

# Gastropod shell size and morphology influence conspecific interactions in an encrusting hydroid

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**ABSTRACT:** Discrete patches of suitable habitat and the consequent aggregation of organisms with similar habitat requirements often intensify competition, particularly among conspecifics. Habitat differences may generate interactions between smaller or larger individuals at variable stages of development in many fungi, plants, and colonial animals. Size-dependent competitive outcomes and effects on sexual reproductive allocation indicate that differences among discrete habitats have potentially profound ecological and evolutionary implications. In the northern Gulf of Mexico, the colonial hydroid *Hydractinia* [GM] colonizes hermit crab-occupied gastropod shells (= microhabitats), which vary greatly in size and morphology. Here, the relationship between the gastropod assemblages available for *H.* [GM] colonization and the frequency of conspecific encounters and sexual status of those colonies involved is documented. Field-collected shells bore 1 to 3 colonies, and the number of colonies per shell increased with shell size. In contrast to previous studies, conspecific encounters were not limited to juvenile colonies. Sexually mature *H.* [GM] colonies generally were not distributed differently among shells with and without conspecifics. Moreover, mature colonies predominated conspecific encounters on large shell species exhibiting certain morphology. Inanimate structures, such as dock pilings and rocky surfaces, provide additional large surfaces for *Hydractinia* colonization in some areas. These results suggest that previous *Hydractinia* spp. studies represent only a subset of the diversity of ecologically relevant possibilities with respect to available substrata. Also, the characteristics of a given microhabitat (e.g. shell) affect competitive outcomes and sexual reproductive characters of its constituent competitors.

**KEY WORDS:** Gulf of Mexico · *Hydractinia* · Sexual maturity · Size-dependent

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## INTRODUCTION

Suitable habitat is often patchily distributed. The boundary separating suitable and unsuitable habitat may be sharp, restricting organisms to discrete habitat patches. Examples are widespread and varied, and include insect larvae (Shorrocks et al. 1984) or saprotrophic fungi (Holmer & Stenlid 1996, Schmit 1999) restricted to dung, vegetable, fruit, or corpse resources, mosses growing on large mammal feces (Marino 1991), water fleas (*Daphnia* spp.) distributed among rock pools (Hanski & Ranta 1983), and freshwater fishes occupying isolated stream pools (Matthews et al. 1994). Characteristics of discrete habitats—such as size, location, heterogeneity, and

scarcity—may exert a strong influence on competitive dynamics among organisms with similar habitat requirements (White & Pickett 1985). Because habitat requirements are likely to be most similar among conspecifics, intraspecific competitive dynamics may be particularly sensitive to discrete habitat characteristics.

Encrusting colonial invertebrates regularly recruit to adjacent surfaces and grow into contact with each other, which often initiates competition for space. Competition may be exacerbated in situations in which larval recruitment to relatively small, discrete substrata makes subsequent contact nearly inevitable. Gastropod shells provide substrata for many invertebrate epibionts (e.g. McDermott 2001). These shells represent discrete microhabitats that vary in many

attributes—including species, size, and inhabitant if present (e.g. live gastropod, various hermit crab species)—all of which can strongly influence epibiont assemblages (e.g. Karlson & Shenk 1983). Hydroid colonies in the genus *Hydractinia* typically encrust hermit crab-inhabited gastropod shells in natural populations and commonly engage in intraspecific competition. The present study focuses on *Hydractinia* spp. colonies in the northern Gulf of Mexico, which colonize at least 13 different gastropod shell species, exhibiting wide variation in both shell size and morphology. Mating experiments between colonies collected in the Gulf and the northwestern Atlantic indicate that colonies in the Gulf of Mexico comprise a new, undescribed species, designated *Hydractinia* [GM] (Cunningham et al. 1991).

*Hydractinia* [GM] shares many similarities with its congeners relating to intraspecific competition. Like most *Hydractinia* species, *H.* [GM] typically encrusts gastropod shells inhabited by pagurid hermit crabs. Colonies are gonochoristic broadcast spawners and disperse among shells via sexually produced planula larvae (Frank et al. 2001). Upon successful larval recruitment, colonies grow asexually by producing repeated structural units (polyps) connected by intervening stolons, and the ectoderm of stolons gradually becomes fused to form an ectodermal mat. In the event that 2 or more larvae successfully recruit to a single shell, conspecific encounters may be inevitable. Indeed, several studies have documented the frequent incidence of multiple colonization of a single shell and/or supply indirect evidence of interference competition between *Hydractinia* spp. conspecifics in natural populations (Yund et al. 1987, Buss & Yund 1988, Yund & Parker 1989, Yund 1991, Hart & Grosberg 1999). In some cases, conspecific encounters may exceed even heterospecific encounters in frequency (Buss & Yund 1988).

