

Growth, Seasonality, and Dispersion of a Population of *Aplysia vaccaria* Winkler, 1955

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Abstract. The growth and spatial dispersion of an intertidal population of the California black sea hare, *Aplysia vaccaria* Winkler, 1955, was studied from October 1995 to October 1996 in North Cardiff Beach, California. Population size peaked in November and then declined to zero the following year, while mean weight peaked in June. Breeding was observed throughout the year. The sea hares were spatially clustered and the aggregation pattern was invariant over time. Individual movements and growth were recorded by tagging 19 animals with internal microchips. Tagged animals grew at a rate of 4.9 g/day and moved an average minimum distance of 2.3 m/day.

INTRODUCTION

Intensive research on the neurobiology of sea hares (Kandel, 1979) has been complemented by field studies of their behavior and ecology (e.g., Carefoot, 1967; Usuki, 1970; Kupferman & Carew, 1974; Audesirk, 1979; Nishiwaki et al., 1975; Susswein et al., 1983; Susswein et al., 1984; Carefoot, 1989; Pennings, 1991a, b; Strenth & Blankenship, 1991; Yusa, 1996). One of the least studied of the sea hare species is *Aplysia vaccaria* Winkler, 1955 (Carefoot, 1987). This may be partly due to its perception as "a secretive animal . . . much more difficult to obtain in numbers" than other sea hares (Winkler, 1957). *A. vaccaria* ranges from California to Baja California (Lance, 1967). The species is reported to be primarily nocturnal (Eales, 1960; Pennings, 1991b) and often immobile (Pennings, 1991b), inhabits rocky coasts and kelp beds (Kandel, 1979), spawns in February and March under rocks in shallow water (Winkler, 1955), and feeds upon *Egregia* spp. (Winkler, 1955; Winkler & Dawson, 1963). There are no published data on the growth rate of *A. vaccaria*, its seasonal abundance or its movements in the field (Carefoot, 1987).

In this study, we report on a dense intertidal population of *A. vaccaria* which we were able to monitor regularly for 1 year. Data collected included population size, individual body masses, and fraction of animals mating. The animals in this population appeared to be clustered into small aggregations. *Aplysia* aggregations have often been described (Kupferman & Carew, 1974; Achituv & Susswein, 1985; Pennings, 1991b), but rarely quantitatively, and their function is still unknown. Sea hares may aggregate primarily for mating purposes or other social functions (Susswein et al., 1984; Carefoot, 1987; Pennings, 1991b). On the other hand, aggregations may be caused by differential larval settlement on preferred habitats, at-

traction of adults to patches of food, or attraction of adults to sites with preferred levels of exposure and tidal action (Pennings, 1991a). Because we had the opportunity to map every animal within a fixed study area on each census, we were able to monitor a number of measures of spatial dispersion to see how these changed with season, mean body size, mating frequency, and density of animals. Microchip tagging, a method new to sea hare biology, successfully provided data on growth and movement for a small number of individuals. The result is the first study of dispersion, growth, and survival on this species.

MATERIALS AND METHODS

Site and Study Period

The study population was monitored from October 1995 to October 1996. The site is an intertidal rocky reef at North Cardiff Beach, San Diego County, California (33°1'N, 117°17'W). At the beginning of our study, there was little sand, much exposed bedrock, and extensive cobbling of the upper strand. A year later much of the beach was covered with sand, and most of the tidepools formerly occupied by *A. vaccaria* were covered. We selected a 15 × 19.85 m rectangular census site with deeply eroded channels and pools which harbored high densities of *A. vaccaria*. The tidal range of this site spans from 25 cm above mean low tide level to 90 cm below mean low tide level. The included channels remained filled with water during the lowest tides (-58 cm), and there were many rock ledges under which the sea hares aggregated. Algae in the study site included *Ulva californica*, *Placodium cartilagineum*, *Laurencia sinicola*, *Ceramium* sp., *Pterocladia capillacea*, *Gelidium purpurascens*, *Acrosorium venulosum*, *Jania crassa*, *Herposiphonia* sp., *Centroceras clavulatum*, *Hypnea valentiae*, *Zonaria far-*

lowii, *Dictyopteris undulata*, *Sphacelaria* sp., *Colpomenia sinuosa*, *Egregia menziesii*, and *Macrocystis pyrifera* drift. The animals in this area were not isolated from human disturbance, although we usually arrived before the low tide and secured cooperation from onlookers in minimizing disturbance to the study site.

