

LIVING ON THE EDGE: JUVENILE RECRUITMENT AND GROWTH OF THE
GOOSENECK BARNACLE *POLLICIPES POLYMERUS*

by

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CHAPTER I

GENERAL INTRODUCTION

Variation in hydrodynamic and biological processes affects recruitment, growth, and survival of marine populations (Barry and Dayton, 1991). These populations are frequently observed in intertidal habitats as patchy assemblages of organisms (Sousa, 1985). The interactions among established individuals and settling larvae are important in explaining the boundaries and maintenance of assemblages in marine systems. In the mid-high rocky intertidal communities on the west coast of North America, the gooseneck barnacle *Pollicipes polymerus* is a conspicuously observed species that forms dense clusters. Gregarious settlement of larvae on adult peduncles may contribute to the dense packing of adult gooseneck barnacles. The aggregated lifestyle of this species implies profound ecological impacts for both juveniles and adults living within clusters, including competition for space and food, which, in turn, impact growth. Considering the ecological costs and benefits of an aggregated lifestyle is important for this species, which is found in clusters of various sizes and, more rarely, as solitary adult barnacles.

Recruitment is an essential process that structures communities because all subsequent interactions within communities depend on its success (Woodin et al., 1995). Chapter I of this thesis focuses on the distribution patterns of larval and juvenile gooseneck barnacles in relation to their recruitment location on adult peduncles and in a

broader context, to their recruitment location within the entire cluster (edge, middle, or center of the cluster). Additionally, it compares the abundance of recruits in different sizes of clusters including small clusters, large clusters, and solitary adult barnacles. The recruitment patterns of recently settled cyprids and juveniles (< 0.5 mm rostro-carinal length) have not been well documented. Furthermore, no one has looked at where the cyprids and juveniles are recruiting within the dense matrix of adults of *P. polymerus*.

Growth of organisms is one of the fundamental components of their life-histories. Important aspects of the dynamics of populations and communities may be elucidated by studying the growth rates of individuals and the variation in growth among and within habitats. Chapter II of this thesis explores the growth rates of juvenile gooseneck barnacles *Pollicipes polymerus* in relation to both cluster size and location within the cluster.

In essence, this thesis explores the recruitment and growth patterns of larval and juvenile gooseneck barnacles in an effort to understand the formation and preservation of the discrete clusters of adult *P. polymerus*. Understanding the recruitment and growth patterns of juveniles of this species of gooseneck barnacle is especially important given both the tradeoffs associated with living in a group and as a solitary individual (reviewed in Buss, 1981) and the competitive relationship between the gooseneck barnacle *Pollicipes polymerus* and the California mussel, *Mytilus californianus* (Paine, 1974; Wootton, 1990).

CHAPTER II

RECRUITMENT PATTERNS OF GOOSENECK BARNACLES *Pollicipes polymerus*

1. Introduction

In the marine environment, many species of benthic invertebrates are known to form dense aggregations. Examples of aggregating species include barnacles, mussels, oysters, vermetid gastropods, serpulid and sabellid polychaetes, sand dollars, crinoids, brittle stars, and ascidians. For sessile organisms, spatial arrangements can negatively and positively impact fitness. A colonization pattern that results in high population densities may cause intraspecific competition for space (Hui and Moyse, 1987; Bertness, 1989) or food (Wu, 1980; Bertness et al., 1998), increased exposure to predation (Fairweather, 1988) or to parasites (Blower and Roughgarden, 1988), or inhibition of settlement caused by larval predation (Woodin, 1976; Young, 1989; Peterson, 1979). These same high populations densities may create substratum stability (Young, 1983), increase feeding efficiency (Merz, 1984; Pullen and LaBarbera, 1991), reduce risk of predation (as cited in Buss, 1981), increase the chances of finding a mate (Wu, 1978), decrease chances of mortality caused by desiccation (Lively and Raimondi, 1987) or wave-borne debris (Shanks and Wright, 1986), or increase interspecific interference

competitive ability (Buss, 1981). In many cases, the opposite arguments can be made for the impacts of colonization patterns on fitness where low population densities occur.

The ecological significance of aggregated distributions of marine invertebrates has received considerable attention. Dalby (1995) tested the hypothesis that aggregated individuals of the ascidian *Pyura stolonifera* would experience stronger effects of intraspecific competition than individuals living outside aggregations and found those inside aggregations grew more slowly; they had shorter body lengths and lighter bodies, tunics, and gonads. McGrorty et al. (1990) found a positive correlation between densities of settled spat and adult densities in beds of the mussel *Mytilus edulis*; he noted that established adults provided protection to the spat, which settled deep within the beds on adult byssal threads. Mauck and Harkless (2001) tested the hypothesis that increased competition and decreased predation should cause barnacles living in groups to spend more time feeding after a predation threat than solitary barnacles. The results indicated that solitary barnacles took longer to resume feeding than did barnacles in a group. The conclusions of Dalby (1995) highlighted a negative consequence of aggregating: intraspecific competition, while those of McGrorty et al. (1990) illustrated a positive interaction between settlers and adults. By comparing solitary and grouped barnacles, the study by Mauck and Harkless (2001) demonstrates some of the tradeoffs of living in a group. Clearly, there seem to be both ecological costs and benefits of an aggregated lifestyle.

In addition to exploring why organisms occur in aggregations, ecologists have studied how these aggregations are formed. Many marine invertebrates have pelagic

larvae that disperse away from the adult habitat and then must return, settle, metamorphose, and grow into sessile, benthic adults. Many explanations may account for how larvae contribute to the aggregative pattern of adults. Three explanations that include settlement processes are 1) larvae settle gregariously in response to contact with their own species (Crisp, 1979), 2) larvae settle associatively in response to another species i.e. surfaces, bio-organic films, and other habitat cues (Crisp, 1979), or 3) larvae accumulate near conspecific adults due to hydrodynamic processes that affect larval supply (Butman, 1987; Possingham and Roughgarden, 1990; Havenhand and Svane, 1991; Walters et al., 1997). Alternatively, aggregations may be due to variation in patterns of mortality after random settlement of the larvae into the adult habitat (Keough and Downes, 1982). Regardless of which one or combination of these explanations contributes to aggregation of a species, recruitment into established conspecific adult habitats must occur in order for the aggregations to be formed, and recruitment must continually take place to sustain the population (Young, 1988). The influence of conspecific interactions, including larval, juvenile, or adult interactions, on the population dynamics of marine systems has been an important focus of many studies (Woodin, 1976; Jensen and Morse, 1984; Svane and Young, 1989; Young, 1990; Hurlbut, 1991; Quinn et al., 1993; Hutchings, 1994; Minchinton, 1997; Gutierrez, 1998; Strasser et al., 1999; Funk et al., 2000).

On the exposed rocky shores of the west coast of North America, the gooseneck barnacle *Pollicipes polymerus* Sowerby forms distinct rosette-shaped clusters that are densely packed (Fig. 1a,b). Solitary individuals are rarely found (Ricketts et al., 1985).

This species occurs in the mid to upper intertidal, especially where there is considerable wave action. The restriction of the animal to locations with strong wave action is believed to be related to feeding behavior of the adults (Barnes and Reese, 1960). A certain level of current flow or turbulence is required before adults will begin feeding actively. Feeding takes place on the backwash of waves.

Some studies have suggested that the aggregative pattern seen in *Pollicipes polymerus* is due to the preferential settlement of cyprids on the peduncles of adults (Fig. 1c,d; Barnes and Reese, 1960; Lewis, 1975 a,b; Hoffman, 1988; Satchell and Farrell, 1993). Living within a cluster of adults might offer juveniles protection from predation, desiccation and strong wave action (Barnes and Reese, 1960). Hoffman (1984) suggested that the preferential settlement of *P. polymerus* cyprids on adult peduncles is a mechanism for allowing the recruits to eventually attach themselves to the primary substratum. He found a size gradient in the distribution of juveniles (0.5 -7 mm RC length) on the adult peduncle where the smallest and most abundant juveniles were attached near the capitulum, while the largest and fewest juveniles were attached basally at the peduncle. He explained this distribution by migration of the juveniles down the peduncle in order to become established on primary substratum.

Because adult gooseneck barnacles occur predominately in distinct clusters, I became interested in how the distribution of larval and juvenile barnacles might help explain the aggregated pattern of adults and contribute to the formation and preservation of these clusters. The gregarious settlement of cyprids, which attach to the adult

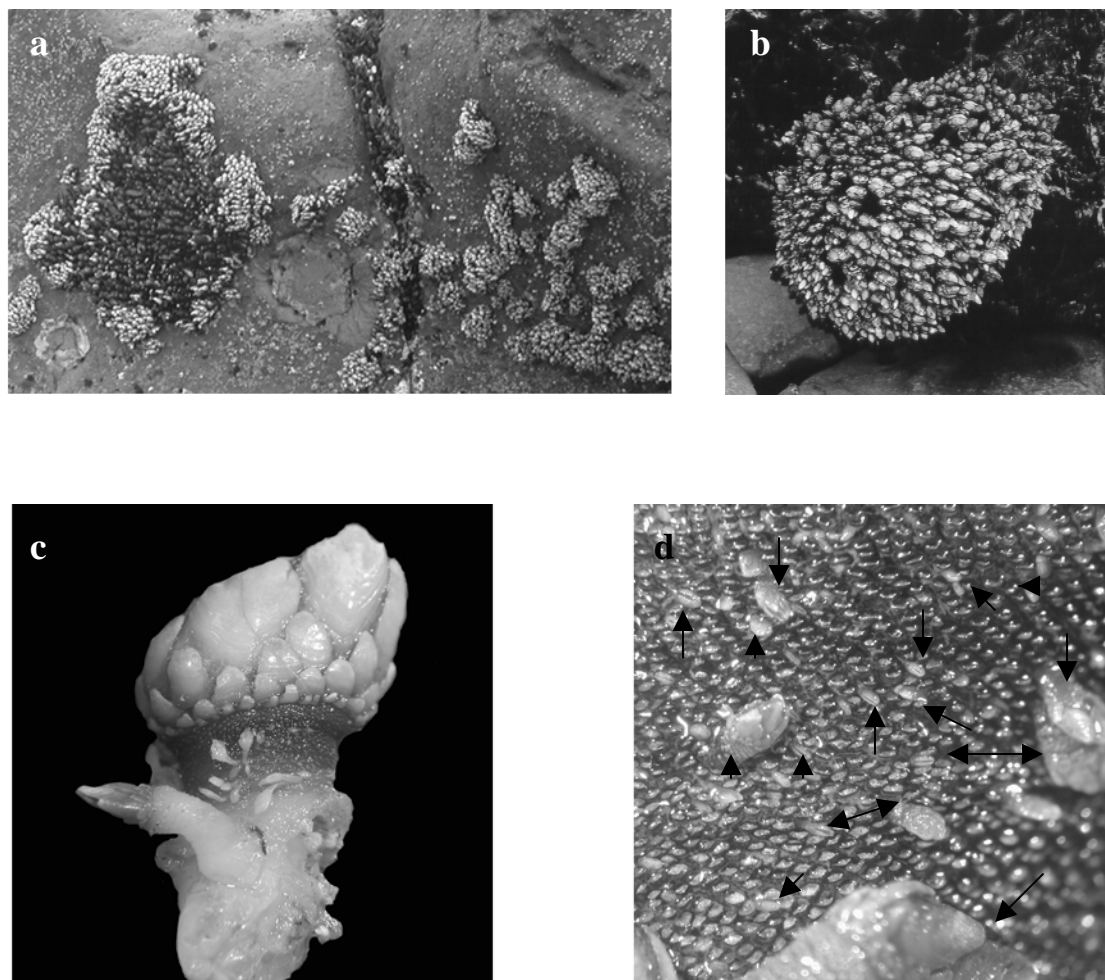


Fig. 1. Photographs of the gooseneck barnacle *Pollicipes polymerus*: a) Rock wall at South Cove, Cape Arago, OR with clusters of gooseneck barnacles and the California mussel, *Mytilus californianus* b) Dense cluster of gooseneck barnacles at Blacklock Point, OR c) Adult gooseneck barnacle with juveniles attached to the peduncle d) Close-up of peduncle with juveniles of varying sizes attached between white spicules. The smaller, cryptic juveniles are barely distinguishable from the peduncular spicules. Arrows indicate juveniles.

peduncle (Fig. 1c,d), provides the opportunity to compare larval and juvenile distribution patterns on the adult peduncle and within the whole cluster. The papers of Hoffman (1984, 1988, 1989) are the only prior investigations of the recruitment patterns of juvenile *P. polymerus* within clusters. At South Cove, Cape Arago, Oregon *P. polymerus* forms discrete clusters of various sizes on vertical surfaces (Fig. 1a) but occurs mixed within beds of *Mytilus* on horizontal surfaces. Gooseneck barnacles are also found as solitary individuals that may be isolated from surrounding organisms or isolated within beds of mussels. The variation in size of clusters and the presence of solitary adult barnacles at South Cove allows comparisons of recruitment patterns for individuals in small and large clusters and on solitary adult barnacles. This study investigates the following questions:

- 1) What is the distribution of recently settled cyprids and juveniles (< 0.5 mm rostro-carinal length, RC) on the adult peduncle in clusters of barnacles and on solitary adult barnacles?
- 2) What are the effects of location within the cluster (edge, middle, center) and cluster size (small, large, solitary adult) on the abundance of juvenile recruits?

2. Materials and Methods

2.1. Study site and Animal collection

Pollicipes polymerus clusters were collected from a sandstone rock wall at the northwest tip of South Cove, Cape Arago, OR (43°18.102 N, 124°23.989 W). The rock wall faces northwest, is 30 meters in length, is located 3 meters above mean low low water (MLLW), and lies at the edge of a large surge channel.

Round clusters of barnacles and solitary adult barnacles located vertically along a 10 meter section of the wall were selected for recruitment studies. Recruitment was examined at three different times. For a Winter 2002-2003 study, three large clusters were selected with diameters of 9-15 cm. For studies in Summer 2003 and Winter 2003-2004 studies, large and small clusters were chosen in pairs (a large and small cluster were found close to each other), and solitary individuals were also studied along the rock wall. Four pairs of clusters were chosen for Summer 2003 and five pairs of clusters were selected for Winter 2003-2004. Although results are not analyzed for pairs, pairs were selected to minimize local microhabitat differences that might exist between clusters at various locations on the rock wall. Small clusters had a diameter of 4-7 cm and large clusters were 8-14 cm in diameter. Clusters were found at intertidal heights of 1.4-2.5

meters above MLLW. Eleven solitary adults located 0.9-2.3 m above MLLW were selected for comparisons with large and small cluster pairs for Summer 2003 and seventeen solitary adults were selected for Winter 2003-2004. In a few cases, there were not enough solitary adults available. Therefore, two adults that were found together were selected instead and one adult was randomly eliminated by removing it from the rock.

Clusters and solitary adults were removed from the rock by drilling around their circumferences with a gas drill and then chiseling away the rock until the underlying rock and its cluster fell off. In some instances, the rock substratum of the clusters and solitary adults had natural cracks that appeared after removing them from the wall. In the laboratory, cracked clusters were repaired with Z-spar underwater marine epoxy (Kop-Coat, Inc.) without damaging the animals. All barnacles were kept in sea tables with unfiltered seawater and airstones for no more than ten days before they were marked and outplanted.

2.2. Marking

Calcein (Sigma # C0875) is a flouochrome that binds to calcium and becomes incorporated into calcified structures of growing animals that are exposed to the chemical (Moran, 2000). Calcein leaves a mark, visible with blue light, on the calcium carbonate plates of the barnacles (Fig. 2b,c). Calcein was used in this study to distinguish the old recruits (marked; Fig. 2b) from the new recruits (unmarked; Fig. 2a) that settled into the cluster after outplanting. A preliminary study was conducted from May 20-28, 2002 to determine the appropriate concentration and time for marking juvenile barnacles. The

brightness of marks on juveniles attached to adults were examined for 3 different concentrations of calcein (100, 120 and 160 mg l⁻¹) at four immersion times (1, 2, 4 and 8 days). All juveniles were marked regardless of the treatment, but marks varied in brightness. The marks on juveniles in concentrations of 120 and 160 mg calcein l⁻¹ were not noticeably different but were brighter than 100 mg l⁻¹, and marks on animals immersed for 4 and 8 days were brighter than those immersed for 1 and 2 days. Therefore, to conserve calcein and save time without compromising marking results, animals were immersed in 12-14 L of seawater at 120 mg calcein l⁻¹ for 4 days. Calcein solutions were made from a stock of 6.25 g l⁻¹ of calcein in distilled water. The calcein solutions, which had an original pH of 2.7, were buffered to ca. pH 6 with the addition of sodium bicarbonate to increase solubility (Wilson, 1987). Clusters (Winter 2002-2003) or clusters and solitaries (Summer 2003 and Winter 2003-2004) were randomly placed into two or four 40 L glass aquarium tanks containing the marking calcein solution. The tanks were placed into a seawater table with water held at 14-16 °C. Each tank had two stir paddles and two air stones to keep the water moving vigorously. Animals were fed once a day with concentrated cultures of the alga *Skeletonema costatum* during the Winter 2002-2003 study or a mixture of *S. costatum* and *Rhodomonas lens* during the Summer 2003 and Winter 2003-2004 studies. Algae were grown in f/2 media (Guillard, 1983). The concentration of *S. costatum* fed ranged from 1x10⁷ cell ml⁻¹ to 1.5x10⁷ cell ml⁻¹ and the concentration of *R. lens* ranged from 1.2x10⁷ to 1.5x10⁷ cells ml⁻¹.

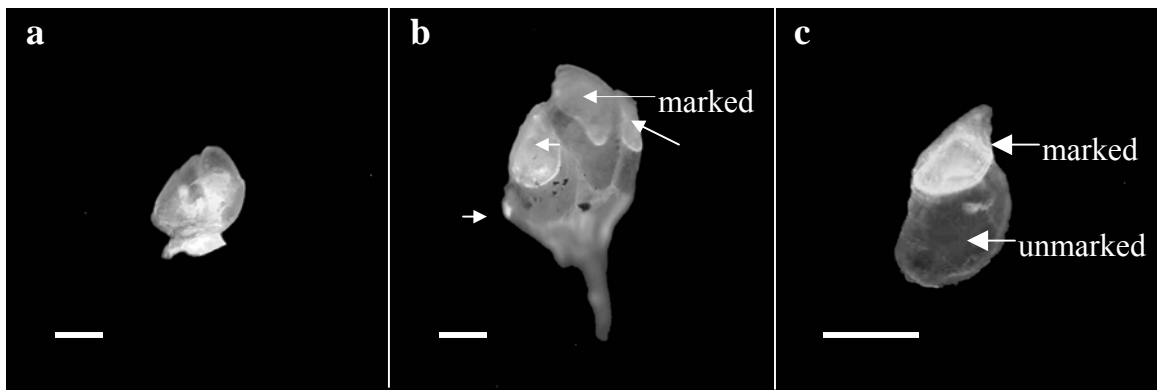


Fig. 2 Epifluorescence photographs of juveniles of *Pollicipes polymerus*. a) Unmarked juvenile b) Juvenile marked with calcein c) Right scutal plate of juvenile marked with calcein. Scale bars are 20 μm .

