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## Competitive equivalence maintains persistent inter-clonal boundaries

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**Abstract** Clear boundaries often separate adjacent conspecific competitors. These boundaries may reflect bordering animal territories or regions of inter-organism contact in mobile and non-mobile organisms, respectively. Sessile, clonal organisms often form persistent inter-clonal boundaries despite great variation in competitive ability among genotypes within a population. I show that neighboring clones in the sea anemone *Anthopleura elegantissima* and three species of the marine hydroid genus *Hydractinia* are more evenly matched in terms of competitive ability than expected by chance. Hypotheses of genetic relatedness or similar environmental regime shared by neighboring clones are inconsistent with the observed similarities between adjacent competitors in one or both taxa. Instead, inter-clonal borders evidently persist as standoffs between evenly matched competitors. Large differences in competitive ability between bordering clones were rarely observed, suggesting that dominant clones quickly displace or eliminate others in competitive mismatches. This ecological parallel between taxa (i.e., competitive equivalence) exists despite several fundamental differences (e.g., geographical distribution, habitat, body size, longevity), suggesting that competitive equivalence may be a widespread determinant of boundary persistence between adjacent competitors.

**Keywords** *Anthopleura elegantissima* · Competitive ability · *Hydractinia* · Local coexistence · Neighbor

### Introduction

Indeterminate vegetative growth combined with absent or limited mobility makes conspecific interactions frequent and unavoidable in many sessile, clonal organisms, including fungi, attached plants, and some invertebrates. Within species, clones may differ greatly in competitive ability (Turkington and Harper 1979; Ellison and Harvell 1989; Buss and Grosberg 1990; de Kroon et al. 1992; Ayre and Grosberg 1995, 1996). Consequently, one or a few highly adapted clones may dominate, at least over limited spatial scales (Sebens and Thorne 1985). In the absence of frequent perturbations or routine high mortality, dominant competitors should displace inferior competitors, if only gradually. Yet high levels of clonal diversity persist locally in both clonal plants (Ellstrand and Roose 1987) and animals (Ayre and Grosberg 1995).

Proximity should facilitate interference competition among clones and enable the proliferation of dominant clones in species exhibiting territorial or agonistic behavior. However, persistent boundaries often demarcate regions of contact between locally co-occurring clones. In clonal marine invertebrates, regions of inter-clonal contact can be particularly striking. Many bordering cnidarian clones, for example, form open contact regions devoid of live tissue (Francis 1973a; Purcell 1977; Shaw 1991; Yund 1991; Ferrell 2004b). Similarly, in a terrestrial setting, maps of foraging territories in neighboring conspecific ant colonies reveal distinct and persistent inter-colony boundaries (Adams 1998). Whether boundaries separate animal territories or regions of inter-organism contact, they can exhibit remarkable persistence. Inter-clonal boundaries persist for up to 4 years in at least one cnidarian species (Francis 1973a), and fire-ant territories remain unchanged unless colony fighting ability (i.e., number of worker ants) is directly manipulated (Adams 2003).

Perhaps the simplest explanation for long-term boundary persistence is competitive equivalence; that is,

