patterns and scales along the Chilean coast. I first highlighted gaps in knowledge of factors potentially influencing larval connectivity of loco. I helped fill these gaps by laboratory experiments showing a nocturnal vertical migration behavior for first stage loco larvae. Subsequently, I developed a biophysical larval dispersal model integrating the effects of several heterogeneous factors along the Chilean coast: available habitat, fecundity, larval transport, growth, vertical migration, and mortality. I used this model to establish connectivity matrices between areas along Chile. From these matrices, I used a clustering algorithm to identify independent loco subpopulations in order to propose a regional management plan, in line with the ecology of the species.

Keywords: fishery, management, loco, connectivity, biology, ecology, larval dispersal, laboratory experiments, biophysical model