2.3. Outplanting

The gooseneck barnacle clusters and solitary adults were outplanted in the field by coating the bottom and sides of the underlying rock of the cluster or solitary adults and the hole on the rock wall from which the animals were removed with a layer of Z-Spar underwater marine epoxy. The cluster or solitary adult was then pressed into the appropriate hole on the wall and held in place while the epoxy was filled into any remaining gaps around the circumference of the cluster. Animals were outplanted to the same location from which they had been removed, and in the same orientation. The animals were left in the field for approximately two months before they were recollected (17 November 2002-14 January 2003= 58 days; 5 May-5 July 2003= 61 days; and 8 November 03-6 January 04= 59 days). The number of clusters and solitary adult barnacles outplanted were different from the numbers that were recovered (Table 1).

Animals were brought back to the lab and stored in 70 % ethanol until they could be processed.

Table 1. Experimental design showing the number of clusters and solitary adults that were recovered after 2 months in the field out of how many that were originally collected and outplanted for three seasons. ## = Recovered/Outplanted

Season	Cluster Size		Solitary Adults
	Large	Small	
Winter 2002-2003	3/3	0/3	0/0
Summer 2003	4/5	4/5	11/25
Winter 2003-2004	5/6	5/7	17/24

2.4. Processing clusters in the lab

Measurements of length, width and height of each cluster were recorded. All adults in clusters were then separated by location relative to the cluster center (edge, middle, and center). A piece of plexiglass with an attached transparency was suspended over the cluster. The transparency contained a circle plot sized to match the circumference of each cluster. The circle plot was then divided into three equal radial sections (edge, middle, center) and twelve 30° angular sections, and the position of each adult as a distance from the center and a compass heading angle from the top (North) of the cluster was recorded. Each adult was subsequently removed from the cluster and placed into a labeled container with 70 % ethanol.

2.5. *Recruitment position on adult P. polymerus*

Peduncle length from its junction with the capitulum to its attachment on the rock was measured with a pair of calipers to the nearest 0.1 mm for each disaggregated adult. The positions of recruits found on the peduncles of adults were recorded as distances on the peduncle and angles around the peduncle. The distance on the peduncle was measured from the junction of the capitulum and peduncle. The relative distance of each recruit was determined by dividing the distance on the peduncle where a recruit was found by the length of the host adult peduncle. The angle measured was 0-360° increasing clockwise where the rostral plate of the capitulum was 0° and the carinal plate was 180°. Each recruit was placed on a microscope slide, their rostro-carinal length was measured to the nearest 0.01 mm with a Leica MZ12 dissecting scope, and then the recruit was glued to a slide. An Olympus compound microscope equipped with epifluorescence was used to distinguish marked recruits (Fig. 2b) from unmarked recruits (Fig. 2a). Calcein has an excitation maximum of 494 nm and an emission maximum of 517 nm (Merck Index, 2003); a blue excitation filter and an XF-23 yellow emission filter (Omega Optical, Inc.) revealed the calcein mark which glowed bright green. Animals without a mark appeared light yellow to off-white in color when viewed under epifluorescence (Fig. 2a) and were distinct from marked animals.

The patterns of juvenile distributions as relative positions on the adult peduncle are presented for all clusters by season (Fig. 3, 4, 5). The distributions of juveniles on solitary adults are presented separately (Fig. 6). Juveniles in clusters and on solitary adults were grouped according to their relative distance down the peduncle and by size

classes of < 0.5 mm, 0.5 mm to 1 mm, and then by 1 mm size classes up to the largest juveniles found; cyprids were grouped separately. For Winter 02-03, size classes greater than 1 mm are not shown because juveniles from 1-8 mm RC represented 16 individuals, $< 3\%$ of the total juveniles recruited during the season and three of the four size classes had fewer than 5 juveniles (Fig. 3). In Summer 2003 (Fig. 4) and Winter 03-04 (Fig. 5), size classes greater than 4 mm are pooled because they represented 21 and 42 individuals, respectively, $< 5\%$ of the total juveniles found in clusters. Size classes of 3-6 mm were pooled for juveniles on solitary adults because there were no juveniles in the 4-5 mm size class, and there was only 1 juvenile in the 5-6 mm size class (Fig. 6).

Juveniles in clusters and on solitary adults were also mapped by their location around the peduncle. The angle on the peduncle was grouped into twelve 30° arcs, with the midpoints of the 12 arcs (0, 30, 60, 90, ... 330) measured in degrees relative to the RC axis. Juveniles in clusters and on solitary adults were divided into 2 size classes of < 0.5 mm RC and > 0.5 mm RC (Fig. 7, 8). Adults that contained no recruits were not included in the linear regressions of different size classes of recruits (Fig. 9).

2.6. *Statistical analyses*

The distributions as a relative distance down the peduncle of juveniles (< 0.5 mm RC) were tested for significant departures from randomness (using a uniform distribution) with the Kolmogorov-Smirnov test. The positions around the peduncle of juveniles in clusters were investigated with circular statistics. For this analysis, juveniles

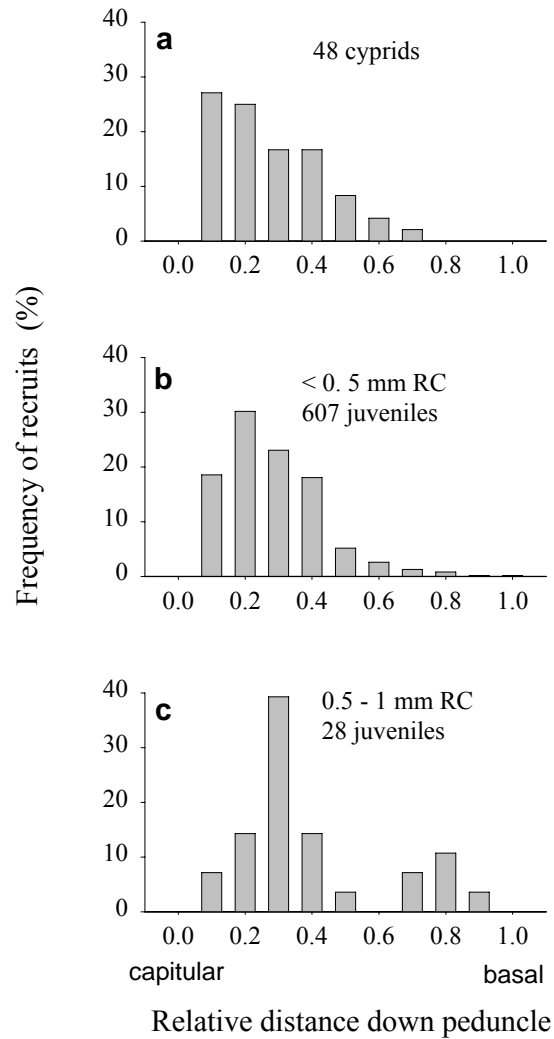


Fig. 3. Distributions of recruits of *Pollicipes polymerus* from clusters shown as a relative distance down the peduncle for one season of recruitment Winter 2002-2003: **a** cyprids, **b** < 0.5 mm juvenile rostro-carinal length (RC), and **c** 0.5-1 mm juvenile RC. 176 adults were sampled.

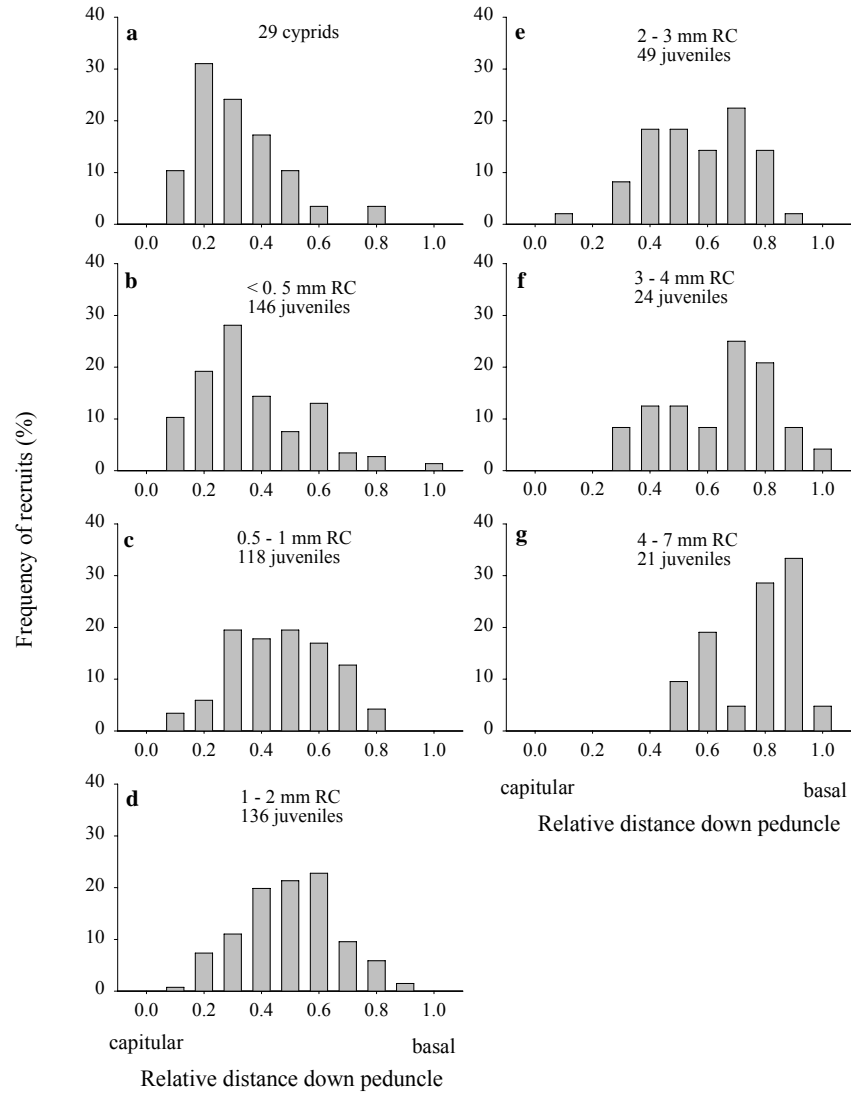


Fig. 4. Distributions of recruits of *Pollicipes polymerus* from clusters shown as a relative distance down the peduncle for one season of recruitment Summer 2003: **a** cyprids, **b** < 0.5 mm juvenile rostro-carinal length (RC), **c** 0.5-1 mm juvenile RC, **d** 1-2 mm juvenile RC, **e** 2-3 mm juvenile RC, **f** 3-4 mm juvenile RC and **g** 4-7 mm juvenile RC. 353 adults were sampled.

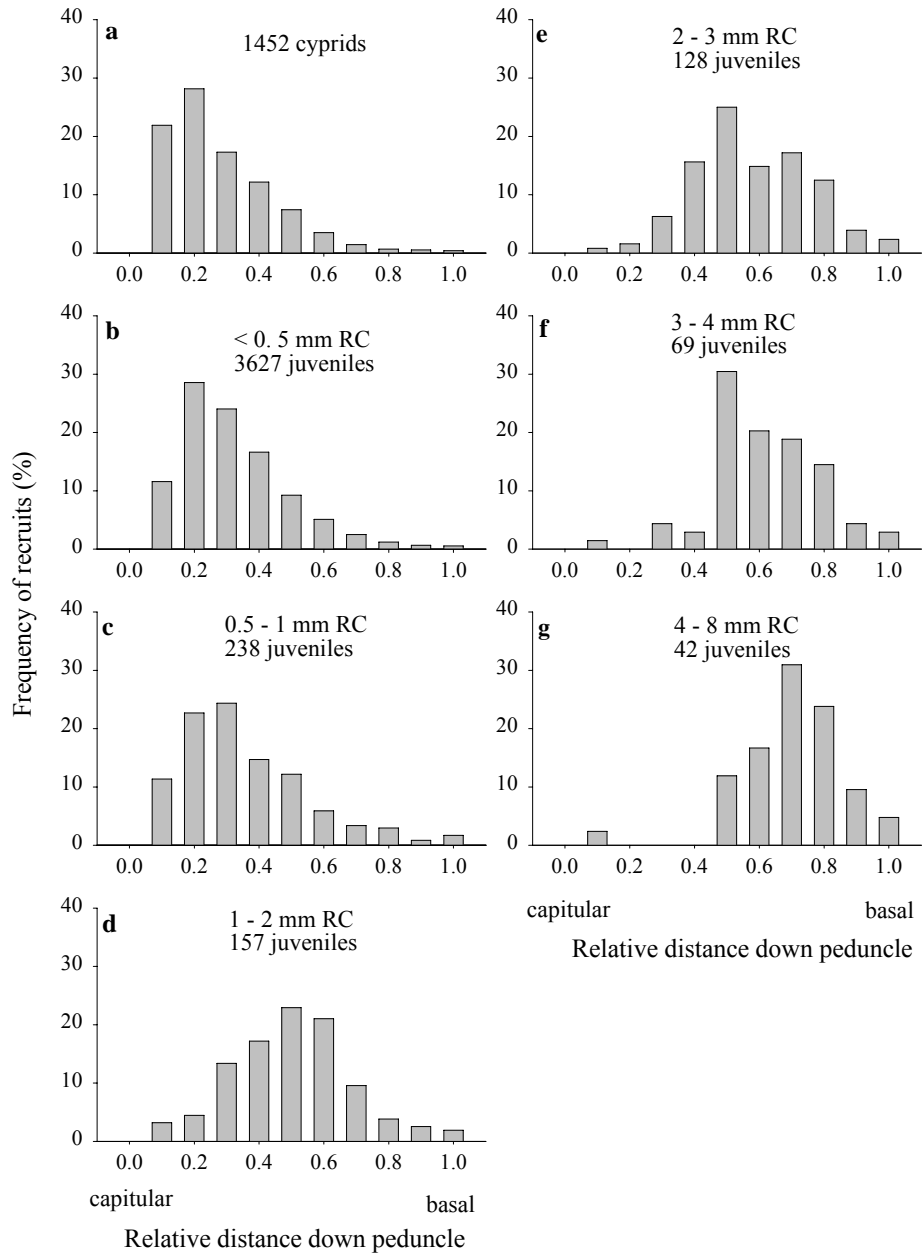


Fig. 5. Distributions of recruits of *Pollicipes polymerus* from clusters shown as a relative distance down the peduncle for one season of recruitment Winter 2003-2004: **a** cyprids, **b** < 0.5 mm juvenile rostro-carinal length (RC), **c** 0.5-1 mm juvenile RC, **d** 1-2 mm juvenile RC, **e** 2-3 mm juvenile RC, **f** 3-4 mm juvenile RC and **g** 4-8 mm juvenile RC. 469 adults were sampled.

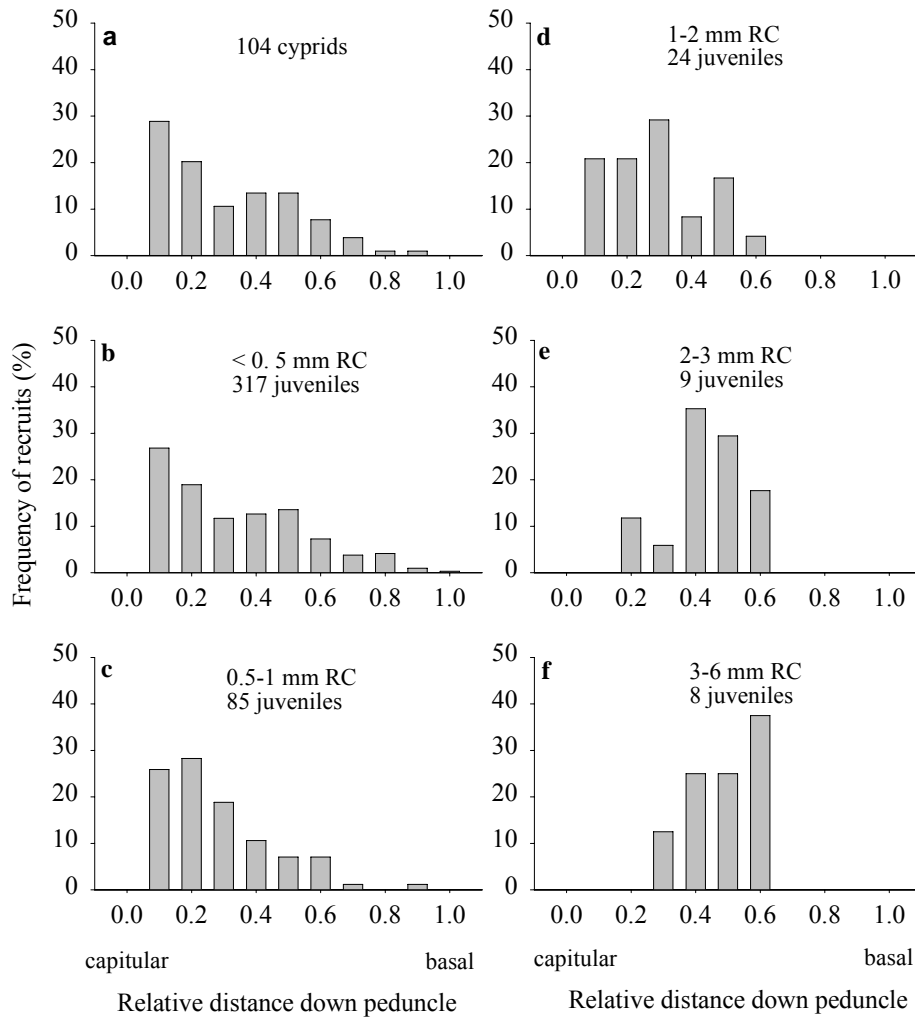


Fig. 6. Distributions of recruits of *Pollicipes polymerus* on solitary adults shown as a relative distance down the peduncle for one season of recruitment Winter 2003-2004: **a** cyprids, **b** < 0.5 mm juvenile rostro-carinal length (RC), **c** 0.5-1 mm juvenile RC, **d** 1-2 mm juvenile RC, **e** 2-3 mm juvenile RC and **f** 3-6 mm juvenile RC. 17 solitary adults were sampled.

