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Seasonality and reproductive periods of the hydroid Clytia gracilis in temperate littoral ecosystems. Is asexual reproduction the prime mechanism in maintaining populations?

María L. Jaubet [a] & Gabriel N. Genzano [a]

[a] Estación Costera J. J. Nágera, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Mar del Plata, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

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ORIGINAL ARTICLE

Seasonality and reproductive periods of the hydroid *Clytia gracilis* in temperate littoral ecosystems. Is asexual reproduction the prime mechanism in maintaining populations?

MARÍA L. JAUBET* & GABRIEL N. GENZANO

Estación Costera J. J. Nágera, Departamento de Ciencias Marinas, Universidad Nacional de Mar del Plata, Mar del Plata, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

Abstract
Hydropolyps inhabiting temperate ecosystems exhibit marked seasonality, and undergo regression as a normal part of their life cycle. In the campanulariid species *Clytia gracilis*, both hydroids and medusae are decidedly seasonal in occurrence. Epizoic colonies of *C. gracilis*, growing on colonies of *Ectopleura crocea*, were collected monthly in the intertidal zone at Mar del Plata, Argentina (38°08′S–57°37′W) during low tide from February 2000 to January 2001. Abundance, seasonality and reproductive periods were analysed. The hydroid reached peak abundance during the summer, yet reproductive structures were scarce and observed in only a few colonies. A remarkable regression period was evident in the cold season. During that period, hydroids of the species had few functional polyps, and the colonies were largely reduced to dormant tissue in the coenosarc of hydrocauli and stolons. Hydranths of *C. gracilis* regenerated during summer and produced a profuse asexual growth by stolonization. Asexual propagation is proposed as the prime mechanism in maintaining these hydroid populations. In comparisons of intertidal and subtidal populations of *C. gracilis*, available hydroid colonies of *Amphisbetia operculata* and *Plumularia setacea* collected from neighboring rocky outcrops (38°10′S–57°30′W), at depths of 18–20 m, during both warm and cold seasons were analysed. As in the intertidal populations, these colonies showed marked stolonal growth at the end of summer.

Key words: *Asexual propagation,* Clytia gracilis, *hydroids, hydromedusae, seasonality*

Introduction

The Medusozoa may be unique among major animal taxa in having a life cycle with two alternative final stages. These comprise an asexual benthic polyp, usually with modular or colonial form, and a typically solitary planktonic medusa representing the sexual phase of the life cycle. The cycle includes the formation of a larval stage which metamorphoses into a new polyp. Although many hydrozoans have both major stages, one or other usually seems to dominate (see Cornelius 1992).

In temperate littoral ecosystems, for instance, some hydroid colonies with metagenetic life cycles can be found throughout the year ('stable' or perennial species; Boero 1994), although their medusae may be released for relatively brief periods only, during favourable seasons. Planktonic stages are absent from the water column during periods of unfavourable temperatures and inadequate food supply. In 'seasonal' species, presence/abundance variations are even more apparent, with hydroids as well as medusae appearing to be absent for prolonged periods. In such species, colonies present marked seasonal patterns in abundance and growth (Coma et al. 2000; Bavestrello et al. 2006; Boero et al. 2008 and information therein).

During unfavourable environmental conditions, the hydranths and coenosarc of hydroids may regress (withdrawing into the stolons, leaving empty perisarc portions) and the colonies survive in an inactive state, usually as dormant coenosarc in the stem or stolons. With the return of favourable conditions, hydranths regenerate from dormant tissues, the
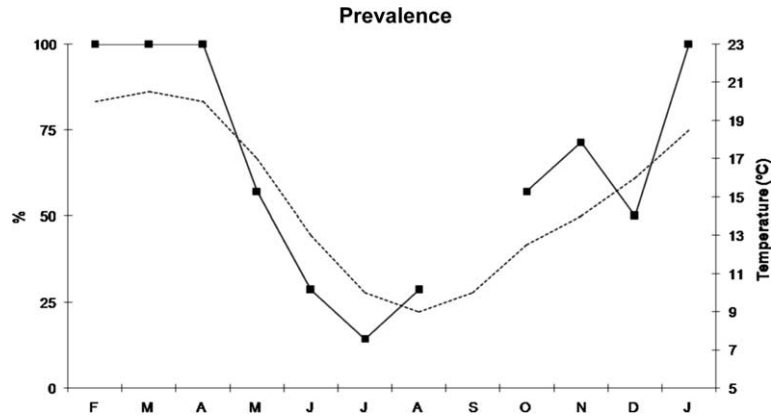
Figure 1. Prevalence of *Clytia gracilis* on *Ectopleura crocea* in the intertidal zone at Mar del Plata throughout the year (except in September, due to adverse weather conditions). Monthly water temperature is indicated by dotted line.