### Shell size and morphology

Differential post-recruitment mortality with regard to position on a gastropod shell restricts to some extent the surface regions that enable successful colonization by *Hydractinia* (Yund et al. 1987). As a result, successful colonizers of a single shell often are located near one another (i.e. approximate intercolony distance  $\leq 5$  mm) (Buss & Yund 1988, Yund & Parker 1989, Yund et al. 1987). Fig. 1 shows that depending on the gastropod species and its corresponding morphology, 2 shell surface regions that yield high postrecruitment survivorship, separated by a larger region of low juvenile survivorship, may exist (Yund et al. 1987, Buss & Yund 1988). Gastropod species possessing a well-developed

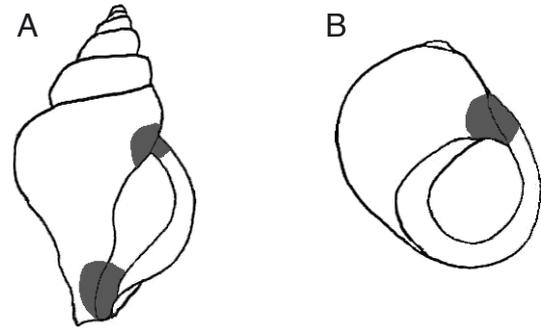


Fig. 1. Shell morphology and successful recruitment position(s). Shaded regions represent areas yielding high post-recruitment survivorship of *Hydractinia* colonies, as reported by Yund et al. (1987), Buss & Yund (1988), and Yund & Parker (1989). Shell regions associated with high juvenile survivorship are found near the aperture where the outer body whorl meets the spire and in and around the siphonal canal. A: Shells with a well-developed siphonal canal (e.g. *Urosalpinx cinerea*) possess 2 regions of high juvenile survivorship separated by a region of low survivorship. B: Shells without a siphonal canal (e.g. *Littoraria littorea*) possess only a single region of high juvenile survivorship

siphonal canal are commonly encrusted by *Hydractinia* colonies in the northern Gulf of Mexico (see 'Results' below). On shells of this morphology, conspecific interactions occur between small or relatively large colonies depending on whether colonies recruit to the same or distant shell positions, respectively (Fig. 1, Yund et al. 1987, Buss & Yund 1988).

In general, the size of competing colonies upon contact increases with the initial distance between recruitment positions on a shell. The potential for greater spatial separation of new recruits increases with shell size regardless of shell morphology, but on shells with 2 distinct regions of high postrecruitment survivorship, this effect may be particularly strong. Importantly, in *Hydractinia*, intraspecific competitive bouts between large colonies differ in 2 key respects from those involving small colonies. The first disparity involves competitive outcomes; the second, sexual reproductive allocation.

### Competitive relationships

Contact between genetically unrelated colonies elicits a highly specialized inducible defense in *Hydractinia* spp. (von Hauenschild 1954, Ivker 1972, Buss et al. 1984, Buss & Grosberg 1990). In such agonistic contests, one or both colonies produce a profusion of tissue branches, or stolons, that swell as a result of accumulating nematocytes loaded with an especially potent nematocyst type, the basotrichous isorhiza (Buss et al. 1984). These hyperplastic stolons (as

termed by Ivker 1972) attempt to overgrow and necrotize the competitor's tissue.

The ability to mount an agonistic attack is tightly linked to gross colony morphology, which has a strong genetic basis (Buss & Grosberg 1990). Asexually derived replicates of some genotypes grow solely by expansion of ectodermal mat tissue ('mat' phenotypes) whereas others grow primarily by stolon proliferation ('stoloniferous' phenotypes) with ectodermal fusion slowly radiating out from the center of the colony. The terms 'mat' and 'stoloniferous' are analogous to 'phalanx' and 'guerilla', respectively, used in the plant literature (Lovett Doust 1981). Colonies exhibit continuous variation between these 2 morphological extremes. Having an increased capacity for hyperplastic stolon production, more stoloniferous colonies dominate in conspecific agonistic encounters (Buss & Grosberg 1990). Despite frequent competition for space, *Hydractinia* colonies found in natural populations differ widely in growth form (Hauenschild 1954, Ivker 1972, McFadden et al. 1984, Yund 1991, Ferrell 2004) and, hence, competitive ability.

Competitive outcomes are size-dependent in *Hydractinia* (Yund et al. 1987, Ferrell 2004). Competitive relationships among small *Hydractinia* colonies are essentially transitive, consistently resulting in rapid overgrowth of the inferior competitor (Yund et al. 1987, Buss & Grosberg 1990, Ferrell 2004). In contrast, contests involving larger colonies are significantly prolonged, and may or may not ultimately end in overgrowth of the inferior competitor. In those cases in which competitive exclusion occurs, competitive reversals may emerge (Yund et al. 1987, Ferrell 2004). The competitive abilities of the colonies involved likely determine the prolonged duration or effective permanence of such encounters (Ferrell 2004).

Much of what is known regarding competition in larger *Hydractinia* spp. colonies involves interspecific competitors. *Hydractinia* spp. are common symbionts occurring on larger, hermit crab-occupied shells (Karlson & Shenk 1983, Shenk & Karlson 1986), and can become established on artificial substrata (Sutherland & Karlson 1977, Karlson 1978), where interspecific encounters are frequent. Larger colonies inhibit colonization of a diversity of interspecific competitors, including gastropods (Shenk & Karlson 1986), and many encrusting species (Sutherland & Karlson 1977, Karlson 1978, McFadden 1986). Once established on dock pilings, individual colonies may be quite long-lived (e.g. up to 2.5 yr; Sutherland & Karlson 1977), encountering many different species as recruitment patterns fluctuate. In this competitive context, *Hydractinia* spp. colonies inhibit growth in the presence of competitors, and expand asexually only in the absence of competitors (Karlson 1978, 1981).

