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Low incidence of clonality in cold water corals revealed through the novel use of a standardized protocol adapted to deep sea sampling

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ABSTRACT

Sampling in the deep sea is a technical challenge, which has hindered the acquisition of robust datasets that are necessary to determine the fine-grained biological patterns and processes that may shape genetic diversity. Estimates of the extent of clonality in deep-sea species, despite the importance of clonality in shaping the local dynamics and evolutionary trajectories, have been largely obscured by such limitations. Cold-water coral reefs along European margins are formed mainly by two reef-building species, *Lophelia pertusa* and *Madrepora oculata*. Here we present a fine-grained analysis of the genotypic and genetic composition of reefs occurring in the Bay of Biscay, based on an innovative deep-sea sampling protocol. This strategy was designed to be standardized, random, and allowed the georeferencing of all sampled colonies. Clonal lineages discriminated through their Multi-Locus Genotypes (MLG) at 6–7 microsatellite markers could thus be mapped to assess the level of clonality and the spatial spread of clonal lineages. High values of clonal richness were observed for both species across all sites suggesting a limited occurrence of clonality, which likely originated through fragmentation. Additionally, spatial autocorrelation analysis underlined the possible occurrence of fine-grained genetic structure in several populations of both *L. pertusa* and *M. oculata*. The two cold-water coral species examined had contrasting patterns of connectivity among canyons, with among-canyon genetic structuring detected in *M. oculata*, whereas *L. pertusa* was panmictic at the canyon scale. This study exemplifies that a standardized, random and georeferenced sampling strategy, while challenging, can be applied in the deep sea, and associated benefits outlined here include improved estimates of fine grained patterns of clonality and dispersal that are comparable across sites and among species.

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1. Introduction

Limited accessibility of the deep sea represents a major obstacle for scientific research. In particular, conducting a rigorous sampling strategy is *de facto* challenging. This logistical difficulty partly explains gaps in our knowledge of major ecological and/or evolutionary trends shaping the evolution and dynamics of deep sea species and populations (but see Pawlowski et al., 2007; Van Dover et al., 2002; Vrijenhoek, 1997; Won et al., 2003), though recent improvements in technology have increased access to deep sea ecosystems. Notably, the empirical studies dedicated to fine-grained patterns of relatedness and associated key processes (such

as spatial distribution of genotypes and recruitment) within populations often require standardized and high density sampling to allow thorough understanding of small scale distribution and dynamics and rigorous inter-site comparisons. Yet, standardization of sampling strategies is rare because the collection of samples is time consuming and technically difficult.

Among deep sea ecosystems discovered during recent decades, cold-water coral (CWC) reefs have been the subject of increasing research efforts to improve our understanding of their extent and role in supporting biodiversity along continental margins. Despite recent efforts, exploration of CWC reefs remains preliminary and fragmentary. These organisms represent the structural basis of key deep ecosystems, forming important three dimensional biological structures (Rogers, 1999). Similar to their shallow-water counterparts, CWC reefs support high biodiversity and biomass (Freiwald et al., 2004; Roberts et al., 2006), providing habitat and nursery for

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numerous marine species (Baillon et al., 2012). Recently, it has been demonstrated that these ecosystems constitute underappreciated hotspots for carbon and nutrient cycling along continental margins (Cathalot et al., 2015). Cold-water coral reefs are distributed worldwide (Cairns, 1994; Zibrowius, 1980), and are particularly prevalent along the European Atlantic continental margin (Freiwald and Roberts, 2005). They are generally reported at depths between 200 and 1000 m, but occasionally are found as shallow as 35 and as deep as 4000 m. The two main reef-building CWCs are the species *Lophelia pertusa* and *Madrepora oculata*, which co-exist in most of the reefs observed in the Northeastern Atlantic Ocean (Arnaud-Haond et al., 2015). These two widely distributed species are known for being partially clonal, i.e. able to alternate between sexual reproduction through the production of gametes, and asexual, vegetative growth through fragmentation (Roberts et al., 2006). In some locations, such as along the European continental margin (Freiwald et al., 1999) and off the southeastern United States (Ross and Nizinski, 2007), *L. pertusa* and *M. oculata* form large carbonate mounds, or reef bioherms, composed of carbonate mud and the skeletal remains of the corals (Roberts et al., 2006). Such bioherms allow corals to grow in an elevated position in the water column where faster flowing waters deliver increased levels of organic particulate food supply (Freiwald, 2002).