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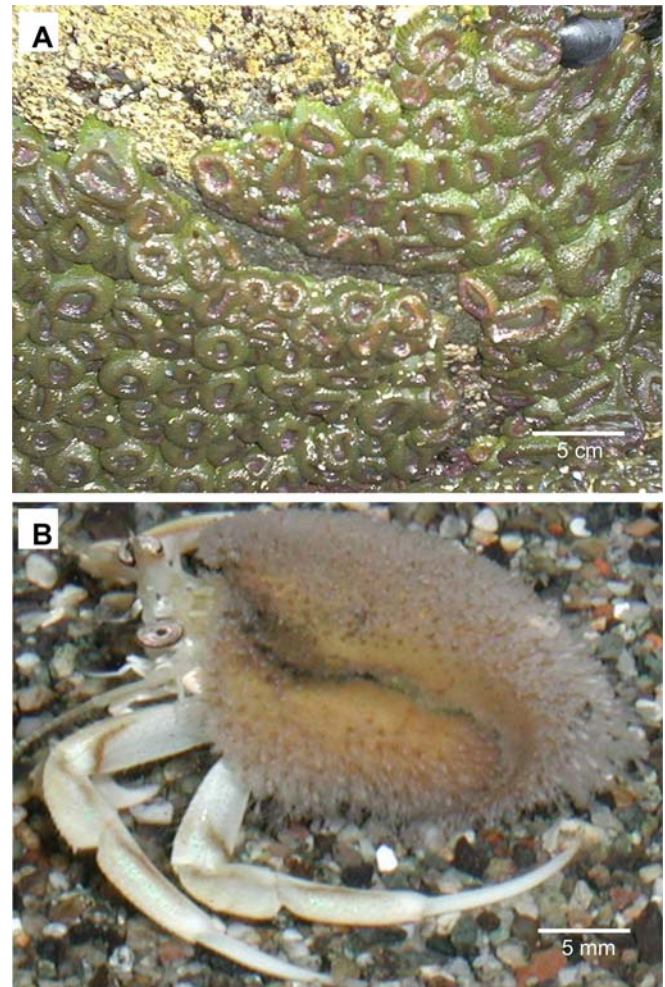
bordering competitors possess equal competitive abilities. Indeed, competitive equivalence is commonly discussed in the context of interspecific competition covering a wide range of organisms (e.g., fungi, Harris 1996; plants, Suding and Goldberg 2001; animals, Connell et al. 2004). Competitive standoffs (often assumed to reflect competitive equivalence) likely contribute to local coexistence of space-limited, benthic invertebrate species (e.g., Connell 1976; Karlson 1980; Connell and Keough 1985; Tanner 1993; Connell et al. 2004), and heterospecific contact between coral species or other sessile invertebrates, such as sponges, sometimes even generates regions of open space demarcating interspecific borders (e.g., Richardson et al. 1979) comparable to vacant regions existing at inter-clonal boundaries. Competitive equivalence of neighboring conspecifics, however, can be very difficult to demonstrate (e.g., Ayre and Grosberg 1995, 1996). At least four other hypotheses might explain contrary findings (the last three discussed in Ayre and Grosberg 1996). First, inferior clones may defend themselves against aggressive neighbors and persist by pre-emption of space even in the face of competition with competitively superior clones. Second, habituation and tolerance developed in response to repeated contacts with neighbors might reduce or eliminate interference competitive interactions. Third, an increased rate of production of competing individuals or structures may compensate for inferior competitive abilities in clonal organisms. Fourth, inferences about inter-clonal dominance made from laboratory assays (or in other artificial settings) may not accurately portray dominance in the field.

The present study examines the relative competitive abilities of neighboring clones in distantly related cnidarians: the sea anemone *Anthopleura elegantissima* and three species of the marine hydroid genus *Hydractinia*. Rigorous studies of inter-clonal dominance using pairs of individual anemones suggest that inter-clonal borders apparently persist despite differences in competitive ability between neighboring *A. elegantissima* clones (Ayre and Grosberg 1995, 1996). Comparable studies in *Hydractinia* spp. have not been performed. Here I consider many neighboring pairs in both *A. elegantissima* and *Hydractinia* spp., and show that neighboring pairs indeed exhibit more similar competitive abilities than expected by chance. Thus, this study makes more complex explanations for boundary stability less likely in these taxa and underscores the importance of competitive equivalence in maintaining stable inter-competitor boundaries.