Sampling and Mapping Methods

On average, we sampled the site every 2–3 weeks during low tides, which occurred sometime between 4 a.m. and 6 p.m. Each *A. vaccaria* was mapped by recording the distance and compass angle measurement from one corner of the study site to the animal; these were later converted to cartesian coordinates relative to the sides of the study rectangle. Each animal was weighed after removing any debris and as much water as possible from its body. Errors in wet mass measures were estimated by returning five individuals to the water, letting them move about for 5 minutes, and then reweighing them three times. The repeatability (a measure of correlation between repeated measures) of mass measurements was very high ($r = .998$, $SD = 7$ g; Falconer, 1989). Mating status of closely opposed animals was determined by inserting a finger under the parapodia to determine whether or not an everted penis joined individuals.

Density Measures

We used two different measures of density. "Absolute density" is the number of sea hares in the study area divided by the total area in the plot. We also computed an "effective density" by dividing the total number of sea hares counted on a census by the minimum convex polygon required to surround them all. This second density measure thus reflects both the number of animals present and their dispersion.

Dispersion Analysis

The study area was partitioned into 81 contiguous quadrats. Twenty-three of these were considered uninhabitable because of lack of sufficient tidepool area and none ever hosted an animal. All but one of the remaining quadrats did harbor *A. vaccaria* at one time or another during the study. In order to determine whether the animals were significantly aggregated on each census, counts in the habitable 58 quadrats were compared to random (Poisson) expectations with a chi-square goodness-of-fit test.

Where dispersions were significantly non-random, pattern was characterized using several measures of intensity and grain (Pielou, 1969). Intensity measures the difference in sea hare density between cluster peaks and spaces between clusters; grain measures the typical distance between cluster centers and the typical area occupied by a cluster. Lloyd's index of patchiness was an intensity measure computed from quadrat counts. This value indicates

the average number of animals found in the same quadrat with a focal animal after correcting for differences in overall densities. A second measure of intensity was computed by assigning all animals within 1 m of a neighbor to a "cluster" and averaging the resulting number of animals per cluster.

Grain was measured in several ways. The first method was to impose a 10×10 cell grid on the study site and construct correlograms to characterize levels of autocorrelation between numbers of animals/cell at varying cell separations. These plots all showed initial positive autocorrelation (as measured by Moran's I) which dropped to zero and then oscillated around the zero line with increasing cell separations. The farthest separation with a significant positive I (after a Bonferroni correction) and that at which I first crossed the zero line were both noted. The two values are rough estimates of average minimal and maximal cluster size (Upton & Fingleton, 1985). A second measure of grain relied on the number of clusters generated by the 1 m proximity rule: the larger the number of clusters per unit area, the finer the grain. The clustering algorithm also drew minimum convex polygons around each cluster, identified the geometrical centers of the polygons, and computed the enclosed areas. The dispersion of the cluster centers was examined using nearest neighbor methods. The areas of the polygons were used as additional measures of grain: larger mean cluster areas implies coarser pattern grain. Cluster areas could be larger because of more animals per cluster, larger distances between nearest neighbors, or both. To tease apart these effects, we measured average nearest neighbor distances for each census.

Intensity and grain are both likely to vary with population density. We plotted a measure of intensity (the logarithm of cluster size) against a measure of grain (the logarithm of the number of clusters) for successive censuses. Points have to move as overall densities change: which variable shifts least over time can be used as an indicator of the possible mechanisms governing dispersion. Because densities steadily decreased from the fourth census on, we confirmed impressions from the grain vs. intensity plot by regressing the logarithms of animal density, cluster size, and cluster number on time, and then comparing the slopes of the three regressions using ANCOVA.

Finally, we examined the regularity with which different areas in the study site were used by ranking habitable quadrats according to the fraction of the total animals they hosted on each census, and comparing the consistency of quadrat ranks over time using Kendall's index of concordance.

Statistics were undertaken on Macintosh computers using the commercially available Statview and JMP packages. The analyses of intensity and grain were largely undertaken using our own dispersion program called An-

telope (available on the Internet at <http://www-biology.ucsd.edu/research/vehrenbury/programs.html>).

Tagging Methods

Nineteen sea hares were tagged (12 in March and seven in May) using number-coded Trovan passive transponder tags, which were later detected and read with a Trovan LID-500 Hand Held Reader held close to the body of the sea hare. Both the tags and reader were obtained from InfoPet Identification Systems, Inc. Transponder tags, weighing only 0.01% of the weight of a typical individual, were injected under the mantle just inside of the left parapodium. This tagging method was selected for several reasons: we found it to be less likely to attract the attention of curious onlookers than external tags, reducing the human disturbance to the study; tagged animals appeared to be healthy and unaffected by the procedure, and continued to increase in mass, as did the rest of the population; the reader was easy to use and detected microchips quickly, even when wrapped in a plastic bag for protection against moisture.