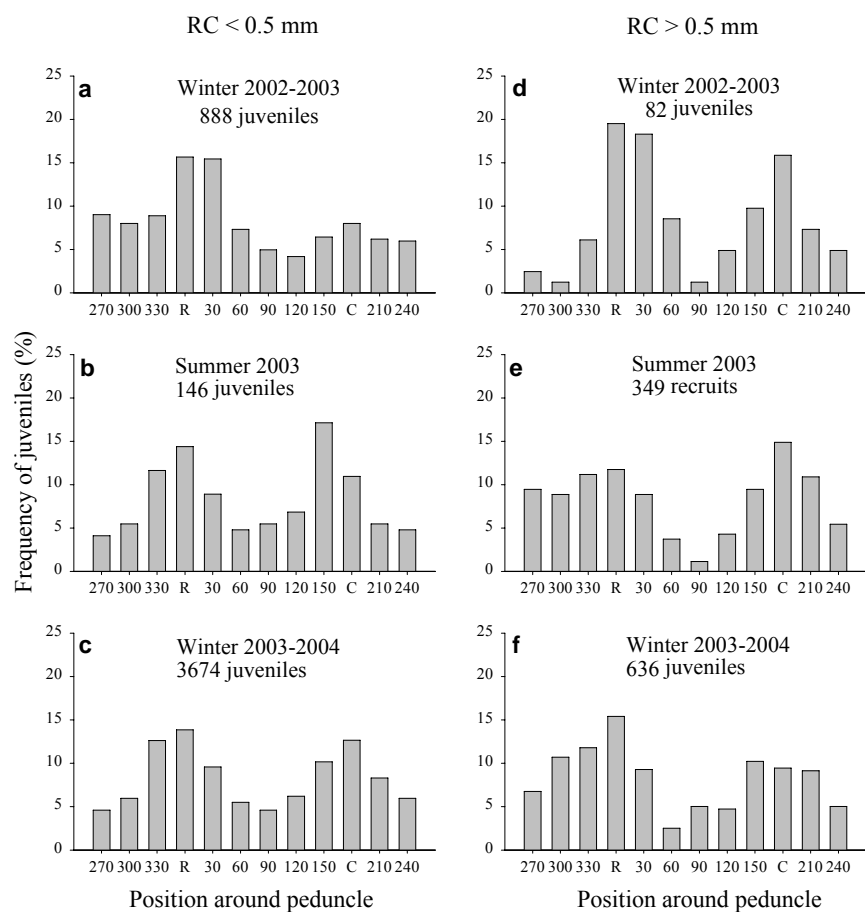


Fig. 7 Distribution of juveniles of *Pollicipes polymerus* from clusters shown as a position in degrees around the adult peduncle. Data are shown for three seasons of recruitment and two size classes of juveniles: **a** Winter 02-03, RC < 0.5 mm, **b** Summer 03, RC < 0.5 mm, **c** Winter 03-04, RC < 0.5 mm, **d** Winter 02-03, RC > 0.5 mm, **e** Summer 03, RC > 0.5 mm and **f** Winter 03-04, RC > 0.5 mm. Ticks on x-axis represent 30⁰ degree sections around the peduncle, continuous from 0-360⁰. Rostrum (R; 345⁰-15⁰) and Carina (C; 165⁰-195⁰) are shown as letters because they distinguish the major axis of the capitulum of the animal.

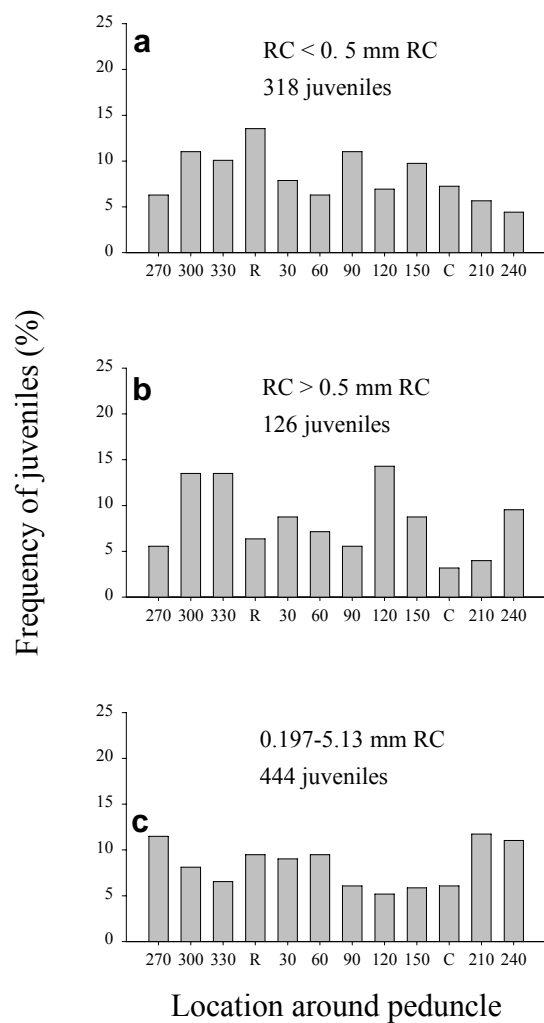


Fig. 8. Distribution of juveniles of *Pollicipes polymerus* on solitary adults shown as a position in degrees around the adult peduncle. Data are shown for one season of recruitment Winter 03-04 and three size classes of juveniles: **a** RC < 0.5 mm, **b** RC > 0.5 mm and **c** 0.197-5.13 mm RC (a, b combined). Ticks on x-axis represent 30° sections around the adult peduncle, continuous from 0-360°. Rostrum (R; 345°-15°) and Carina (C; 165°-195°) are shown as letters because they distinguish the major axis of the capitulum of the animal.

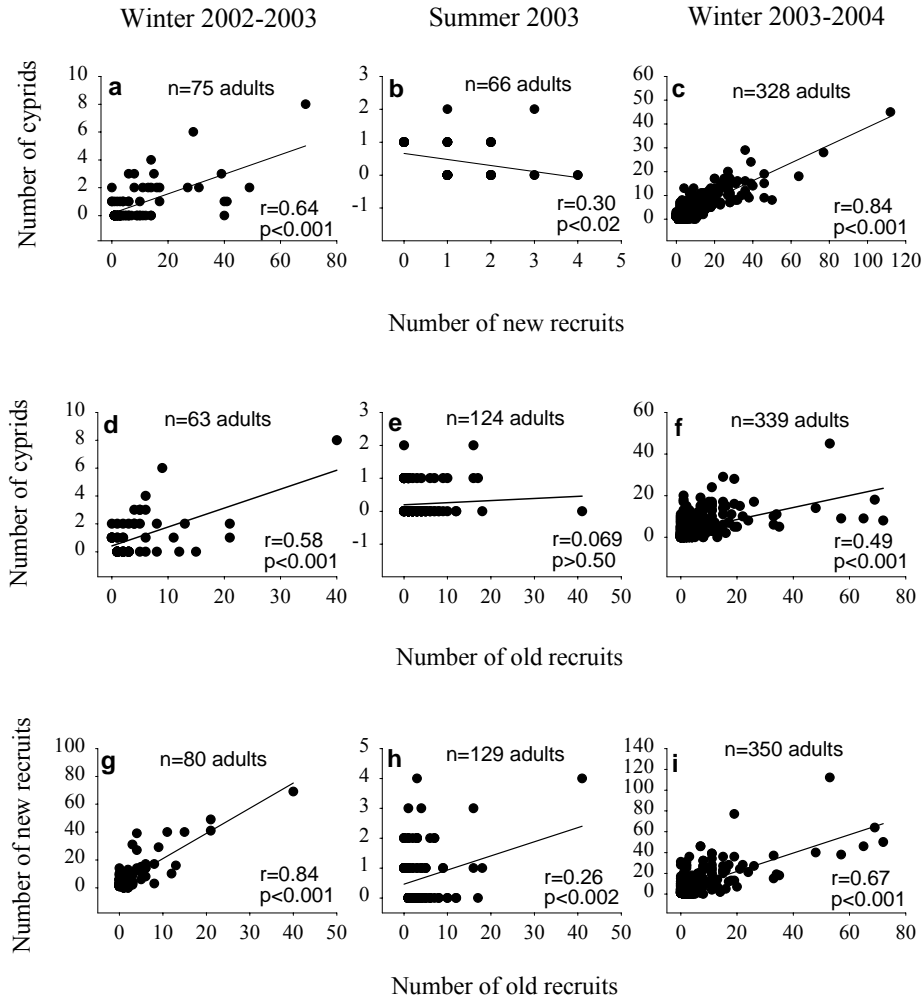


Fig. 9. Linear regressions of number of cyprids vs. number of new recruits of *Pollicipes polymerus*, number of cyprids vs. number of old recruits of *P. polymerus*, and number of new recruits vs. number of old recruits of *P. polymerus* for three seasons of recruitment: **a, d, g** Winter 2002-2003, 294 adults sampled; **b, e, h** Summer 2003; 353 adults sampled and **c, f, i** Winter 2003-2004, 469 adults sampled. Note different scales for x and y-axes.

in clusters were not divided into size classes because there was a similar distribution pattern for all sizes. Data were analyzed by a single degree rather than grouped degrees because the distributions were multimodal. Bimodal distributions were transformed into unimodal ones by doubling the angles in order to test for significance with the Rayleigh goodness-of-fit test for randomness; z values are reported for $n > 200$ and r values are reported for $n < 200$ (Batschelet, 1981). Then, the distribution was tested for bimodality by fitting a multimodal distribution using the density function of a multimodal von Mises distribution with 2 modes: $f(\phi) = \frac{1}{2\pi I_0(\kappa)} \exp[\kappa \cos 2(\phi - \theta)]$ (Batschelet, 1981). Recruitment data were analyzed using the statistical programs Statistica 6.1 and Systat 9.0. The data were transformed to their natural logarithms to remove some of the skewness resulting from variation in the numbers of adults represented in each location and to satisfy the assumption of homogeneity of variance which was tested using Cochran's test at $p < 0.05$ (Underwood, 1997). The assumption of normality was met in most cases, but two groups in the summer 2003 study violated this assumption. Recruitment data were analyzed with an analysis of variance (ANOVA) to test for differences in the effects of location within the cluster and of cluster size on recruitment. Because the Winter 2002-2003 experiment had clusters of one size, it was not included in the initial statistical analysis. Recruitment, the dependent variable, was defined as the ratio of the mean number of recruits to the number of adults in each location. Cluster size and location within cluster were the fixed factors tested; season was included as an additional random factor. Since experiments were replicated across multiple seasons, variation in treatment effects among seasons was investigated. The final model omitted

interactions that included season because these seasonal effects were absent. For significant results, Tukey's HSD or Unequal-N HSD post-hoc tests were used to determine which groups were different. In a separate ANOVA, the effects of location and season were tested on recruitment in large clusters in order to include data from the Winter 2002-2003 experiment. The final model for this analysis also omitted an interaction term (season by location) because there was no variation in treatment effects among seasons. A separate two-way ANOVA was performed to test for differences in recruitment among solitary adults, large clusters, and small clusters. Size was tested as a fixed factor and season as a random factor with recruitment as the dependent variable. Since recruitment to solitary adults was highly variable between seasons and season was not a factor of interest, a separate one-way ANOVA was performed for the Winter 2003-2004 data with size as the fixed factor and recruitment as the dependent variable.

3. Results

3.1. Distribution of larvae and juveniles on the adult peduncle: relative distance down the peduncle

Cyprids (0.22-0.28 mm width and 0.37-0.51 mm length), and juveniles (0.16 to 7.46 mm rostro-carinal length) were found attached to peduncles of adult *P. polymerus* as well as to the peduncles of juveniles. Therefore, recruits were defined as cyprids and juveniles (including those both unmarked and marked with calcein) that were attached to

adult peduncles and excluded cyprids and juveniles attached to the peduncles of other juveniles. Adults were defined as individuals in the cluster that were attached to primary substrate. This distinction is important because a few of the adults (< 15 %) were small enough to be defined as recruits, 4-7.5 mm RC, but they were attached to primary substrate and not to a host peduncle.

Juvenile size varied between seasons. In the summer experiment, 30 % of the juveniles found in clusters were < 0.5 mm RC while more than 85 % of the juveniles in clusters were this size in both winter studies. 72 % of the juveniles on solitary adults were < 0.5 mm RC in Winter 2003-2004. There was only one juvenile found on solitary adults in the summer study, and there were no solitary adults studied in Winter 2002-2003.

The distributions as a relative distance down the peduncle of cyprids and juveniles from clusters and solitary adults were predominately unimodal, but peaks occurred at different relative distances on the peduncle for different size classes. Juveniles < 0.5 mm RC length were not randomly distributed on the adult peduncle (Fig. 3b, K-S $d=0.504$, $p<0.001$; Fig. 4b, K-S $d=0.325$, $p<0.001$; Fig. 5b, K-S $d=0.407$, $p<0.01$; Fig. 6b, K-S $d=0.336$, $p<0.01$); cyprids (Fig. 3a, 4a, 5a, 6a) and juveniles > 0.5 mm RC length (Fig. 3c, 4c-g, 5c-g, 6c-f) were also not randomly distributed on the adult peduncle. In both winter studies, the smallest, most abundant juveniles on clusters were found at relative peduncle distances of 0.1-0.2 (Fig. 3a, 5a, 6a) while in the summer study, the smallest juveniles on clusters were found at relative distances down the peduncle of 0.2-0.3 (Fig. 4a). On solitary adults, the smallest juveniles were found at the very top of the peduncle,

at relative distances down the peduncle of 0-0.1 (Fig. 6a). As juveniles increased in size, their relative positions on the peduncle shifted downward (Fig. 3c, 4c-g, 5c-g, 6c-f). There was a clear gradient in sizes and abundance on the peduncle with more abundant, smaller juveniles found at the top of the peduncle and fewer, larger juveniles found at the bottom of the peduncle. The smallest juveniles on clusters and solitary adults were found from the top to the bottom of the peduncle; however, the largest juveniles were usually absent from the top of the peduncle (Fig. 4e-f, 5f, 6e). Larger juveniles (1-5.13 mm) on solitary adults were never found below a relative distance of 0.6 of the way down the peduncle (Fig. 6b-e), whereas larger juveniles in clusters were distributed to the bottom of the peduncle (Fig. 4b-f, 5b-f).

3.2. Distribution of larvae and juveniles on the adult peduncle: position around the peduncle

The juveniles on clusters from both size classes were not randomly distributed around the adult peduncle (Fig. 7; Winter 2002-2003, $z=35.97$, $p<0.001$; Summer 2003, $z=34.51$, $p<0.001$; Winter 2003-2004, $z=304.81$, $p<0.001$). In all seasons, the distribution of juveniles on adult peduncles from clusters was bimodal. Juveniles were found below the rostrum (0°) and below the carina (180°). In Winter 2003-2004, the mean angles of recruits were 354° and $177^\circ \pm 34.7^\circ$, in Summer 2003 the mean angles of recruits were 352° and $176^\circ \pm 34.8^\circ$, and the mean angles of recruits for Winter 02-03 were 10° and $185^\circ \pm 36.4^\circ$.

On solitary adults, juveniles < 0.5 mm RC were not distributed randomly (Fig.

8a, $z=5.09$, $p < 0.01$); however, juveniles > 0.5 mm RC were distributed randomly around the peduncle (Fig. 8a, $r=0.11$, $p > 0.369$). Smaller juveniles were most abundant under the rostrum (0°), and the mean angle of recruits < 0.5 mm RC on solitary adults was $21^\circ \pm 37.9^\circ$. Larger juveniles were more abundant around $300-330^\circ$ and 120° . Below the rostrum and below the carina were not locations of intense recruitment for larger juveniles on solitary adults, as these same locations had been for juveniles of all size classes in clusters. In fact, when size classes of juveniles on solitary adults were combined, the location of juveniles is random (Fig. 8c, $z=0.41$, $p > 0.10$).

3.3 Recruitment of cyprids and juveniles in clusters

The abundance of cyprids was significantly positively correlated with new and old recruits in the Winter studies; however, the abundance of cyprids was significantly negatively correlated with new recruits and the abundance of cyprids was not significantly correlated with old recruits in the Summer study (Fig.9; Table 2). In all seasons, the abundance of new recruits was significantly positively correlated with old recruits (Fig. 9g,h,i; Table 2). For all seasons, cyprids and new recruits and new recruits and old recruits were more strongly correlated than were cyprids and old recruits.

Recruitment results were analyzed further for old and new recruits combined, and excluding cyprids because: 1) there were large differences in the numbers and sizes of recruits between seasons (30 % of juveniles were less than 0.5 mm RC in the summer experiment; 85 % of the juveniles were this size in both winter studies, 25 % of the

Table 2. Linear regression results of different size classes of recruits (cyprids, new recruits, old recruits) of *Pollicipes polymerus* found on adults (n) in three seasons.

<i>Relationship</i>	<i>Season</i>	<i>n</i>	<i>r</i>	<i>p</i>
cyprids vs. new recruits	Winter 2002-2003	75	0.64	< 0.001
	Summer 2003	66	0.30	< 0.02
	Winter 2003-2004	328	0.84	< 0.001
cyprids vs. old recruits	Winter 2002-2003	63	0.58	< 0.001
	Summer 2003	124	0.07	> 0.50
	Winter 2003-2004	339	0.49	< 0.001
new recruits vs. old recruits	Winter 2002-2003	80	0.84	< 0.001
	Summer 2003	129	0.26	< 0.002
	Winter 2003-2004	350	0.67	< 0.001

recruits were cyprids in Winter 03-04, while 5 % and 6 % of recruits were cyprids in the Summer 2003 and Winter 2002-2003, respectively) 2) there was a significant positive linear relationship between all size classes (cyprids, new, old) of recruits in the Winter studies, but the relationship between cyprids and old recruits was weaker (Fig. 9), and 3) a later study (see Chapter III of this thesis) reports on growth rates of some of the same juveniles counted for recruitment studies. By combining new and old recruits and omitting cyprids, comparisons of three replicate seasons could be made without sacrificing the summer data, and connections between recruitment and growth would be morappropriate if most of the same individuals were considered. Growth rates for cyprids were not estimated with the methods used in this study.

