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Effect of the bat star, *Asterina miniata*, on recruitment of the giant kelp, *Macrocystis pyrifera*

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Leonard, George H., M.S.

San Jose State University, 1993

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EFFECT OF THE BAT STAR, ASTERINA MINIATA, ON RECRUITMENT
OF THE GIANT KELP, MACROCYSTIS PYRIFERA

A Thesis

Presented to

The Faculty of the Department of Biology
San Jose State University

In Partial Fulfillment

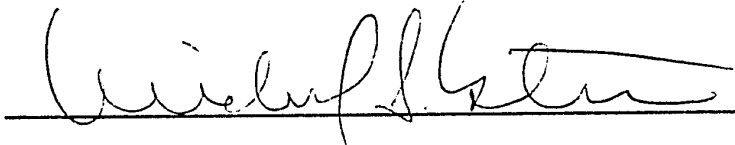
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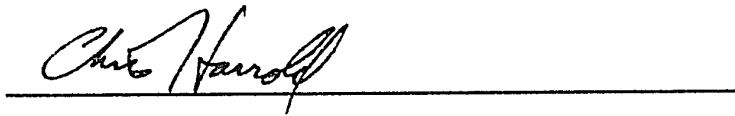
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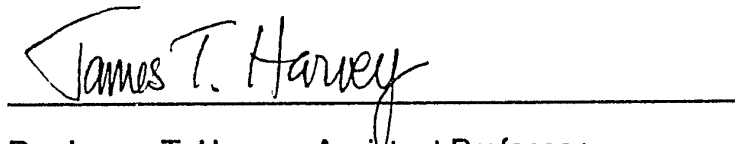
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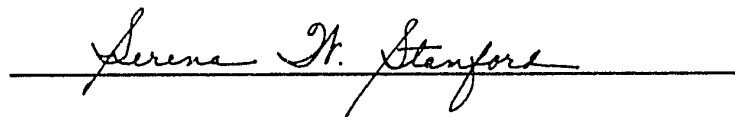


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ABSTRACT

EFFECT OF THE BAT STAR, ASTERINA MINIATA, ON RECRUITMENT OF THE GIANT KELP, MACROCYSTIS PYRIFERA

by George H. Leonard

The common bat star, Asterina miniata, can be abundant in central California kelp forests. Its effect on recruitment of the giant kelp, Macrocystis pyrifera, was addressed through laboratory grazing experiments, a field experiment, and modelling of feeding behavior. In the laboratory, A. miniata significantly decreased the percent cover of sporophytes that developed from one-week-old gametophytes and the percent cover of two-, six-, and seven-week-old sporophytes. All blades remaining at the end of these experiments subsequently died. A large scale bat star removal and addition experiment in the field showed that depth significantly affected kelp recruitment. Although grazing was statistically insignificant, a trend of increasing recruitment with decreasing bat star density was found. Simple modelling suggested that A. miniata (at the high densities maintained during the experiment) could graze nearly 100% of the substratum over the 90-day experiment. However, visible recruitment was seen in less than 30 days and over this time 36% of the substratum was predicted to have remained ungrazed. M. pyrifera of 3 to 5 cm in length may thus obtain a refuge in size from A. miniata grazing through rapid growth. These results indicate this generalist grazer does not have a major impact on giant kelp abundance but may contribute to small scale patterns of dispersion.

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As with most Moss Landing thesis projects, this one involved a good deal of field work. Without the help of innumerable Moss Landing students, I would still be pondering how to get into the field. Specifically, the assistance of Cassandra Roberts, James Downing, Lawrence Honma and Ross Clark was crucial in collecting the data and all provided friendly advice throughout this project. I will fondly remember 'three dive days' and each ritualistic yet dyspeptic 'run-for-the-border'!

Finally, without the encouragement of my wife, Tara, I would never have completed this project, let alone applied to graduate school. I am forever grateful to her for the courage to move across the country with me. If this thesis is at all legible, it is because of her meticulous editing. Thank you, Tara, for all you have taught me over the last ten years.

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Introduction

The factors that control recruitment, growth and survival of Macrocystis pyrifera (henceforth Macrocystis) have long been of interest to ecologists. Kelp forests are one of the most productive marine habitats (Chapman, 1974) and support numerous species of fish, invertebrates and algae. Light (Luning, 1980, 1981; Deysher & Dean, 1984, 1986a, 1986b; Dean & Jacobsen, 1984; Reed & Foster, 1984), temperature (Van den Hoek, 1982), nutrients (North & Zimmerman, 1984; Zimmerman & Kremer, 1984) and water motion (Foster, 1982; Ebeling et al., 1985; Dayton et al., 1992) affect Macrocystis populations over large temporal and spatial scales (Dayton, 1985; Schiel & Foster, 1986). On a local scale, variability in hard substrata (Gerard, 1976; Foster, 1982), sedimentation rates (Devinny & Volse, 1978) and wave exposure (Wheeler, 1980; Ebeling et al., 1985; Foster, 1986; Tegner & Dayton, 1987; Harrold et al., 1988; Seymour et al., 1989; Tegner & Dayton, 1991; Dayton et al., 1992) can affect the distribution of kelp.

Dayton et al. (1984) suggested that unlike most physical factors, biological factors (e. g., interspecific competition, self thinning and grazing) affect small scale variability in kelp distribution and abundance. Except for sea urchins (Leighton, 1971; Harrold & Pearse, 1987), the effect of grazers on kelp distribution has been studied less intensely than physical factors (Hsiao & Druehl, 1973; Schiel & Foster, 1986). Sea urchins, changing from feeding on drift algae to attached plants, can cause massive decreases in kelp abundance (Dean et al., 1984). Decreases in abundance of drift algae, caused by storms, may induce this change in sea urchin behavior and transform areas from kelp dominated regions to 'barren zones' (Harrold & Reed, 1985).

With the exception of sea urchins, only a few other subtidal kelp grazers have been examined. Gastropods (Schiel, 1981; Watanabe, 1983), isopods (North, 1964; Barrales & Lobban, 1975), and mussels (Santelices & Martinez, 1988) have varying effects on kelp abundance. Herbivorous fish greatly affect Macrocystis abundance in southern California (North, 1976; Harris et al., 1984) but are rare in central California kelp forests (Foster & Schiel, 1985).

The common bat star, Asterina miniata (henceforth Asterina), is abundant and patchily distributed in central California kelp forests (Araki, 1964; Gerard, 1976; Foster & Schiel, 1985). As an omnivore, it feeds on carrion and drift algae (Gerard, 1976) by everting its stomach over food. Digestion occurs externally. Bat stars often evert their stomachs on bare rock or encrusting coralline algae where no visible food is present. Araki (1964) hypothesized that in these cases Asterina may obtain nutrition from bacteria, detritus, algal spores and dissolved organic carbon.