## Sexual status

Delayed overgrowth or persistent standoffs between larger conspecifics influence sexual reproductive characters in *Hydractinia* (Ferrell 2004). Several authors (Abrahamson 1975, Hughes & Cancino 1985, Harvell & Grosberg 1988) have hypothesized that clones can maximize fitness by postponing the allocation of energy to sexual reproduction until extrinsic factors limit asexual growth. Empirical support for this prediction includes clonal plants (Abrahamson 1980) and colonial marine invertebrates (hydroids: Hauenschild 1954, Braverman 1974, Stebbing 1980, Ferrell 2004; bryozoans: Harvell & Grosberg 1988; ascidians: Yamaguchi 1975, Harvell & Grosberg 1988). Among the various growth-limiting conditions implicated in these studies are the size of colonizable substrata, unfavorable aquatic conditions, simulated predatory grazing, and intraspecific competition. For example, von Hauenschild (1954) demonstrated that substrate-limited *Hydractinia* spp. colonies attained sexual maturity much sooner than genetically identical colonies encrusting unlimited substrate (mean age of first reproduction = 46 vs 125 d), and sexually mature colonies possessed as few as 2 feeding polyps. A similar effect has been demonstrated in response to intraspecific competition. In those cases where the agonistic assault is unlikely to result in overgrowth (e.g. large colony size), *Hydractinia* spp. colonies exhibit increased investment in future reproduction (Ferrell 2004). Thus, the size of competing colonies upon contact effects critical differences in the nature of conspecific interactions.

Considerable potential for conspecific interactions involving large, in addition to very small, colonies exists in *Hydractinia* [GM]. Because this hydroid commonly encrusts a variety of gastropod shells, the likelihood of conspecific interactions between relatively large colonies may vary depending upon shell characteristics. Here, I present the results of field studies indicating that the size and morphology of gastropod shells influences the frequency of conspecific encounters and sexual status of competing colonies.

## MATERIALS AND METHODS

**Field studies.** All live *Hydractinia* [GM] colonies encountered (approx. 0.5 to 1.5 m deep) during field surveys at 4 different sites along the Florida panhandle coast in the Gulf of Mexico were hand collected by the author (Fig. 2). *H.* [GM] colonies were found encrusting gastropod shells inhabited by 1 of 2 species of pagurid hermit crabs, *Pagurus longicarpus* or *P. pollicaris*, living on mud or sand flats. Collection dates, given in the Fig. 2 legend, ranged from June 1999 to September 2001.

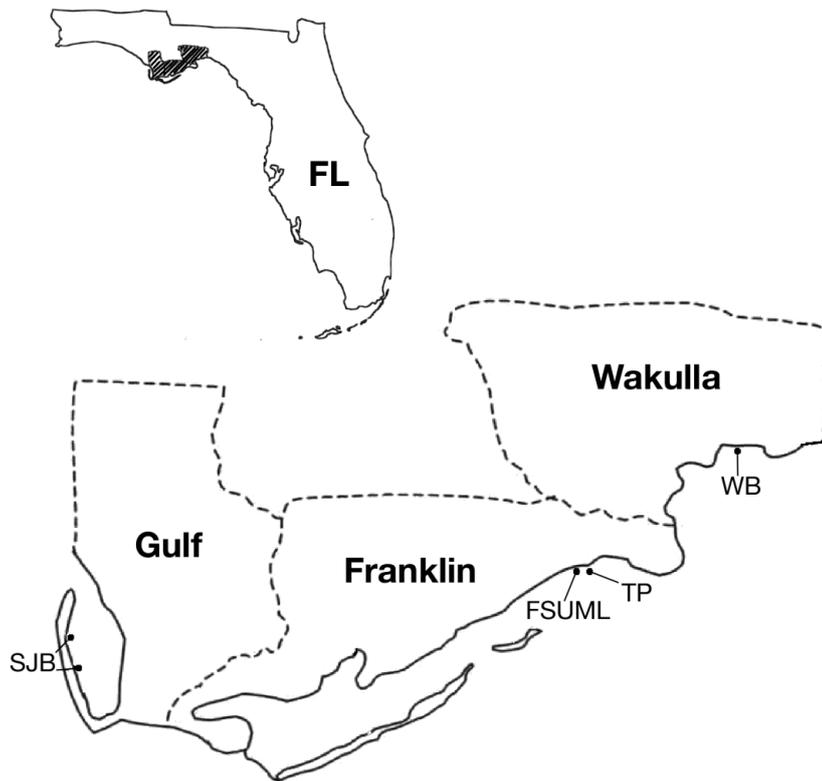


Fig. 2. Map of *Hydractinia* [GM] collection sites in Florida, USA. Hermit crabs (*Pagurus longicarpus* and *P. pollicaris*) inhabiting gastropod shells colonized by *H. [GM]* were collected at these 4 sites in the Gulf of Mexico, spanning 3 northern Florida counties (Gulf, Franklin, Wakulla). Site abbreviations and collection dates are as follows: WB = Wakulla Beach, June–July 2000; TP = Turkey Point, March–June 2000, October 2000, December 2000, April 2001; FSUML = Florida State University Marine Lab, June 2000, October 2000, December 2000, April 2001, August 2001; SJB = St. Joseph Bay, June–November 1999, February 2000, September–October 2000, April 2001, August–September 2001. Data from 2 nearby sites in SJB were very similar, and were therefore pooled to simplify later figures

For all hydroid-colonized shells, the gastropod species and maximum shell length (except at the Florida State University Marine Laboratory [FSUML] site) were recorded. Maximum shell length was measured using calipers and estimated to the nearest 0.5 mm. The number of *H. [GM]* colonies per shell was also recorded. Shells bearing more than 1 colony possessed 2 or 3 discrete areas of *H. [GM]* colonization. Sometimes these colonies were not in contact with one another, but often possessed borders exhibiting evidence of agonistic behavior. In these cases, hyperplastic stolons radiating out from bordering edges of each colony were tightly intertwined with one another, generating a suture-like appearance to the naked eye. Finally, the sexual status of each colony was noted. Colonies were categorized as sexually immature (juvenile) or mature. Sexually mature colonies possessed ripe gonophores (containing either sperm or eggs), which were easily identified using a dissecting

microscope, whereas juvenile colonies lacked these structures.