The number and size of recruits varied considerably among adults and locations in all clusters. Because of the unequal samples sizes of adults in each cluster location, recruitment is presented in two ways. First, recruitment was explored as the percentage of adults vs. the number of recruits where the number of recruits are grouped into categories: 0, 1-5, 6-10 recruits, etc. (Fig. 10, 11, 12). Second, recruitment was analyzed statistically as the ratio of the number of recruits to the number of adults in each location to account for the uneven distribution of adults in each location (Fig. 13). In one cluster from the Winter 2002-2003 study, not all adults were sampled and recruitment was defined as the ratio of the number of recruits to the number of adults sampled in each location.

The frequency distribution of recruits on adults was non-random in all experiments. There were high percentages of adults with no recruits in all locations and sizes of clusters. In Winter 2002-2003, 56, 84, and 81 % of adults on the edge, in the middle, and in the center, respectively, had no recruits (Fig. 10). In large clusters during Summer 2003, 58, 82, and 95 % of adults on the edge, in the middle, and in the center, respectively, had no recruits (Fig. 11). In the Winter 2003-2004 study, the percentage of adults in large clusters with no recruits for each location was 15, 35, and 54 %, while the percentage of adults in small clusters with no recruits for each location was 30, 54, and 25 % on the edge, in the middle, and in the center, respectively (Fig. 12). The frequency of adults with zero recruits was higher on the inside of the cluster than the edge of the cluster.

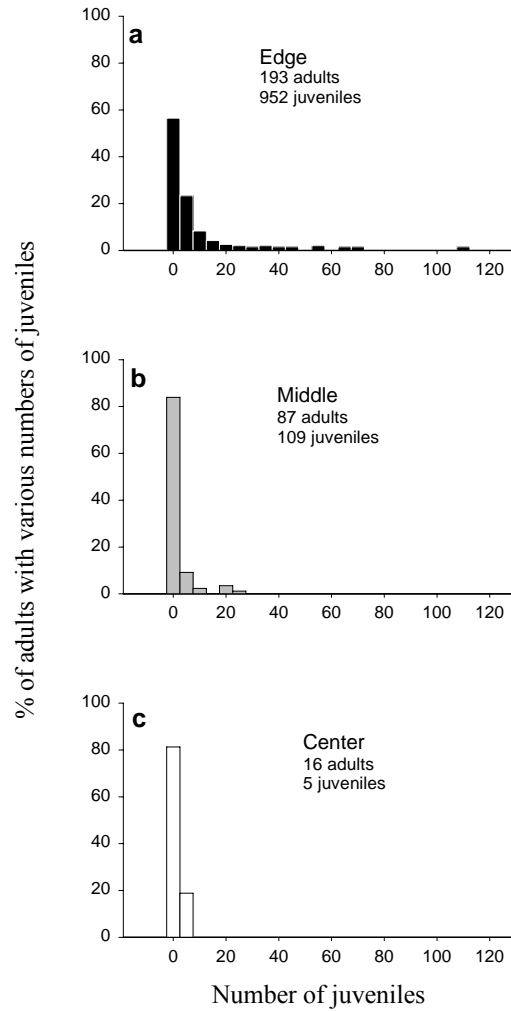


Fig. 10. Distribution of juveniles per adults of *Pollicipes polymerus* from large clusters for one season of recruitment Winter 2002-2003 and three cluster locations: **a** edge, **b** middle and **c** center.

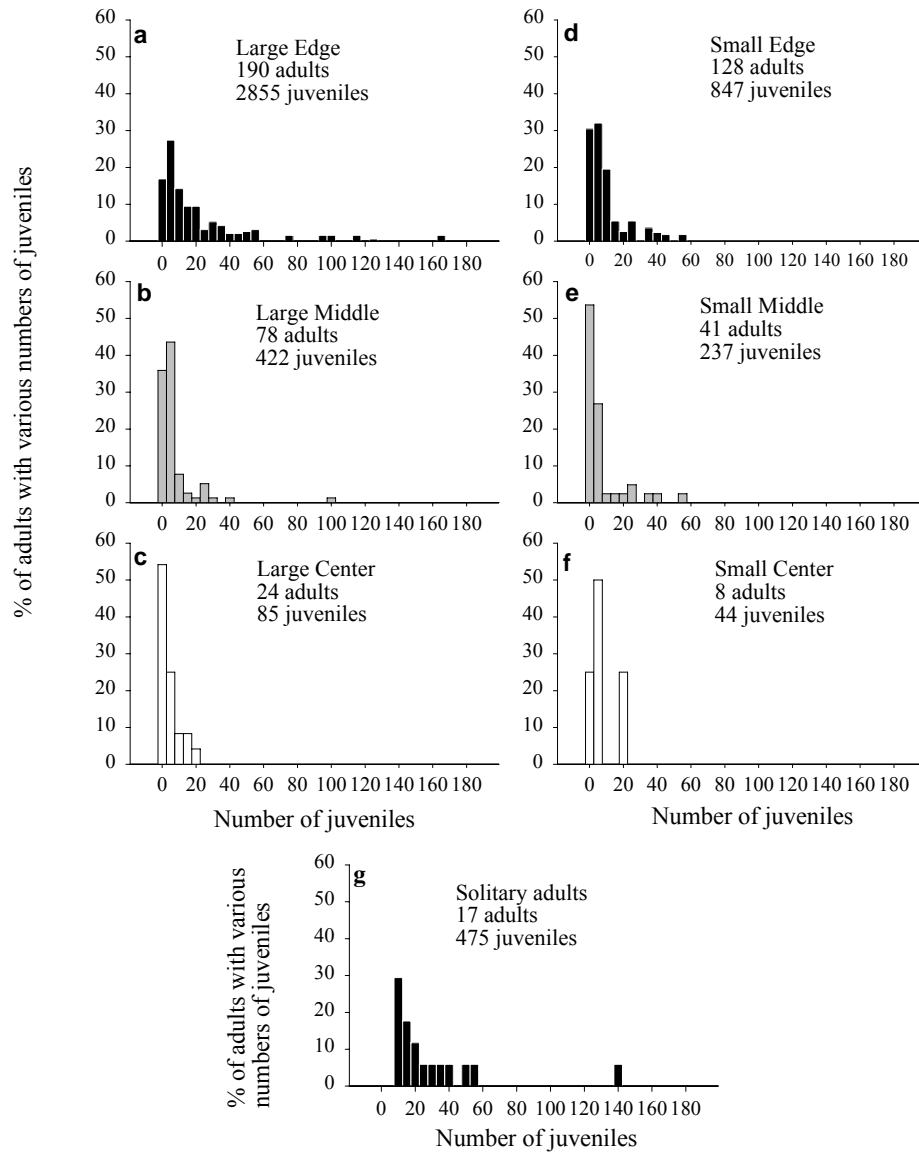


Fig. 12. Distribution of juveniles per adult of *Pollicipes polymerus* from clusters for one season of recruitment Winter 2003-2004, three cluster sizes (large, small, solitary adults), and three cluster locations (edge, middle, center): **a** large, edge **b** large, middle **c** large, center **d** small, edge **e** small, middle **f** small, center and **g** solitary adults

Recruitment was highly patchy in every cluster. In fact, on average 22 % of the recruits in a cluster were found on one adult and on average 47 % of all recruits in a cluster were found on three adults (Fig. 13). In all seasons, the frequency distributions of recruits per adult were positively skewed. This positively skewed distribution was stronger for the edge and middle locations and resulted from many adults with no recruits or low numbers of recruits and a few adults with high numbers of recruits.

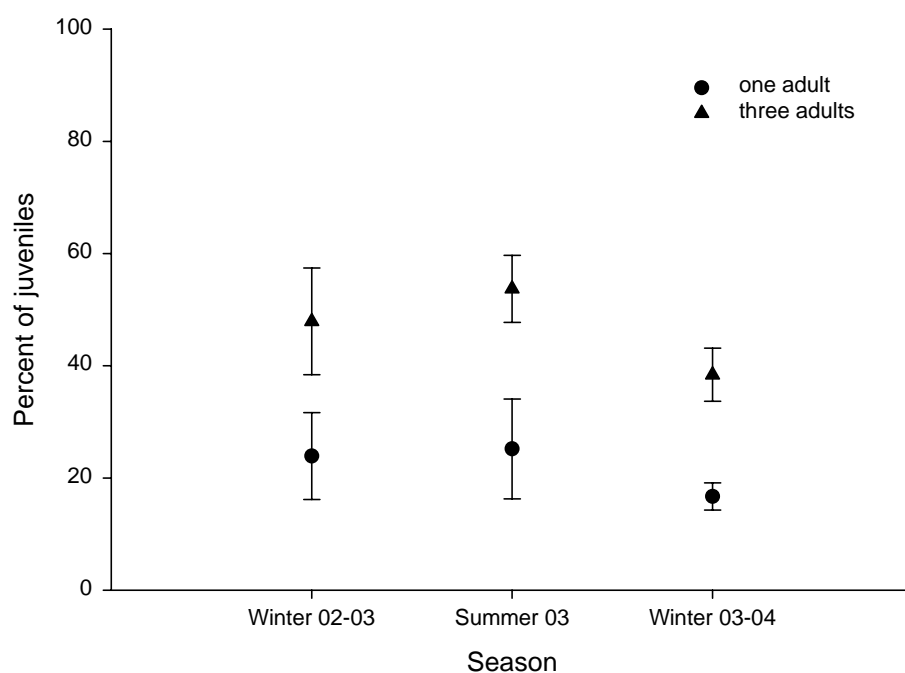


Fig. 13. Percent of juveniles of *Pollicipes polymerus* from clusters found on one adult and on three adults for three seasons of recruitment: Winter 2002-2003, n= 3 clusters; Summer 2003, n=8 clusters; and Winter 2003-2004, n=10 clusters. Error bars are ± 1 SE.

3.4. The effects of location within the cluster and cluster size on recruitment

The distribution of the mean number of recruits per adult as a function of both location within the cluster and cluster size was similar across seasons for large and small clusters but not for solitary adults (Fig. 14). The number of juveniles per adult varied considerably between clusters; however, there was a significant effect of location (Table 3, $p < 0.003$). Significantly more juveniles per adult were found on the edge of clusters than in the center of clusters ($F_{2,47}$, $p=0.003$). There was no significant difference between the number of juveniles per adult found on the edge of clusters and the middle of clusters ($p=0.069$) or between the middle and center of clusters ($p=0.427$). However, the mean number of juveniles per adult decreased from the edge to the center of the cluster (LS means for edge 1.80, middle 1.21, and center 0.89 recruits adult⁻¹). There was no significant effect of cluster size (Table 3, $p=0.87$) for large and small clusters and no significant interaction between location and size ($p=0.49$). An additional statistical analysis testing the effect of location in large clusters from three seasons confirmed these results (Table 4, $p < 0.001$) and showed that significantly more juveniles were found on edges of clusters than in either the middle ($p=0.009$) or center locations of the cluster ($p < 0.001$). Again, there was no significant difference between recruitment in the middle and center of clusters ($p=0.17$).

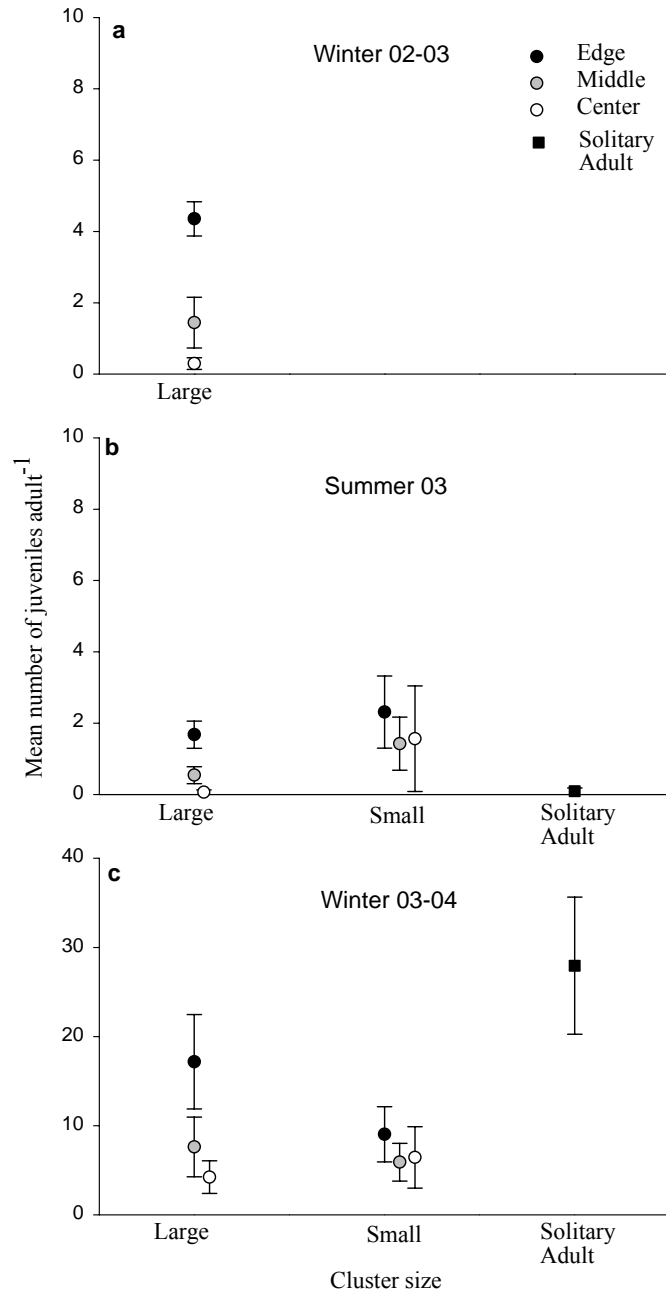


Fig. 14. Mean number (± 1 SE) of juveniles of *Pollicipes polymerus* per adult in three locations of clusters (edge, middle, center) and three sizes of clusters (large, small, solitary) for three seasons of recruitment: **a** Winter 02-03; 3 large clusters, **b** Summer 03; 4 large clusters, 4 small clusters, and 11 solitary adults and **c** Winter 03-04; 5 large clusters, 5 small clusters, and 17 solitary adults. Note the different scales on y-axis.

Table 3. Analysis of variance for Summer 2003 and Winter 2003-2004 recruitment of juveniles of *Pollicipes polymerus* in clusters with season, size, and location as main effects.

Effect	df	MS	F	p
Season	1	20.086	33.957	0.001
Size	1	0.016	0.028	0.869
Location	2	3.798	6.420	0.003
Size x Location	2	0.434	0.734	0.485
Residual	47	0.592		

Table 4. Analysis of variance for Winter 2002-2003, Summer 2003, and Winter 2003-2004 recruitment of juveniles of *Pollicipes polymerus* in large clusters with season and location as main effects.

<i>Effect</i>	<i>d</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Season	2	7.712	20.397	0.001
Location	2	4.930	13.040	0.001
Residual	31	0.378		

The effect of cluster size was looked at in more detail by comparing recruitment on solitary adults, small clusters and large clusters. There was no significant effect of cluster size or season (Table 5; size, $p=0.89$; season, $p=0.093$), but there was a significant interaction of cluster size and season (Fig. 15, $p<0.001$). Because recruitment was negligible on solitary adults in Summer 03 (mean of 0.09 recruits adult⁻¹), the effect of cluster size on recruitment in Winter 2003-2004 was tested separately. The results of this ANOVA indicated a significant cluster size effect (Table 6; $F_{2,44}$, $p<0.001$). Recruitment

on solitary adults in this season was significantly higher than recruitment on large ($p=0.008$) and small ($p=0.002$) clusters.

Table 5. Analysis of variance for Summer 2003 and Winter 2003-2004 recruitment of juveniles of *Pollicipes polymerus* in clusters and on solitary adults with season and size as main effects.

Effect	df	MS	F	p
Season	1	66.490	9.269	0.093
Size	2	0.851	0.121	0.892
Season x Size	2	7.011	11.577	0.001
Residual	76	0.592		

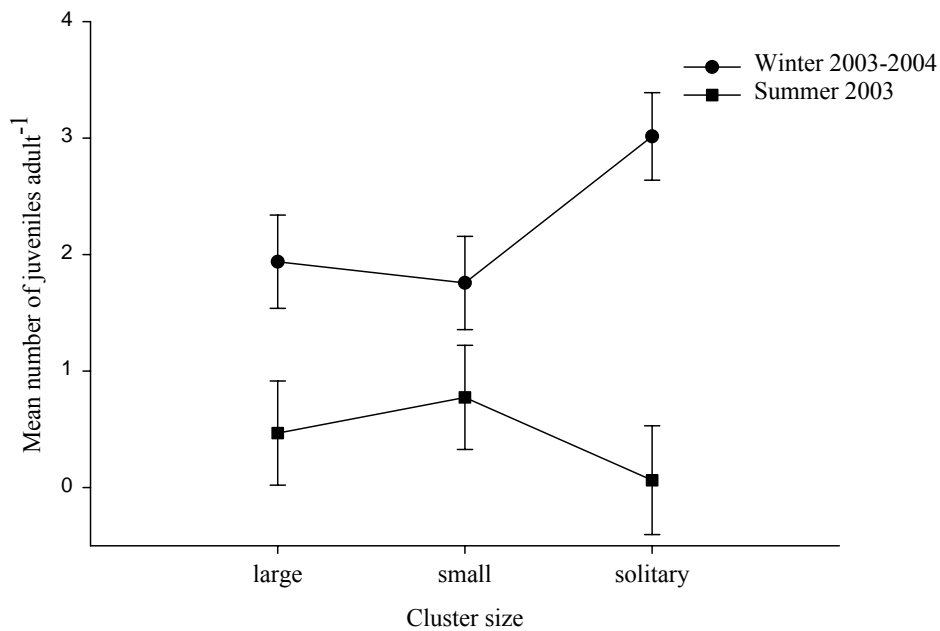


Fig. 15. Interaction plot of a two-factorial ANOVA of mean number of juveniles per adult of *P. polymerus* with cluster size (large, small, solitary) and season (winter, summer) as main effects. Vertical bars denote 0.95 confidence intervals.

Table 6. Analysis of variance for Winter 2003-2004 recruitment of juveniles of *Pollicipes polymerus* in clusters and on solitary adults with size as a main effect.