colony increase rapidly and medusal buds are formed over very short time intervals; their release occurs in pulses restricted to shorter periods (Hughes 1977; Calder 1990; Brinckmann-Voss 1996; Boero et al. 2008; Genzano et al. 2009b).

The presence of tolerant or resistant stages in hydrozoans with complex metagenic life cycles may explain prolonged absences of sessile hydroid colonies and their medusae from aquatic ecosystems, and their sudden reappearance at certain times of the year.

Clytia gracilis (Sars, 1851) is a species with a distinct seasonality of both its hydroid and medusa stages. This campanulariid has been widely reported in tropical and temperate waters around the world (see Cornelius 1995) and it is frequently found in the shallow littoral zone of Buenos Aires (Genzano 1994; Genzano et al. 2009a). Hydroids of the species are abundant during warm seasons, but they are rarely found during colder periods of the year (Genzano 1994). Its medusae are extremely rare at any time (see Genzano et al. 2008a).

The goals of this study were to analyse the seasonal changes in abundance, colony size and activity of sexual reproduction so as to determine the role of asexual reproduction in maintaining the population of hydroids of *Clytia gracilis*.

Materials and methods

The coastal area of the city of Mar del Plata is characterized by the presence of quartzite rocks originating in the mountainous system of Tandilia (SE of Buenos Aires province). The intertidal rocky fringe comprises both exposed and sheltered areas, such as channels and crevices, inhabited by many benthic organisms. This intertidal zone is characterized by dense beds of the small mytilid *Brachidontes rodriguezii* (D'Orbigny, 1846) (up to 5 cm of length) established on natural or artificial hard substrates (Scelzo et al. 1996).

Valves of this mytilid are frequently colonized by *Ectopleura crocea* (Agassiz, 1862) (Anthoathecata; Tubulariidae) a species widely distributed around the world, which is the most abundant hydroid in the intertidal fringe. *E. crocea* forms dense clumps usually comprising more than 100 stems each, which occur all year round, reaching maximal abundance
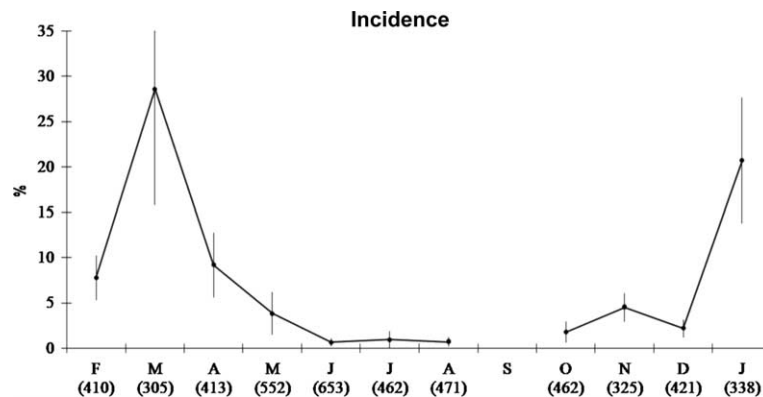