**Statistical analysis.** Contingency  $\chi^2$  tests of independence were used to evaluate whether colony reproductive status (juvenile vs sexually mature) depended upon the absence/presence of conspecifics. In those cases in which expected values were sufficiently small ( $\leq 5$ ), Fisher's exact test of independence was used instead. Tests were performed on data segregated among sites or gastropod shells as well as pooled data.

To evaluate whether the reproductive status of colony pairs—'both juvenile,' 'both mature,' or '1 juvenile and 1 mature'—found on individual shells conformed to expected frequencies, a goodness-of-fit  $\chi^2$  was used assuming a random distribution of juvenile and mature colonies among doubly-colonized shells. Shells bearing  $>2$  colonies were not included in this analysis. Using the observed frequencies of juvenile ( $p$ ) and mature ( $q$ ) colonies, expected frequencies for colony pairs—both juvenile ( $p^2$ ), both mature ( $q^2$ ), or 1 juvenile, 1 mature ( $2pq$ )—according to the following equation:  $p^2 + 2pq + q^2 = 1$  were generated. One or more small expected values resulted from segregating data among sites; thus, the test was performed on pooled data only.

## RESULTS

The frequency with which multiple colonizations of *Hydractinia* [GM] were observed on field-collected shells varied between sites ( $\chi^2_{\text{calc}} = 18.9$ ,  $df = 3$ ,  $p < 0.0001$ ). At some sites, such as Wakulla Beach (WB) and Turkey Point (TP), multiply-colonized shells constituted  $<10\%$  of all colonized shells whereas at St. Joseph Bay (SJB) multiple colonizations were observed on  $>25\%$  of colonized shells (Fig. 3). An intermediate frequency of multiple colonizations ( $\sim 15\%$ ) was observed at FSUML.

Observed differences in the frequency of multiple colonizations were accompanied by clear differences in the type and size of gastropod shells available at these sites. *Hydractinia* [GM] encrusted a variety (13 species total) of shells at field sites over a large size range of mean shell lengths ranging from 12.4 mm in the mud snail *Nassarius vibex* to 57.1 mm in the pear whelk *Busycon spiratum* (Fig. 4). The smallest and

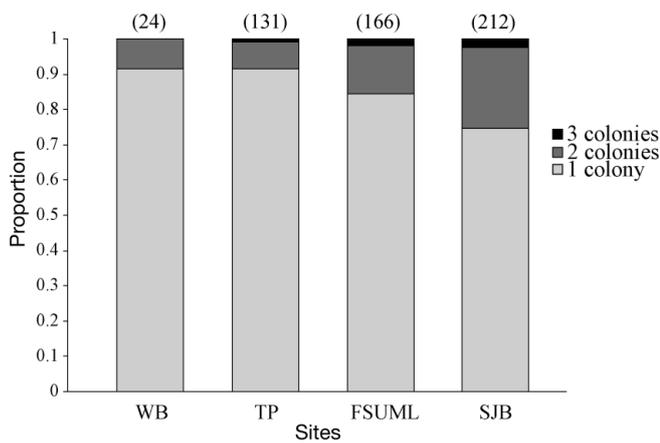


Fig. 3. Abundance of multiply-colonized shells at *Hydractinia* [GM] collection sites. The proportion of hydroid-bearing shells collected bearing 1, 2, and 3 colonies is listed per site. Site abbreviations and collection dates are listed in Fig. 2. Sample sizes are given in parentheses

largest individual shells encountered were 7.5 mm and 73.0 mm in length, respectively (data not shown). At WB, hermit crabs associated with *H.* [GM] inhabited primarily small shells, such as *Nassarius vibex* and *Littoraria irrorata* (Figs. 4 & 5). As a result, hydroid-

Table 1. Variation in shell length among sites. Shell length data include all hydroid-bearing shells regardless of gastropod species. 1-way ANOVA with Bonferroni pairwise comparisons shows that mean shell lengths differed among all sites (adjusted  $\alpha = 0.0167$ ). Site abbreviations and collection dates are given in Fig. 2, and sample sizes are given in Fig. 3

Site	Mean (mm)	95% CL
WB	17.7	(15.9, 19.5)
TP	24.1	(22.3, 26.9)
SJB	41.6	(39.7, 43.4)

colonized shells at WB were significantly smaller than those at TP and SJB (Table 1). Mean shell length differed among all sites in the following manner: WB < TP < SJB. Colonized shells at SJB were, on average, over twice as large as those at WB and nearly twice as large as those found at TP (Table 1).