The 14 tagged animals that were recaptured on subsequent censuses were mapped and weighed. Because our data are limited to those animals that stayed within the study site, and assume a straight line of travel between the two points on subsequent days, our estimates of individual movements are highly conservative. Because we could sample the study area exhaustively, tagged animals not found on one census, but found later, must have emigrated outside the site and then returned. For the census when they were not detected, we recorded the minimum distance between last capture site and the edge of the study area. This is again a conservative estimate of movement over that period given that we routinely searched the immediate area around the study site for tagged animals; hence any sea hares moving out and back into the site must have gone even farther than the value recorded. Mean movement/day was calculated using data from censuses on 5 consecutive days in March (Days 156–160 of the study).

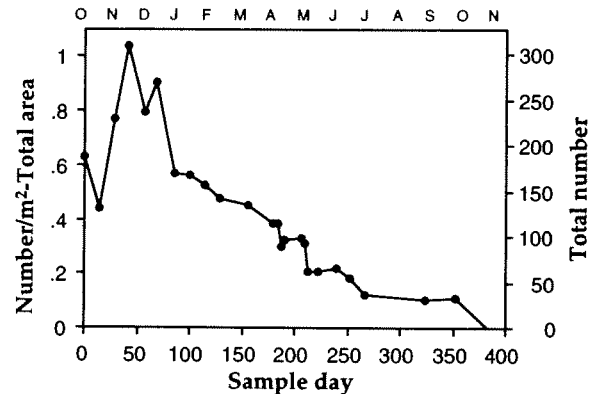
Estimates of short-term movements were obtained by observing 16 animals during four low-tide periods in April (Days 183, 185–187). Each animal was followed for 2 hours between 10 a.m. and 3 p.m., and its location was mapped on a diagram of the study site every 15 min.

RESULTS

Density, Growth and Mating Patterns

The number of sea hares in the study site peaked in November (Day 42) at 310 animals and an absolute density of 1.04 individuals/m²; the corresponding effective density was 1.63 individuals/m². The population then steadily decreased to zero by October of the following year (Figure 1).

a) Absolute density



b) Effective density

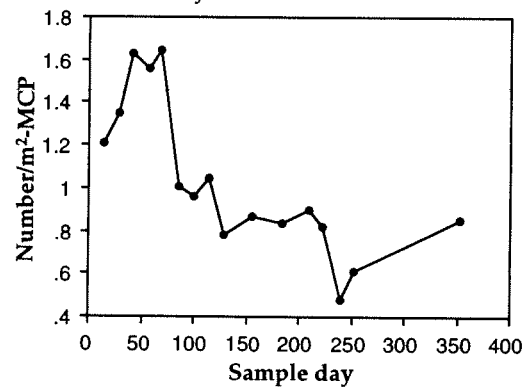


Figure 1

Density of *A. vaccaria* in the study area vs. sample day. a. Absolute density calculated by dividing the number of individuals by the total area of the study site. b. Effective density calculated by dividing the number of individuals by the minimum convex polygon around them (calculated in Antelope). Months are indicated at the top of the figure.

Mean body mass increased in a roughly linear fashion from 372 g in October to the peak of 1105 g in June (Day 239); this corresponds to an average increase of 3.1 g/day (Figure 2). June was also the only time that animals with weights below 180 g were observed; however, these were few in number. The smallest individual found was 30 g. The decrease in mean mass after the June peak was not due to further recruitment of small individuals, but instead to a rapid drop in maximum body size. Because minimal body sizes concurrently increased, this was a period in which the range of body sizes in the site was dramatically reduced.

Body size histories for 13 tagged animals are summarized in Figure 3. All but two samples were taken before the mass peak in June. Although the general trend for the tagged animals is an increase in mass, we observed both rises and falls over the short term. Whether these reflect egg-laying bouts, food shortages, or other constraints on

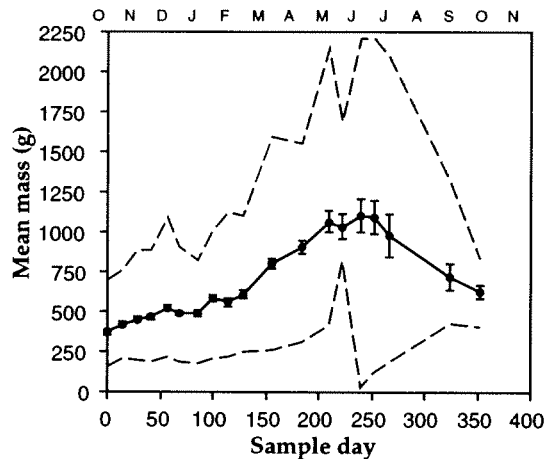


Figure 2

Mean mass of the population vs. sample day (solid line). Bars represent 1.96 standard errors of the mean. Dashed lines indicate maximum and minimum masses for each census. Months are indicated at the top of the figure.