Effect	df	MS	F	p
Size	2	7.510	8.779	0.001
Residual	44	0.8554		

Discussion

4.1. Distribution of recruits on the adult peduncle

On both adults from clusters and on solitary adults, the most abundant, smallest juveniles were located near the tops of the adult peduncles and the least abundant, largest juveniles were attached closer to the bottoms of the peduncles. Cyprids and recently settled juveniles were also located at the tops of the peduncles, just above the next respective size class. Hoffman (1984) reported a similar pattern but did not include cyprids or recently settled juveniles less than 0.5 mm rostro-carinal length. The distribution of recruits could be explained by 1) adult peduncle growth, 2) differential juvenile growth, 3) differential mortality 4) temporal settlement patterns, 5) juvenile migration, or 6) a combination of settlement and juvenile migration. New peduncle tissue is primarily added at the junction of the capitulum and the peduncle (Darwin, 1851; Chaffee and Lewis, 1988). After 9 days, Chaffee and Lewis (1988) documented visible

bands produced in 24 % of *P. polymerus* 7-17 mm RC at the junction of the capitulum and peduncle, though they did not report any dimensions of the band. Therefore, recruits settling at the top of the peduncle, probably shift relatively lower on the peduncle as new peduncle tissue is added above them, and growth automatically creates a gradient in sizes over time as new recruits continually attached to the top of the adult peduncle. However, in this scenario, recruits should not get closer to the bottom of the peduncle as the peduncle grows above them. The recruits should always remain at a fixed distance above the substrate unless the base of the peduncle deteriorates, and there is no evidence for deterioration of the peduncle. Consequently, the growth of the adult peduncle cannot fully explain the gradient in sizes of juveniles on the peduncle.

The distribution of recruits on the peduncle may be due to differential growth of juveniles that settled at the top and bottom of the peduncle. Hoffman (1984) discussed a shading effect (Cimberg, unpublished in Hoffman, 1984), where juveniles at the proximal end of the peduncle may grow slower because they are competing for food with the canopy of adults above them. The shading effect hypothesis may, however, be unlikely because juvenile and adult gooseneck barnacles have different modes of feeding. Adult barnacles feed by cirral extension (Barnes and Reese, 1959), while juveniles feed by cirral pumping, beating, and extension (Lewis, 1981). Juveniles shifted their feeding activity to extension with increasing size (Lewis, 1981). The variety of juvenile feeding behaviors in contrast to a single adult feeding behavior might allow the juveniles to compete with adults for food. Even if juveniles and adult barnacles were competing heavily for food, causing juveniles at the top of the peduncle to suffer from food

limitation compared to those at the bottom, the growth rate of juveniles at the bottom would have to be extremely fast in order to account for the observed distribution pattern of recruits. The few studies that have measured growth rates of juveniles in the field have reported rates such as 0.0067-0.033 mm RC day⁻¹ for juveniles 3-4 mm RC (Lewis and Chia, 1981), 0.039 mm RC day⁻¹ for juveniles 3.6-19 mm RC (Page, 1986), and 0-0.029 mm RC day⁻¹ for juveniles 0.296-7.48 mm RC (Chapter III of this thesis). These rates are too slow to explain the large differences (e.g. 7 mm RC) in juvenile sizes in the size gradient of juveniles on the adult peduncle if recruits settled in the same season.

A third hypothesis that may account for the distribution of recruits is differential mortality of recruits at the top and bottom of the peduncle. Adults are attached to the substrate and laterally at the bases of other adult peduncles but are not found along adult peduncles, whereas settlers are found along adult peduncles. Therefore, the cyprids and new recruits at the top of the peduncle may have died while the settlers found at the bottom survived and grew into new adults. However, this hypothesis seems unlikely given the high rates of mortality of spat and the few numbers of cyprids that settled at the bottom.

A fourth possibility for the distribution of recruits on the peduncle is random settlement followed by differential growth and survival of recruits at the top and bottom of the peduncle. Recruits would have to settle randomly along the peduncle, grow faster at the bottom of the peduncle than the top, and survive better at the top of the peduncle than at the bottom. However, in this study the majority (57-72 %) of the cyprids and unmarked juveniles (new recruits) that settled into clusters or on solitary adults were

found at the very top of the peduncle, a relative distance of 0.0-0.3 (Fig. 3a,b Fig. 4a,b Fig. 5a,b, Fig. 6a,b). Furthermore, the highest frequency of cyprids were always found above the next larger size class, juveniles < 0.5 mm RC.

A fifth hypothesis for the gradient in sizes of juvenile barnacles on the adult peduncle is migration of juveniles down the adult peduncle. Hoffman (1984) proposed that juveniles eventually attach to the primary substratum with limited mobility, as “foot-loose” barnacles. He described how juveniles may move by producing peduncular extensions at the distal end of the peduncle (Hoffman, 1984, 1989). Chaffee and Lewis (1988) reported that thickenings and small extensions of the peduncle were produced at the base of the animal. Hoffman (1984, 1989) and I both observed red bulges lacking peduncular spicules at the distal portion of the peduncle on both adults and juveniles attached to adults. Although neither Hoffman nor I tested the mobility of juveniles, there have been three studies that reported mobility in lepadomorph barnacles (Kugele and Yule, 1993, 2000; Woll, 1997).

Kugele and Yule (1993) observed tracks of cement from juveniles on peduncles of adult *P. pollicipes*. Tracks increased in width along the distance from the start of the track and matched the diameters of juvenile peduncles, thus indicating directed locomotion of juveniles. Also, when adults were suspended upside down in tanks, the direction of tracks from attached juveniles changed toward the capitulum but was still downward. A few studies (Kugele and Yule, 2000; Woll, 1997) followed specific juveniles (2-12 mm RC) for periods of 58 to 251 days and reported movement ranging from 20–190 $\mu\text{m day}^{-1}$ and, in three cases, larger juveniles (8-12 mm RC) moved off the

host peduncle onto the substrate. However, there is no evidence in the literature of small recruits moving up the peduncle; thus, migration alone cannot account for the distribution of many, small recruits at the top of the peduncle and few, large recruits at the bottom.

From the data presented in this study, the most logical explanation for the gradients in size and abundance of recruits distributed on the adult peduncle is that cyprids settled at the top of the peduncle (Fig. 3a, 4a, 5a, 6a) and then migrated down the peduncle as they grew (Fig. 3b-c, 4b-g, Fig. 5b-g, Fig. 6b-g). The abundance of cyprids and new recruits was probably high because of gregarious settlement (Barnes and Reese, 1960; Lewis 1975a, b; Hoffman 1988; Satchell and Farrell, 1993), and the abundance of large juveniles was probably low because of the high rates of mortality of spat during the first 2-3 weeks after settlement (Hoffman, 1989). The few, large juveniles at the bottom of the peduncle may represent recruits that settled at the top, grew, and survived the migration to the bottom of the peduncle.

4.2. Distribution of recruits around the adult peduncle

The distributions of juveniles from clusters around the adult peduncle, aggregated at particular locations on the adult, are not surprising given the gregarious settlement of barnacles (Knight-Jones, 1954; Crisp, 1961); however, why they are aggregated most frequently below the rostrum and carina of the adult and not at other locations around the peduncle may be related to the orientation of the barnacles in flow and the effects of the cluster on flow past individual barnacles.

Barnes and Reese (1960) observed that over a restricted area, most of the adults in groups of *P. polymerus* orient their capitula in the same direction. They noticed that the adults were feeding on the backwash of waves with the anterior face of the cirral net against the incoming waves. The feeding efficiency of a group of tightly packed adults is linked to the orientation of the capitula. I speculate that settling cyprids are probably concentrated at the particular locations below the rostrum and carina of the adult because of the interaction of flows through the cluster and around the capitula and peduncles of individual barnacles. The individuals in a cluster may act as a filter, creating dead spaces around their peduncles below the rostrum and carina. The rough cylindrical peduncle, unlike the capitulum, is covered with tightly packed, symmetrically arranged calcareous spicules that make grooved depressions perfect for settling cyprids (Barnes and Reese, 1960). The flow around the capitulum is probably decelerated around the rostrum and carina but accelerated along the sides (scutal and tergal plates) due to flow around a cylinder, where the water reaches the highest velocity laterally because the cylinder blocks the path of flow, but the water becomes fixed at upstream and downstream boundaries of the cylinder (Vogel, 1994).

Young and Cameron (1989) looked at the effects of larval predation by *Balanus eburneus* on recruitment of bryozoans. At the smallest scale, they studied recruitment differences of bryozoans between the regions of the barnacle shell influenced by the cirral feeding stroke and other regions of the shell. They found fewer larval bryozoans on the rostral and carinal plates than on the lateral or carinolateral plates of individual barnacles. This pattern is the opposite trend from the spatial distribution of juveniles of

P. polymerus, which did not settle on the capitular plates like the bryozoan larvae did. Instead, juveniles of *P. polymerus* were found most frequently below the rostral and carinal plates on the adult peduncle (Fig. 7). The study by Young and Cameron (1989) is important because it documented very small scale spatial effects on recruitment. Similar to Young and Cameron (1989), this study found differences in recruitment of *P. polymerus* at a very small spatial scale. Young and Cameron (1989) suggested that larvae in flows above the carinal plate have high chances of being caught by the cirri during feeding, and those that aren't caught may be swept in the posterior-anterior direction (i.e. from the carinal to the rostral plate) by the currents made from the cirral stroke. Perhaps, the action of the cirri in adult gooseneck barnacles sets up a current that directs the larvae toward the rostrum and carina, where they settle below on the peduncle. *P. polymerus* larvae may manage to escape the adult cirri because their cirri do not have a regular beat as in balanomorphs, but are extended for long periods of time. Alternatively, gooseneck barnacle larvae may be caught and then rejected, similar to larvae of *Bugula neritina*, by adults and end up encountering the locations below the rostrum and carina because of different forces (Young and Cameron, 1989) that expel them.

Another idea that may explain the distribution of juveniles below the rostrum and carina is related to the activity of the peduncle. Barnes and Reese (1960) noted that the peduncle undergoes changes of shape by retracting, expanding, and bending movements. Time lapse photographs of adult individuals indicated that bending movements were from side to side rather than from anterior to posterior (Barnes and Reese, 1960). Since adults are tightly packed into clusters, they may rub the sides of their peduncles against

each other while bending, decreasing the numbers of larvae that settle or survive below the lateral plates because they may be abraded away. The dense arrangement of clusters and lateral bending movements of the peduncle may also increase the numbers of larvae found below the rostrum and carina since these locations on the peduncle may be less likely to rub or abrade juveniles away if bending movements are occurring from side to side.

The lack of other adults surrounding solitary adult barnacles may explain why solitary adult barnacles had a different distribution of juveniles around the peduncle (Fig. 8). Solitary gooseneck barnacles may experience flows that are different than clustered gooseneck barnacles and settling cyprids may be able to contact more surface area of the solitary peduncle without the presence of other adults. The flows around the solitary adult barnacles are probably more haphazard and less directed than flows that are filtered by a cluster of individuals, thus allowing cyprids to settle more randomly around the peduncle (Fig. 8c).

4.3. Distribution of juveniles in clusters: frequency per adult

The juvenile barnacles from clusters and on solitary adults were distributed nonrandomly on adults in all locations. There are several possible reasons that might explain the highly patchy distribution of juveniles on adults.

The abundance of cyprids was a good predictor of both the abundance of new and old recruits in the Winter studies and the abundance of new recruits was a good predictor of the abundance of old recruits in all seasons (Fig. 9, Table 2). Gregarious behavior has

been demonstrated in many marine invertebrate groups (Knight-Jones and Stevenson, 1950; Moyses and Knight-Jones, 1965; reviewed in Burke, 1986). However, gregariousness in barnacles has only been less well documented for lepadomorph than balanomorph barnacles (Knight-Jones, 1954). Barnes and Reese (1960), Lewis (1975a,b), Hoffman (1988), and Satchell and Farrell (1993) attributed the aggregative pattern of *P. polymerus* to the preferential settlement of cyprids on peduncles of adults. Hoffman (1988) experimentally confirmed that the presence of conspecifics induced the settlement of larvae when he placed scored and pitted terra cotta tiles 2 m from the seaward end of the seawater intake pipe at Scripps Institution of Oceanography. *P. polymerus* aggregations were regularly scraped from this end of the pipe because they block water flow through the pipe. Twenty days after the plates had been in the pipe, initial settlement of cyprids of *P. polymerus* occurred, and twenty eight days after their placement, he noticed distinct aggregations of cyprids with a maximum number of 15 larvae per aggregation. The positive linear relationships I found between abundance of cyprids and new and old recruits (Fig. 9a,c,d,f) provides further support for the gregarious settlement of larvae of *P. polymerus*.

In a different study, natural variation in recruitment rate of four intertidal barnacles, including *Pollicipes polyermus*, was used to examine how the density of settling barnacles influenced the spatial pattern of recruits (Satchell and Farrell, 1993). They found that 75 % of the settling plates with *P. polymerus* had aggregated settlement, while three balanomorph species recruited in random spatial patterns on 64-93 % of the settling plates. Furthermore, 3-8 cyprids of *P. polymerus* settled in contact with each

other, and their degree of aggregation increased significantly with the density of settlers. Although Satchell and Farrell (1993) did not look at *P. polymerus* recruitment on adult peduncles, the settlement and recruitment densities of this species on settling plates indicated that cyprids were strongly attracted to conspecific cyprids. Both studies, Hoffman (1988) and Satchell and Farrell (1993), found non-random distributions of recruits that I also found on adult peduncles. Explaining why peduncles of one or three particular adults were selected over the hundreds to choose from by an average of 22 or 47 % of all recruited juveniles (Fig. 14) may be more related to physical forces than larval choices.

One possibility to explain these patterns is that those adults were particularly attractive. Larval settlement cues may be produced directly by conspecific organisms. For example, in barnacles and polychaetes, exposure to extracts of adults or tubes of conspecific adults has been shown to enhance settlement (Larman and Gabbott, 1975; Jensen and Morse, 1984; reviewed in Walters et al., 1997). By chance alone, one cyprid that settled on a particular adult may have attracted another etc. until there was a dense patch on that adult. However, if we assume that chance alone did not account for the distribution of juveniles and most adults would be capable of producing similar cues, the answer to why only a few were selected out of hundreds of adults may be found by considering hydrodynamic reasons rather than active larval choices to cues produced by adults.

A second possibility to explain the patchy distribution patterns of juveniles per adult is that cyprids were passively accumulated in flows around clusters and deposited in

pockets around a particular adult or a few adults. The arrangement of the three adults with the most recruits in clusters may help explain the passive deposition of larvae. Sometimes the adults with the most recruits occurred in different cluster locations (edge, middle, center) but were in the same quadrat of the cluster, creating a radial pattern out from the center of the cluster. Another indication that hydrodynamics may be important in explaining the distribution of juveniles was the patchy distribution of juveniles on one side of the cluster. By sampling adults around the entire cluster, this study found that adults with the highest numbers of recruits typically were found on the landward side of the cluster (Fig. 16). Perhaps, the combination of hydrodynamics entraining cyprids in pockets near particular adults in the cluster and on a certain side of the cluster and gregarious larval settlement that resulted in their attachment to particular adult peduncles explains the unique distribution patterns of juveniles of *P. polymerus* in clusters.

Finally, the patchy distribution may be explained by random settlement on most adults with differential survival on a few adults; however, this seems unlikely given the three replicate seasons of recruitment. This alternative hypothesis is also discussed further in the next section.

4.4. Distribution of juveniles in clusters: the effects of location within the cluster and cluster size

The number of juveniles on an adult varied with location in the cluster. There was a significantly higher abundance of juveniles on adults at the edges of clusters than the center of clusters (Fig. 13). In large clusters, the number of juveniles per adult

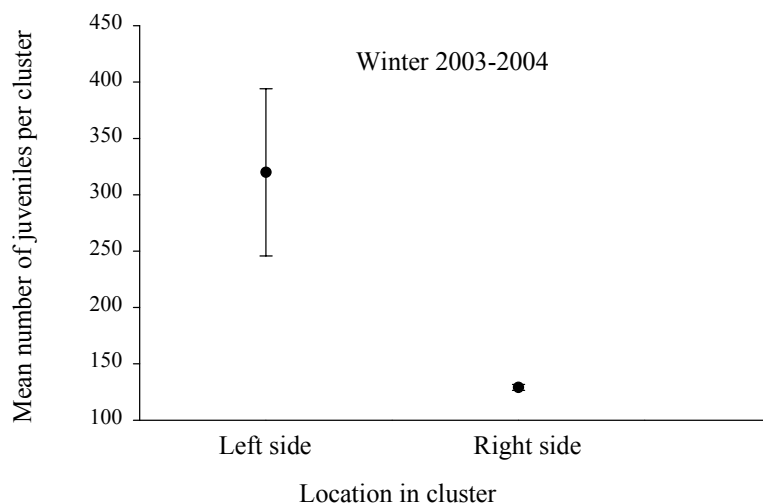


Fig. 16. Mean number of juveniles found on the left side (landward) and the right side (seaward) of the cluster for one season of recruitment Winter 2003-2004. The mean number of juveniles in all locations on the right side vs. the left side of the cluster were compared by treating adults located at a compass angle of $0-180^{\circ}$ as the right side with 0° marking the top of the cluster and adults located at a compass angle of $181-360^{\circ}$ as the left side of the cluster.

increased from the center to the edge of the cluster. A variety of factors might account for the strong relationship between recruitment and the edges of clusters. Given the gregarious behavior of cyprids of *P. polymerus* to conspecific adults (Barnes and Reese, 1960; Lewis, 1975a, b; Hoffman, 1988; Satchell and Farrell, 1993), it is possible that cyprids receive a cue from adults in a cluster and then contact edge adults first and attach to their peduncles. There may be reduced flows of water, i.e. skimming flows, inside the cluster due to collective action of adult peduncles trapping or depositing larvae at the edges of clusters (Eckman, 1983; Wetthey, 1986; Butman, 1987; Gregoire et al., 1996;

Walters et al., 1997), which may lead to more water and more larvae coming into contact with barnacles at edges compared to the center of clusters.

An example of the interaction of conspecific cues and hydrodynamics that support the hypotheses stated above comes from a field experiment that examined the effects of small-scale flows and chemical cues associated with conspecifics on the settlement of barnacle larvae of *Elminius modeusts* and *E. covertus* (Wright and Boxshall, 1999). They looked at the effects of conspecifics and flow disruption on the settlement of cyprids by using different settlement plates (live, casts, and flat surfaces) with different densities of barnacles (clustered, uncrowded, and no barnacles). They found higher settlement on clustered and uncrowded plates containing live barnacles than those same plates with casts of adult barnacles. In addition, there was low settlement on plates with no barnacles and on flat control plates. Considering the outcome of their experiments, they suggested that a combination of flows around the physical structure of adult barnacles (live or casts) and conspecific presence explained the settlement patterns of cyprids.