Asterina's digestive enzymes break down cellulose, the main constituent of plant cell walls (Araki, 1964). Feeding bat stars often produce bleached spots on encrusting coralline and drift algae indicating degradation of photosynthetic pigments and damage of cell walls. Several authors have proposed community-wide effects of feeding Asterina (Schiel & Foster, 1986; Harrold & Pearse, 1987). Asterina grazing may cause mortality of gametophytes, young sporophytes, or propagules of benthic invertebrates. Bat stars grazed Macrocystis gametophytes on glass slides outplanted to the Point Loma kelp forest (Dayton et al., 1984) and altered successional patterns on plexiglass plates on Naples Reef (Breitburg, 1985). Foster (1975) postulated that Asterina grazing may limit bryozoan abundance and Day & Osman (1981) found bat star

grazing increased byzoan diversity. Invertebrates may graze on microscopic stages of other algae in both intertidal and subtidal habitats (Jones, 1946; Breen & Mann, 1976; Chapman, 1981, 1984; Bertness et al., 1983) but this idea has rarely been tested. Asterina, because of its high densities and unique feeding behavior, may be a cause of mortality for young giant kelp. Bat stars probably do not affect adult sporophytes and rarely feed on small sporophytes in the field. Any grazing effect would occur at the microscopic stage of the plant.

The effects of Asterina on early recruitment success also can be placed in the theoretical framework of plant-animal interactions. Lubchenco and Gaines (1981) argued that the expected damage by an herbivore on a plant is a function of the probability an herbivore will encounter a plant, the conditional probability of eating at least part of the plant once encountered and the change in fitness of the plant if eaten. Generalist herbivores usually have less impact on their prey species than specialists because one alga has a refuge from grazing by the presence of other algae in the diet. That is, the probability of encounter decreases as number of prey in the herbivore's diet increases. This can be offset because the probability of encounter increases with an increase in density of the herbivore. Specialists usually have major impacts because they target one or few specific prey (have high rates of encounter). Gaines and Lubchenco (1982) noted that in many subtidal habitats grazers and algae coexist. They postulated that coexistence was a function of the three variables discussed above and the alga's recruitment and growth rates. Edible species therefore can persist (with high individual turnover rates) at densities similar to those of inedible species if their recruitment and growth rates are sufficiently high. As a generalist, Asterina provides a test of Lubchenco and Gaines' (1982)

hypothesis: can a generalist herbivore greatly impact a prey species through incidental feeding?

Changes in spatial variability of prey species may be a function of the type of predation (Schneider, 1992). Schneider's hypothesis suggested Asterina is a 'clearer' rather than a 'thinner' because it is a slow-moving invertebrate. 'Clearers' feed at random locations without regard to initial prey densities (thereby increasing variability) whereas 'thinners' only feed in areas where prey density is above the mean (thereby decreasing variability). 'Thinners' usually are highly mobile predators whereas 'clearers' often have limited movements. Presence of the bat star, therefore, should increase spatial variability of Macrocystis recruitment whereas its removal should decrease variability.

The purpose of this study was to determine if Asterina miniata contributes to small scale variability in giant kelp recruitment and whether this effect potentially impacts population dynamics of kelp. Laboratory experiments were used to determine if grazing killed kelp gametophytes and young sporophytes. A large-scale bat star removal and addition study was used to determine whether Asterina grazing affects recruitment success in the field. Modeling movement and feeding behavior were used to calculate the potential impact of Asterina grazing on Macrocystis populations and compare this potential with actual results from field studies. Finally, results from this study were used to test several theoretical issues of plant-animal interactions.

Methods and Materials

Laboratory Grazing Experiments

Grazing experiments were done at the Monterey Bay Aquarium from July 1991 through January 1992. Macrocystis spores were settled onto glass microscope slides or roughened plastic plates using the techniques of Reed et al. (1991). To encourage spore release, sporophylls were subjected to a 30 second salinity shock in distilled water followed by two hours in the dark at 5° C. This treatment had no effect on the viability of spores. The resultant spore solution of 1 to 6 x 10⁶ cells ml⁻¹ was diluted to 5 x 10³ cells ml⁻¹ with 0.45 µm sterile filtered seawater. Substrata were covered to a depth of approximately 2 cm with this solution and spores were settled in the dark at 15° C for 24 hours. This resulted in approximately 40 to 50 spores mm⁻². After 24 hours, cultures were transferred to sterile seawater enriched with PES growth medium (Provosoli, 1968) and were grown in the incubator at 15° C under 20 to 25 µE m⁻² s⁻¹ light on a cycle of 12hr light and 12hr dark. Aeration from a small aquarium pump provided water circulation. Growth media were changed biweekly. Germanium dioxide, to retard diatom growth (2ml l⁻¹ media of 250 mg l⁻¹ stock), and antibiotics, to retard bacterial growth (1ml l⁻¹ media of 100 g l⁻¹ penicillin and 50 g l⁻¹ streptomycin stock), were used sparingly and only as necessary.

Four experiments were done to test the susceptibility of gametophytes and sporophytes to Asterina grazing. Gametophytes were subjected to grazing after one week of growth and sporophytes after two, six and seven weeks of growth. One-week-old gametophytes and two-week-old sporophytes were

grown on slides whereas six- and seven-week-old sporophytes were grown on roughened plastic plates.

Two experimental tanks (+ bat stars) and two control tanks (- bat stars) were used. They measured 55 cm x 85 cm and were filled to a depth of 15 cm. This shallow depth minimized the bat stars' tendency to climb up the tank walls. Tanks were lit from above with 'cool white' fluorescent fixtures on a cycle of 12hr light and 12hr dark. Light levels averaged $25 \mu\text{E m}^{-2} \text{s}^{-1}$. This supported the growth of Macrocystis but retarded growth of benthic diatoms. Sand-filtered seawater entered tanks at approximately $4 \text{ litres min}^{-1}$, resulting in a theoretical residence time of less than 20 minutes. Twenty Asterina were starved for one week and then ten were added to the experimental tanks. An average of four to five bat stars remained on the bottom of a tank while five to six remained on the walls. These densities approximated those found in the field. Experimental substrata were added to the tanks approximately two hours later.

Four slides were placed in each tank for experiments on one-week-old gametophytes and two-week-old sporophytes, whereas three plates were placed in each tank for experiments on six- and seven-week-old sporophytes. Allocation of treatments, replicates and slides was random in all four experiments. This resulted in a fully nested design with two levels of a single factor (+/- grazing), two replicates of each treatment and three or four replicate substrata nested within each tank.

Grazing experiments were run for one week. Because Asterina often ignored the slides under these laboratory conditions, this amount of time ensured they grazed the substrata. After one week, the density of sporophytes that developed from the one-week-old gametophytes was determined under

200x magnification with a compound microscope. For the two-week-old sporophytes, the density of blades was determined under 100x magnification. Percent cover on the six- and seven-week-old sporophyte plates was measured using a 100 point grid under 120x magnification because blade density was too high to count. Nested analysis of variance was used to examine treatment effects after the assumption of homogeneity of variances was tested. Data usually had to be transformed using Taylor's power law (Elliot, 1971) to meet this assumption.