feeding is unknown. Note that some tagged individuals show synchronous increases and decreases in mass, whereas others show quite asynchronous patterns. The average increase in mass for tagged animals was 4.9 g/day over the time period they were followed; this can be compared to a 3.2 g/day average increase in the unmarked population over the same time period. There was a great deal of variance in growth rate ($SD = 8.7$ g, $SE = 2.3$ g) with some tagged animals even losing weight over the period they were monitored. Growth rate of tagged animals was unrelated to their initial weights ($r^2 = 0.02$, $df = 13$, $P > 0.5$). The lower growth rate for the population as a whole during this period when compared to the tagged animals is at least partly due to the appearance of small individuals in the population in June.

In every census, some fraction of the population, between 3% and 43%, was found mating. Both time of day (morning vs. afternoon; Figure 4a) and tide height (Figure 4b) were found to have a significant effect on the fraction of total individuals mating (analysis of covariance on transformed data, $r^2 = 0.51$, $df = 23$, $P = 0.002$). The results indicate that more individuals were mating in the morning censuses ($P = 0.007$) and when the low tide was relatively higher ($P = 0.008$). There was also a significant interaction effect between tide height and time of day on the fraction mating ($P = 0.004$). However, it is impossible to separate the effects of time of day and season, as most of the morning censuses occurred in the spring and summer and most of the afternoon censuses occurred in the fall and winter. Although the number of egg masses was not quantified, newly laid eggs were observed in the study site throughout the entire year's sampling.

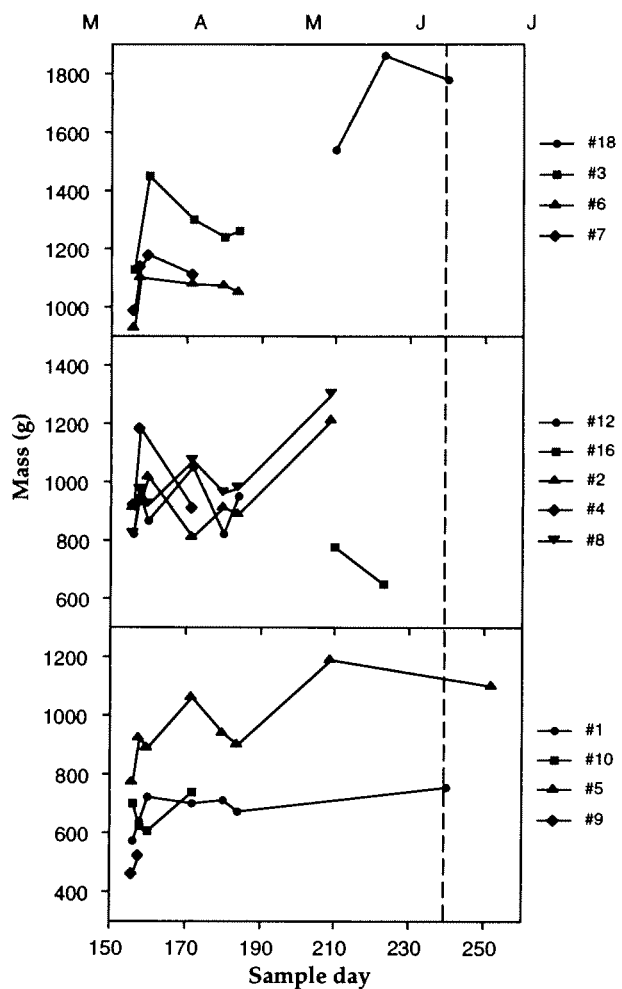


Figure 3

Body size histories for 13 tagged animals which were recaptured and reweighed. Months are indicated at the top of the figure.

Dispersion

Even after uninhabitable quadrats were removed from the analyses, animals were found to be significantly clustered in space on every census (all $\chi^2 > 23$, minimal $df = 3$, and all $P < 0.0001$). Correlograms showed strong positive autocorrelation of animal densities over an average range of 3.4 m, and a drop to zero correlation for quadrats separated by an average 5.3 m (see example in Figure 5). Mean cluster size within a census (using a 1 m linkage rule) ranged from 4.1–12.1 animals/cluster when all individuals were considered, and from 6.2–23.0 when only clusters with more than two individuals were tallied. Mean numbers of clusters in the site ranged from 14–34 including singletons and pairs, and from 8–20 when only clusters larger than two were considered. Clus-