Settlers at the edges of clusters could have higher survival if cluster edges have: higher food availability, reduced crowding by adults, reduced predation, or less severe sedimentation. Studies on feeding of adults in clusters found correlations between location in the cluster and food capture (Pullen and LaBarbera, 1991, Ekman and Okamura, 1998). Ekman and Okamura (1998) used models of bryozoan colonies to explain that zooids located at the upstream colony edge would capture more particles than zooids located at the downstream edge and in the colony interior. Likewise, Pullen and LaBarbera (1991) found that acorn barnacles located at the upstream edge and top of

clusters captured more food particles than barnacles located at the downstream edge of clusters. The studies by Pullen and Labarbera, 1991 and Ekman and Okamura, 1998 are more applicable to adult gooseneck barnacles though because the juveniles are on peduncles below the adult feeding canopy and may be competing with adults for food (Page, 1986). Edges of clusters may be exposed to higher fluxes of phytoplankton than centers of clusters (Svane and Ompi, 1993) because flow rates are most likely slow inside the cluster and faster around the edge (Vogel, 1994).

Juveniles that recruit to the center of a cluster may be surrounded by more adults than juveniles that recruit to the edges. The negative effects of crowding on survival in barnacles has been addressed (Grant, 1977; Wethey, 1983, Bertness et al., 1998). Grant (1977) found a correlation between early mortality and settlement density of recruits of *Balanus balanoides*. He reported that 90 % mortality occurred within 5 months in areas of dense settlement (60 spat per cm²) due to crowding associated with growth. Wethey (1983) observed differences in size and mortality of individuals of *B. balanoides* at high and low population densities; barnacles at high population densities were smaller and had higher rates of mortality than individuals at low population densities.

Hoffman (1989) observed nemertean predators feeding on small juveniles (1 mm RC length) of *P. polymerus*, though he did not note the locations of these juveniles. Barnacle clusters provide habitats for many species of invertebrates including flatworms, crabs, amphipods, and snails, which may reside within the protected clusters. Perhaps, these predators rarely venture to the edges of clusters, which would be potentially dangerous locations for predators of their own.

When disaggregating clusters, I noticed algae, surf grass, sand, fishing line, and other debris surrounding the bases of adult peduncles in the centers of clusters. Hoffman (1989) made a similar observation. The coarse debris may cause higher mortality in young juveniles in centers of clusters, but may not affect juveniles that settled on the edge, where the debris is less abundant.

Cluster size was not as important in determining the abundance of recruits as location within the cluster. If recruitment is higher at the edges than in the center (Fig. 13), then the circumference (edge) of a cluster is more important in determining the abundance of recruits than the area of the cluster (large or small). The significant difference in numbers of recruits per adult on edges of large and small clusters compared to middle and center locations of large and small clusters and the lack of a difference in numbers of juveniles per adult between edges of large and small clusters supports this argument (Fig. 13).

The high recruitment ($28 \text{ recruits adult}^{-1}$) found on solitary adults in the Winter 2003-2004 study (Fig. 13c) and the very low recruitment ($0.09 \text{ recruits adult}^{-1}$) found on solitary adult barnacles in the Summer 2003 (Fig. 13b) study may be due to seasonal differences in recruitment because the abundance of juveniles from clusters was also lower in the Summer 2003 than Winter 2003-2004 (Fig. 13b,c). Raimondi (1990) found that settlement and recruitment of *Chthamalus* varied at almost all temporal and spatial scales that he measured and that the majority of the variability was due to differences between sampling period.

Another explanation for the differences in recruitment on solitary adults between Summer 2003 and Winter 03-04 is differential survival of recruits (from spat to juveniles) on solitary adults. Hoffman (1989) found that 51 solitary adult barnacles of *P. polymerus* sampled over 4-6 weeks in March 1985 had an average of 8.2 spat per adult and an average of 0.99 juveniles per adult. However, he noted that survival from spat to juvenile was highest on solitary adults (12.1 %). This study found the highest recruitment on solitary adult barnacles compared to clusters during the Winter 03-04 (Fig. 13c), which may suggest that more recruits were settling on solitary adults but not surviving to sizes where they reach the substrate and form new colonies (Fig. 6). If juveniles do survive then solitary adult barnacles may represent the sites of future clusters. Whether solitary adult barnacles are remnants of destroyed clusters (Lewis pers. comm. of Hoffman, cited in Hoffman, 1989) or founders of new clusters cannot be determined from the snapshots of recruitment that Hoffman and this study presented.

By looking at recruitment separately in each cluster, it was evident that the location of the cluster on the rock wall may have been more important than cluster size. In most cases, if a small cluster had high recruitment, its paired large cluster also had high recruitment. The same was true for paired clusters showing low recruitment. This pattern was true for all paired clusters in the Winter 03-04 study and was true for 3 out of 4 pairs of clusters in the Summer 03 study (Fig. 17). Although this study did not address site-specific spatial variation in recruitment, sites separated by meters to tens of meters (small-spatial scales) have attributed variation in settlement to a variety of causes: larval

preferences for chemical, physical and biotic aspects of the substratum, differences in larval distribution due to small scale current patterns, aggregative larval behavior in the water column, or spatial differences in larval predators in the water column (reviewed in Gaines et al., 1985).

4.5. Conclusions

Conspecific adults were very important in structuring the patterns of distribution and abundance patterns of recruits found on adult peduncles and within the cluster, and the abundance of juveniles related to location within the cluster and cluster size. The patterns of recruits (cyprids, new, old) settling near other cyprids and juveniles (Fig. 9) may contribute to the distinct aggregations of adults of this species.

The results of this study have important implications for spatial competition between gooseneck barnacles *Pollicipes polymerus* and California mussels, *Mytilus californianus*, which are closely associated on rocky cliffs exposed to the Pacific Ocean. Wootton (1993) described several ways in which the California mussels could outcompete gooseneck barnacles: 1) *M. californianus* could squeeze out *P. polymerus* because mussels have rigid external shells while gooseneck barnacles have flexible peduncles and rely on high-pressure hydrostatic skeletons to resist crowding, 2) *P. polymerus* grows too slowly to take over all of the available space before the California

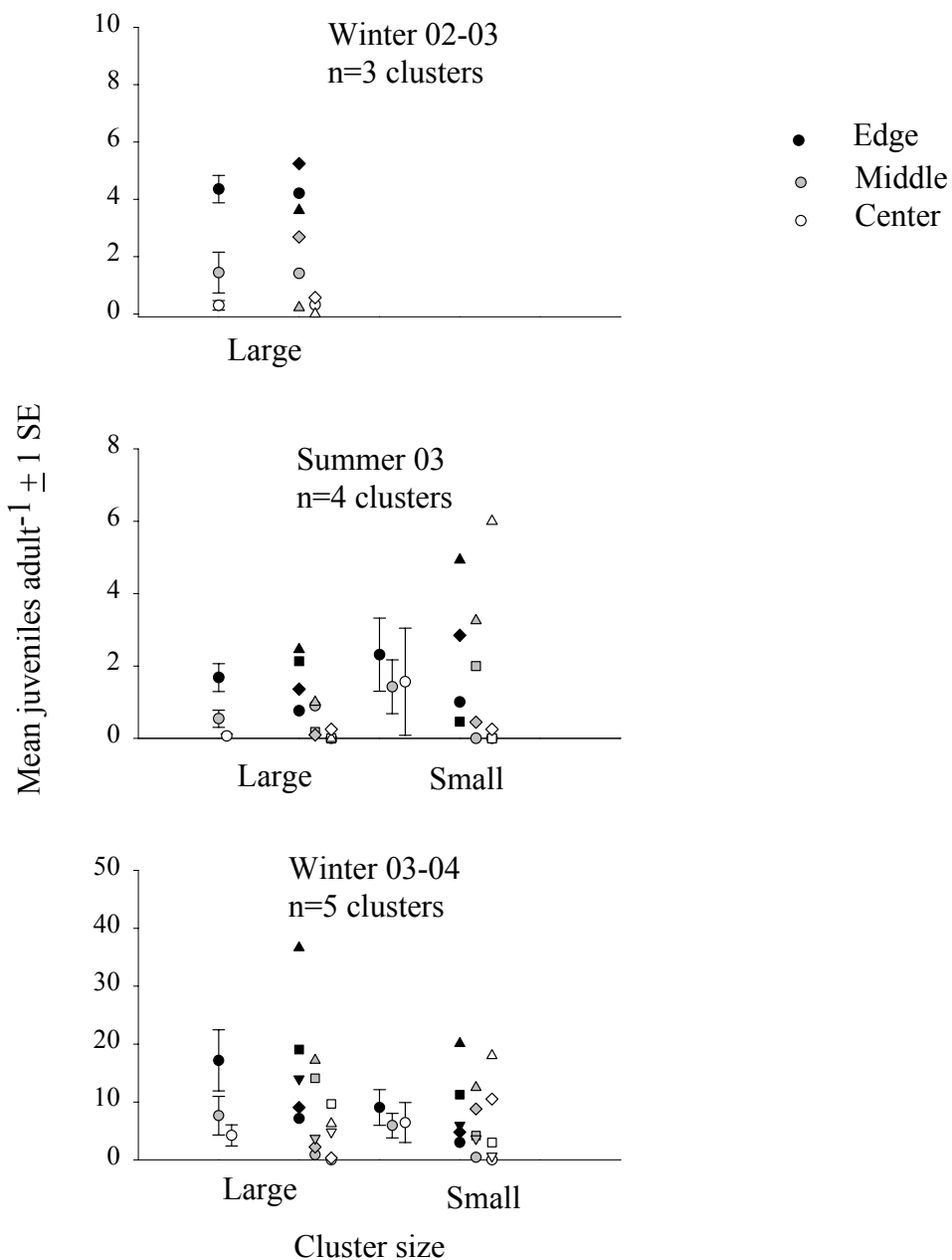


Fig. 17. Scatter plots of mean number of juveniles per adult for each cluster for three seasons of recruitment shown next to the data from Fig. 12. Each symbol of the scatter plots represent a different cluster, large and small clusters with the same symbol represent pairs.

mussel settles, and 3) *M. californianus* can recruit to gaps as adults from surrounding mussel beds. If solitary individuals of *P. polymerus* grow quickly into clusters, and clusters continue to grow from their edges, forming large clusters, then *P. polymerus* may more effectively compete with the *M. californianus*. More specifically, Paine (1974) and Wootton (1990) documented that on vertical walls, the intertidal community was dominated by *P. polymerus* rather than *M. californianus* due to the lack of gull predation on these vertical walls. It has also been suggested that *M. californianus* may be a poor competitor for space on vertical surfaces because their attachment by byssal threads is weaker than the cement attachment of a thick basal peduncle of gooseneck barnacles. However, on vertical and horizontal surfaces at South Cove, Cape Arago, mussels and gooseneck barnacles occur together. The results of this study showed that clusters added new individuals to their edges, thus creating dense aggregations which may help *Pollicipes* compete successfully against co-occurring individuals of *M. californianus*.

The highly patchy recruitment (Fig. 14) of juvenile gooseneck barnacles predominately on edges of clusters (Fig. 10a, 11a,d 12a,d, 13) may suggest differences in growth rate and survival of recruits located at different locations within the cluster. Some studies have shown that sites of abundant larval settlement of invertebrates were negatively related to high mortality (Grosberg, 1981; Davis 1987) and low growth (Burshek, 1988; Dirnberger, 1994). If edges of clusters are intense locations of recruitment of cyprids and juvenile gooseneck barnacles, perhaps they are also sites of high growth rates and survival.

BRIDGE

" From the most refined of saints
As naturally grow miscreants,
As barnacles turn Solan-geese
In the islands of the Orcades."

“Having traveled from the grasses growing in the bottom of the fenny waters, the woods, and mountains, even unto Libanus itself; and also the sea, and bowels of the same, we are arrived at the end of our History: thinking it not impertinent to the conclusion of the same, to end with one of the marvels of this land (we may say of the world) . . . There are found in the North parts of Scotland and the Island adjacent, called Orcades, certain trees whereon do grow certain shells of a white color tending to russet, wherein are contained little living creatures, which shells in time of maturity do open, and out of them do grow

those little living things, which falling in the water do become fowls, which we call Barnacles; in the North of England trant geese, and in Lancashire tree geese; but the other that do fall upon the land perish and come to nothing (Fig. 18).”

John Gerarde, (1597:1392)

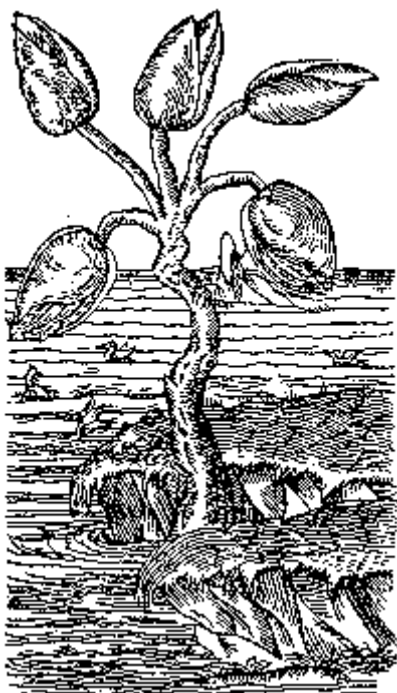


Fig. 18. The legendary Barnacle tree on the Isle of Man depicting the mussel-shaped shells of the tree that would grow until they split open, revealing geese that would hang by their bills until mature and then drop into the sea (Gerarde, 1597).

CHAPTER III

THE EFFECTS OF LOCATION WITHIN THE CLUSTER AND CLUSTER SIZE ON GROWTH RATES OF *Pollicipes polymerus*

1. Introduction

In a broad context, life-histories of organisms are viewed as their lifetime patterns of growth, development, storage, and reproduction (Begon et al., 1990). One of the most conspicuous components of a life-history is individual size, and all organisms increase their size by growth. In fact, many ecologists have devoted their research to patterns of life-history traits associated with growth. By studying the growth rates of individuals and the variation in growth among and within habitats, one can begin to understand some of the dynamics of populations and communities.

The effects of high population density on growth rates of organisms has been well studied; however, there have been comparatively few studies that have focused on these issues for sessile, aggregating organisms (Bertness and Grosholz, 1985; Holbrook et al., 1991; Dalby, 1995; Bertness et al., 1998). Because high population densities are inherent in aggregations, any negative consequences of high population densities on life-history components including growth, survivorship, feeding success, or fecundity must represent a trade-off for the individuals that have formed aggregations. Interestingly, three of the

four studies mentioned above found negative relationships between high population density and growth. Bertness and Grosholz (1985) reported that individual growth rates of the mussel *Geukensia demissa* were reduced at high densities. Isolated individuals of the sea-palm, *Postelsia palmaeformis*, had blade growth rates that were five times greater than canopy or understory plants in aggregations (Holbrook et al., 1991). Ascidians, *Pyura stolonifera*, inside aggregations grew more slowly than those outside aggregations (Dalby, 1995). In contrast, Bertness et al. (1998) studied the dynamics of acorn barnacle hummocks (tall, densely packed individuals) and found that shells of hummocked individuals were larger and tissue growth was higher compared to solitary individuals. Clearly, the majority of these studies indicated negative consequences of high population densities on growth; regardless, these organisms were found more frequently in aggregations with isolated individuals observed occasionally.

Few studies have looked at growth rates in aggregations of lepadomorph barnacles. In general, growth has been studied more extensively in balanomorph barnacles than in lepadomorphs (Anderson, 1994). This is surprising given that the growth pattern of pollicipedines (a subgroup within lepadomorphs), where the carinal primordium is shifted anteriorly (future basal position in balanomorphs), was of major significance in creating a system from which the balanomorph form could evolve (Anderson, 1994). Nevertheless, cirrepedes are a unique group of arthropods, in which to study growth because they grow by accretion of exoskeletal structures and development of permanent calcareous plates (Anderson, 1994).

A lepadomorph cirripede, *Pollicipes polymerus*, occurs commonly in the mid-upper intertidal on the northeastern Pacific coast and forms dense clusters. Studies have suggested that the dense cluster formation may be due to the gregarious settlement of the larvae on adult peduncles (Barnes and Reese, 1960; Lewis, 1975 a,b; Hoffman, 1989; Satchell and Farrell, 1993). Because of the naturally occurring clusters of aggregating adults and the gregarious settlement of cyprids, I became interested in the consequences of these adult aggregations on the growth rates of juveniles in different locations within the cluster. Growth of adult gooseneck barnacles *Pollicipes polymerus* has been more thoroughly studied than juvenile growth (Barnes and Reese, 1960; Paine, 1974, Newman and Abbott, 1980; Lewis and Chia, 1981; Page, 1986; Hoffman, 1988, 1989).

At South Cove, Cape Arago, OR on vertical rock surfaces, gooseneck barnacles are found in clusters of varying size and as solitary individuals. Since high population density is known to affect growth in barnacles, studying clusters of different sizes might elucidate the effects of aggregation on growth rates in juveniles of *Pollicipes polymerus*. However, the growth of juveniles, especially in the early stages, is hard to measure because of their small size and cryptic nature (Southwood, 1978). In order to study growth rates in the field, a method for marking juveniles was necessary. A recent study showed that calcein, a fluorescent label that binds to calcium and becomes incorporated into growing calcium carbonate structures, is a suitable marker for newly hatched juvenile snails, *Nucella ostrina* (Moran, 2000). Moran found that calcein provides a long-lasting, easily visible mark on the shell that could be used to measure shell growth. Because the shell of gooseneck barnacles is made up of external calcareous plates and

contains calcium carbonate like the shell of a gastropod, calcein can also be used as a method to study growth rates of juveniles of *Pollicipes polymerus*. Using calcein as a marker, this study addresses the following question:

What are the effects of location within the cluster (edge, inside) and cluster size (large, small, and solitary adult barnacles) on the growth rates of juveniles of *Pollicipes polymerus*?

I studied the mean growth rates of juveniles over a two month period. It uses a mark and recover method that is, to my knowledge, unique for studying growth in juvenile barnacles. The method of calcein tagging allowed growth of specific individuals to be followed through time in the field. Using this method, clusters were not destroyed initially, and therefore estimates of individual growth were made from juveniles growing within intact clusters.

2. Materials and Methods

2.1. Study site and Animal collection

For growth studies, I used the same clusters and solitary adults of *Pollicipes polymerus* that were collected for recruitment studies (see Chapter II).

2.2. Marking, Outplanting and Processing in the lab

The methods for marking, outplanting, and processing the animals were identical to those used for recruitment studies (see Chapter II).