After preliminary counts, experimental substrata were returned to the incubator for growth under ideal light and nutrient conditions. This allowed estimation of plant recovery and survival after Asterina grazing. After one additional week, random slides or plates were examined under a microscope for signs of healthy sporophytes. Percent survival was estimated visually.

Observations suggested that bat star exudate might contribute to Macrocystis mortality even without direct grazing. This was tested in a single experiment on two-week-old sporophytes. Four tanks were divided with plastic egg crate, allowing free exchange of seawater but denying bat stars access to half of the tank. Presence of Asterina alone did not visually impact kelp survival. In fact, grazing had a very localized effect (see Results). Therefore, this split design was not used in subsequent experiments.

Field Experiment

The field study was done from March 12 to June 12, 1992 in Stillwater Cove, Carmel Bay, California [35° 34' N, 121° 56' W; see Reed & Foster (1984) for site description]. Three reefs, between 10 and 17 m depth, that

supported growth of Macrocystis and Pterygophora californica were cleared of these algae to encourage kelp recruitment. Macrocystis also was cleared along a 4 m band outside the reefs to prevent shading by plants at the edges. A healthy population of Macrocystis surrounded all three reefs throughout the experiment. One replicate of each of three treatments (control, bat star removal, bat star addition) was established on each of the three reefs. The order of treatments along each reef was intentionally different to reduce any potential influence of one treatment on another. Size of experimental plots was 45 to 104 m² (mean = 71 ± 6 (SE) m², n=9).

Asterina were removed from three plots and added to three plots biweekly. The number of bat stars that reentered removal plots was recorded. Several hundred bat stars were added to addition sites such that densities were increased from 1-3 individuals m⁻². Bat stars were evenly spread to minimize agonism (Wobber, 1975) due to crowding.

After 90 days, the number of small brown blades (excluding identifiable juvenile Pterygophora californica) and Asterina were counted in each plot using 19 to 21, 1-m² quadrats. Depth was recorded for each quadrat. The number of quadrats sampled was the maximum that could be sampled in two dives. An average 30% of a plot was sampled with 19 to 21 quadrats. Quadrats were located using random compass bearings and distances, avoiding edges of the plots. The location of each quadrat was marked to prevent resampling.

Data were analyzed using a single factor analysis of covariance with depth as the covariate. The assumption of homogeneity of slopes was tested by examining the treatment x depth interaction term. The assumption of homogeneity of variances for recruitment and depth data was tested using a

Cochran's test (Winer, 1971) and data were retested after transformations were performed. Quadrats nested within each plot were averaged before analysis. Power analysis was used to determine the likelihood of correctly rejecting a false null hypothesis when the analysis of covariance was non-significant (Cohen, 1988). The detectable effect size and needed sample size for 80% power were also calculated.

Movement and Feeding Behavior

Movement and feeding behavior of Asterina were examined to determine whether enhancing bat star abundance during the field experiment had altered their behavior. At the end of the field experiment, all macroalgae were cleared from an addition and control plot. Bat star densities were again manipulated biweekly. These conditions assumably simulated those that existed during the first month of the experiment.

Asterina behavior was monitored on three days and two nights from July 30 to September 13, 1992. Seven bat stars in each plot were gently labelled with a grease pencil and their locations (to the nearest cm) were determined using an x,y coordinate system. Sea star positions were determined every two hours from 0800 to 1800 (daylight hours) and from 1800 to 0600 (evening hours). The period from 0600 to 0800 was never sampled. No attempt was made to compensate for this lack of data.

Feeding status was determined at each observation by gently tugging on each bat star. Asterina feeds by everting its stomach and sucking to the bottom and this can be easily sensed. It was unlikely that the marking technique or method of determining feeding status greatly altered behavior of the bat stars. If

it did, distance moved would decrease or increase throughout the day and night sampling periods. However, this only occurred during the day.

The ability of the technique to correctly determine feeding status was independently tested by turning over a group of randomly chosen animals (n=175). Tugging was 91.4% accurate at detecting the feeding status of a population of which 70.3% were feeding.

The percentage of individuals that moved and distance travelled during the two-hour time periods were determined using data from the control and addition plots. Distance was calculated, assuming travel in a straight line, by using the equation $D = (\Delta x^2 + \Delta y^2)^{1/2}$ where $\Delta x = x_t - x_{t-1}$ and $\Delta y = y_t - y_{t-1}$. Number of different locations ('feeding spots') at which each bat star was feeding during day and night at both the control and addition plots was also determined. No inferential statistics were applied to these data because of a lack of independence across time periods and unequal replication during day and night monitoring.

Grazing Probability Model

The probability that a given area could escape grazing was computed using the data of bat star movement and feeding behavior and this was used to interpret results of the field experiment. A simple, theoretical model was developed to calculate the proportion of the bottom that would not be grazed during a given time period. This also represents the proportion of the entire kelp population that should escape grazing. This was done by calculating the probability that a given area would not be grazed in one day and using the geometric probability distribution to determine the probability of that area

remaining ungrazed for an additional number of days. This model assumes that movement and feeding behavior occur randomly and it permits bat stars to return to a previously grazed spot simply through random movement. The equation used was:

$$\text{Probability} = [1 - (\rho \cdot \# \text{ spots}/\text{total spots})]^t$$

where

ρ = the density of bat stars (# m⁻²)

spots = the number of different locations on which a bat star feeds during a 24 hour period

total spots = the number of these spots that are in a 1 m² quadrat

t = time (in days)

The density of bat stars used in this model was that maintained during the field experiment as well as two greater, hypothetical densities. The number of feeding spots in a day was determined by summing the number found during day and night hours. Because there was no difference in number of spots used by bat stars at the control and addition plots, these data were combined. Total number of spots was a function of the size of these spots. This size was calculated from the area of the everted stomach assuming this area was a circle (πr^2), with 'r' the radius of the everted stomach. Size of the everted stomach was measured on all feeding bat stars in 27 6-m² quadrats, located at three haphazardly chosen sites in Stillwater Cove.

Results

Laboratory Grazing Experiments

The density and percent cover of Macrocystis gametophytes and sporophytes decreased significantly when subjected to Asterina grazing in the laboratory (Fig. 1). Bat star grazing significantly decreased the number of sporophytes that developed from one-week-old gametophytes ($F=58.679$, $p=0.017$). Gametophytes were still present at the end of the experiment, however, Asterina grazing inhibited fertilization or development of the female gametophytes. Grazing also significantly decreased the density of two-week-old sporophytes ($F = 61.41$, $p=0.016$) mainly by removal of plants during feeding. Similarly, percent cover of six- and seven-week-old sporophytes was also significantly decreased by grazing ($F_{6 \text{ week}} = 18.719$, $p=0.049$, $F_{7 \text{ week}} = 84.114$, $p=0.012$). Decreases in percent cover of these older sporophytes, although significant, were not large. Percent cover was 94.2 to 95.4% on control plates and 78.8 to 82.7% on grazed plates.