### Study species

*A. elegantissima* forms extensive clonal aggregations composed of hundreds to thousands of tightly packed, genetically identical anemones in northeastern Pacific rocky intertidal habitats (Sebens 1982b), whereas *Hydractinia* spp. are found along coasts in the North

Atlantic and Gulf of Mexico (Cunningham et al. 1991), and typically encrust shells inhabited by hermit crabs inhabiting soft sediments. *A. elegantissima* expands asexually at a slow rate (Sebens 1982b). Clonal aggregations may take many years to successfully establish (i.e., consisting of at least 100 individuals, as defined in previous studies) but then likely persist for several decades (Sebens 1982b, 1983). In contrast, *Hydractinia* spp. can colonize all available substratum provided by a single shell and attain sexual maturity over the course of a single season (Yund et al. 1987; Yund 1991), and may persist for several years on fixed substrata (Sutherland and Karlson 1977). Despite these differences, striking parallels exist with respect to intraspecific competition.



**Fig. 1** Naturally bordering clones. **a** Bordering aggregations of the clonal sea anemone *A. elegantissima* in the Pacific rocky intertidal. A narrow strip of bare rock separates two large aggregations, each composed of genetically identical individuals generated by asexual reproduction. All anemones have withdrawn their tentacles during a low-tide event, and barnacles encrust the rock surface in the upper left portion of the photograph. **b** Bordering colonies of the marine hydroid *Hydractinia* [GM] in the northern Gulf of Mexico. The irregular line on this hermit crab-occupied shell demarcates the border between two adult colonies, each composed of hundreds of genetically identical individual polyps generated by asexual reproduction

Both *A. elegantissima* and *Hydractinia* spp. grow into contact with neighboring clones frequently and behave aggressively toward unrelated conspecifics. Extensive, conspicuous inter-clonal borders may arise from agonistic interactions in both *A. elegantissima* (Francis 1973a; Ayre and Grosberg 1996; Fig. 1a) and *Hydractinia* spp. (Yund et al. 1987; Ferrell 2004b; Fig. 1b). “Warrior” polyps (Francis 1976; Ayre and Grosberg 1996), armed with densely packed aggressive tentacles, line inter-clonal borders in *A. elegantissima*. These aggressive tentacles, or acrorhagi, are not used in feeding but are packed with dense batteries of nematocysts, and located just below the more numerous feeding tentacles (Francis 1973b). Similarly, neighboring *Hydractinia* colonies mutually develop highly specialized aggressive tissues along regions of contact. Aggressive tissues, or hyperplastic stolons (Ivker 1972), form as existing tissues recruit and discharge especially potent nematocysts (Buss et al. 1984). Although aggressive tentacles (in *A. elegantissima*) or tissues (in *Hydractinia* spp.) are often induced by the presence of a competitor, not all clones are equally equipped to produce them and behave aggressively (Buss and Grosberg 1990; Ayre and Grosberg 1995). Thus, clones differ in their agonistic capabilities.

In *A. elegantissima*, the number of acrorhagi borne by warrior polyps determines competitive dominance. Warriors with more acrorhagi generally behave more aggressively and win agonistic contests (Ayre and Grosberg 1995). Acrorhagial allocation, number of acrorhagi standardized by basal diameter (an indicator of body size), thus serves as a proxy for competitive ability. In *Hydractinia* spp., growth form determines competitive dominance. Growth form has a strong genetic basis, as indicated by high clonal repeatability, in at least three *Hydractinia* species (Buss and Grosberg 1990; Yund 1991; Ferrell 2004a). Colonies of different genotypes vary greatly in the production of tissue branches, or stolons, during growth. Some colonies produce very few or no stolons; others generate a profusion of stolons, but most exhibit growth forms intermediate between these two extremes. Colonies with more stolons develop hyperplastic stolons more readily, and therefore dominate in agonistic contests (Buss and Grosberg 1990). Colony growth form (number of stolon tips) thus serves as an indicator of competitive ability.