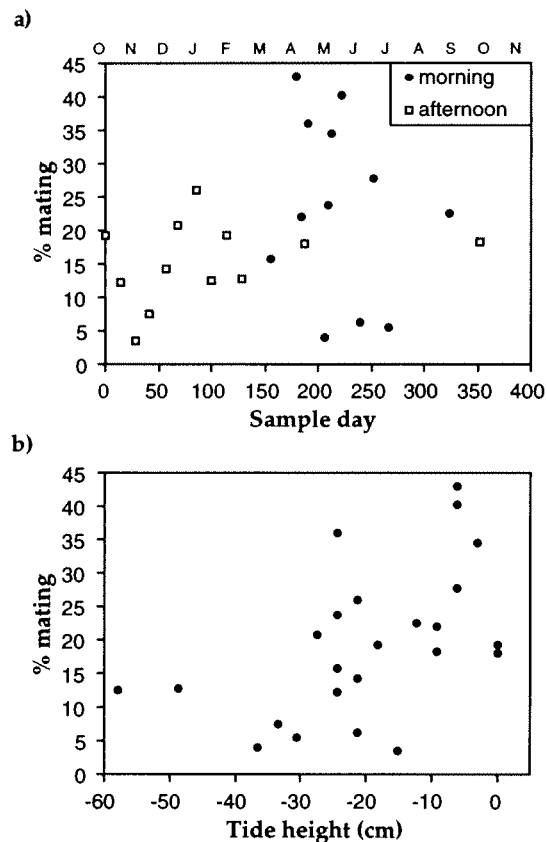


Figure 4

a. Percent of total individuals which were mating in each census. Squares represent afternoon censuses, circles represent morning censuses. Months are indicated at the top of the figure. b. Percent of total individuals which were mating vs. tide height in each census.

ter size and cluster number were uncorrelated ($r = -0.159$, $t = 0.534$, $P > 0.5$).

Population density equals the product of mean cluster size and cluster density. Thus, variation in population density or population size (given the fixed area of our study site) can be completely explained by the independent variations in cluster size and number; whichever of these has the larger variation will dominate variations in density. For our samples, the coefficient of variation in cluster size was 41.4%, whereas it was only 26.6% for cluster number. This suggests that most of the variation in density was due to changes in cluster size. This is confirmed in Figure 6a, which summarizes how mean cluster size and number each varied as population size decreased over time. The relative stability of cluster number when compared to cluster size is demonstrated statistically in Figure 6b. Here, the logarithms of density, cluster size, and cluster number are regressed against sample date over the period of population decline. The regres-

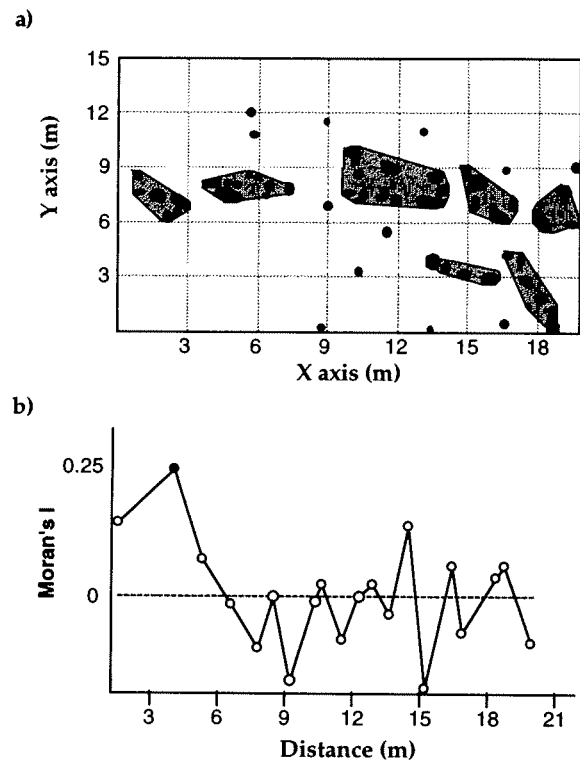


Figure 5

a. Dispersion and size of clusters using 30 cm linkage rule (dark stipple) and 1 m linkage rule (light stipple) for census on 19 December 1995 (Day 69). A total of 270 animals were recorded on this census. b. Correlogram based on a 10×10 grid for above sample. Dark circle at distance of 3.75 m corresponds to Moran's I of 0.241 ($P = 0.00275$). This is just slightly greater than the $P = 0.0025$ required by a Bonferroni correction given an overall significance level of 0.05 and 20 tests.

sions show a rate of drop in number of clusters which is significantly slower than that for cluster size or overall density, but statistically similar rates for drops in cluster size and population density. This again suggests that density decreases were accomplished as reductions in numbers of animals/cluster, not in the number of clusters. This linkage between density and cluster size is also indicated by a plot of Lloyd's index of patchiness vs. sample day (Figure 6c). There is no significant trend here indicating that once variations in density have been taken into account (a fundamental focus of this index), the intensity of the spatial pattern is invariant over time.