Sporophytes had visible signs of bat star grazing. Two-, six- and seven-week-old sporophytes were highly bleached (yellowish-green) and had lost much of the characteristic light brown of laboratory grown laminarian sporophytes. Cytoplasm had coalesced as dark clumps in the center of the cells. These grazing effects, however, were localized. In a rare instance when only part of a slide was grazed, blades at the grazed border were only partially bleached (Fig. 2).

There was no post-grazing recovery of any Macrocystis blades. In all cases, percent mortality on control slides or plates was near 0%, whereas on

grazed slides or plates it was approximately 100%. Although algal tissue was still present, it was clearly dead.

Field Experiment

Removal or addition of Asterina in the field did not have a statistically significant effect on kelp recruitment (Table 1a). However, depth of the plot, analyzed as a covariate, did explain a significant proportion of the recruitment variability (Table 1a and Fig. 3). As depth of the plot increased, density of recruits decreased. There was no significant difference in overall depth of the three treatments (Table 1b). Depths at the nine plots ranged from 11.2 to 15.4 m but because treatments were blocked by reef there was no overall difference in depth of the three treatments. Although not statistically significant, increased recruitment occurred with removal of Asterina, whereas decreased recruitment occurred when Asterina was added (Table 1a). High variability, particularly in removal plots, prevented the ANCOVA from statistically detecting this trend.

Densities of bat stars during the field experiment were significantly less than controls in the removal plots but were not significantly greater than controls in the addition plots (Table 1c). After 90 days, there was a statistically significant difference in Asterina density between removal and control plots and removal and addition plots. Although not significant, there were greater densities of bat stars in addition versus control plots. Bat stars likely fled from addition plots due to increased agonism from increased densities and because of disturbance of moving the animals.

The power of these statistical tests to detect differences in recruitment was 37%. To increase power to 80%, with the same effect size, would require

doubling replication from n=3 (9 plots total) to n=6 (18 plots total). A recruitment density ratio of 2.90:1 between treatments would have to exist to be detected statistically at $\alpha = 0.05$ with only 3 replicates. The maximum ratio between removal and addition treatments in this field experiment was 2.22:1.

Movement and Feeding Behavior

There was great variability in feeding and movement patterns of Asterina. During the day the average percentage of bat stars that moved at the addition and control plots was similar (Fig. 4a,b). From 47 to 75% of the bat stars moved, with no trend throughout the day. This indicated marking and handling did not alter the behavior of bat stars. Variability in average percentage of bat stars that moved was greater during the evening than the day (7%-71%), but there was no clear trend between addition and control plots. In general, it appeared that the percentage that moved was less during the evening than the day and that the percentage decreased throughout the night until the early morning hours (Fig. 4b).

Asterina moved an average 9 to 67 cm 2 hr^{-1} (Fig. 4c,d). In general, this distance was less at night. Distance moved was usually (9 of 11 periods) less in the control vs. addition plots. Distance moved during the evening remained low and relatively constant throughout.

There was little variability in average number of feeding spots during the day and night for bat stars in control and addition plots (mean \pm 1 SE: Day: Addition = 2.33 ± 0.15 , Control = 2.20 ± 0.23 ; Night: Addition = 2.30 ± 0.10 , Control = 2.60 ± 0.5). Bat stars were found on an average 2.3 spots during the day and 2.5 spots during the night (Table 2). The overall average was 4.73

spots day⁻¹ (Table 2).

In general, there were few differences in the behavior of control and manipulated bat stars. For logistical reasons, these studies were not conducted immediately after densities were manipulated, but usually 1 to 2 days later. Asterina must have fled the plots, because over the course of the experiment a total of 35 bat stars m⁻² were added but densities sampled at the end of the experiment averaged only 5.7 m⁻². These numbers suggest increased movement rates and decreased feeding rates probably occurred but were likely ephemeral. Observations suggested normal behavior was probably attained within 1 day.

Grazing Probability Model

Estimates made using density of bat stars, number of feeding spots per day and size of the everted stomach (Table 2) indicated the proportion of Macrocystis gametophytes and sporophytes that should escape grazing in one day was 99.8 to 99.5% for bat star densities of 0.3 to 18.0 individuals m⁻² (Fig. 5). This value decreased exponentially with time, most rapidly during the first 30 days. The model predicted that during the 90-day experiment, 85.4%, 14.8% and 4.7% of the population would escape grazing in the removal, control and addition plots, respectively. Signs of Macrocystis recruitment, however, were visible within the first 30 days of the experiment at all plots. The model predicted that during the first 30 days, 36.2% of the population should remain ungrazed in addition plots whereas 52.8% should remain ungrazed in control plots. Hypothetical bat star densities of 9.0 individuals m⁻² would leave only 0.8% and 18 individuals m⁻² would leave 0.0% of the population ungrazed during the 90

days. For the first 30 days, as much as 19.8% (at 9.0 bat stars m^{-2}) and 3.6% (at 18.0 bat stars m^{-2}) of the population would survive.

Discussion

Laboratory Grazing Experiments

Laboratory experiments indicated that Asterina grazing kills microscopic gametophytes and young sporophytes of Macrocystis. This appears to result from inhibition of development of gametophytes and degradation of photosynthetic pigments of juvenile sporophytes. However, this effect was localized and only occurred directly under a feeding bat star. Digestion enzymes may not travel far from a bat star's stomach or may be rapidly diluted in the surrounding seawater (Araki, 1964).

Observations in the laboratory indicated once a bat star's stomach was everted, the grazing effect occurred in a matter of hours. These observations agree with an average 4.08 hours spent on a feeding spot in the field. Observations also indicated that movement of bat stars over slides without feeding on them had no effect on gametophyte or sporophyte survival.

No alternate prey were provided in the laboratory experiments. In the field, Asterina feed on drift algae and carrion if present. If these food items were present in the tanks, bat stars likely would not have grazed the slides. In Stillwater Cove, however, drift algae are rare and greater than 70% (mean \pm 1 SE = $72.4 \pm 3.9\%$; n=27) of bat stars have their stomachs everted on bare rock or encrusting and articulated coralline algae. Laboratory conditions, therefore, simulated field conditions where most bat stars fed on substrata that would be exposed to Macrocystis propagules.