Shell length was positively associated with the number of colonies per shell (linear regression: shell length [mm] = 9.05 × [no. of colonies] + 24.59, pooled data,  $p < 0.0001$ ,  $r = 0.24$ ). This trend persisted ( $p < 0.05$ ) even within a single site (SJB). It was found that the frequency of multiple colonizations on SJB shells comparable in size to those found at WB and TP approximate the frequency observed at WB and TP. For example,

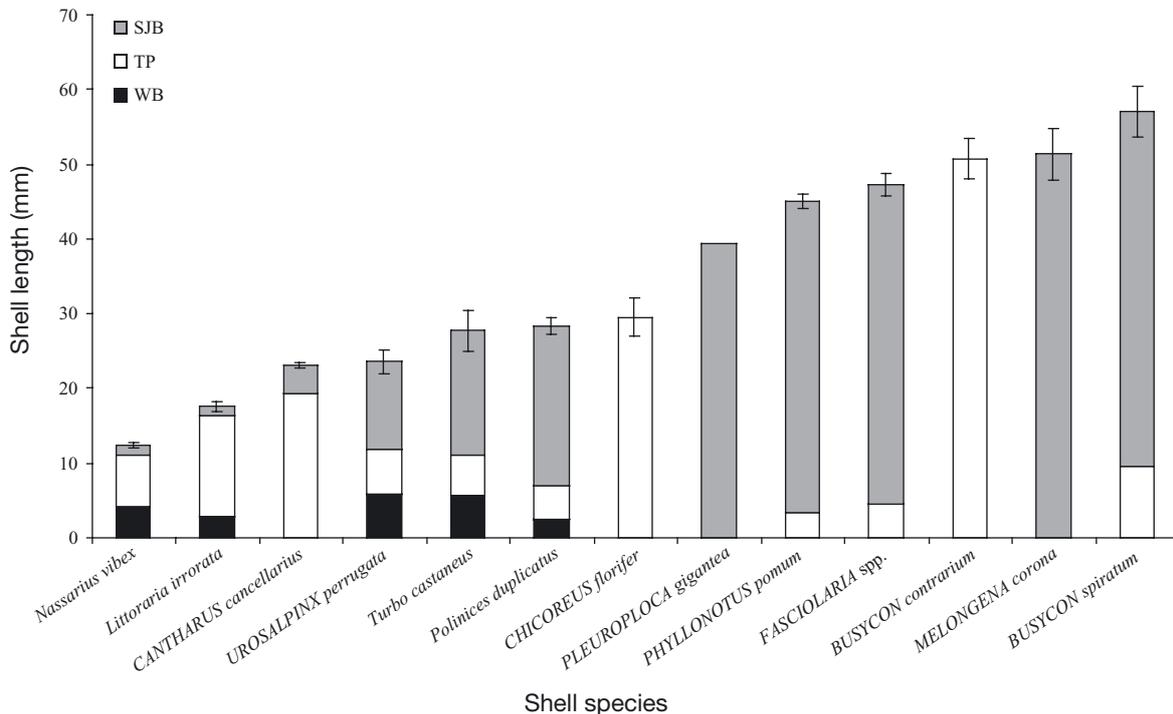


Fig. 4. Variation in size and morphology of gastropod shells inhabited by hermit crabs (*Pagurus longicarpus* and *P. pollicaris*) at *Hydractinia* [GM] collection sites. The mean ( $\pm$ SE) shell length of hydroid-bearing shells collected from field sites (WB, TP, SJB) is listed by gastropod species in ascending order. Capital lettered genera indicate shells with a well-developed siphonal canal, likely providing 2 spatially segregated regions of high juvenile survivorship (see Fig. 1A). Bar shading represents the proportional distribution of each shell species among sites. *Fasciolaria* spp. includes *F. lilium hunteria* and *F. tulipa*

subsets of SJB shells including only those  $\leq 30$  mm and  $\leq 25$  mm in length exhibited only 15.4% (4/26) and 11.8% (2/17) multiple colonizations, respectively.

Many colonies encrusting multiply-colonized shells were sexually mature, bearing ripe gonophores (Table 2). Although only 33, 23, and 25% of these colonies were mature at WB, TP, and FSUML, respectively, 74% (62/84) of these colonies at SJB were mature (Table 2b). Tests of independence indicated that colony sexual status was not generally associated with the presence of conspecifics; this was found when including only those shells bearing exclusively juvenile or sexually mature colonies (Table 2a) and when including all colonies (Table 2b). At TP, however, multiply-colonized shells were less likely to bear mature colonies. WB exhibited a similar trend, albeit statistically non-significant. The lack of significance may be attributable to small sample size. If Table 2a is modified to include all multiply-colonized shells with at least one mature colony (rather than only those shells bearing mature colonies exclusively), results remain unchanged except that, at SJB, multiply-colonized shells were more likely to harbor mature colonies ( $37/40 = 93\%$ ) than singly-colonized shells ( $134/169 = 79\%$ ). Although clear, this trend is not statistically significant ( $\chi^2_{\text{calc}} = 3.79$ ,  $df = 1$ ,  $p = 0.051$ ).

Fig. 5 shows that the gastropod shells colonized at WB and TP differed markedly from those at SJB. Most notably, *Littoraria irrorata* accounted for a large portion (~50%) of colonized shells at WB and TP (Fig. 5). Regardless of the presence of conspecifics, most colonies encrusting *L. irrorata* were juvenile (Table 3). On all other shell species in which multiple colonizations were observed (except *Polinices duplicatus*), the