## Materials and methods

### *Anthopleura elegantissima*

During low-tide outings in May/June 2002, I collected up to 20 anemones per aggregation from 3 to 7 pairs of bordering *A. elegantissima* aggregations (Fig. 1a) per site at 8 field sites in Barkley Sound, BC, Canada (Table 1). In an effort to sample anemones with the greatest allocation to acrorhagi production (i.e., “warrior” polyps; Francis 1976; Ayre and Grosberg 1996), I chose to

**Table 1** *Anthopleura elegantissima* field collection sites in Barkley Sound, BC, Canada

Site	Latitude/longitude
Brady's Beach	48°50'N/125° 9'W
Dixon Island	48°51'N/125°7'W
Helby Island	48°51'N/125°10'W
Pachena Bay	48°47'N/125°7'W
Ross Islets	48°53'N/125°10'W
Sandford Island	48°52'N/125°10'W
Seppings Island	48°50'N/125°12'W
Wizard Islet	48°52'N/125°11'W

collect individuals located within approximately 10 cm of the aggregation edge. Individuals were collected entirely from the inter-clonal border region when possible. After using a dull knife to pry exposed anemones from the rocky substrate, I placed them in re-sealable bags or small, plastic jars and transferred them to an outdoor, flowing seawater table. I maintained anemones unfed in seawater tables for up to 7 days before determining acrorhagial allocation. All damaged anemones, as evidenced by ruptured basal discs or body columns, were discarded.

Before inspecting them with a dissecting microscope, I relaxed intact anemones by placing them in a glass petri dish containing a 25% seawater solution of 0.1 M MgSO<sub>4</sub>. After 1–2 h, I examined each anemone individually. Using a transparent ruler affixed to the microscope specimen stage, I estimated the diameter of the basal disc (= basal diameter or BD) to the nearest 0.5 mm. I then used forceps to peel back feeding tentacles as necessary to count the acrorhagi. Basal diameter measurements were used to standardize acrorhagi counts for anemone body size (number of acrorhagi/basal diameter). For each clone, I calculated its mean acrorhagial allocation as the number of acrorhagi, divided by the basal diameter, averaged over 20 polyps.

### *Hydractinia* spp.

During summer 2003, I hand-collected *Hydractinia* colonies while snorkeling or wading in shallow water (0.5–2 m deep) at 14 field sites in the northern Gulf of Mexico and northwestern Atlantic (Table 2). *Hydractinia* colonies were identified to one of three species (*Hydractinia* [GM], *Hydractinia polyclina*, *H. symbiolongicarpus*) by morphometric characters (Buss and Yund 1989) and comparisons of species ranges (Cunningham et al. 1991, Folino and Yund 1998) with site of collection. ([GM] is the designation given by Cunningham et al. 1991 to an undescribed *Hydractinia* species that is found in the northern Gulf of Mexico). I selectively sampled only shells occupied by hermit crabs with hydroid growth over at least 80% of the external shell surface. After transporting colonies and host crabs to the laboratory, I recorded the number of adult colonies on each shell and then selected shells with two adult colonies (i.e., colonies

with ripe gonophores containing either sperm or eggs) separated by a distinct inter-clonal boundary (Fig. 1b). Within 24 h of collection, I obtained tissue samples to determine colony growth form according to the protocol outlined below. Otherwise, colonies and host crabs were maintained in aerated wet tables for up to 5 days and fed 2-day-old brine shrimp nauplii (Ocean Star International, Pro 100) daily until tissue samples were obtained.

For each colony, I used a microscalpel to excise five small portions of colony tissue, each including five to ten feeding zooids. Thus, tissue explants were standardized for colony size. I then used (8-lb test) monofilament thread to secure each tissue explant individually to a plain glass microscope slide. Slides were transferred to standard plastic slide boxes (from which the tops and bottoms had been removed to permit water movement) and suspended in a single aquarium containing re-circulated 1- $\mu$ m-filtered seawater (temperature  $\sim$ 18°C, salinity  $\sim$ 28 ppt). Explants were fed 2-day-old brine shrimp nauplii daily. After 7 days of growth, colonies were removed, rinsed thoroughly in 70% ethanol and air-dried. I later counted the number of stolon tips, an indicator of colony growth form.