Field Experiment

Algal recruitment was significantly affected by depth but not Asterina grazing in the field experiment. Depth affects recruitment of many algae, including Macrocystis (Foster & Schiel, 1985). It may decrease light levels below that necessary for development of gametophytes or growth of young sporophytes (Dean & Jacobsen, 1984; Dayton, 1985; Schiel & Foster, 1986; Santelices, 1990). The lower limit of Macrocystis kelp forests in central California is from several meters to over 30 m depth at which there is generally 1% of surface irradiance (Luning, 1981). It was remarkable that the effect of depth on kelp recruitment in this experiment was observed in the narrow range of 10 to 17 meters depth. Although kelp grows to at least 25 m depth in Stillwater Cove (G. Leonard, personal observation), 10 to 17 m may represent the depths where there is a rapid decrease in recruitment, at least during the time of this study. Reefs were chosen to have similar depths, but even slight differences resulted in statistically significant differences in kelp recruitment. Dayton et al. (1992) found similar effects of depth on recruitment in the Point Loma kelp forest in southern California.

Although the effect of grazing was not statistically significant, a trend was evident. When bat stars were completely removed, mean recruitment was 19.1 recruits m⁻² compared to 10.9 recruits m⁻² in control plots. When bat star densities were artificially increased, recruitment was 8.6 recruits m⁻². This trend strongly indicated Asterina grazing caused small scale variability in kelp recruitment but other factors, including depth and its effect on light, were more important. The lack of statistical significance in this relationship was likely due to low power (37%) of the analysis of covariance and the high variability inherent

in this system. To increase power to 80% would require doubling the number of replicates from 3 to 6 (18 plots total). The confines of Stillwater Cove and logistical difficulties prevented such an expansive field experiment.

Lack of significance can also be partially attributed to Reef 3. The removal and addition plots on this reef were at the greatest depths of the nine plots, whereas the control plot was of intermediate depth. The removal and addition plots on Reef 3 also had the lowest initial density of Asterina. Bat stars added to the addition plot rapidly fled. There was a linear relationship between the number added to the addition plot and the number found entering the adjacent removal plot at the time of the next manipulation ($r^2=0.499$, $p=0.001$; $n=19$). No such relationship occurred for the other two reefs. Consequently, the number of recruits at the removal plot and density of bat stars at the addition plot were low on Reef 3. These plots contributed to an insignificant grazing effect and an insignificant overall difference between Asterina density at addition and control plots.

The considerable recruitment that occurred even under enhanced Asterina densities suggested long-term effects of bat star grazing on kelp recruitment are probably minimal even if short-term effects were statistically significant. Recruitment densities of approximately 10 individuals m^{-2} found in this experiment commonly decrease to adult densities of only 0.1 to 0.3 individuals m^{-2} (Dayton et al., 1992). This self-thinning is partly due to intra-specific competition for light (Dean et al., 1989; Reed, 1990) and wave and storm induced mortality (Tegner & Dayton, 1987, 1991; Dayton et al., 1992). Dean et al. (1989) calculated that a ten-fold increase in number of juvenile kelp plants would result in only a two-fold increase in number of adults. In this study,

removal of bat stars resulted in more than twice the number of recruits but this likely would not impact the adult population because of the strong density-dependent mortality of Macrocystis. Even under high bat star predation enough kelp plants probably survive to contribute to the adult population.

Asterina may only have major impacts when recruitment conditions are poor (e.g., low light or low nutrients). During this field experiment, however, recruitment conditions were excellent. Clearing the canopy resulted in high light levels and nutrient concentrations were non-limiting. Bat star grazing may be strong enough to prevent recruitment under poor conditions when number of potential recruits is small and their growth rate is slow due to physiological constraints. This would increase the time recruits were susceptible to grazing.

Grazing Probability Model

Gaines and Lubchenco (1982) stated that the effect of a grazer on its algal prey is a function of density and grazing rate of the herbivore and recruitment and growth rate of the alga. Results of the grazing probability model indicated Asterina's grazing rate is low relative to the recruitment and growth rate of giant kelp. The density of Asterina maintained in addition plots (5.7 individuals m⁻²) could graze an estimated 95% of the bottom during the 90 day experiment. Visible recruitment, however, occurred within 30 days after the experiment began and by 90 days many of these plants were several meters in height. The estimated proportion of the population that should have remained ungrazed through 30 days was 36.2% at addition plots and more than 50% at control plots (Fig. 5). Although Asterina densities were relatively high during this experiment, bat stars did not graze enough spots in one day to have a major

impact over the first month of the experiment.

The probability model predicts that for bat stars to have a larger impact on Macrocystis they would have to occur at higher densities than maintained during the field experiment. The probability that Macrocystis will escape grazing is a function of bat star density, time and the size at which giant kelp is no longer susceptible to bat stars. An increase in density should decrease the probability that a given plant will survive. The probability model indicated that as bat star densities increased, the proportion of a population that remained ungrazed decreased most rapidly during the first 30 days (Fig. 5). From 35 to 50% of a population should remain ungrazed over 30 days at bat star densities from 3.6 to 5.7 individuals m^{-2} . Even at bat star densities of 9.0 individuals m^{-2} , a large percentage of the population (19.8%) should escape grazing over this time. These latter densities have been seen in other areas of Stillwater Cove and other local kelp forests (G. Leonard, personal observation; Gerard, 1976) but were not maintained during the field experiment. Bat stars probably would not greatly affect kelp populations even at these higher densities because at least 20% of the plants should survive. Increased abundances of other food sources, such as drift algae, also may decrease the grazing effect as number of bat stars grazing on rock and encrusting coralline algae decrease. Densities of 18.0 individuals m^{-2} would permit only 3.6% of the population to survive over 30 days but these densities are highly unlikely in nature.

This model appeared robust. The number of recruits when bat stars were absent was back-calculated using the percent of the bottom theoretically ungrazed over 30 days at the three Asterina densities and actual number of recruits measured at those densities in the field experiment. These three

separate calculations estimated recruit densities of 20.1 to 23.8 individuals m^{-2} with no bat star grazing. This density of recruits was well within the range normally seen in the field (Reed & Foster, 1984). The ability of these three independent calculations to yield the same value suggested the model was robust.

Robustness was also suggested because the model's conclusions did not rely heavily on the accuracy of the number of different feeding spots. Allowing number of feeding spots to vary within 2 standard errors of the mean yielded an estimated percent survival of 31.5 to 41.6% (versus 36.2% at the mean number of feeding spots) at bat star densities of 5.7 individuals m^{-2} . At bat star densities of 3.6 individuals m^{-2} , this yielded values of 48.4 to 57.7% survival (versus 52.8% at the mean number of feeding spots). Conclusions of the model did not change appreciably even though percent survival varied slightly.

Bat stars were observed only twice actively grazing on juvenile sporophytes in the field. These plants were 5 to 10 cm in length. Under laboratory conditions, however, Asterina actively grazed reared sporophytes from 3 to 28 cm and rapidly killed them. These sporophytes had abnormal morphologies due to limited water motion in the growing chambers and were contaminated by benthic diatoms due to growth under high light conditions. A combination of altered morphology and diatom contamination may produce extensive grazing in the laboratory that does not occur naturally in the field. Similar problems were found by Stevenson (1992) for Patiriella calcar, a close relative of Asterina. This intertidal sea star frequently ate Patiriella exigua in the laboratory but rarely in the field.