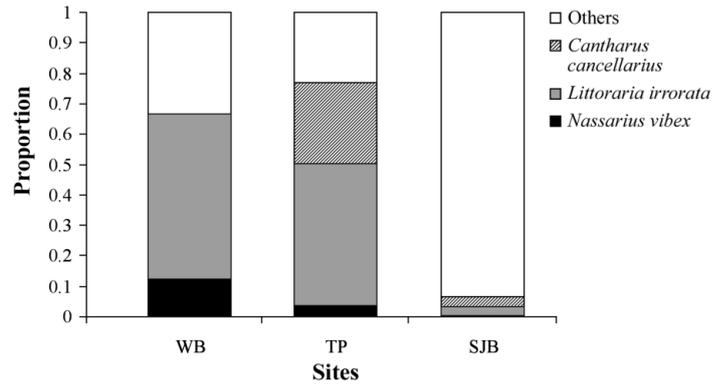


Fig. 5. Hydroid-colonized gastropod shell composition and size at *Hydractinia* [GM] collection sites. Proportion of hydroid-bearing shells composed of *Nassarius vibex*, *Littoraria irrorata*, *Cantharus cancellarius*, and other gastropod species listed in Fig. 3 (see Fig. 2 for abbreviations)

opposite was true. That is, regardless of the presence of conspecifics, most colonies were sexually mature. In the case of *P. duplicatus*, colonies on multiply-colonized shells, although typically mature, bore a significantly larger proportion of juvenile colonies than did singly-colonized shells (Table 3). When pooled over all sites, however, *H.* [GM] colonies on multiply-colonized shells were equally as likely to be juvenile or sexually mature (Tables 2 & 3).

Colony pairs of the same sexual status (i.e. both juvenile or both mature) occurred more frequently on the same shell than expected if colonies were randomly distributed among shells (Table 4). The preponderance of juvenile-juvenile versus mature-mature colony pairs, however, differed among sites. Juvenile-juvenile

Table 2. *Hydractinia* [GM]. Relationship between presence of conspecifics and sexual maturity among sites. The absence and presence of conspecifics corresponds to singly- and multiply-colonized shells, respectively. Sexually mature colonies possess ripe gonophores (containing either sperm or eggs). Tests of independence—Contingency  $\chi^2$  or Fisher's Exact Test—were used to examine whether (a) the number of shells bearing *only* juvenile or sexually mature colonies depended upon the presence of conspecifics, and (b) the total number of juvenile or sexually mature colonies depended upon the presence of conspecifics. Site abbreviations and collection dates are listed in Fig. 2.  $\chi^2_{\text{crit}, 0.05} = 3.84$ ,  $df = 1$ ; statistically significant results are in bold

Site	Conspecifics	a			b		
		# shells with <i>only</i> juvenile	# shells with <i>only</i> mature	Result	# juvenile colonies	# mature colonies	Result
WB	Absent	6	15	Fisher: $p = 0.25$	6	15	Fisher: $p = 0.11$
	Present	2	1		4	2	
TP	Absent	45	76	<b>Fisher: <math>p = 0.007</math></b>	45	76	<b>Fisher: <math>p = 0.001</math></b>
	Present	7	1		17	5	
FSUML	Absent	111	31	Fisher: $p = 0.52$	111	31	$\chi^2_{\text{calc}} = 0.161$
	Present	17	4		40	13	
SJB	Absent	35	134	Fisher: $p = 0.23$	35	134	$\chi^2_{\text{calc}} = 0.97$
	Present	3	22		22	62	
Overall	Absent	197	256	$\chi^2_{\text{calc}} = 1.12$	197	256	$\chi^2_{\text{calc}} = 2.27$
	Present	29	28		83	82	

Table 3. *Hydractinia* [GM]. Relationship between presence of conspecifics and sexual maturity among gastropod shell genera. Tests of independence — Contingency  $\chi^2$  or Fisher's Exact Test were used to examine whether the total number of juvenile or sexually mature colonies depended upon the presence of conspecifics. Shell

Shell	Conspecifics	# juvenile colonies	# mature colonies	Result
<i>Littoraria</i>	Absent	146	28	$\chi^2_{\text{calc}} = 1.79$
	Present	56	17	
<i>Polinices</i>	Absent	7	55	$\chi^2_{\text{calc}} = 10.1^{**}$
	Present	11	16	
<i>Phyllonotus</i>	Absent	9	45	$\chi^2_{\text{calc}} = 0.04$
	Present	5	22	
<i>Fasciolaria</i>	Absent	16	50	$\chi^2_{\text{calc}} = 0.63$
	Present	9	19	
<i>Melongena</i>	Absent	2	4	Fisher: p = 0.59
	Present	2	6	
<i>Busycon</i>	Absent	1	5	Fisher: p = 0.75
	Present	0	2	
Overall	Absent	181	187	$\chi^2_{\text{calc}} = 0.06$
	Present	83	82	

interactions accounted for 66 to 74 % of colony pairs at WB, TP, and FSUML but only 8 % (3/36) of SJB pairs (Table 4). Instead, most colony pairs (22/36 = 61 %) at SJB involved 2 sexually mature colonies. Pooled among all sites, shells bearing colony pairs were equally as likely to bear 2 juvenile (29/72 = 40 %) or 2 mature (28/72 = 39 %) colonies whereas interactions between juvenile and mature colonies occurred less frequently (15/72 = 21 %).

**DISCUSSION**

Conspecific encounters in *Hydractinia* spp. are not limited to small, juvenile colonies. As a rule, sexually mature *Hydractinia* [GM] colonies are not differentially distributed among singly- or multiply-colonized shells. In fact, mature colonies may predominate on multiply-colonized shells depending on the local gastropod shell assemblage available for encrustation. Among-site disparities in shell relative abundance appear to be tightly linked to differences in the frequency of conspecific encounters as well as the sexual status of those colonies involved.