### Statistical analysis

For both *A. elegantissima* and *Hydractinia* spp., simulated pairs were generated by pairing all possible combinations of co-occurring (but not bordering) clones within a site. A *t*-test was used to examine the difference in acrorhagi/BD ratio for *A. elegantissima* between

bordering and simulated clonal pairs. In *Hydractinia* spp., two-way ANOVA was used to examine differences in number of stolon tips between the three species and between bordering and simulated clonal pairs. A Contingency  $\chi^2$  was used to test whether the frequency of shells with  $>1$  adult colony differed between the three *Hydractinia* species.

In addition, model II regression analysis (Sokal and Rohlf 1995) was performed on the mean acrorhagi/BD ratio (*A. elegantissima*) or mean number of stolon tips (*Hydractinia* spp.) for each neighboring clonal pair (i.e., *x*-axis = clone A, *y*-axis = clone B). Neighboring pairs were assigned letters A or B haphazardly. To test whether the haphazard assignment of clones to the *x*- or *y*-axis biased regression results, ten additional regression analyses were performed in which each member of a clonal pair was randomly assigned to the *x*- or *y*-axis.

### Results

In *A. elegantissima*, number of acrorhagi was strongly correlated with anemone basal diameter, or BD ( $F_{1,1060} = 439.1$ ,  $P < 0.0001$ ). Acrorhagial allocation (acrorhagi/BD) of bordering pairs of clonal aggregations was strikingly similar. Mean acrorhagial allocation of bordering pairs exhibited a 1:1 relationship (Fig. 2a). All ten additional regression analyses, in which members of clonal pairs were randomly assigned to the *x*- or *y*-axis, yielded identical results and confirmed the 1:1 relationship. Differences in mean acrorhagial allocation did not exceed 1.0 for 89% (32/36) of bordering pairs. Large inter-clonal differences in agonistic capabilities (difference in mean acrorhagial allocation  $> 2.0$ ) were observed only once (the "outlier" identified in Fig. 2a). The three remaining pairs exhibited differences of 1.01, 1.15, and 1.40. The mean difference in acrorhagial allocation between bordering pairs was compared to that of simulated clonal pairs, which were generated by pairing co-occurring (but not bordering) clones. Simulated pairs exhibited significantly greater differences in acrorhagial allocation compared to bordering pairs [difference in mean acrorhagi/BD ratio = 0.88 (sim) vs 0.53 (bord);  $t_{314, 0.05} = 3.22$ ,  $P = 0.0014$ ]. Pairs of anemones collected within an aggregation never exhibited unilateral or mutual aggression in laboratory assays (data not shown), indicating that individuals within an aggregation were indeed clonemates, as previous studies have also confirmed (Sebens 1982b; Ayre and Grosberg 1995).

In all three *Hydractinia* species, adult colonies sharing extensive inter-colony borders exhibited remarkable similarities in growth form, as inferred from the mean numbers of stolon tips (Fig. 2b). As in the analogous situation in *A. elegantissima* (Fig. 2a), a 1:1 relationship existed between the mean number of stolon tips of bordering pairs of *Hydractinia* colonies. In all ten additional regression analyses, in which members of neighboring pairs were randomly assigned to the *x*- or

**Table 2** *Hydractinia* spp. field collection sites

Species	Site	Latitude/longitude
<i>Hydractinia</i> [GM] <sup>a</sup>	FSUML <sup>c</sup> , Turkey Point, Fla.	29°55'N/84°19'W
	NOAA <sup>d</sup> , St. Andrew Bay, Fla.	30°0'N/85°44'W
	St. Joseph Bay State Park, Fla.	29°47'N/85°23'W
	<i>H.</i> <i>sympylongicarpus</i> <sup>b</sup>	
<i>H.</i> <i>sympylongicarpus</i> <sup>b</sup>	Brenton Cove, R.I.	41°30'N/71°20'W
	Cotuit Bay, Mass.	41°40'N/70°25'W
	Lighthouse Point, Conn.	41°13'N/85°23'W
	Round Cove, Mass.	41°43'N/70°00'W
	WBNER <sup>e</sup> , Waquoit Bay, Mass.	41°33'N/70°31'W
<i>H. polyclina</i> <sup>b</sup>	West Falmouth Harbor, Mass	41°36'N/70°39'W
	Glen Cove, Me.	44°10'N/69°5'W
	Lowe's Cove, Me.	43°55'N/69°35'W
	Pemaquid Beach, Me. St. George River, Me.	43°47'N/69°30'W 44°0'N/69°15'W