These results indicated that rapid growth provided Macrocystis a size

refuge from Asterina grazing. Rapid plant growth minimizes mortality from grazers in both terrestrial and marine communities (e.g., Harper, 1977; Montgomery, 1980; Sousa et al., 1981; Underwood & Jernakoff, 1981; Lubchenco, 1980, 1983). Adult giant kelp are not impacted by bat stars because of the large size of this life history stage. Plants from 2 to 5 cm, however, also appear immune to Asterina grazing in the field. Although the size of this refuge is important, it is the rate at which this size is reached that appears crucial. Thus, the limited impact of Asterina on Macrocystis populations is likely because kelp gametophytes and young sporophytes are only vulnerable when they are microscopic and rapidly reach a size Asterina can not graze. Similar conclusions were reached by Menge (1975) and Lubchenco (1980) for Littorina and Fucus in rocky intertidal zones of New England.

It is unlikely that Macrocystis had a temporal or spatial refuge from Asterina grazing but these were not directly tested. Asterina abundances in Stillwater Cove did not change seasonally and feeding patterns were not markedly different throughout the year (G. Leonard, personal observation). This makes it unlikely that Macrocystis would have a temporal refuge due to seasonal inactivity of bat stars. Asterina is a generalist feeder (Gerard, 1976; Harrold & Pearse, 1987) and in Stillwater Cove, bat stars fed on nearly all surfaces, including bare rock, encrusting coralline algae, articulated coralline algae, sessile invertebrates, drift algae and carrion. Any surface suitable for spore settlement and development was likely grazed by bat stars. Spores that settled within micro-topographic features of rock surfaces, however, may have survived grazing because they were physically sheltered from bat star digestive enzymes. Unlike rock surfaces in the field, laboratory substrata were smooth

glass slides and all spores and gametophytes were susceptible to the digestive enzymes. Conversely, a refuge provided by structural features in the field may be offset by increased mortality due to decreased light levels or increased sedimentation rates (Devinny & Vorse, 1978; Deysher & Dean, 1986a).

Agonism in bat stars (Wobber, 1975), particularly at high densities, may have resulted in changes in either number of feeding spots or time spent on each spot but I assumed they remained unchanged. If time of each feeding bout decreased as densities increased, there would be a density at which the duration of feeding would not cause algal mortality. Alternatively, as density of Asterina increased, the time each bat star remained on one spot might increase. This might provide a spatial refuge from bat star grazing even with higher densities. Other conditions that cause a bat star to spend more time on the same spot (such as increased water motion) may similarly result in a spatial refuge from grazing.

I assumed that every time a bat star fed on a spot in the field, 100% of the young kelp recruits died. This may be a function, however, of feeding intensity and time. Under laboratory conditions, young Macrocystis were bleached by grazing and did not survive. In the field, some feeding bouts produced bleaching whereas others did not. This may be a function of amount of digestive enzyme extruded and duration of the feeding bout.

These modelling results suggest giant kelp acts as a weed (sensu Foster, 1992). Its high reproductive rate and rapid growth allow Macrocystis to escape grazers that feed directly on the substrate. Sea urchins are one of the most important grazers of Macrocystis because even large adult kelp plants can be eaten. Sea urchins kill adults of all sizes by grazing through

the haptera and primary dichotomy (Leighton, 1971; Harrold & Pearse, 1987) resulting in removal of whole, intact plants from the population. Grazing by Tegula spp. (Foster & Schiel, 1985) and Norrisia norrisi (Leighton, 1971) may also impact plants of all sizes by facilitating stipe breakage during storms. Certain herbivorous fishes may cause intermediate effects because Macrocystis is not eaten when larger than 10 cm (Harris et al., 1984). Alternatively, plants of all sizes may be susceptible to fish grazing when kelp plants are in low densities or isolated stands (Grant et al., 1982). Excessive fish grazing may have thwarted attempts to populate artificial reefs with kelp in southern California (North, 1968; Grant et al., 1982). Kelp plants are susceptible throughout their lives to some types of grazers but seem vulnerable to Asterina only for the first few weeks to one month after settlement.

Theoretical Considerations

These results support Gaines and Lubchenco's (1982) theory that generalist grazers usually do not greatly impact algal populations. For Asterina, this is probably because it does not specifically eat Macrocystis. Although the probability of grazing a plant (at the microscopic stage) once encountered is nearly 100% and the decrease in fitness if eaten is absolute (the plant is killed), the probability of encounter in any given day is low. The overall probability of damage, therefore, is also low. A similar argument was used by Prince and LeBlanc (1992) to explain how Codium fragile escaped Strongylocentrotus droebachiensis grazing in laboratory experiments. If Asterina were selectively feeding on gametophytes and small sporophytes of giant kelp, few plants could survive to adulthood even at moderate bat star densities. My results support

Paine's (1992) hypothesis that most links in food webs are weak. Foster (1992) has also questioned the importance of grazing on the structure of algal assemblages in intertidal and subtidal habitats of the north-east Pacific. Of seven species Paine (1992) studied, only two had strong, negative impacts on their algal prey. He postulated that the 'interaction strength' of most predators and prey is weak and that even with high grazing rates enough plants survive to produce viable adult populations. Asterina appears to be an example of a grazer with weak 'interaction strength'.

One striking result from the field experiment was the high variability in recruitment at small spatial scales, especially in plots with enhanced bat star densities. Schneider (1992) has argued that slow moving predators, such as bat stars, are 'clearers'. This hypothesis predicts that by feeding at random locations without reference to initial prey densities, 'clearers' often increase the spatial variability of their prey species. Highly mobile predators, such as birds, that feed only in areas of high prey abundance and stop feeding when local densities reach average densities, are 'thinners'. Their presence should decrease spatial variability in prey populations. Thus, one would predict that areas of high bat star density should have highly variable Macrocystis densities (measured as the coefficient of variation) whereas areas with few Asterina should exhibit low variability in dispersion. Within plots at Stillwater Cove, variability was greater, but not statistically so, in the addition plots compared to the removal plots (mean CV \pm 1 SE: 0.860 ± 0.095 vs. 0.640 ± 0.104 ; $t = 1.567$, $df = 4$, $p = 0.192$). This trend suggests that at scales of tens to hundreds of meters, Asterina may act as a 'clearer'. If bat stars had been maintained at greater densities during the field experiment, this trend likely would have been

statistically significant.

Conclusions

In summary, depth contributed to different levels of Macrocystis recruitment in Stillwater Cove and grazing by Asterina may have played a secondary role in limiting early stages of kelp recruitment. Bat star grazing caused mortality of gametophytes and juvenile sporophytes in the laboratory. A general trend of increased recruitment with decreased bat star densities was observed in the field. Substantial recruitment, however, occurred in high density plots and a model indicated more than 36% of the bottom would remain ungrazed in these plots during a 30 day period. Macrocystis appears most susceptible to Asterina grazing during this time. These results support the theory that generalist herbivores have a lower impact on plant populations than specialists. Although its effect may be minor, Asterina may be one of a suite of grazers including bacteria, protozoans, meiofauna, filter feeders, and small invertebrates (Osman et al., 1992; Trowbridge, 1992) that affect early succession of algal communities (Dayton, 1985). The effect of these grazers and other factors that contribute to small scale variability in algal recruitment remain to be investigated.

