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NOTE

Recruitment and mortality of the temperate coral *Cladocora caespitosa*: implications for the recovery of endangered populations

Diego K. Kersting · Núria Teixidó · Cristina Linares

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Abstract Long-lived species are characterized by low recruitment and mortality. In these species, longevity buffers low recruitment, but when catastrophic disturbances alter mortality, recruitment becomes critical for population recovery. In this study, we assessed basic biological traits—recruitment, post-settlement growth, and the mortality of juvenile corals—and related these factors to the adult mortality of one of the most important populations of the Mediterranean reef-building coral *Cladocora caespitosa* over a period of 6 yr. Adult mortality and recruitment rates were low ($\sim 1\ \%$ and 0.30 recruits $\mathrm{m}^{-2}\ \mathrm{yr}^{-1}$, respectively), whereas the juvenile colony mortality was comparatively high (29 % in the smallest size-class, <5 polyps). The low recruitment rates will hardly balance the recurrent climate-related mortality that has affected this population. Conservation plans and inclusion in the protection lists are urgently needed, given the escalating threats and slow dynamics of this species.

Keywords Recruitment · Mortality · *Cladocora caespitosa* · Long-lived species · Mediterranean Sea

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D. K. Kersting (✉) · C. Linares
Departament d'Ecologia, Universitat de Barcelona (UB), 08028 Barcelona, Spain
e-mail: diegokersting@gmail.com

N. Teixidó
Institute of Marine Sciences (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

Introduction

Marine coastal habitats are being affected by multiple stressors such as overexploitation, habitat loss, invasive species, and climate change (Chapin et al. 2000; Halpern et al. 2008; Polunin 2008). Given these cumulative disturbances, corals are declining worldwide at unprecedented rates (Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Knowledge of population dynamics, especially demographic processes, is crucial to assess the viability of coral populations (Done 1992; Bellwood et al. 2004; Hughes et al. 2010). Recruitment and survival are essential for population recovery after disturbances (Connell et al. 1997; Hughes et al. 2000; Adjeroud et al. 2007; Coles and Brown 2007), and these traits are even more critical in long-lived, slow-growing species (Hughes and Tanner 2000). Long-lived species are characterized by low recruitment rates. Whereas in natural conditions, these low rates are buffered by their longevity and low adult mortality (Edmunds 2000; Hughes and Tanner 2000; Adjeroud et al. 2007; Coles and Brown 2007; Linares et al. 2007), under catastrophic impacts, these species are highly vulnerable due to their slow dynamics (Hughes and Tanner 2000; Linares et al. 2007).

The endemic scleractinian *Cladocora caespitosa*, the unique zooxanthellate reef-building coral from the Mediterranean Sea, is a long-lived, ecosystem engineer species whose bioconstructions have become very rare in the Mediterranean (Kružić and Benković 2008; Kersting and Linares 2012). One of the major threats to this coral in recent years has been recurrent warming-related mass mortalities, which have seriously affected *C. caespitosa* in many Mediterranean sites (Rodolfo-Metalpa et al. 2005; Garrabou et al. 2009; Kersting et al. 2013a). There have been several studies of the population dynamics of tropical

Fig. 1 *Cladocora caespitosa* recruit (*scale bar* 0.5 cm)

corals (e.g., Edmunds 2000; Hughes and Tanner 2000; Smith et al. 2005; Guzner et al. 2007), temperate gorgonians (Linares et al. 2007, 2008), and solitary corals (Goffredo et al. 2004) during the last decade, but no study of the recruitment and natural mortality of temperate colonial scleractinian corals, particularly of *C. caespitosa*.

The main goal of this study was to assess recruitment, post-settlement growth, and the mortality of juvenile corals and to relate these factors to the adult mortality of one of the most important *C. caespitosa* populations in the Mediterranean Sea over a period of 6 yr. This information is crucial for evaluating the potential resilience of the endangered reefs of this species.

Materials and methods

We studied a population of *C. caespitosa* in Illa Grossa Bay (at 5–20 m depth; 39°53.825′N, 0°41.214′E; Columbretes Islands, NW Mediterranean; Kersting and Linares 2012). Adult mortality rates were assessed from 2006 to 2012, and recruitment rates were measured between 2007 and 2012.

Recruitment was quantified annually using 50 × 50 cm quadrats in permanent plots on subvertical and horizontal substrata (24 and 12 plots, respectively). Recruitment was taken to be the number of new individuals who settled and survived long enough to be recorded, as in other coral recruitment surveys (e.g., Connell et al. 1997; Salinas-de-Leon et al. 2013). Surveys were made approximately five months after *C. caespitosa* reproduces, when algal cover is lowest (March, i.e., the end of winter–beginning of spring), thus maximizing the detection of new recruits. Using the naked eye, the smallest recruit we observed was a two-polyp stage (Fig. 1), which should be at most 1 yr old (see below). In addition to the permanent quadrats, between 25 and 50 haphazardly placed quadrats were surveyed annually in the same location and depth range in order to obtain more recruitment data covering a larger area within the bay.