2.3 Growth

In addition to marking animals for recruitment studies, calcein was used to estimate growth. When calcein is incorporated into the growing calcium carbonate of the capitular plates of the barnacles, the plates are marked (Fig. 2c). When animals are returned to the field, the new plate material that is added during growth is unmarked (Fig. 2c). Marked recruits were distinguished from unmarked recruits with epifluorescence, and the rostro-carinal length was measured in the same way as for the recruitment studies (see Chapter II). All marked recruits were sampled in Winter 2002-2003, Summer 2003, and in two clusters from Winter 2003-2004. Due to the high abundance of recruits and the lack of time, the remaining eight clusters collected in Winter 2003-2004 were sampled randomly with a minimum of nine recruits from a given location (edge, inside) in each cluster. Recruits with a calcein mark were placed in 6 % sodium hypochlorite to dissolve away the tissue between the capitular plates. The capitular plates were then glued to a microscope slide. A digital camera attached to the compound microscope was used to photograph the capitular plates under epifluorescent light. Optimas software was used to determine the area of the marked and unmarked (growth) portions of the plates. Because the capitular plates of barnacles grow in thickness and in area through laminar

accretion or basal marginal accretion (Anderson, 1994), the entire original plate was stained.

In order to estimate the growth rate of juveniles over two months, the relationship between the rostrum-carinal length (RC) and the area of the scutal (S) and tergal (T) plates was determined using nonlinear regression (Ebert and Russell, 1994). Because measurements of rostrum-carinal length and capitular plate area are both subject to errors, a Model II regression was chosen to estimate the relationship because it incorporates variation in both variables, and non-linear regression was chosen because it may be more appropriate for describing relationships that do not pass through the origin (Ebert and Russell, 1994). From the results of this analysis, (initial) rostrum-carinal length at the time of marking (RC_t) was estimated. Rostrum-carinal length at time of marking, RC_t , was estimated using the rostrum-carinal length at time of collection, RC_{t+2} , together with the square root of final and initial (marked) scutal plate area, S_{t+2} and S_t : $RC_t = RC_{t+2} + \alpha (S_{t+2}^\beta - S_t^\beta)$, where α and β are the allometric parameters estimated by nonlinear regression of RC vs. S (Ebert, 1998). RC_t length was estimated from both the scutal and tergal plate areas in Winter 2002-2003 and Summer 2003, but only the scutal plate area was used in Winter 2003-2004. Data are presented for the scutal plate only because all seasons have a measurement of growth rate estimated from this plate and because there was slightly less variation associated with the allometric parameters estimated by nonlinear regression of (final) RC at time of collection (RC_{t+2}) vs. (scutal plate area)^{1/2}. Separate estimates were made for juveniles > 1mm RC and < 1 mm RC. When the nonlinear regression of final RC vs. (final scutal plate area)^{1/2} was made without splitting

the data into 2 size groups, I found a linear relationship between final RC and final scutal plate area at $RC < 1$ mm and a curvilinear relationship at $RC > 1$ mm; splitting data into size groups has been rationalized by others (Hentschel, 1998).

With Model II nonlinear regression giving an estimate of initial RC length at time of marking, the growth rates of juveniles were calculated. Because there was a positive linear relationship between change in RC ($RC_{t+2} - RC_t$) and final RC (RC_{t+2}), (Fig. 19; Winter 2002-2003, $p < 0.001$, $r = 0.69$; Summer 2003, $p < 0.001$, $r = 0.61$; Winter 2003-2004, $p < 0.001$, $r = 0.81$), growth rate was represented as $(RC_{t+2} - RC_t) / RC_{t+2}$ to reduce the effects of size-specific growth.

A mean growth rate for all juveniles on an adult was calculated for each adult because the particular location of the adult in the cluster is likely to affect juveniles growing on it.

2.4 Statistical analyses

Growth data were analyzed using the statistical programs Statistica 6.1 and Systat 9.0. The data were transformed to their natural logarithms to remove some of the skewness resulting from variation in growth rates. The assumption of homogeneity of variance was tested using Cochran's test at $p < 0.05$. (Underwood, 1997). The assumption of normality was tested with Kolmogorov-Smirnov and Lilliefors's test at $p < 0.05$; this assumption was violated for one group in Winter 2003-2004.

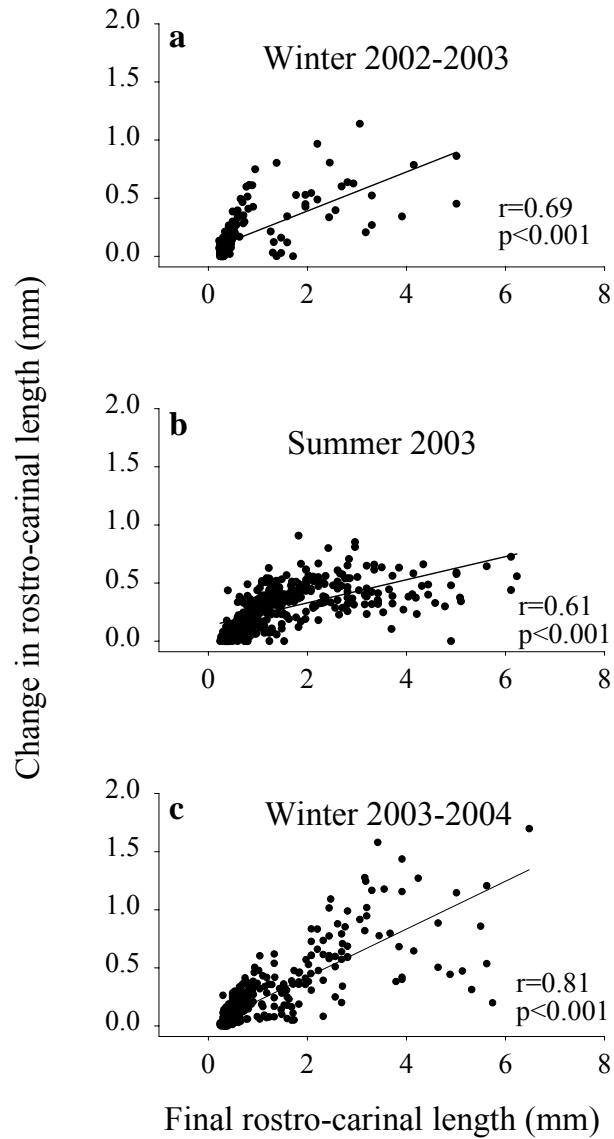


Fig. 19. Linear regression of change in rostro-carinal length (mm) vs. final rostro-carinal length (mm) of juveniles of *Pollicipes polymerus* for three seasons of growth: **a** Winter 2002-2003, $n=249$ juveniles **b** Summer 2003, $n=414$ juveniles and **c** Winter 2003-2004, $n=464$ juveniles.

Growth data were analyzed with an analysis of variance (ANOVA) to test for differences in the effects of location within the cluster (edge, inside) and cluster size (large, small, solitary adult). The locations middle and center have been combined into the “inside” location for growth analyses because recruits in the center location were not abundant enough to treat center as a separate location (see Chapter II). Because the Winter 2002-2003 experiment had clusters of only one size (large), this experiment was not included in the initial statistical analysis. Location within the cluster and cluster size were the fixed factors tested; season was included as an additional random factor. Growth, the dependent variable, was defined as the mean growth rate of recruits per adult. The final model was run without interactions that included season because variation in treatment effects among seasons was absent.

Growth in large clusters was compared in a separate ANOVA with the effects of location within the cluster and of season in order to include data from the Winter 2002-2003 study. The final model for large clusters omitted an interaction term (season by location) because this term was non-significant in a preliminary test.

In order to test for differences in growth due to cluster size, a separate two way ANOVA was performed. Cluster size (large clusters, small clusters, and solitary adult barnacles) was tested as a fixed factor and season as a random factor with growth as the dependent variable. Since growth for solitary adults was highly variable between seasons, due to one recruit representing growth for solitary adults in Summer 2003, artificial data were generated for Summer 2003 juveniles on solitary adults so that the sample size matched the smallest sample size ($n=38$) and the largest variance of the six

treatments, but the mean (0.133) for the one original individual stayed the same. These data were combined with the original data for Winter 2003-2004 and the large and small cluster data for Summer 2003, and the two-way ANOVA was rerun. Because of the significant interaction between growth on solitary adults in Winter 2003-2004 and the other treatments (Fig. 20), an additional separate one-way ANOVA was performed for the Winter 2003-2004 experiment with cluster size as the fixed factor and growth as the dependent variable. When results were significant, an Unequal HSD post-hoc test was used to determine which groups were different from each other.

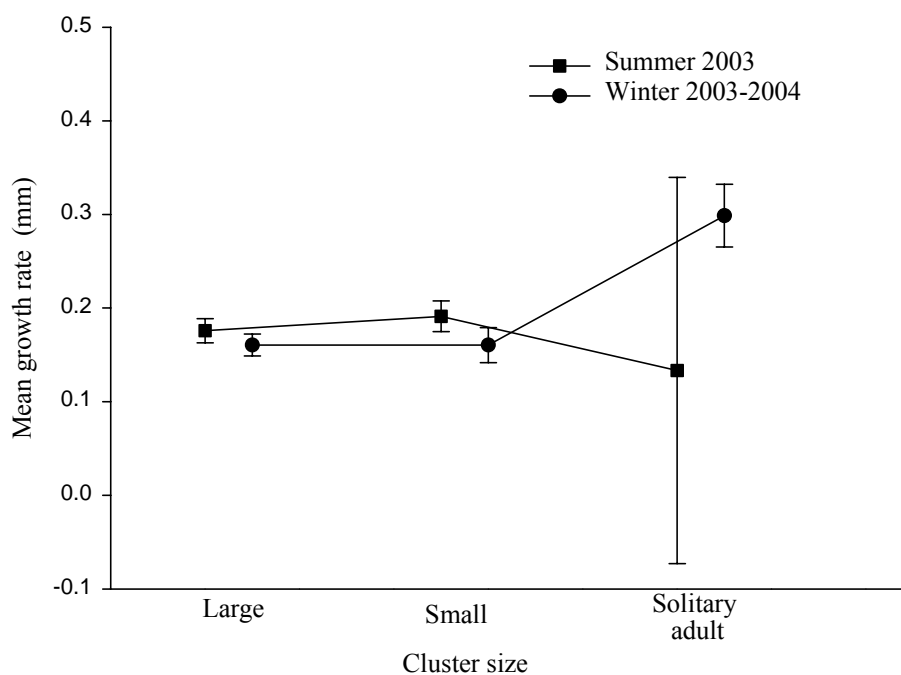


Fig. 20. Interaction plot of a two-factorial ANOVA of mean growth rate of all juveniles on an adult juveniles of *Pollicipes polymerus* with cluster size (large, small, solitary adult) and season (summer, winter) as main effects. Vertical bars denote 0.95 confidence intervals.

3. Results

3.1 The effect of location within the cluster on growth

Growth rates of juveniles in both locations (edge, inside) were highly variable; however, there was a significant effect of location within the cluster for two seasons (Table 7, $F_{1, 832}$, $p < 0.001$). In 6 out of 8 clusters during Summer 2003, juveniles on the edge of clusters had higher growth rates than juveniles on the inside (Fig. 21b). One small cluster did not have any marked juveniles on the inside location, and juveniles from one small cluster had higher growth rates on the inside of the cluster (Fig. 21b). In Winter 2003-2004, juveniles in 9 out of 10 clusters showed that grew faster on edges than on the inside of clusters (Fig. 21c). One cluster had mean growth rates of juveniles on edges (0.176 mm) that were almost equal to juveniles on the inside (0.175 mm); however, there was more variance associated with the inside location than the edge location (inside, ± 0.092 SE; edge, ± 0.022 SE; Fig. 21c). Mean growth rates of juveniles on the inside were greater than juveniles on the edge for one small cluster. When clusters of the same size were combined for a season, it was clear that juveniles had higher growth rates on the edges of clusters than on the inside (Fig. 22) for both Summer 2003 and Winter 2003-2004.

Table 7. Analysis of variance for Summer 2003 and Winter 2003-2004 growth of juveniles of *Pollicipes polymerus* from clusters with season, size, and location as main effects.

Effect	df	MS	F	p
Season	1	0.047	4.370	0.037
Size	1	0.018	1.683	0.195
Location	1	0.220	20.553	0.001
Size x Location	1	0.00034	0.031	0.859
Residual	832	0.011		

3.2. The effect of cluster size on growth

There was no significant effect of cluster size (Table 7, $p=0.20$) on growth for large and small clusters and no significant interaction between location and size ($p=0.86$).

An additional statistical analysis testing the effect of location in large clusters from three seasons solidified these results (Table 8, $F_{1, 797}$, $p < 0.001$). In large clusters, juveniles located at the edge of the cluster had significantly higher growth rates than those juveniles located on the inside of the cluster.

Table 8. Analysis of variance for Winter 2002-2003, Summer 2003, and Winter 2003-2004 growth of juveniles of *Pollicipes polymerus* from large clusters with season and location as main effects.

Effect	df	MS	F	p
Season	2	0.275	20.459	0.001
Location	1	0.324	24.137	0.001
Residual	797	0.013		

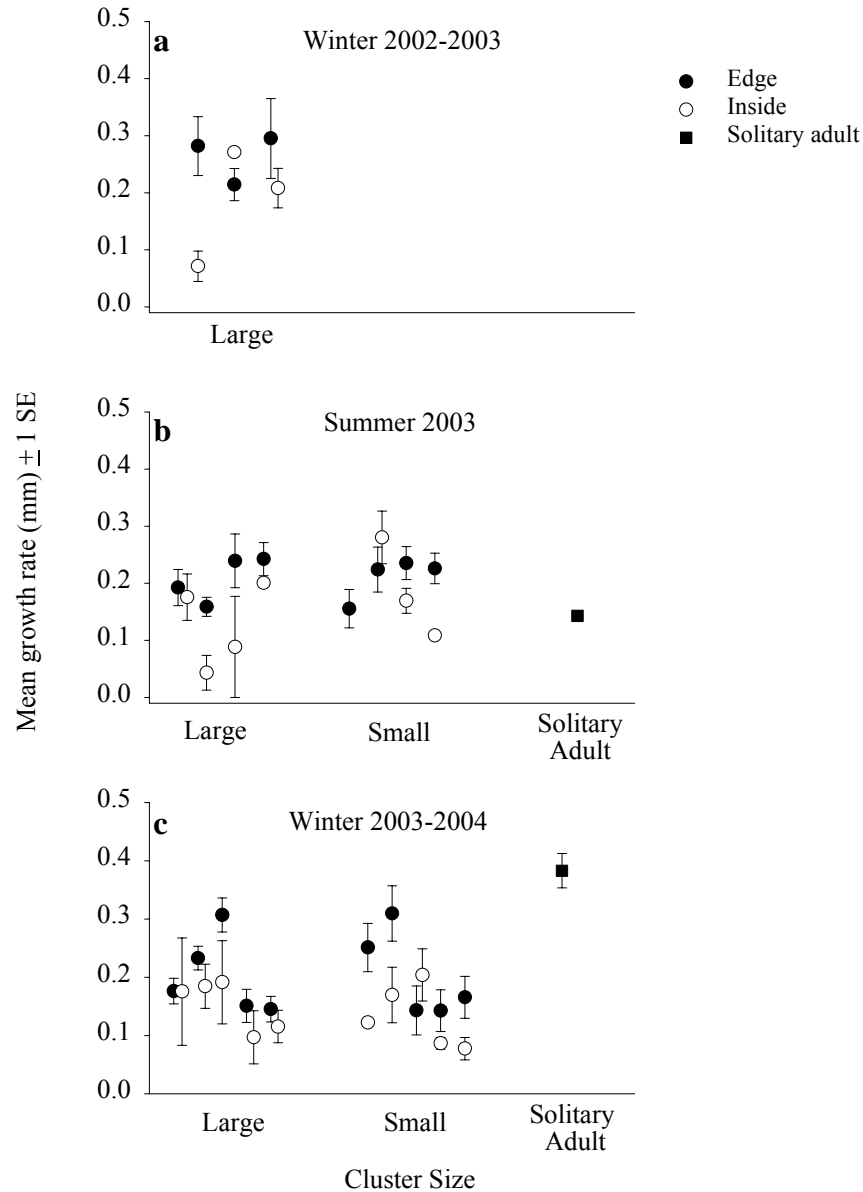


Fig. 21. Mean growth rates of juveniles of *Pollicipes polymerus* in two locations of clusters (edge, inside) and three sizes of clusters (large, small, solitary) for three seasons of growth: **a** Winter 02-03; 3 large clusters **b** Summer 03; 4 large clusters, 4 small clusters, 11 solitary adults, and **c** Winter 03-04; 5 large clusters, 5 small clusters, 17 solitary adults. Growth rate is defined as change in rostrum-carinal length (RC)/final RC. Mean growth rates were calculated for all juveniles on each adult. Data are shown for each cluster.

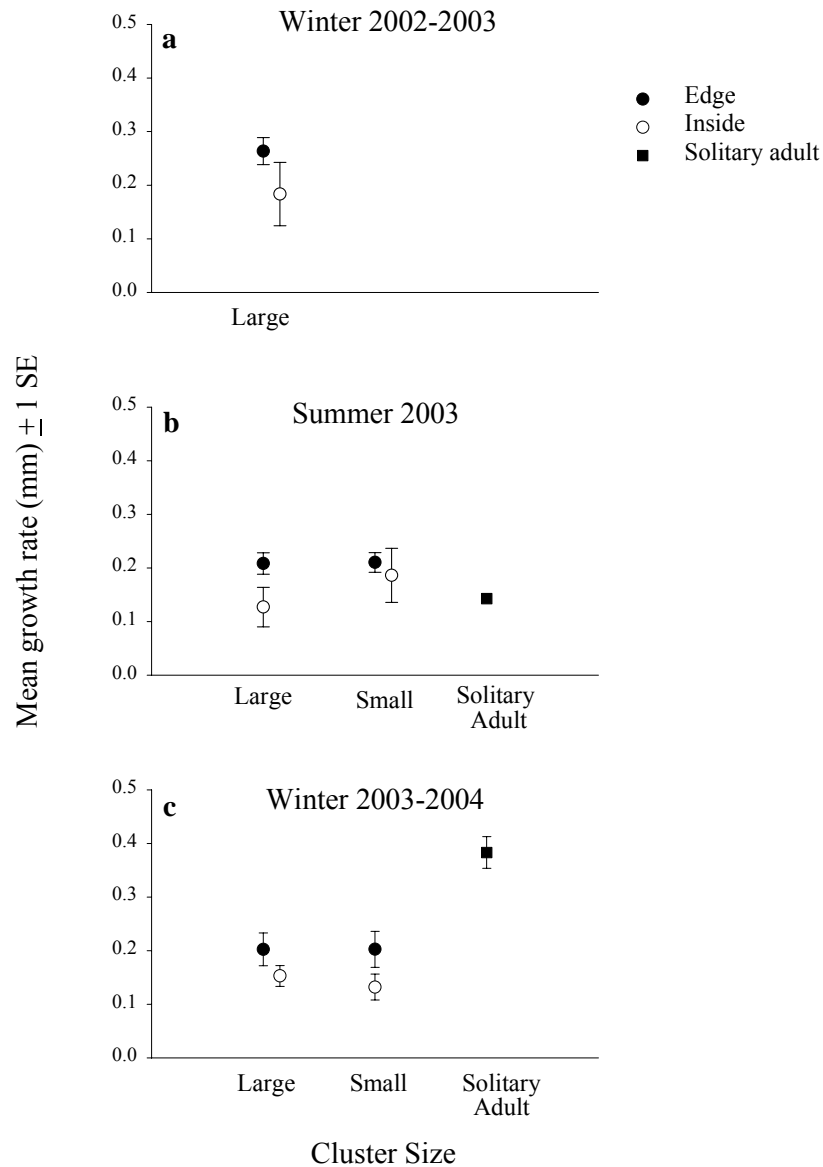


Fig. 22. Mean growth rates of juveniles of *Pollicipes polymerus* in two locations of clusters (edge, inside) and three sizes of clusters (large, small, solitary) for three seasons of growth: **a** Winter 02-03; 3 large clusters **b** Summer 03; 4 large clusters, 4 small clusters, 11 solitary adults, and **c** Winter 03-04; 5 large clusters, 5 small clusters, 17 solitary adults. Growth rate is defined as change in rostro-carinal (RC) length/final RC length. Mean growth rates were calculated for all juveniles on each adult.