<sup>a</sup>Collected May-July 2003; [GM] is the designation given by Cunningham et al. (1991) to an undescribed *Hydractinia* species found in the northern Gulf of Mexico

<sup>b</sup>Collected August 2003

<sup>c</sup>Florida State University Marine Laboratory

<sup>d</sup>National Oceanic and Atmospheric Administration facility

<sup>e</sup>Waquoit Bay National Estuarine Research Reserve

y-axis, the 1:1 relationship was confirmed. Simulated pairs, generated by matching colonies collected at the same site (but not on the same shell), exhibited greater differences in growth form than did bordering pairs [difference in mean number of stolon tips = 8.0 (sim) vs 5.7 (bord);  $F_{1,396} = 5.29$ ,  $P = 0.022$ ]. Significant differ-

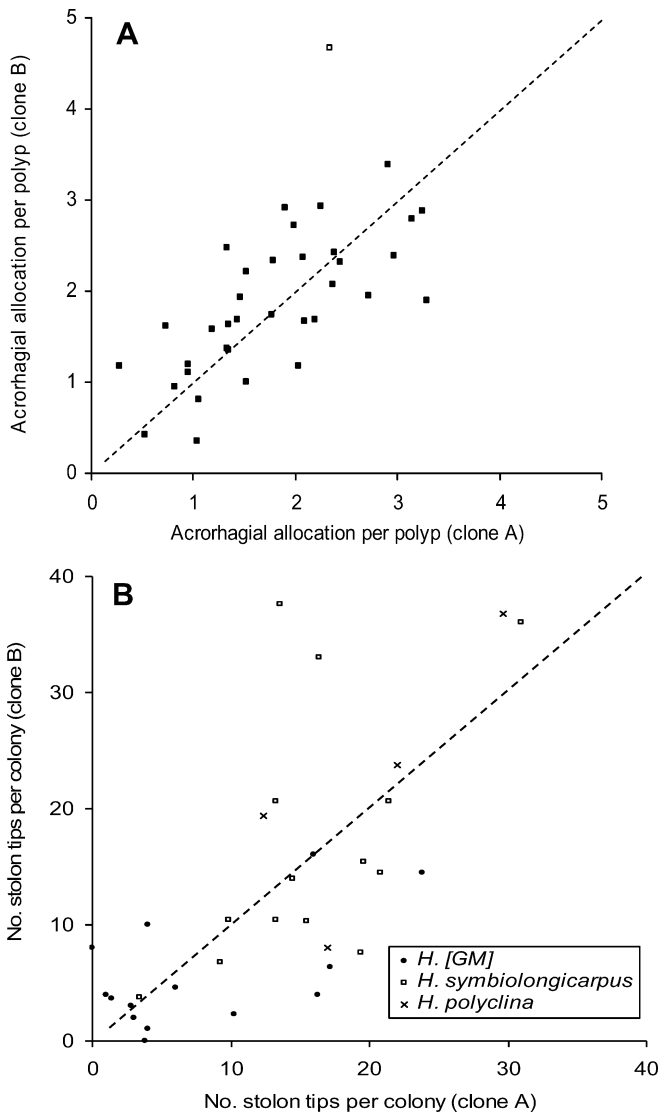
ences in growth form between species were also detected ( $F_{2,396} = 6.72$ ,  $P = 0.0013$ ). The differences in mean number of stolon tips between simulated and bordering pairs for *Hydractinia* [GM], *H. symbiolongicarpus*, and *H. polyclina* colony pairs were 4.92, 6.23, and 6.25, respectively.