Figure 2. Incidence ($\pm$ SE) of *Clytia gracilis* on *Ectopleura crocea* in the intertidal zone at Mar del Plata throughout the year (except in September, due to adverse weather conditions). The total number of stems of *E. crocea* analysed is indicated in parentheses.
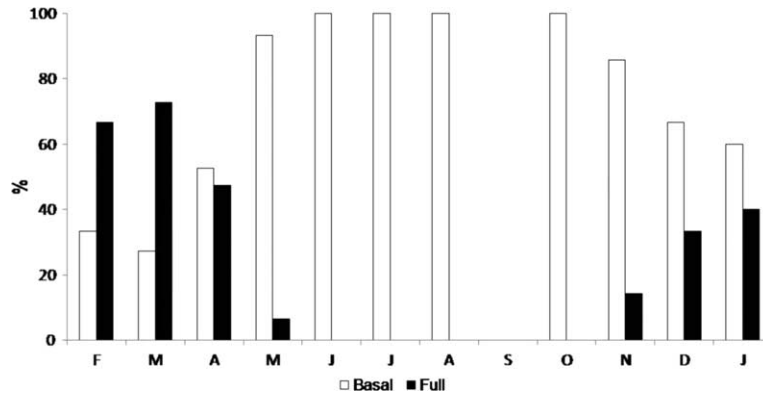
Figure 3. Frequency of stems of *Ectopleura crocea* colonized only on the basal portion and fully covered by *Clytia gracilis* (100% of coverage).

during the warm season (October–April). Stems of *E. crocea* are the most frequent substrate of the small epizoic hydroid *Clytia gracilis* (Leptothecata; Campanulariidae) (see Genzano 1994; Genzano & Rodriguez 1998).

The tidal regime is regular and semidiurnal, ranging between 0.90 and 0.60 m, but is subject to the weather conditions. The large rocky blocks that characterize the intertidal zone extend several miles seaward to a depth up to 20–25 m, constituting isolated outcrops where the mussel *Mytilus platensis* (D'Orbigny, 1846) is the dominant organism.

Water temperatures vary from season to season, with lows of close to 7°C in autumn and winter, and highs reaching 18–19°C in summer (up to 21°C in the intertidal fringe) (Genzano et al. 2002; Genzano & Zamponi 2003).

Investigations were carried out in the intertidal zone of Punta Cantera, Mar del Plata, Argentina (38°08′S–57°37′W). Epizoic colonies of *C. gracilis* attached to colonies of *E. crocea*, the most frequent basibiont (substrate organism) of this campanulariid (Genzano & Rodriguez 1998), were collected monthly.

Sampling was conducted during low tide from February 2000 to January 2001 between 9:00 and 11:00 am (except in September, due to adverse weather conditions). Basibiont clumps were removed from a crevice perpendicular to the coastline with a stainless steel spatula and fixed in situ in a 5% neutralized formaldehyde solution. Each clump of this basibiont on a bivalve was considered as one colony. A possible sample area effect was minimized by choosing clumps 4–5 cm in height which occupied the total area of mytilid valves 2.5–3cm in height (see Genzano et al. 2002).

Between seven and nine basibiont colonies were analysed each month to determine the prevalence, incidence and abundance of epizoic *C. gracilis*. Prevalence was calculated as a percentage of

E. crocea clumps colonized by the campanulariid. The incidence of epizoic fauna was calculated as a percentage of stems of *E. crocea* colonized by *C. gracilis* (see Genzano & San Martin 2002). Differences during the year were evaluated by means of a non-parametric Kruskall–Wallis test, as the data did not meet the assumptions of normality and homoscedasticity. Differences in frequencies of stems of *E. crocea* partially or fully colonized by *C. gracilis* (100% of coverage) was tested by χ^2 test.

Later, colonies of *C. gracilis* were removed from their substrata and size frequencies (number of pedicels per colonies) and percentage of mature colonies (with gonothecae) were calculated.

Complementary observations were conducted in vivo during February 2007 to observe the release of medusae. Colonies of *E. crocea* colonized by mature colonies of *C. gracilis* from the same location were isolated in a plankton net suspended in an aquarium with constantly aerated seawater. The plankton net (opening 15 cm and 200-μm mesh size) was suspended vertically and its opening held 5–10 cm above the water surface, so that any released medusae remained trapped in the net and concentrated in the collector (Genzano & Kubota 2003). Some of the colonies were maintained in the aquarium until December 2007, to observe periods of regression/ regeneration of hydranths.