Many empirical studies of competition within discrete habitats have focused on interactions between species (e.g. Hanski & Ranta 1983, Marino 1991, Holmer & Stenlid 1996, Schmit 1999), despite the fact that conspecifics likely share most similar habitat requirements and therefore compete most intensely. In prolonged conspecific interactions, *Hydractinia* spp. competitors may ameliorate competitive effects by adjusting sexual reproductive characters. Notably, however, at least one

hydractiniid hydroid may disperse asexually via fragmentation (Bavestrello et al. 2000). To the extent that among-shell dispersal requires sexual reproduction, compensatory effects involving sexual reproductive characters may be more, or less, probable in the face of competition.

**Shell size and morphology**

An overwhelming majority of studies maintain that conspecific agonistic contests in *Hydractinia* spp. involve small, juvenile colonies (Yund et al. 1987, Buss & Yund 1988, Buss & Grosberg 1990, Yund 1991, Hart & Grosberg 1999, Van Winkle & Blackstone 2002). The present study suggests that this conclusion is likely attributable to the size and species of gastropod shells available for

*Hydractinia* spp. colonization. Previous studies of intraspecific competition have been conducted on northwestern Atlantic *Hydractinia* species, *H. polyclina* and *H. symbiolongicarpus*. The discrete gastropod substrata encrusted by both of these species are relatively small in size (Buss & Yund 1989) and often possess a morphology such that only one shell region yields high juvenile colony survivorship (Yund & Parker 1989); thus, conspecific contests largely involve small, typically juvenile, colonies. However, such uniformity in size and morphology of colonizable shells is

Table 4. *Hydractinia* [GM]. Sexual reproductive status of colony pairs on individual shells. Sexually mature colonies possess ripe gonophores (containing either sperm or eggs). Shells bearing >2 colonies were not included. Goodness-of-fit  $\chi^2$  test was used to examine whether data conformed to expected frequencies of juvenile–juvenile, mature–mature, and juvenile–mature pairs, respectively (see 'Materials and methods', subsection 'Statistical analysis' for explanation of null model). Small expected values preclude separate analysis within sites; thus, a statistical result is given only for pooled data. Expected values are given in parentheses below observed values. \*\*\*significant at p < 0.0001 ( $\chi^2_{\text{crit}, 0.05} = 5.99$ , df = 2)

Site	Juvenile–juvenile	Mature–mature	Juvenile–mature	$\chi^2_{\text{calc}}$
WB	2	1	0	-
TP	7	1	2	-
FSUML	17	4	2	-
SJB	3	22	11	-
Overall	29 (18.5)	28 (17.5)	15 (36.0)	24.5***

not typical of all field situations. Indeed, mean shell length of hydroid-colonized shells at SJB (~42 mm) greatly exceeds even the maximum shell length reported in some northwestern Atlantic *Hydractinia* spp. populations (Buss & Yund 1988). *Hydractinia* spp. commonly associate with larger hermit crabs and consequently larger shells both in the northwestern Atlantic (Karlson & Shenk 1983, Shenk & Karlson 1986, Buss & Yund 1989) and the northern Gulf of Mexico (the present study).

The availability of a variety of larger, colonizable shells creates an ecological situation fostering interactions between larger, often sexually mature, colonies (in addition to small colonies). Other substrata suitable for *Hydractinia* spp. growth provide still larger surfaces for colonization. These include man-made structures (e.g. dock pilings; Sutherland & Karlson 1977, Karlson 1978) and rocks (author's pers. obs.). Previous *Hydractinia* spp. studies accurately describe the nature of conspecific interactions encountered at focal study sites but may represent only a subset of the diversity of ecologically relevant possibilities with respect to gastropod shells and other colonizable substrata.

The size of *Hydractinia* spp. colonies upon contact depends upon at least 3 factors: the distance between successful colonizers, the respective growth rates of the colonies involved, and whether colonies derive from temporally distinct recruitment events. Of particular interest is intercolony distance, which may be determined, at least in part, by the gastropod species available for colonization. In *H. polyclina* and *H. symbiolongicarpus*, the initial intercolony distance is typically very small; thus, colony growth rates have a near negligible effect on determining colony size at contact, as intercolony contact will occur rapidly regardless of growth rate. Even when ignoring recruitment site preferences, intercolony distance is limited in principle by the small shell size utilized by these species. This is not true of all *Hydractinia* species, however. For example, *H. symbiopollicaris* associates primarily with a hermit crab species *Pagurus pollicaris*, that generally occupies much larger gastropod shells (e.g. *Polinices duplicatus* and *Busycon* spp.) than those colonized by *H. polyclina* and *H. symbiolongicarpus* (Buss & Yund 1989). Similarly, *H. [GM]* associates with hermit crab species (*P. pollicaris* and *P. longicarpus*) inhabiting both small and large shells. Comparatively large gastropod shells encrusted by *H. symbiopollicaris* and *H. [GM]* not only differ in size, but also the shell morphology of many of these gastropods indicates the presence of 2 spatially discrete shell surface regions with high juvenile survivorship. The number of hydroid recruits per shell is positively associated with shell size (Buss & Yund 1988, the present study), and the distance between the 2 regions enabling successful colonization also increases

with shell size. Thus, the intercolony distance between some portion of *H. symbiopollicaris* and *H. [GM]* recruits may depend critically on shell morphology and size.