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Table I: Results of three, one way ANOVAs on *Macrocystis* recruitment in field experiment manipulating *Asterina* density. Treatment had three levels of grazing; removal, control and addition of *Asterina*. (A): Recruits, transformed using $\ln(x+1)$, were number of brown blades m^{-2} excluding identifiable *Pterygophora californica*. Depth of each plot was analyzed as a covariate. Treatment x Depth interaction term was non-significant ($F_{2,3}=0.873$, $p=0.502$). Depth was measured in meters at MLW and was transformed using Taylor's power law to meet the assumption of homogeneity. Means ± 1 SE are adjusted least square means from the ANCOVA. (B): Depth of each plot was transformed as in (A). (C): Bat star density was transformed using $\ln(x+1)$. Treatments that were not statistically significant by the Bonferroni a posteriori test are connected by a line. NS = non-significant ($p>0.05$).

(A): Recruits					
Source of Variation	Sum of Squares	Df	Mean Square	F Ratio	P Value
Treatment	0.867	2	0.433	4.124	0.088 NS
Depth	0.920	1	0.920	8.754	0.032
Error	0.525	5	0.105		
	Addition <u>8.60 \pm 2.74</u>	Control <u>10.87 \pm 4.36</u>	Removal <u>19.11 \pm 8.82</u>		
(B): Depth					
Treatment	8.9 x 10 ⁵	2	4.4 x 10 ⁵	0.567	0.595 NS
Error	4.7 x 10 ⁶	6	7.8 x 10 ⁵		
	Addition <u>13.44 \pm 1.22</u>	Control <u>12.29 \pm 0.37</u>	Removal <u>13.33 \pm 1.01</u>		
(C): Bat Star Density					
Treatment	4.219	2	2.110	19.390	0.002
Error	0.653	6	0.109		
	Addition <u>5.70 \pm 1.27</u>	Control <u>3.66 \pm 0.93</u>	Removal <u>0.25 \pm 0.17</u>		

Table II: Measured and calculated parameters used in the grazing probability model. Densities of Asterina were those maintained during the field study and two hypothetical densities. The radius of the everted stomach was measured on all feeding bat stars in 27 quadrats at three haphazardly chosen locations in Stillwater Cove. Effective area was calculated from the stomach radii. Number of feeding spots was obtained from the movement study. Values in the parentheses are sample sizes. Probability of not being grazed is calculated from the geometric probability function.

(A) Density of <u>Asterina</u> (# m ⁻²)		
1) Addition	5.7 ± 1.3	(3)
2) Control	3.7 ± 1.0	(3)
3) Removal	0.3 ± 0.2	(3)
4) Hypothetical 1	9.0	
5) Hypothetical 2	18.0	
(B) Stomach Radius (mm)	18.2 ± 0.9	(27)
(C) Effective Area (mm ²)	1235.5 ± 105.7	(27)
Feeding spots during day (#)	2.28 ± 0.12	(3)
Feeding spots during night (#)	2.45 ± 0.20	(2)
(D) Feeding spots during whole day (#)	4.73 ± 0.32	(2)
(E) Time (days)	Range: 1-90	

Probability of not being grazed: $[1 - \{(D \cdot A) / (1 \times 10^6 / C)\}]^E$

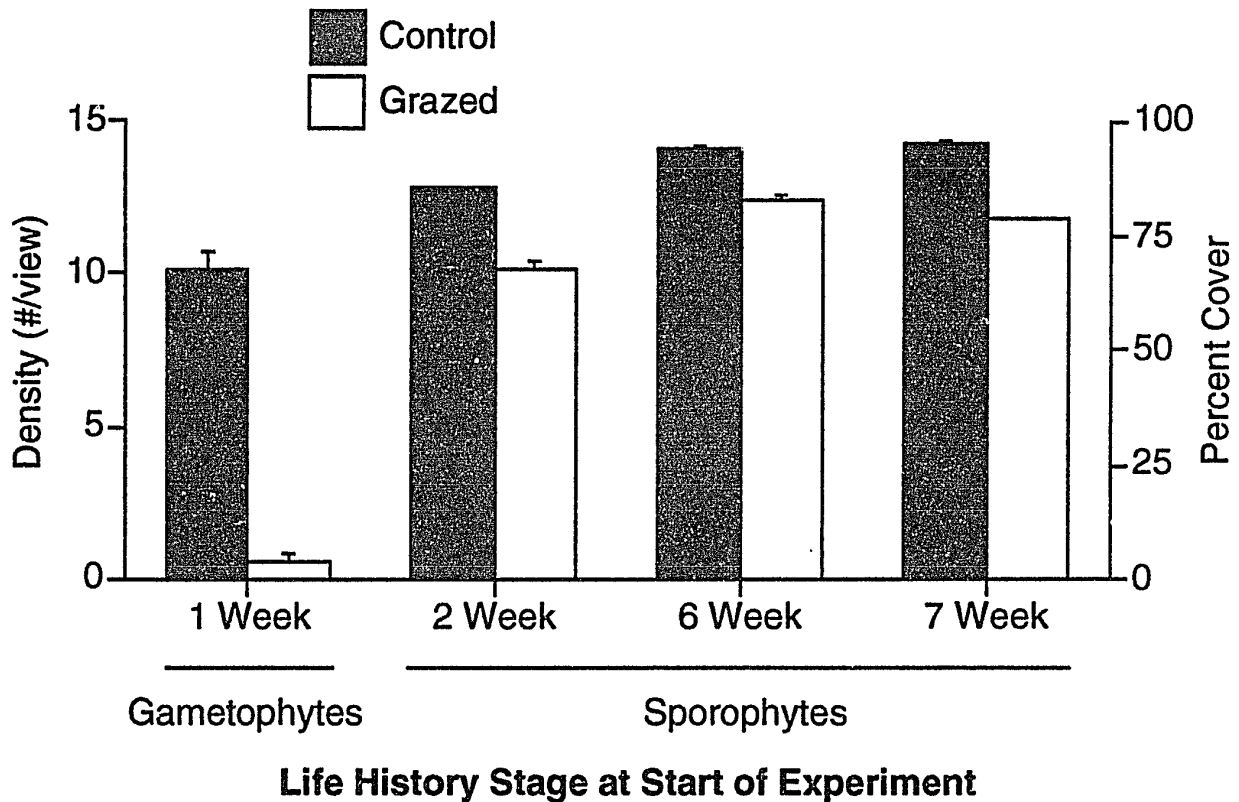


Fig. 1. Effect of *Asterina* grazing on *Macrocyctis* abundance in the laboratory. Measurements of density are for 1-week-old gametophytes (field of view = 0.403 mm²) and 2-week-old sporophytes (field of view = 1.617 mm²). Measurements of percent cover are for 6 and 7-week-old sporophytes. Data are mean \pm 1 s.e. Life history stage is that at the beginning of the 1 week experiment. By the end of the experiment, the 1-week-old gametophytes had become sporophytes.