In order to compare intertidal and subtidal populations of *C. gracilis*, 39 colonies collected during January–March and 16 collected during June–August were analysed. Epizoic colonies attached to hydroid clumps of *Amphisbetia operculata* (Linnaeus, 1758) and *Plumularia setacea* (Linnaeus, 1758), were the most frequent substrates of *C. gracilis* in deeper areas (Genzano et al. 2002). Basibionts were collected by SCUBA from neighbouring rocky outcrops (38°10′S–57°30′W), at depths of 18–20 m.
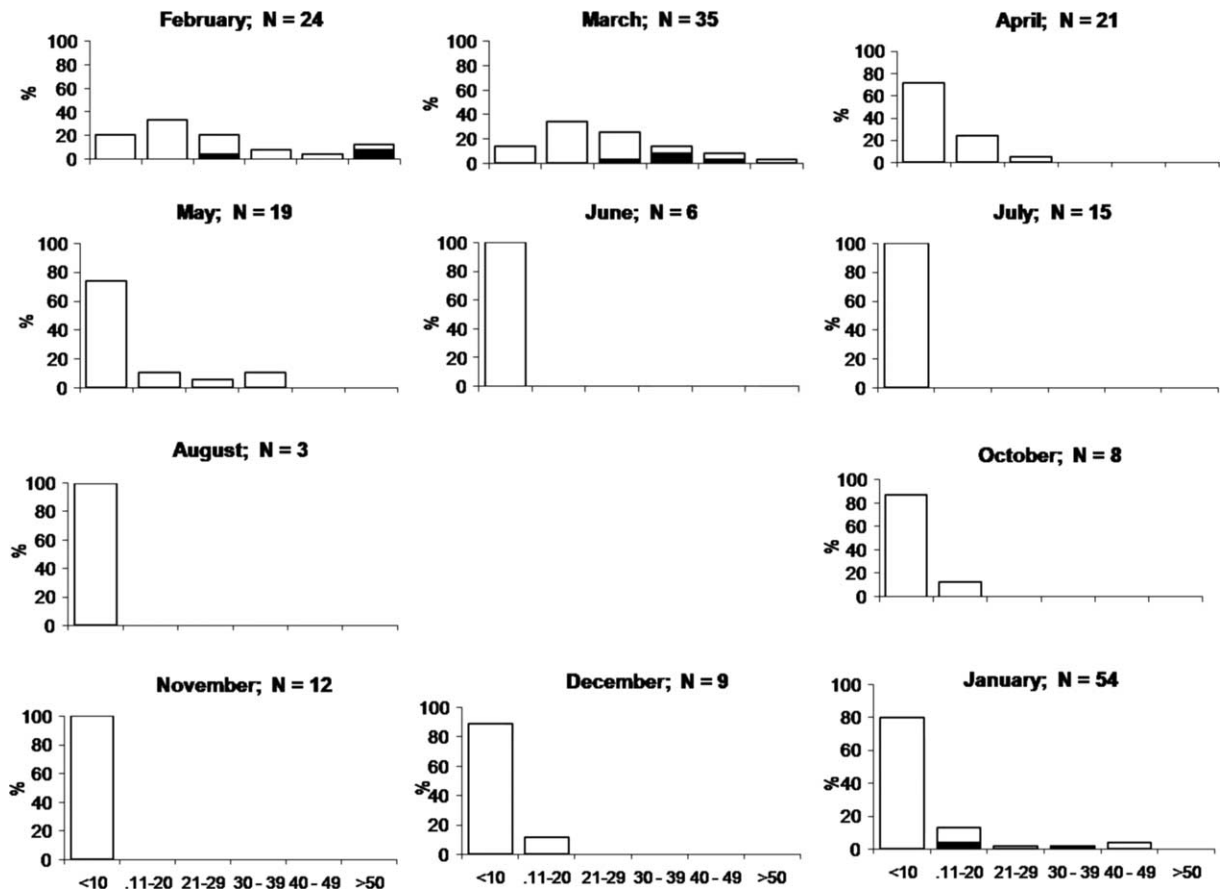
Figure 4. Size frequency distribution (number of hydranths per colony) of *Clytia gracilis*. N = number of analysed colonies. Black bars represent mature colonies.