In CWC, sexual reproduction occurs either in the water column or in the maternal colony through the fertilization of eggs. Gametes then develop into planula larvae that are dispersed via the water column. Their post-dispersal recruitment initiates the formation of a colony, corresponding to a unique genetic individual, as observed for the coastal gorgonian *Corallium rubrum* (Costantini et al., 2007a, 2007b). Clonal reproduction is expected to occur through the fragmentation of colonies, where broken fragments form new colonies. This mimics the phenomenon of clonal elongation, which is well known for terrestrial and marine plants (Arnaud-Haond et al., 2012; Douhovnikoff et al., 2005; Schmid and Harper, 1985). The release of asexual larvae may represent a second source of clonal reproduction, although Dahl et al. (2012) suggest that asexually produced larvae do not occur in *L. pertusa*. Fragmentation leads to the potential for multiple occurrences of a genet, a unique genetic individual, occurring in different geographic locations as ramets deriving from a common sexual event (*sensu* Eriksson (1993)). Partial clonality deeply influences the population dynamics and evolutionary trajectories, including the ability to disperse, occupy space and colonize new environments during periods of climate change, or to recolonize depleted environments such as reefs heavily impacted by deep sea trawling (Fossa et al., 2002; Roberts and Hirshfield, 2004). Notably, this life-history trait impacts the fine-grained (i.e. intra-population) genotypic and genetic structure, as shown for both terrestrial (Vekemans and Hardy, 2004) and marine species (Becheler et al., 2010; Blanquer et al., 2009; Dahl et al., 2012; Hammerli and Reusch, 2003; Shurin et al., 2009), through spatial competition among established clones and equilibrium between migrant recruitment and vegetative growth. Statistical descriptors of clonality are largely influenced by sampling scheme and strategy (Arnaud-Haond et al., 2007) and relevant assessment of clonal features requires standardized sampling. The extent of clonality and the estimate of fine-grained genetic structure should account for multiple occurrences of identical genotypes (ramets). It is therefore necessary to obtain geographical information for each sampling unit (Arnaud-Haond et al., 2007).

Although the literature on clonal reproduction is abundant for shallow-water corals (Baums et al., 2014, 2006; Boulay et al., 2012; Coffroth and Lasker, 1998; Foster et al., 2007; Hunter, 1993; Pinzón et al., 2012), very few studies have thus far addressed the issue of clonal versus sexual reproduction in CWC. An assessment of the degree of clonality, in Eastern North Atlantic *L. pertusa* reefs,

suggests highly variable levels of clonal richness among sites, from cases in which all colonies exhibit distinct genotypes, to the other extreme where most colonies originated from the same clonal lineage and share the same multi-locus genotype (MLG) (Le Goff-Vitry et al., 2004). The highest rates of clonality could not be explained by edge effects of species range known to favor a high rate of clonality (Alberto et al., 2005; Baums et al., 2006), as the studied sites were well within the range of *L. pertusa* populations. Furthermore, samples were obtained via blind trawling so observations may have accurately reflected among-site variation of clonality, but may have been due to the technical artifact of analyzing distinct parts of a single colony fragmented during the trawling, leading to a) an overestimation of intra-site clonality and b) a possible associated overestimation of genetic structure among reefs. In contrast, a local and thorough analysis of a deep reef in Sweden that was exhaustively sampled with geolocation of colonies to map clonal lineages, showed extensive clonal elongation reaching tens to hundreds of meters (Dahl et al., 2012). However, this last study reported results for a single reef of *L. pertusa*, therefore, the extent of clonality for this species and its variation across larger spatial scales remains poorly understood. No genetic studies performed on *M. oculata* exist. Here, we aimed to:

1. Propose a realistic and tested sampling strategy and protocol for deep sea organisms, involving georeferenced sampling according to random coordinates in quadrats of standardized shape and size,
2. Characterize the spatial pattern and extent of clonality in both *L. pertusa* and *M. oculata* reefs at the scale of the Bay of Biscay, using seven and six microsatellites markers, respectively, to discriminate MLGs,
3. Present an analysis of the regional and fine-grained spatial genetic structure within and among reefs.

2. Material and methods

2.1. Study sites

The continental slope of the Bay of Biscay is regularly cut by a succession of canyons connecting the continental shelf and the abyssal plain. In this area, CWC reefs are typically located between 600 and 900 m depth, standing mostly above soft sediment. In general, reefs in Bay of Biscay are relatively sparse, with heterogeneous density, while size of colonies varies among sites. Eight canyons were explored and sampled during the BobEco cruise

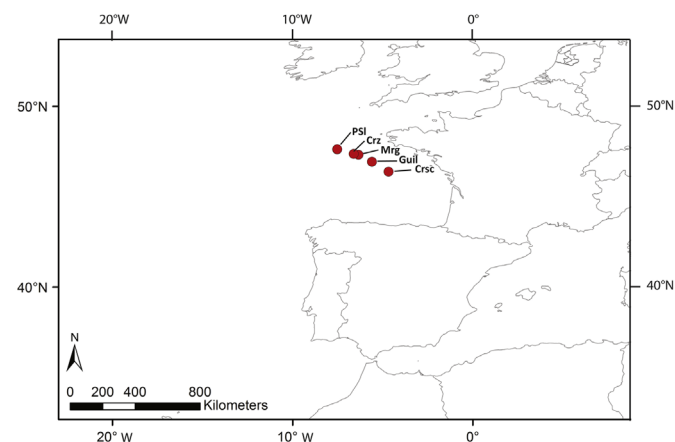


Fig. 1. Canyons sampling locations in the Bay of Biscay in the NE Atlantic Ocean. These reefs are colonized by both *Lophelia pertusa* and *Madrepora oculata*. Canyons of: le Croisic (Crsc); le Guilvinec (Guil); Morgat (Mrg); Crozon (Crz); Petite Sole (PS).

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