### Competitive relationships

To date, competitive relationships among small colonies have been emphasized in *Hydractinia* spp. and are consequently well understood. Small colony interactions proceed rapidly to competitive exclusion of the inferior competitor, yielding essentially transitive dominance hierarchies (Yund et al. 1987, Buss & Grosberg 1990, Ferrell 2004). In comparison, our understanding of larger colony interactions lags far behind. Yund et al. (1987) found evidence of competitive reversals and significantly prolonged agonistic interactions (possibly standoffs) in larger colony interactions even when considering only a single competing pair of genotypes. Ferrell (2004) also observed the incidence of prolonged or standoff interactions and competitive reversals when including larger colonies but demonstrated that competitive outcomes remained independent of colony size only in those interactions involving the best competitors. The strong size-dependence of competitive outcomes in *Hydractinia* spp. complements the hypothesis that colonies are likely adapted for agonistic interactions and competitor overgrowth early in colony development (Yund et al. 1987, Van Winkle & Blackstone 2002).

Studies of interpecific competition further indicate that larger *Hydractinia* spp. colonies prevent competitive exclusion. *Hydractinia* spp. are known to endure prolonged competitive interactions with a variety of species (Sutherland & Karlson 1977, Karlson 1978, McFadden 1986, Shenk & Karlson 1986). In these standoffs, *Hydractinia* spp. generally do not attempt to overgrow competitors but instead inhibit their growth (Sutherland & Karlson 1977, Karlson 1978). As a result, colonies change little in size during such interactions, increasing in size through asexual expansion only when adjacent space is unoccupied (Karlson 1978, 1981). Other clonal cnidarians employ similar growth inhibition strategies in interspecific contests, resulting in competitive standoffs (Karlson 1980). Some clonal cnidarians, including *Hydractinia* spp. (see 'Materials and methods'), generate conspicuous borders separating large colonies or clonal aggregations while engaging in agonistic interactions with conspecifics (Francis 1973, Purcell 1977, Shaw 1991). If borders remain stable, they reflect competitive standoffs. Indeed, Francis (1973) demonstrated that such borders are quite stable in the sea anemone *Anthopleura elegantissima*, persisting up to 4 yr. As in interspecific competition, *Hydractinia* spp. may employ a defensive,

growth inhibitive strategy in intraspecific contests between larger colonies.

Future studies should track the temporal stability (or instability) of apparent standoffs found between naturally occurring *Hydractinia* spp. colonies, and evaluate the relative competitive ability of those colonies involved. Likewise, long-term monitoring of large colony, conspecific interactions in an experimental setting may be revealing.

### Sexual status

*Hydractinia* spp. colonies are known to increase investment in future reproduction when contacting conspecifics given overgrowth-inhibiting conditions (Ferrell 2004). As a result, it is perhaps not surprising that sexually mature colonies often were found encrusting multiply-colonized shells in the present study. That is, an accelerated onset of sexual maturity in neighboring colonies may account, at least in part, for this finding. Experimental studies have demonstrated that a variety of clonal organisms may modify sexual reproductive characteristics (e.g. age/size at sexual maturity, reproductive allocation) in response to growth-limiting factors, including intraspecific competition (von Hauenschild 1954, Braverman 1974, Yamaguchi 1975, Abrahamson 1980, Stebbing 1980, Harvell & Grosberg 1988, Ferrell 2004). However, field observational confirmations of this experimental result are rare. For example, *Didemnum moseleyi* ascidian colonies exhibit reduced sexual reproductive allocation in naturally crowded conditions (Stocker & Underwood 1991). Naturally crowded *Hydractinia* [GM] colonies (i.e. those on multiply-colonized shells), however, were not less likely to be sexually mature than isolated colonies; in fact, in some cases, crowded colonies were predominantly sexually mature. Thus, the distribution of juvenile and mature colonies among singly- and multiply-colonized shells observed in this study is consistent with the notion of conspecific-induced changes in reproductive characters in *Hydractinia* spp..

Alternately, the similar sexual status of colonies on single shells could result from simultaneous recruitment and similar maturation rate of co-occurring colonies. The synchronization of maturation rate would be enhanced further if the co-occurring colonies were related. The reproductive biology of *Hydractinia* spp. makes this scenario possible, and it therefore cannot be dismissed. However, co-occurring mature colonies may persist for months (author's unpubl.), suggesting that similar sexual status does not occur simply as a consequence of synchronized recruitment and colony development prior to rapid overgrowth by the dominant competitor.

### Trends in competitive ability and colony morphology

Shell size and the incidence of interactions between sexually mature colonies varied among field sites in *Hydractinia* [GM]. Interactions between mature colonies encrusting large shells may represent competitive standoffs or, at the very least, permit sexual reproductive opportunities (albeit limited) to inferior competitors prior to overgrowth. This type of conspecific encounter also appears likely in other *Hydractinia* species (such as *H. symbiopollicaris*), which associate with relatively large hermit crab species and therefore may encrust large gastropod shells frequently. Among-population or among-species differences in the likelihood of competitive interactions involving juvenile versus mature colonies may be reflected in differences in the relative abundance of poor versus good competitors. Yund (1991) showed that superior competitors (i.e. stoloniferous growth forms) are more abundant in populations with more frequent intraspecific competition in *H. polyclina*, providing evidence for selection on competitive ability (larger colony interactions are rare in *H. polyclina*). Conversely, in those populations or species in which larger colonies commonly engage in intraspecific competition, selection for superior competitive ability may be relaxed. Competitively dominant genotypes should be less abundant in these populations or species. Given that the primary determinant of competitive ability is gross colony morphology (Buss & Grosberg 1990), this prediction can be tested by comparing the relative abundance of different colony morphologies among populations or species.

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