Shells with >1 adult colony occurred with variable frequency in the three *Hydractinia* species ( $\chi^2 = 16.9$ ,  $df = 2$ ,  $P < 0.001$ ). Shells with >1 adult colony comprised 21% (25/122) of colonized shells in *Hydractinia* [GM] but only 10% (16/160) in *H. symbiolongicarpus* and 4% (4/111) in *H. polyclina*.

## Discussion

In both *A. elegantissima* and *Hydractinia* spp., adjacent clones in the field are more evenly matched in terms of competitive ability than expected by chance. Inter-clonal borders may be quite long-term, persisting up to 4 years in *A. elegantissima* (Francis 1973a). Comparable, long-term studies of border persistence have not been conducted in *Hydractinia* spp., but preliminary field monitoring and the lack of observable aggression and inter-clonal tissue contact at some borders indicate long-term border persistence, at least in *Hydractinia* [GM]. Assuming that inter-clonal borders examined in the present study were stable, boundary persistence evidently requires competitive equivalence in these sessile, clonal animals. Competitive mismatches, however, proceed to competitive exclusion rapidly (Ferrell 2004a), and therefore were observed only rarely.

Two alternative explanations for this trend (Fig. 2) do not apply to at least one of these taxa. First, neighboring clones may be close genetic relatives (e.g., full or half siblings, parent-offspring). This hypothesis appears plausible in *Hydractinia* spp., in which sexually produced larvae disperse little if at all and may remain together as a clutch before attaching to hermit crab-occupied shells, and genetic evidence exists that a significant portion, albeit small, of co-occurring *H. symbiolongicarpus* juveniles is full or half siblings (Hart and Grosberg 1999). Whether a significant portion of co-occurring adult colonies are close genetic relatives is unknown. In contrast, the reproductive ecology and processes of recruitment and clonal establishment in *A. elegantissima* combine to make it very unlikely that close genetic relatives develop adjacent clonal aggregations. Sexually produced, planktotrophic larvae likely spend >30 days in the plankton prior to settlement (Siebert 1974). Successful recruits inhabit structurally complex habitats, such as dense aggregations of mussels (Sebens 1982b; Ayre and Grosberg 1995) or barnacles (Ayre and Grosberg 1995). To establish a clonal aggregation, a recruit must generate asexually derived polyps (Sebens 1982b), eventually move out of the complex habitat of initial recruitment (Sebens 1982a; Ayre and Grosberg 1995), and compete for space with other genotypes (Sebens 1982b), many of which likely



**Fig. 2** Relative competitive abilities of adjacent clonal pairs. **a** Mean acrorhagial allocation per polyp (number of acrorhagi/BD) of bordering *A. elegantissima* clones. Basal diameter, *BD*, refers to the diameter of the anemone basal disc. The mean acrorhagial allocation of each clone represents the number of acrorhagi, divided by the basal diameter, averaged over 20 polyps. The slope is not significantly different from 1 ( $y = 1.07x$ ; 95% CL: 0.95, 1.19; Model II regression, Sokal and Rohlf 1995). When an “outlier” (unfilled symbol) is omitted, this result remains unchanged ( $y = 1.02x$ ; 95% CL: 0.91, 1.12). **b** Mean number of stolon tips per colony replicate of bordering *Hydractinia* colonies on doubly colonized shells. Data represent three species: *Hydractinia* [GM], *H. polyclina*, and *H. symbiolongicarpus*. The slope is not significantly different from 1 ( $y = 1.09x$ ; 95% CL: 0.91, 1.27). The dotted lines indicate the relationship expected with identically matched clones:  $y = 1.0x$ . Clones or colonies were assigned letters A or B haphazardly

originated from temporally or spatially independent sexual reproductive events. Second, adjacent clones experience similar environmental regimes and may exhibit morphological similarities accordingly. This hypothesis may apply to *A. elegantissima*, in which estimates of competitive ability were obtained from direct measurements of field-collected animals. However, estimates of competitive ability in *Hydractinia* spp. were obtained from measurements of laboratory-reared, clonal replicates maintained under uniform conditions, thereby eliminating any potential effects of environmental variability. Thus, hypotheses of genetic relatedness or similar environmental regime fail to account fully for these results.