Differences in colony size and numbers of gonothecae per colony in both environments were tested by means of a non-parametric Mann–Whitney test since the data did not meet the assumptions of normality and homoscedasticity.

Results

Colonies of *Clytia gracilis* were present in the study area throughout the year, but seasonal cycles of abundance and activity were marked. Colonies reached peak abundances during the summer period (January–April), when all basibiont colonies of *Ectopleura crocea* were colonized by *C. gracilis* (Figure 1).

Periods of maximum colonization on hydrocauli of *E. crocea* by *C. gracilis* were observed in January (20.7%) and March (28.6%); (H = 43.67784, P < 0.0001). Incidence of epizoic fauna was lower between May and December, correlating with decreases in temperature, and minimum values were observed in winter (June–August) when *Clytia* colonies stop growing and undergo a marked regression period. In July, *C. gracilis* was found on only four stems (0.95%) from a single colony of *E. crocea* (14.3%) (Figure 2).

Remarkable stolonal growth of colonies of *C. gracilis* was noted during the summer (January–March), with a high number of *E. crocea* stems being fully covered by this epibiont (up to 70%, n = 164). During the coldest months of the year (June–November), *C. gracilis* colonies occurred only on the basal portion of the basibiont stems (χ^2 = 46.33; P < 0.001, n = 43) (Figure 3).

The widest range of colony sizes of *C. gracilis* was found in summer (January–March), with a minimum of three pedicels and maximum of 118 pedicels per colony (Figure 4). During the winter season (June–August), a regression period was evident. The number of pedicels per colony was lower than in warm periods, averaging 3.3 pedicels per colony in June, 2.1 in July, and 2.0 in August. During the latter month, only three small colonies of *C. gracilis*, colonizing the basal portion of hydrocauli of *E. crocea*, were found. These colonies had only one active hydranth, the remaining pedicels contained only regressed coenosarcs.

The formation of reproductive structures (gonothecae, Figure 5a) was evident only in a few mature colonies found during warm periods (6% of mature colonies in January, 13% in February, and
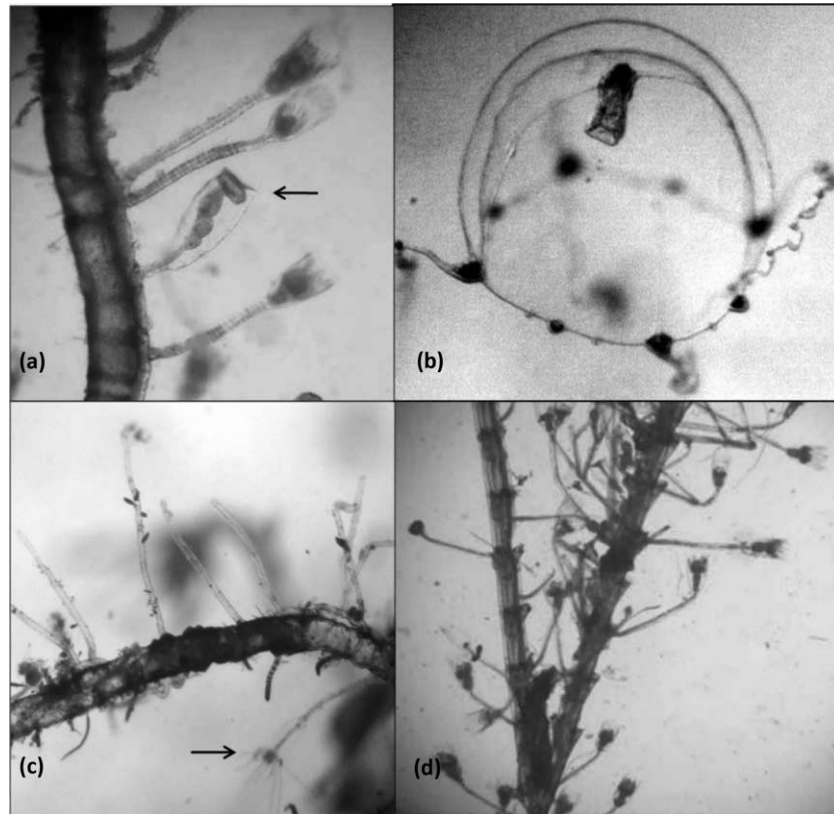
Figure 5. (a) Colony of *Clytia gracilis* attached to stem of *Ectopleura crocea*. Gonotheca is marked by the black arrow; (b) medusa of *Clytia gracilis*, 3 days old; (c) colony of *Clytia gracilis* in regression (most of the pedicels are empty). The unique active hydranth is indicated by the black arrow; material kept in aquarium, August 2007; (d) *Clytia gracilis* on *Amphisbetia operculata* stems from the subtidal zone at Mar del Plata. Scale bar = 0.5mm

