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Wind-induced variability in larval retention in a coral reef system: A biophysical modelling study in the South-West Lagoon of New Caledonia

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ABSTRACT

In the present work, a biophysical dispersal model is used to understand the role of the physical environment in determining reef fish larval dispersal patterns in the South-West Lagoon of New Caledonia. We focus on a reef fish species, the humbug damselfish *Dascyllus aruanus*, to investigate seasonal variability of simulated larval retention at the scale of a reef patch and at the scale of the lagoon, and to explore links between larval retention and wind variability. The model shows that retention exhibits considerable temporal variability and periodically reaches values much larger than anticipated. Non-zero larval settlement occurs over a large part of the lagoon. Nevertheless, settlement values decrease quickly away from the natal reef and mean dispersal distances are of order 25–35 km. Cross-correlation analyses indicate that weather conditions characterized by strong south east trade winds lead to low retention rates at both local (reef) and regional (lagoon) scales. By contrast, subtropical weather conditions characterized by weak winds result in high retention rates. These results suggest that large-scale weather regimes can be used as proxies for larval retention of the humbug damselfish in the South-West Lagoon of New Caledonia. Nevertheless, relatively small mean dispersal distances suggest that metapopulation dynamics occur on relatively small spatial scales.

1. Introduction

The fragmentation of marine coastal habitats results in a geographical separation of local populations. Links among local populations are possible via the movement of individuals. When these connections are strong enough to have a measurable impact on local populations' growth rates, these populations constitute a metapopulation (Sale et al., 2006) and the exchanges between them are referred to as demographic connectivity (Cowen et al., 2007). Knowledge of demographic connectivity is required to understand metapopulation dynamics and the persistence and resilience of marine populations to anthropogenic pressures (Bernhardt and Leslie, 2013), particularly in the context of implementing networks of marine protected areas (Sale et al., 2005). While progress has been made with older life stages, the larval dispersal component of connectivity has long been viewed as a black-box due to the many difficulties associated with directly observing a multitude of small individuals in a marine environment. In the past decade, advances in biophysical modelling (Miller, 2007) and empirical techniques for connectivity assessment (e.g. genetic parentage analysis using DNA microsatellites and otolith transgenerational tagging) have permitted detailed investigation of early life dispersal (reviewed in Levin, 2006; Cowen and Sponaugle, 2009; Leis et al., 2011; Kool et al., 2013), especially in coral reef systems (Jones et al., 2009). Although numerous marine species have pelagic larval durations that may last several weeks, Cowen et al. (2000) showed more than 10 years ago that the spatial scales of

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larval dispersal were not as large as anticipated (only 10–100 km vs. several hundreds of km as was previously thought). This result suggested that larval local retention (i.e. the ratio of the number of larvae that settled back to their natal population to the total number of larvae released there, Botsford et al., 2009) could be important for the functioning and structure of marine populations. Since then, the idea of small scale demographic connectivity ensured by larval retention has been supported by modelling studies e.g. in the Great Barrier Reef in Australia (James et al., 2002), the Caribbean (Cowen et al., 2006; Chérubin et al., 2011), Hawaii (Christie et al., 2010) and the Indo-Pacific Ocean (Treml et al., 2012). Field observations also reported high levels of self-recruitment (i.e. the ratio of the number of larvae that settled back to their natal population to the total number of larvae that settled there, Botsford et al., 2009) e.g. for reef fish species in Papua New Guinea (Almany et al., 2007; Planes et al., 2009; Saenz-Agudelo et al., 2012; Berumen et al., 2012), the Caribbean (Hogan et al., 2012) and the Great Barrier Reef (Harrison et al., 2012; van der Meer et al., 2012).

The present challenge of larval dispersal research is to find out if this relatively "closed" population dynamics is the rule or the exception, and to understand its causes: does it result from local oceanography, larval life history traits, larval behavior, or a combination of these biotic and abiotic drivers? Local oceanography (currents, water residence time) has been shown to be of great importance for explaining relatively closed population dynamics (Paris and Cowen, 2004; Treml et al., 2012). Among life history traits, the length of the larval precompetency period, i.e. the period of time in which larvae may not settle (Jackson and Strathmann, 1981), has been shown to be a key driver for local retention within the natal population (Black and Moran, 1991; Paris and Cowen, 2004; Treml et al., 2012). Whereas the precompetency period of reef-building coral larvae is relatively short (between 2 and 5 days, Heyward and Negri, 2010), it can reach several weeks for other reef species (Staaterman et al., 2012; Butler et al., 2011; Soria et al., 2012). Concerning larval behavior, several studies demonstrate that fish larvae have sensory capabilities coupled with strong swimming capabilities (Leis, 2010) that facilitate local retention through homing. For instance, larvae are capable of olfactory discrimination and prefer the odor of their home reef (Gerlach et al., 2007). Acoustic (e.g. Radford et al., 2011) and sun compass mechanisms (Mouristen et al., 2013) have also been suggested to allow pelagic larvae to locate their natal reef. Modelling studies show that early active larval movement associated with orientation behavior is a mechanism for self-recruitment (James et al., 2002; Paris et al., 2005; Staaterman et al., 2012).