The area of clusters as measured by the 1 m clustering rule is negatively correlated with sample day ($r^2 = 0.735$, $P = 0.0002$). Since it is also positively correlated with mean cluster size ($\ln(\text{cluster area}) = 2.1 \ln(\text{cluster size}) - 5.3$; $r^2 = 0.871$, $P = 0.0001$), the decrease in cluster area could simply reflect the demonstrated drop in mean cluster sizes over the season. However, the 2.1 coefficient

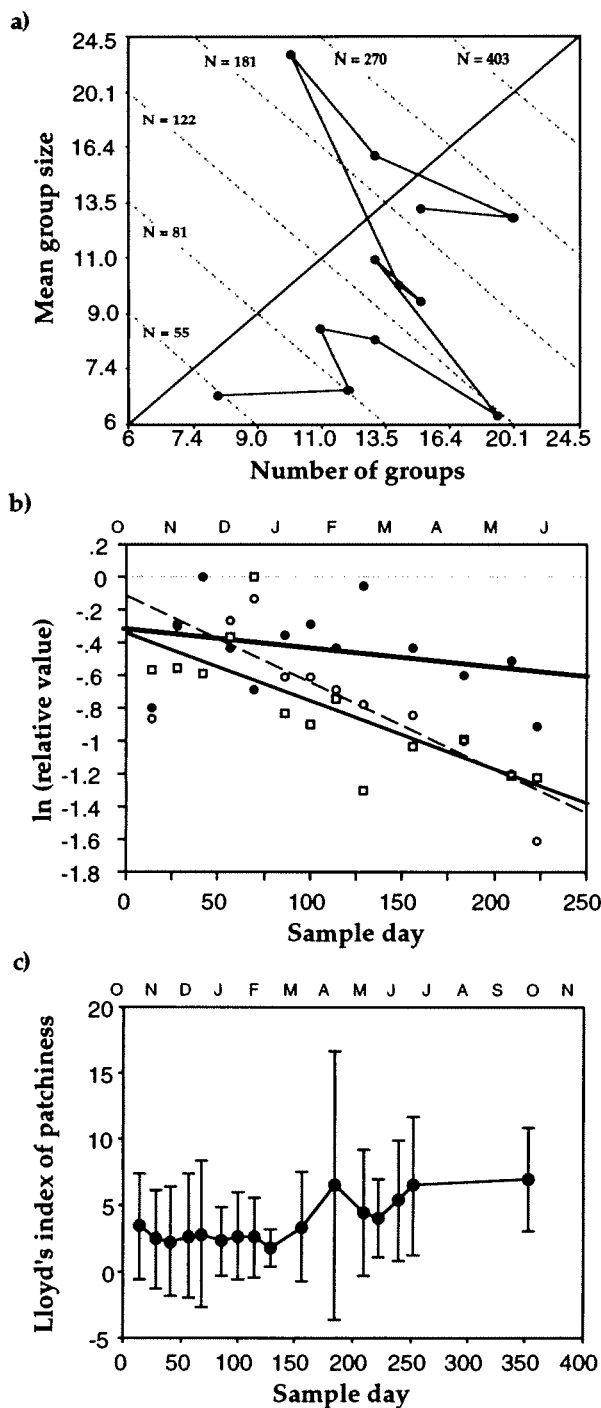


Figure 3

a. Mean cluster size vs. number of clusters for successive censuses after population peak. Clustering uses 1 m rule and only shows groups greater than two individuals. Note logarithmic axes which cause isopleths of equal density to plot as straight lines with a slope of negative one (dotted lines with selected densities indicated). As density decreases, points must move closer to low-

in the log-log regression implies that cluster area depends upon the square of the number of animals in a cluster. Were each animal to require the same amount of space around it, and animals settled in clusters with efficient packing, cluster area should depend only on the first power of cluster size. A likely explanation is that the area added to a cluster per animal is not a constant. In fact, a regression of area/cluster member vs. sample date shows a highly significant decrease over the season ($r^2 = 0.684$, $P = 0.0005$). This could arise either because individuals crowd more closely together later in the season, or because they do not pack into clusters efficiently. Mean nearest neighbor distances range from 14–25 cm, but show no seasonal effects ($r^2 = 0.035$, $P = 0.542$). Thus, the answer is not variation in individual spacing. Because the animals tend to aggregate around the margins of large boulders, their within-cluster dispersion is often curvilinear. This could easily increase the area of enclosing polygons at rates faster than were animals to pack in a contiguous fashion.