14% in March). These structures were very scarce (1–6 gonothecae per colony, averaging 2.3; SE = 0.88) and they occurred only in the largest colonies (up to 20 pedicels) (Figure 4). In aquarium studies, mature colonies released only two medusae (February) which survived for just a short time (3 days) (Figure 5b).

Intermittent periods of regression and regeneration of hydranths were observed in vivo. During the winter, at temperatures of 8°C, all colonies were small, immature, and had numerous pedicels devoid of coenosarcs. Only a few contained active hydranths, feeding on detritus (Figure 5c).

Colonies of *C. gracilis* ($n = 64$) collected at the end of summer (February–March) from nearby
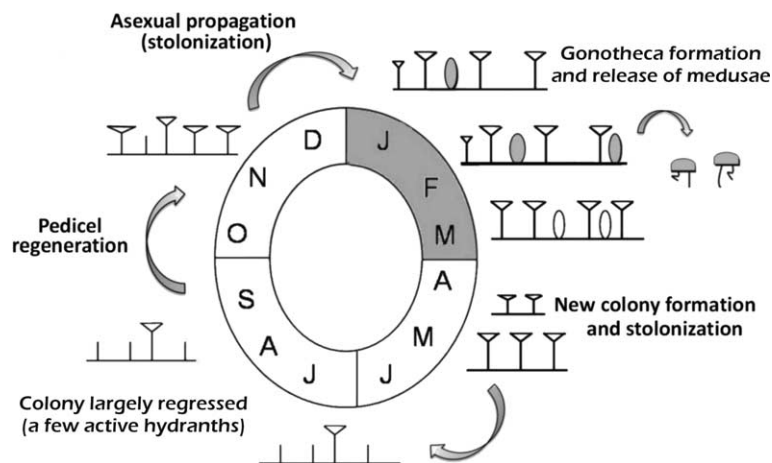

Figure 6. Scheme representing the annual cycle of *Clytia gracilis* in the coastal community of Mar del Plata. The coloured area represents the sexual reproductive period.

sublittoral rocky outcrops (Figure 5d) were larger (exceptionally up to 254 pedicels) than those from the intertidal zone ($Z = 2.97$; $n_1 = 30$; $n_2 = 24$ pedicels per colony; $P < 0.01$). Like the intertidal population, these colonies showed marked stolonal growth during this season.

Sexual reproductive activity in colonies from deeper waters (18–20 m) was also evident only during the warm season. Numbers of gonothecae per colony were higher in subtidal colonies than in intertidal ones ($U = 36$; $n_1 = 17$ vs. $n_2 = 3$; $P < 0.01$), and the percentages of mature colonies was greater (up to 56.7%). However, as with intertidal populations, reproductive structures were very scarce and present only for a brief period in the summer season. During cold months, only small colonies with less than 20 pedicels (mean 6 pedicels) and few functional polyps were observed. Dormant coenosarc was evident in most of the hydrocauli and stolons.

The annual cycle of *C. gracilis* in the study area is illustrated in Figure 6, where seasonal regression/regeneration of hydranths, asexual reproduction by stolonization, and medusa release period are indicated.

Discussion

Temperate littoral benthic ecosystems are subjected to great environmental variability. Fluctuating physical factors influence the annual cycles of epifaunal species such as hydroids, and many of them show marked seasonal patterns in growth, abundance, and reproduction (Giangrande et al. 1994; Coma et al. 2000).