In this study we investigate the roles of local meteo-oceanography, precompetency period and homing behavior in determining reef fish larval retention in the South-West Lagoon of New Caledonia (SWL). The oceanography of the SWL has been particularly well studied over the last 40 years through in situ measurements and numerical models that provide insights on sediment transport and biogeochemical dynamics in the lagoon (Jarrige et al., 1975; Douillet, 1998; Faure et al., 2010; Ouillon et al., 2010; Fuchs et al., 2012). Previous studies using Lagrangian tracers show that the SWL is well mixed by the joined action of tide currents, winds and swell which results in a rather low average water residence time (defined as the time needed for a water particle to leave the lagoon) of 11 days (Jouon et al., 2006; Ouillon et al., 2010). If we assume, as a first approximation, that larvae of marine species are passive entities during their precompetency period, and are therefore advected like water parcels, the short water residence time found in the SWL has enormous consequences for larval retention: species with a larval precompetency period longer than 11 days will be mostly flushed out of the lagoon.

In this study we focus on a coral reef damselfish, *Dascyllus aruanus*, a species that has precisely a precompetency period of ~11 days (see Section 2.3). We use a three-dimensional biophysical model to investigate larval retention of *Dascyllus aruanus* and its seasonal variability inside the SWL. We first describe the study species and region focusing on the oceanographic context. The biophysical model is then described and used to assess larval retention at two different spatial scales: SWL scale ("natal lagoon retention") and local patch reef scale ("natal reef retention"). We define (1) "natal lagoon retention" and (2) "natal reef retention" as the ratio of the number of larvae released at the natal reef that settled (1) on any of the settlement reefs including the natal reef or (2) only on the natal reef, to the total number of larvae released at the natal reef. Larval retention was simulated under two opposite hypotheses regarding homing behavior: a strict-homing hypothesis and a no-homing hypothesis. Finally, to stress out the role of the local meteo-oceanography on larval retention, our results are linked to the synoptic-scale variability of the low-level circulation in New Caledonia that we can describe through the so-called weather regimes (Lefèvre et al., 2010). A sensitivity study is conducted using a longer (3 weeks) precompetency period and different larval release depths.

2. Material and methods

2.1. Study area

New Caledonia (19–23°S, 163–168°E) is an island located in the South West Tropical Pacific 1500 km east of Australia. The New Caledonia lagoon is surrounded by a barrier reef of exceptional size (1600 km in length, the second longest double barrier reef in the world, after the Great Barrier Reef) and is listed as a UNESCO World Heritage Site since 2008. The work presented here focuses on the South-West Lagoon of New Caledonia (SWL) which surrounds Nouméa, the island's main city (Fig. 1). A network of 13 Marine Protected Areas (MPAs) has been established in this area to mitigate the increasing anthropogenic pressure on the lagoon. The SWL covers an area of about 2000 km^2 delimited by the coast on the eastern side and the barrier reef on the western side, extending from the Mato pass in the south to the Ouaraï pass in the north. Depth averages 20 m and varies from less than 1 m around islets to 60 m inside canyons. The lagoon ranges in width from 5 km (northern limit) to 40 km (southern limit) with a length along the north-west/south-east axis of about 100 km, and is connected with the Pacific Ocean by several deep passes.

2.2. Local meteo-oceanography in summertime

The two main forces driving circulation in the SWL are tides and winds (Douillet, 1998). Wind-induced current velocities are approximately one order of magnitude higher than velocities generated by tides (Ouillon et al., 2010). Austral summer (from October to March) is dominated by southeasterly trade winds blowing from 60° to 160° at speeds averaging 8 m s^{-1} (Pesin et al., 1995). Recently, Lefèvre et al. (2010) identified four weather regimes occurring in New Caledonia during austral summer through an objective classification applied to remote sensed winds for nine summer seasons from 1999 to 2008 (Table 1). Three of these weather regimes (regimes 1, 3 and 4) exhibit low-level circulation dominated by SE trade winds. Regime 1 captures a strong, near steady and alongshore trade wind flow, averaging 8 m s^{-1} and is referred to here as "Strong SE Trade-wind". This regime is the most frequent, accounting for slightly less than a third of the austral summer days. Long spells of regime 1 are more favorable to the flushing of the lagoon by driving a general north-west drift. The SWL is thus mainly fed with oceanic waters at its southern end, through the different passes of the barrier reef as described