Previous reports of differences in competitive ability between adjacent *A. elegantissima* clones (Francis 1976; Ayre and Grosberg 1996), based on laboratory assays between pairs of individual anemones, are compatible with the findings presented here. Neighboring clones in this study did not exhibit exactly identical agonistic capabilities (scatter around  $y=1.0x$ ; Fig. 2), and relatively small competitive inequalities may in fact be discernible in laboratory assays between individual polyps. However, extremely large differences between neighboring pairs were rarely observed, although the potential existed (Fig. 2). Only by considering many clonal pairs simultaneously was their relative similarity elucidated.

The degree to which competitive equivalence contributes to prolonged inter-clonal interactions depends on the frequency of persistent borders in natural populations. Although common in *A. elegantissima* throughout its geographical range (Sebens 1982b; Francis 1973a; Ayre and Grosberg 1996), inter-clonal borders occur with different frequencies in the three *Hydractinia* species examined here (see Results). Shells with > 1 adult colony were most frequently encountered in *Hydractinia* [GM] (21%), but occurred with considerably less frequency in *H. symbiolongicarpus* (10%) and *H. polyclina* (4%), respectively. Site-specific variation also exists. In *Hydractinia* [GM], for example, up to 30% of hydroid-colonized shells may bear > 1 adult colony (Ferrell 2004b). Therefore, while persistent inter-clonal interactions may play an important role in *A. elegantissima* and *Hydractinia* [GM], their role in *H. symbiolongicarpus* and *H. polyclina* may be less important.

Space-limited, benthic invertebrate species regularly engage in prolonged interspecific competitive interactions (Connell 1976; Karlson 1980; Connell and Keough 1985; Tanner 1993; Connell et al. 2004). However, as with persistent inter-clonal borders, prolonged interspecific contests do not necessarily imply competitive equivalence as abiotic constraints may preclude elimination even between competitors of unequal competitive abilities. For example, desiccation stress through air exposure during low tide may prevent interspecific overgrowth in competing corals in shallow but not deeper water (Tanner et al. 1996; Connell et al. 2004). Studies of intraspecific competition enable unambiguous tests of competitive equivalence by examining compo-

nents of competitive ability in both competitors using identical units of measurement. Several authors have proposed that the likelihood of interspecific competitive equivalence increases with the diversity of mechanisms employed by competing species, such as overgrowth, overtopping, or aggressive attacks with digestive filaments or filaments (Chornesky 1989; Tanner 1993; Chadwick-Furman and Rinkevich 1994). Within species, however, competing clones employ a single mechanism of interaction (or at least fewer, more similar mechanisms than in interspecific contests). The data presented here indicate that competitive equivalence maintains inter-clonal standoffs in *A. elegantissima* and *Hydractinia* spp. despite the use of a single competitive mechanism in each of these taxa.

Comparable results from relatively small, fast-growing species and a large, slow-growing species indicate that competitive equivalence may be a common determinant of inter-clonal boundary persistence in sessile organisms, including fungi, plants, and many invertebrates. Competitive equivalence may play a similar role in territorial boundary disputes in mobile animals. Diverse animals—insects, fish, birds and mammals—commonly occupy adjacent territories and defend their territory by fighting or display (reviewed in Adams 1998). Territorial boundaries in mobile animals may also be formed by competitive equivalence (Adams 2001, 2003), as has often been assumed (but rarely tested; Adams 2003) in models of territory size (Adams 1998, 2001; Maynard Smith 1982). Thus, competitive equivalence may maintain stable boundaries between adjacent competitors in a diversity of taxa and ecological settings.

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