Hydrozoan colonies inhabiting these areas may undergo a seasonal regression as a normal part of their life cycles. These colonies appear to be absent during unfavourable seasons. However, they do not disappear completely from their respective communities; instead, they remain as resting stages with living tissue stored until the next favourable season (see Hughes 1977; Boero 1984; Calder 1990; Petersen 1990; Boero et al. 1992).

While present in the study area throughout the year, colonies of *Clytia gracilis* underwent a marked seasonal cycle of activity and growth. Maximum abundances were attained during the summer period, clearly related to elevated water temperatures. In contrast, colonies bore few functional hydranths during colder months, and coenosarc in hydrocauli and stolons was dormant. With the return of optimal conditions, hydranths of *C. gracilis* regenerated, and profuse asexual growth by stolonization was evident.

The stolonization process in *C. gracilis* involves the emergence of a stolon from the hydrorhiza that separates from the parent colony and forms a new colony. This mechanism is clearly related to colonization of new (usually living) substrates, reducing the interspecific competition for the space. Hughes (1977) suggested that this strategy explains the distal occupation by *Clytia hemisphaerica* (Linnaeus, 1767) on colonies of *Nemertesia antennina* (Linnaeus, 1758). This 'guerrilla' strategy also avoids the negative effects of sediment deposition, since epizoic colonies are mainly found climbing on hydrocauli of other larger hydroid colonies (Genzano 1998; Genzano & Rodriguez 1998).

The alternation between dormant and active benthic states is considered the primary asexual reproductive mechanism accounting for seasonal cycles of abundance and relative scarcity in this species. Notably, sexual reproduction occurs only during a brief period in summer, and even then few reproductive structures (gonothecae) are formed and few medusae are released to the water column. This reproductive pattern was similar in both intertidal and sublittoral populations.

Differences were noted in size and number of gonothecae per colony in intertidal and subtidal populations of *C. gracilis*. Larger sizes and greater numbers in the sublittoral may be due to more stable environmental conditions in deeper waters (Genzano & Zamponi 2003). The intertidal fringe is characterized by conditions of higher stress that may lead to an increase in asexual reproduction and in the process of fragmentation of *C. gracilis* colonies. Increased asexual reproduction under adverse conditions has been widely reported (e.g. autotomy of hydranths in a hydroid referred to as '*Zelounies estrambordi*', a nomen nudum; production and release of frustules in *Obelia geniculata* (Linnaeus, 1758); strobilation of certain bougainvillioid hydroids; see Gravier-Bonnet 1992; Jarms & Tiemann 1996; Bavestrello et al. 2000; Slobodov & Marfenin 2004).

Gonotheca formation is known to be rare in some species of hydroids, and certain epizoic forms have suppressed sexual reproduction entirely (Garcia Rubies 1987; Gili & Hughes 1995; Genzano et al. 2009a). Literature reports of the medusae of *C. gracilis* in nature are scarce and geographically restricted; meanwhile, the polyp is nearly cosmopolitan and frequently reported in coastal areas (Cornelius 1995). The broad geographic range of the species is likely attributable to rafting of hydroids on floating structures (see Cornelius 1992), rather than dispersal by the medusa. Moreover, colonies of *C. gracilis* are sometimes known to be planktonic, flourishing in the water column without attachment to any substrate (Cornelius 1995; Avent et al. 2001; Adamik et al. 2006). Thus, dispersal by water currents of free-living planktonic colonies may also occur.

Successful asexual strategies that currently maintain populations of this species may explain why its medusal stages are extremely scarce in planktonic communities of the area (Genzano et al. 2008a), even though its hydroids are very frequent in the benthic community (Genzano et al. 2009b).

In species with metagenetic life cycles, abundances of planktonic medusae reflect a response of benthic polypoid stages to several factors. Changes in environmental conditions may affect hydroid populations and trigger unusual blooms of medusae that commonly occur at very low densities and frequencies (Genzano et al. 2008b). Knowledge of the ecology of both life stages is crucial to understanding and interpreting spatial patterns and abundance in different communities (Mills 2001; Miglietta et al. 2008).

Acknowledgements

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