If the 58 habitable quadrats are ranked according to the fraction of animals they harbor on each census, there is a high degree of repeatability in quadrat rank over the season (Kendall's index of concordance, $\chi^2 = 249$, $df = 56$, $P < 0.0001$). In fact, the same 17.5% of the quadrats host an average 48% (95% CL = 40–56%) of the animals on any census, and of these, the top 9% harbor an average 24% (CL = 18–30%) of the population.

Individual Movements

Minimum values for the cumulative distances traveled since first capture date are shown in Figure 7a. A conservative estimate of the minimum mean distance traveled per day by 11 tagged animals on 5 subsequent days is 2.3 m/day ($n = 42$, $SE = 0.3$). Eleven of the 42 dis-

←

er left corner of graph. Diagonal from upper right to lower left indicates trajectory points would follow were decreases in density accommodated by equivalent decreases in cluster size and cluster number. The fact that most points are below this diagonal indicates that drops in density are largely borne by drops in cluster size; cluster number remained relatively stable over the study period. b. Rates of seasonal decrease in overall density of animals on the study plot (open circles and dashed line), numbers of clusters (filled circles and dark solid line), and mean cluster sizes (squares and thin solid line). All measures normalized by dividing by maximum value for season and transformed using logarithms. Results of ANCOVA indicate a significant overall effect of sample day ($F_{2,29} = 44.1$, $P = 0.0001$) and measure ($F_{1,29} = 7.8$, $P = 0.0001$). Post hoc tests using both Fisher's LSD and Scheffe tests indicate significant differences in slopes of density vs. number of clusters ($P = 0.014$ and $P = 0.046$ respectively), and cluster size vs. number of clusters ($P = 0.0006$ and 0.0024), but not between density and cluster size ($P = 0.222$ and 0.478). c. Lloyd's index of patchiness over time. Bars represent 1.96 standard errors of the mean.

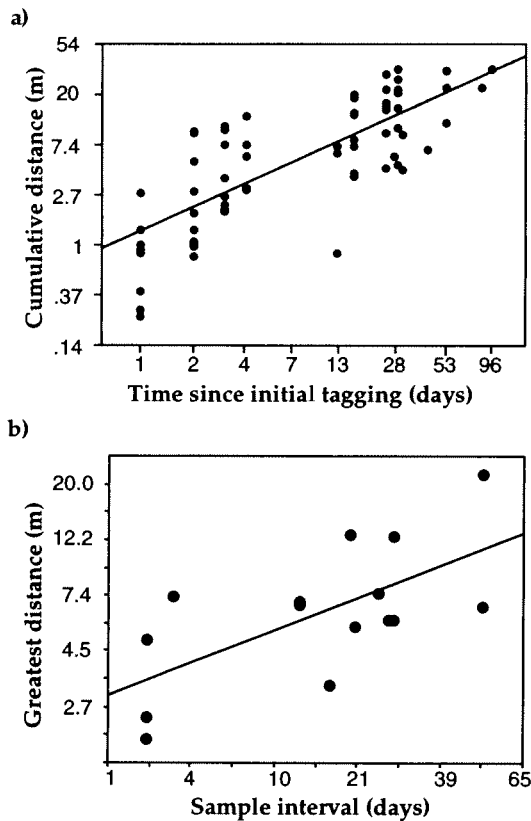


Figure 7

a. Conservative estimates for cumulative distance traveled by each of the tagged animals over the time that they were recaptured. Regression equation is $\ln(\text{cumulative distance}) = 0.28 + .70 \ln(\text{time})$ ($r^2 = 0.57$, $df = 69$, $P < 0.0001$). b. Distance between two most distal capture locations vs. time interval between capture events for each of the tagged animals. Regression equation is $\ln(\text{max distance}) = 0.53 + 0.58 \text{ time}^{0.3}$ ($r^2 = 0.43$, $df = 14$, $P = 0.0078$).

tance measurements are based on estimates of the minimum distance traveled by animals leaving or returning to the study site, and two values are missing because the animals left the study site, but did not return on the consecutive days. Figure 7b shows the greatest distance between two recapture sites for each tagged animal as a function of the time interval between the corresponding recaptures. Maximum distances between recapture sites range from 3–12 m and increase significantly with the interval between recaptures. Direct observations of individual movements during low-tide periods indicate that *A. vaccaria* move an average of 0.92 m/hour (SD = 1.4, SE = 0.24), and that movement is restricted when the tide is especially low (ANOVA, mean for -3 cm and -6 cm tides = 1.5 m/hr, mean for -12 cm tides = 0.5 m/hr, $p = 0.04$). During these observation periods, sea hares were seen grazing on *Ulva*, smaller red and brown algae

on the sides of rock ledges, and drifting pieces of *Macrocystis* and *Egregia* trapped in deep tidal pools.