Annual juvenile mortality rates and colony growth through budding (asexual buds are produced by reorganizing a small area on the exosarc; Rodolfo-Metalpa et al. 2008) were obtained by monitoring permanent plots. Juvenile colonies were assigned to three size-classes, <5, 5–10, and >10 polyps, with colony diameters of approximately <1, 1–1.5, and >1.5 cm, respectively. The number of new fully developed buds in each colony was normalized to the total number of polyps in the colony (see Rodolfo-Metalpa et al. 2008) in order to compare budding rates among size-classes (Fig. 2).

Natural adult mortality was estimated by monitoring 250 adult colonies (colony diameter >3 cm) annually along a permanent transect in the study area between 5 and 20 m depth. The initial position of the transect was chosen randomly, and each colony was tagged using numbered plastic tags attached to the rock with putty. Sketches and photographs of each colony were taken annually. Adult mortality and recruitment rates could not be measured in the same quadrats due to the size of the adult colonies, which may reach over 150 cm in diameter (Kersting and Linares 2012). Natural mortality differs from the warming-related mortality that has affected this species over the last decade, in which it is mostly caused by breakage of colonies through the combined action of boring organisms and hydrodynamics (Schiller 1993). Warming-related mortality, on the other hand, is clearly identifiable because sizable patches of necrotic tissue are seen at the end of summer (Kersting et al. 2013b). For the quantification of natural mortality, colonies were counted as dead if they broke off entirely.

Generalized linear mixed models (GLMM) with a Poisson distribution and a logit link function were used to test for differences in recruitment as a function of substrata (fixed factor) and time (random). GLMMs are used to model data that can cope with repeated measurements over time (Zuur et al. 2009). One-way PERMANOVA, using Euclidian distances, was used to test both differences in the annual polyp budding rates and differences in mortality rates between juvenile colony size-classes. The analyses were computed using lme4 package (Bates et al. 2013) implemented in R (R Development Core Team 2011) and Primer v6 with the PERMANOVA + add-on package (Anderson et al. 2008).

Fig. 2 Juvenile colony in 2010 (*left*) and in 2011 (*right*) (*scale bar* 0.5 cm)

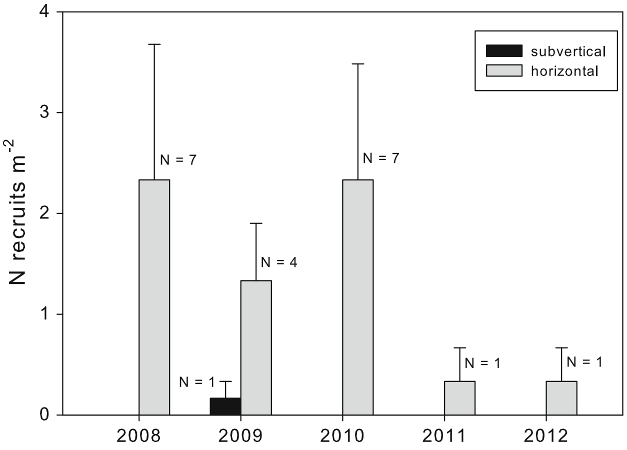

Fig. 3 Annual recruitment in permanent quadrats on *subvertical* and *horizontal* substrata (mean ± SE). The number of new recruits in the total surveyed area (*N*) is shown

Results and discussion

Annual adult mortality rates of *C. caespitosa* were low (1.06 ± 0.28 % yr^{-1}; ±SE). Recruitment rates were also low (0.31 ± 0.09 and 0.33 ± 0.13 recruits m^{-2} yr^{-1} (±SE) in permanent plots and random quadrats, respectively). These traits are typical of a slow-growing species (Kersting and Linares 2012). Comparisons with recruitment rates for other scleractinian corals are difficult due to the different assumptions and methods (Harrison and Wallace 1990), but annual recruitment rates for the long-lived tropical scleractinian *Porites lobata* (Coles and Brown 2007) were similar to our results, while recruitment rates were 1–2 orders of magnitude higher for other tropical corals (Glassom and Chadwick 2006).

Annual recruitment rates differed significantly between horizontal and subvertical substrata ($Z = 4.4$, $p < 0.0001$) and among years ($Z = -0.4$, $p < 0.0001$). Annual recruitment on horizontal substrata ranged from 0.33 ± 0.33 to 2.33 ± 1.15 recruits m^{-2} yr^{-1} (±SE), while new recruits were only recorded on subvertical substrata in 2009 (0.17 ± 0.17 recruits m^{-2} yr^{-1} (±SE); Fig. 3). The differences between substratum types may come about because eggs of *C. caespitosa* have a mucus coating (Kružić et al. 2008) and may also be negatively buoyant. These characteristics are likely to promote self-recruitment, as has been reported in some tropical coral species (Sammarco and Andrews 1988; Ayre and Hughes 2000).