The effect of cluster size was examined in more depth by comparing growth in large clusters, small clusters, and on solitary adult barnacles. There was no significant effect of cluster size or season (Table 9; size, $p=0.70$; season, $p=0.29$) and there was no significant interaction of season and cluster size ($p=0.14$). However, by looking at the interaction plot of this analysis (Fig. 20), it becomes clear that the 0.95 confidence intervals of the summer 2003, solitary adult treatment overlaps all of the other treatments because only one individual represents this treatment. If, instead, I treat the variation around the summer 2003 solitary adult treatment the same as the variation associated with the winter 2003-2004 solitary adult treatment (because this treatment has the highest variation and the lowest sample size ($n=38$) of the six treatments), and rerun the ANOVA, then the results show significant effects of cluster size and season (Fig. 23, Table 10; size, $p<0.001$; season, $p<0.001$), and there is a significant interaction of season and cluster size ($p=0.002$).

Table 9. Analysis of variance for Summer 2003 and Winter 2003-2004 growth of juveniles of *Pollicipes polymerus* from clusters and on solitary adults with season and size as main effects. This analysis has original sample sizes for juveniles from clusters and juveniles on solitary adults.

Effect	df	MS	F	p
Season	1	0.014	1.151	0.285
Size	2	0.009	0.421	0.704
Season x Size	2	0.022	2.008	0.135
Residual	870	0.011		

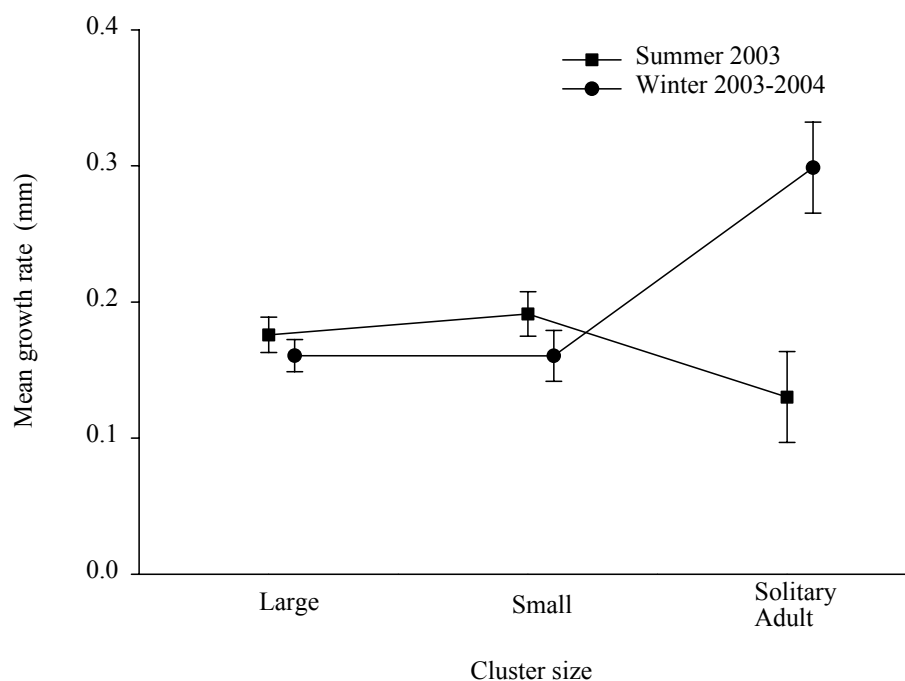


Fig. 23. Interaction plot of a two-factorial ANOVA of mean growth rate per adult of juveniles of *Pollicipes polymerus* with cluster size (large, small,=solitary adult) and season (summer, winter) as main effects. Vertical bars denote 0.95 confidence intervals. Data for the Summer 2003 solitary adult treatment represents the original mean from a sample size of one, but has the same variation and sample size ($n=38$) associated with the Winter 2003-2004 solitary adult treatment.

Table 10. Analysis of variance for Summer 2003 and Winter 2003-2004 growth of juveniles of *Pollicipes polymerus* from clusters and on solitary adults with season and size as main effects. This analysis has original samples sizes for juveniles from clusters for both seasons and juveniles on solitary adults during Winter 2003-2004; however, artificial data were generated for juveniles on solitary adults during Summer 2003.

Effect	df	MS	F	p
Season	1	0.202	18.289	0.001
Size	2	0.316	28.708	0.001
Season x Size	2	0.072	6.511	0.002
Residual	907	0.011		

Because growth on solitary adults was represented by one individual in Summer 2003 but is represented by 38 individuals on solitary adults in Winter 2003-2004, the effect of cluster size on growth in Winter 2003-2004 was tested separately (Table 11). These results indicated a significant cluster size effect ($F_{2, 461}$, $p < 0.001$). Growth of juveniles on solitary adult barnacles in this season was significantly higher than juvenile growth in large clusters ($p < 0.001$) and small clusters ($p < 0.001$). This separate test also confirmed that there was no significant difference between juvenile growth rates in large clusters and small clusters ($p=0.99$) by season.

Table 11. Analysis of variance for Winter 2003-2004 growth of juveniles of *Pollicipes polymerus* from clusters and on solitary adults with size as a main effect.

Effect	df	MS	F	p
Size	2	0.333	28.608	0.001
Residual	461	0.012		

4. Discussion

4.1. The effect of location within the cluster on growth

The location of juvenile barnacles within the cluster significantly influenced how fast they grew over a two month period (Fig. 22). Average growth rates of juveniles over

2 months on edges ($0.22 \text{ mm} \pm 0.01 \text{ SE}$) of clusters were 1.4 times higher than average growth rates of juveniles located on the inside ($0.16 \text{ mm} \pm 0.014 \text{ SE}$) of clusters (Fig. 22). Growth rate differences may be due 1) intraspecific competition for space between juveniles and adults and 2) intraspecific competition for food between juveniles and adults.

Competition for space between juveniles and adults in clusters may be more severe for inside juveniles than edge juveniles because inside juveniles may experience crowding by adults that are located on all sides of them whereas some edge juveniles are only surrounded on one side by the adjacent ring of adults, just interior to the edge of the cluster. The negative effects of high population densities on growth have been shown by some studies (Thorp and Barthalmus, 1975; Bertness and Grosholz, 1985; Holbrook et al., 1991). By manipulating and maintaining population densities of the green hydra, *Hydra viridis*, at 20, 70, 120, and 170 hydras per 40 ml culture solution, Thorp and Barthalmus (1975) found a significant inverse relationship between population density and population growth rate, measured as the mean number of new individuals per adult hydra. Bertness and Grosholz (1985) found that individual growth rates of ribbed mussels, *Geukensia demissa*, were significantly reduced at high densities; and furthermore, the decrease in growth rates was most prominent in the smallest size class of juveniles (30-40 mm length). Holbrook et al. (1991) compared blade growth rates between clumped and isolated sea-palms, *Postelsia palmaeformis*, where clumped plants were defined as plants located within a dense stand and isolated plants were at least 30

cm from their nearest neighbor. They found that blades of isolated individuals grew five times faster than blades of clumped plants.

A few studies have even looked at the effects of spatial position on growth rates of mussels in aggregations or patches (Okamura, 1986; Newell, 1990; Svane and Ompi, 1993). Okamura (1986) found that blue mussels, *Mytilus edulis*, located on the edges of large groups (21-28 mussels group⁻¹) grew an average of two times faster than those in the centers of large groups. A different experiment by Okamura (1986) compared growth of individuals in large groups of living mussels and model mussels and found that the individuals in the treatment with model mussels did not experience the negative effects on growth that were observed for individuals associated with live mussels. In order to explain their results, they discuss crowding as a mechanism of intraspecific competition: as live mussels grow, they exert a physical force on their neighbors (Harger, 1972). Since organisms on edges have neighbors on one side or on both sides, they may experience reduced effects of crowding while organisms in the center of groups, always surrounded by neighbors on all sides, should experience more extreme effects of crowding (compression, overgrowth). Thus, juvenile barnacles on the inside of clusters may have slower growth rates compared to juveniles on edges because they are being “squeezed” by their adult neighbors.

Newell (1990) also looked at the effects of spatial position on growth rates of *M. edulis* by spreading mussel seed at commercial bottom culture operations, allowing mussels to grow and form patches over 12-18 months, and then sampling cores of mussels from the edges of patches and middle of patches. He found that mussels located

at the edge of large patches (10 m diameter) had significantly larger shell lengths and greater dry tissue weight than mussels in the middle of patches. A study by Svane and Ompi (1993) tested the effects of spatial position of individuals on the size distribution within and between patches in beds of *M. edulis* and concluded that the mean size (dry flesh weight and shell weight) of mussels along an edge of a patch was greater than that of mussels on the insides of patches. One hypothesis that they address for this size difference is that crowding creates physical disturbances, where neighboring mussels may impair the shell openings of other mussels by exerting pressure on their shells. Because the size of the shell opening controls pumping rate and therefore, consumption and growth, interference by crowding is linked to food competition. Frechette et al. (1992) found that food and space limitation interacted and resulted in size-specific differences where only small mussels were affected by crowding. In the present study, morphological differences in the capitula or peduncle length between juvenile barnacles on edges and inside the cluster were not compared; however, all of the studies on mussels show a similar pattern to this study, where the location of the organism in the patch or cluster impacted its growth and final size.

A second factor that may be important in explaining growth differences between barnacles located at the edge and inside of clusters is reduced intraspecific competition for food between adults and juveniles on edges compared to adults and juveniles on the inside. This explanation assumes that 1) juveniles on the inside suffer more severe effects of crowding than juveniles on the edge and 2) differential food capture will translate into differences in growth. The influence of high densities of animals on food

depletion has been documented (Merz, 1984, Peterson and Black, 1987; Petersen and Riisgard, 1992). Furthermore, studies have shown differential food capture based on the position of suspension feeding animals within dense aggregations of polychaetes, octocorals, barnacles, phoronids, and bryozoans (Merz, 1984; Patterson, 1984; Pullen and LaBarbera, 1991; Johnson, 1990; Ekman and Okamura, 1998). Patterson (1984) looked at octocoral colonies feeding on cysts of brine shrimp at different flow speeds (2.5, 9.0, 19.0 cm s^{-1}) in both low and high turbulence environments. Because gooseneck barnacles live and feed in high wave energy environments, his results for high turbulence environments make interesting parallels. He found unequal prey capture distributions around the circumference of the colonies in low turbulent environments but not in high turbulence. He also found that in the vertical direction, prey capture showed a bimodal distribution, where polyps located at the highest and lowest height of the colony captured the most prey, and polyps at intermediate heights captured the least. For gooseneck barnacles, his results may indicate that food capture is equal around the edges of clusters and in the vertical direction, barnacles located on the edges and center (top of the cluster) capture more food than barnacles in the middle section of the cluster. Interestingly, there were very few juveniles located on center adults, with the majority of growth rates estimated from juveniles on middle adults. Perhaps, juveniles on edges capture more food than juveniles in the middle of clusters based on the idea of their different vertical positions in the cluster influencing the amount of prey they can capture. However, these results are probably most relevant to adult barnacles because juveniles are on adult peduncles below the feeding canopy of adults. Edge juveniles may be less restricted by

adults because they have more direct access to flows whereas inside juveniles are well buried by adults.

4.2. The effect of cluster size on growth

Cluster size was less important in explaining differences in growth of juvenile barnacles than location within the cluster because growth rates of juveniles in small and large clusters were similar (Fig. 22b,c); however growth rates of juveniles on solitary adults were almost twice as fast (1.9x) as juveniles in clusters (Winter 2003-2004).

Group size has been shown to negatively affect growth in marine invertebrates. Studies addressing this relationship for mussels found that isolated individuals and individuals in small groups (6-9 mussels) grew more than individuals in large groups (21-28 mussels) (Okamura, 1986). However, her study and most other studies that have looked at the effects of group size on growth have focused on adults. In gooseneck barnacles, the influence of adults or other juveniles on the growth of juveniles is complex given that juveniles are growing on the peduncles of adults and are typically concentrated on a few adults. This study did not address these interactions on the growth of juveniles; however, there was an interesting trend between cluster size and location within the cluster on the growth of juveniles.

For the seasons that compared the effects of small and large cluster size on growth (Fig. 21b,c), the mean growth rates of juveniles on the inside of clusters were faster than edges for two small clusters. This trend may be explained by the fact that the difference between the edge and the inside of a small cluster is less defined than the edge and inside

of a large cluster. For example, differences in growth due to food flux are more likely to affect juveniles in large clusters than small clusters because food flux on the inside of a 10 cm diameter large clusters is probably much lower compared compared to flux on the inside of a 5 cm diameter small cluster.

The differences in how resources (food, space) affect a solitary individual and clusters are even greater and may be an important factor in explaining the large differences in growth rate between juveniles on solitary adults and juveniles in clusters during the Winter 03-04 study. Juveniles on solitary adults may grow faster than juveniles in clusters because they have access to more water and potentially higher abundances of phytoplankton and they are not experiencing any interference (crowding) from surrounding adults. On the other hand, juveniles in clusters may be exposed to water from which food particles have most likely been filtered by the cluster, and they are surrounded at least on one side if not on all sides by adults.

4.3. Conclusions

The trade-offs associated with living in aggregations or as solitary units may explain why solitary gooseneck barnacles are pioneers for new clusters, especially given the fast growth rates of juveniles on solitary adults (Fig. 22c). Since solitary adults are rarely found (Ricketts et al., 1985), they may quickly grow into clusters, reaping the benefits of an aggregated lifestyle. Merz (1984) and Bertness et al. (1998) compared feeding currents of polychaetes and particle capture rates of barnacles, respectively between clusters and solitary animals. They both found significant differences between

clustered and solitary animals, where animals within clusters experienced higher feeding currents and higher particle capture rates than solitary animals. Clearly, the formation of clusters implies advantages in feeding and thus, overall growth of the cluster that must outweigh the disadvantages from competitive interactions between cluster members living in such close proximity. The cluster may offer other advantages, in addition to greater feeding efficiency, that must compensate the advantage of potentially faster growth of solitary adults and juveniles on solitary adults (most likely due to lack of crowding rather than food limitation).

Buss (1981) described a benefit of group living in bryozoan colonies, which he called increased interspecific interference competitive ability. He showed that high densities of the bryozoan, *B. turrita* negatively impacted the weight gain per colony, yet larvae form groups which grow into dense adult colonies. In a different experiment, he showed that *S. errata* colonies overgrew low density colonies of *B. turrita*; however, at high densities, *B. turrita* were not overgrown and the other colony was growing slower or not at all. He concluded that the interspecific competitive ability of *B. turrita* was density dependent. The competitive relationship between gooseneck barnacles, *Pollicipes polymerus* and California mussels, *Mytilus californianus* has been well described (Paine, 1974; Wootton, 1990). Perhaps, clusters of *Pollicipes polymerus* are able to compete more effectively with mussels, *Mytilus californianus* than solitary gooseneck barnacles which may be easily overgrown by mussels. On vertical surfaces, larger clusters of gooseneck barnacles would clearly increase their attachment strength and secure their

position on a substrate whereas mussels, attached by thin byssal threads, may be more easily pushed off or down the substrate.

CHAPTER IV

CONCLUDING SUMMARY

The objective of this thesis was to provide a better understanding of the distribution and growth of juveniles of benthic marine invertebrates living within dense aggregations. Since living within an aggregation may have both ecological costs and benefits for the individual members, the many examples of aggregating species in benthic marine environments are both interesting and puzzling. The example chosen to study in this thesis, the gooseneck barnacle *Pollicipes polymerus*, is even more interesting because of the gregarious settlement of larvae on adults.

Chapter II of this thesis has offered a detailed look at the distribution and abundance patterns of larvae and juveniles of *P. polymerus* in four different ways: 1) as the distribution and abundance of larvae and juveniles on adult peduncles, which were studied as a relative distance down the peduncle and as a position around the peduncle for juveniles in both clusters and on solitary adults, 2) as the distribution and abundance of juveniles within the cluster, 3) as the abundance of juveniles in different cluster locations, and 4) as the abundance of juveniles in clusters of varying size. Chapter III of this thesis gives a comparison of growth rates of juveniles in two different location within the cluster (edge, inside) and three sizes of clusters (large, small, and solitary adults).

Results described in both chapters indicate that there may be important differences in recruitment and growth between clusters and solitary adults that may help

explain how clusters are formed and maintained and how *P. polymerus* may compete with the California mussel, *M. californianus*. The discussion of the recruitment and growth patterns also leads to a very important future direction of this research, which involves hydrodynamics. Determining if and how larvae are influenced by flows around the cluster may elucidate the peculiar patchy distribution of larvae on particular adults. Also, experiments that test the effects of location in the cluster and cluster size on food capture of adults and larger juveniles might resolve questions about competition among adults or between juveniles and adults. The potential results of experiments examining hydrodynamics around clusters may contribute to understanding the unique clusters of adults of *Pollicipes polymerus* and may be applicable to other aggregating benthic invertebrates.

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