DISCUSSION

Most sea hares are thought to have maximum life cycles of 1 year (Miller, 1960; Carefoot, 1967; Audesirk, 1979; Carefoot, 1987; Strenth & Blankenship, 1991). While we were unable to follow tagged individuals for their full lifetime, the temporally changing weight distribution for the population does not contradict the possibility of a year-long life cycle for *A. vaccaria*. If we assume that the mean weight of the population was increasing at the same rate before this study as during the increasing portion of this study, the estimated recruitment time of this population would have been June–July, 1995. This, in combination with the presence of small individuals in June 1996, indicates a late spring or summer recruitment time for *A. vaccaria*. There is evidence of some overlapping of generations, as small animals were present with the largest individuals in June. The scarcity of small animals and absence of juveniles smaller than 30 g may reflect a low recruitment rate for the year of this study, or may indicate that juveniles recruit to other locations or habitat types. The increase in amount of sand within the study site was not quantified, but may have contributed to the decline of the population. Very few dead animals were found during the last censuses, and these were quickly washed offshore. It is important to note that because this study population was not a closed one, the measured changes in density and mass cannot be entirely attributed to the seasonal patterns of settlement, growth, and death, but could also be caused by migration into and out of the site.

A. vaccaria is described as the largest gastropod in the world with record sizes of 14 kg and 99 cm (Behrens, 1991). To attain such large body sizes in 1 or 2 years would require a rapid growth rate. While both population averages and tagged animals showed rapid growth, individuals in this study did not approach these record sizes. There are several possible explanations for the large difference in body sizes between record animals and those in this study: there may be greater variance in lifespan than what is seen in most sea hares, such that record animals live longer than 1 or 2 years; the study site may be a marginal or lower quality habitat for *A. vaccaria*; while there was sufficient food in the site to attract and support growth for record densities of these animals, it may not have been the amount or quality required for record growth rates in such a dense population. Our observations show that the *A. vaccaria* diet is considerably broader than suggested by Winkler & Dawson (1963).

The data on individual movements support the claim that the activity of intertidal sea hares is often restricted during extremely low tides due to exposure to the air (Kupferman & Carew, 1974; Carefoot, 1987). Our finding

that members of this population are less likely to mate during the lowest low tides may be explained by the fact that many animals were partially exposed. The resulting reduction in movement is likely to reduce encounter rates with potential mates, and dessication may make it physically difficult for sea hares to mate. The significantly higher levels of mating in the morning censuses of April, May, and June might be explained by time of day, season, or both. If *A. vaccaria* are indeed nocturnal (Eales, 1960; Pennings, 1991b), they may initiate mating during the night and then continue on into the morning. It is also possible that they mate more in the spring, allowing for high levels of recruitment in the summer. In any case, it is clear that *A. vaccaria* are not limited to reproducing in February and March (Winkler, 1955), but spawn year-round.

The dispersion data show that, like other sea hares, *A. vaccaria* is characterized by dense aggregations, and that as densities vary seasonally, the number and spacing of clusters is strongly conserved. This could arise because the animals are willing to travel a limited distance to join a cluster, and thus the spacing of clusters depends only on the area of the site and this typical range, or it could arise because there are favored locations in which clusters might form. The consistency in location of clusters supports the latter possibility. Pennings (1991b) noted that aggregations of *A. californica* often appeared in the same locations as previous aggregations, indicating a preference for certain sites, either because those sites are more environmentally suitable or because they were previously occupied, leaving olfactory cues as a basis for subsequent aggregations. Our data indicate that this site-fidelity is also true for *A. vaccaria*.

Microchip tagging of individuals showed that they moved across an average of 6 m of the study site during the 2 weeks between censuses (as indicated by the greatest distances between recapture locations), and some moved completely across or even out of the 15 × 19.85 m study site. The minimum average daily movements of 2 m were themselves as great as the typical distances between clusters (about 1–3 m). Average hourly movements of 0.92 m also allowed for a great deal of movement between clusters, even during low tides. Tagged individuals were found in different clusters in subsequent recaptures, and the sizes of clusters varied above and beyond global density changes. All of these results suggest that the dispersion patterns are not simply the consequence of initially patchy recruitment of larvae, but rather that these very mobile animals are actively aggregating. Given normal movements, each animal thus has a choice of many groups that it could join.

An earlier study (Winkler, 1955) suggested that reproduction in *A. vaccaria* was limited to a few winter months. The fact that the animals aggregate year-round could then have been construed as evidence against clustering as a mating strategy. Our data show clearly that clustering and

breeding are both maintained year-round, normal ranging allows access to multiple clusters, and most clusters contain mating animals. It thus remains possible that clustering in *A. vaccaria* is related to mating strategies as has been suggested for other members of the genus (Audesirk, 1979; Carefoot, 1987; Pennings, 1991b).

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