Our findings are consistent with the overall paucity of sexual recruits in marine clonal organisms (Hughes and Jackson 1985; Garrabou and Harmelin 2002; Teixidó et al. 2011). In long-lived species, longevity and a low natural mortality buffer the low recruitment rates (the storage effect; Warner and Chesson 1985), so low rates of recruitment may maintain high adult coral abundances because these are the result of the accumulation of recruits over many years (Edmunds 2000; Hughes and Tanner 2000; Adjeroud et al. 2007; Coles and Brown 2007). In this context, pulses of high recruitment may drastically influence adult abundance (Edmunds 2000). However, problems arise when catastrophic disturbances become more frequent and mortality exceeds sporadic recruitment (Hughes et al. 1999; Adjeroud et al. 2007). This could be the case with the *C. caespitosa* population in the Columbretes Islands, which has suffered recurrent climate-related mortality since 2003 (Kersting et al. 2013a).

Cladocora caespitosa colonies appear to reproduce annually (Kersting et al. 2013b), and the low recruitment

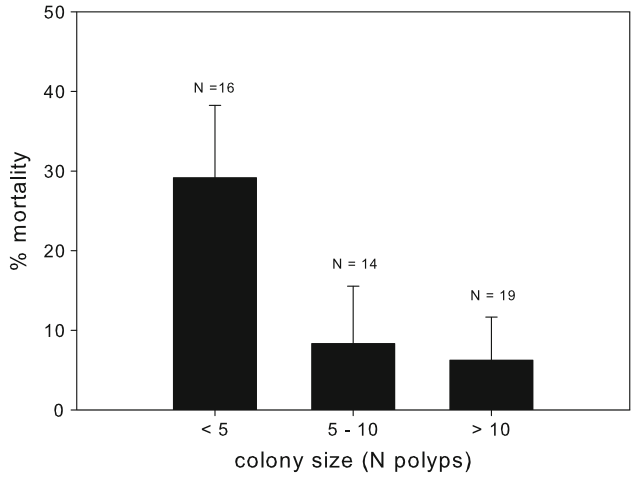

Fig. 4 Variation in the annual juvenile mortality (mean ± SE) with colony size based on the permanent quadrats. The total number of colonies in each size-class (*N*) is shown

rates seem to be caused by high juvenile mortality rather than low reproductive output. While the natural mortality rates in adult *C. caespitosa* colonies were low ($\sim 1\ \%\ \mathrm{yr}^{-1}$), juvenile colony mortality could be high ($29\ \%\ \mathrm{yr}^{-1}$ for colonies < 5 polyps; Fig. 4) and mortality rates did not differ among the three size-classes ($F_{2,9} = 2.21$, $p = 0.269$). Annual mortality of juvenile colonies during the study was much higher than the average incidence of warming-induced necrosis in this population ($\sim 4\ \%\ \mathrm{yr}^{-1}$, Kersting et al. 2013a), so this difference is most probably attributable to natural causes. Although juvenile corals may show great spatiotemporal variability in mortality rates, which makes comparisons difficult even within the same species (Edmunds 2000), the mortality rates for the smallest size-class of *C. caespitosa* colonies were similar to those of tropical scleractinian corals [e.g., *Siderastrea radians* ($23\ \%\ \mathrm{yr}^{-1}$) or *Porites* spp. ($27\ \%\ \mathrm{yr}^{-1}$): Edmunds 2000; Red Sea corals ($27–33\ \%\ \mathrm{yr}^{-1}$): Glassom and Chadwick 2006]. The early life stages in corals are characterized by low survivorship, but survivorship increases appreciably with colony size (Vermeij and Sandin 2008). Juvenile *C. caespitosa* colonies grew in polyp number by asexual budding. The smaller colonies grew significantly faster through this mechanism (1.14 buds $\mathrm{polyp}^{-1}\ \mathrm{yr}^{-1}$), reaching higher budding rates per polyp than larger juvenile colonies (0.33–0.43 buds $\mathrm{polyp}^{-1}\ \mathrm{yr}^{-1}$; $F_{2,34} = 4.44$, $p < 0.05$).

Overall, the slow dynamics and reduced recovery potential highlight the vulnerability of the coral *C. caespitosa* to the global change-related impacts that are affecting this species in Mediterranean coastal waters (Kersting et al. 2013a, 2014). This species and its unique reefs should be seriously considered for urgent inclusion on the national and international lists of threatened species.

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