Fig. 2. Partially grazed, two-week-old sporophyte from the laboratory grazing experiments.

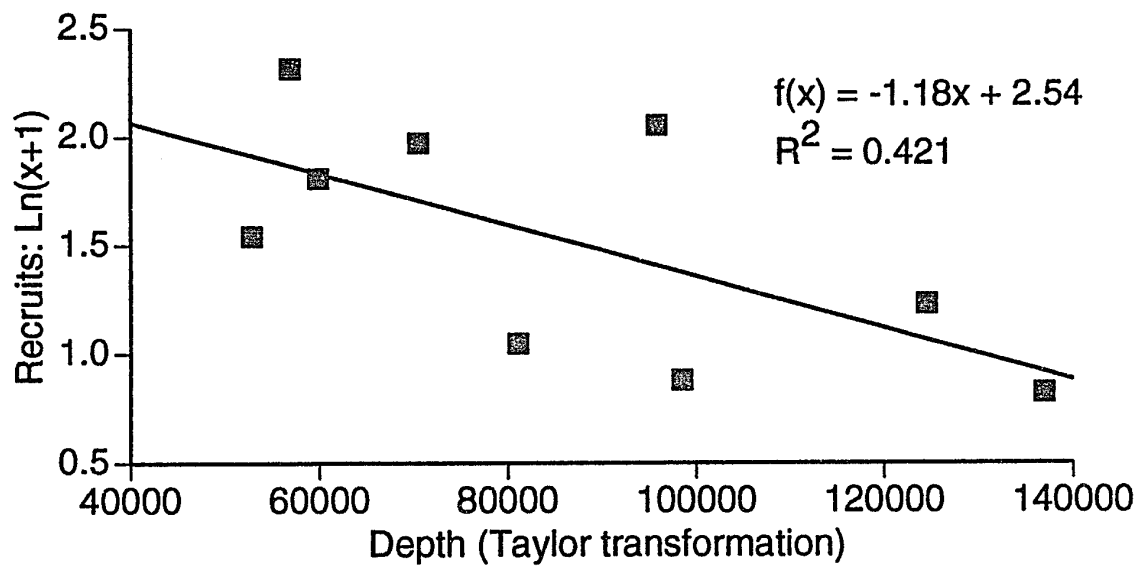


Fig. 3. Relationship between number of recruits and depth of the experimental plots. Recruits (# per square meter) were transformed by $\ln(x+1)$. Depth (m at MLW) was transformed by Taylor's power law. This relationship was significant in the analysis of covariance.

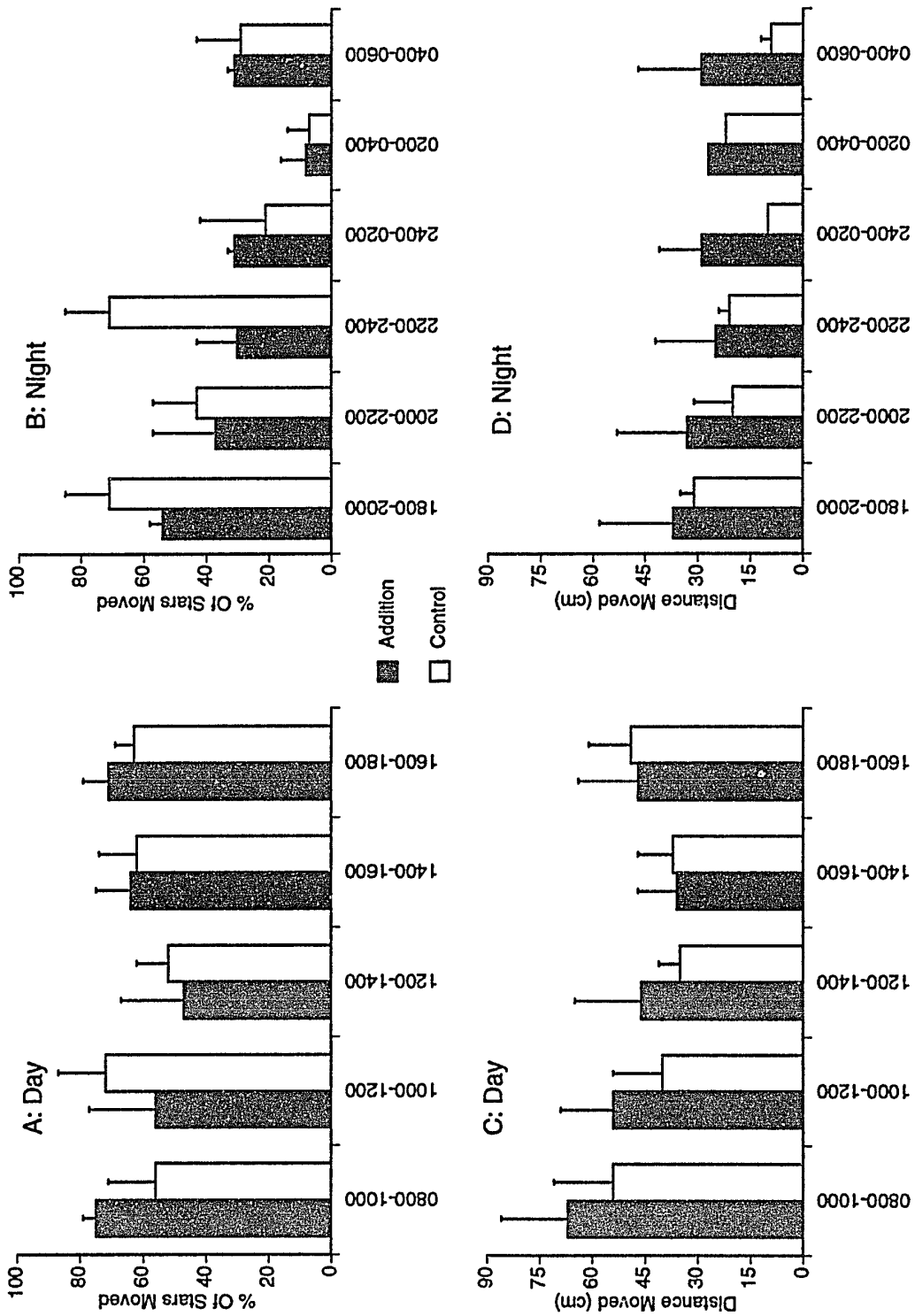


Fig. 4. Percentage of *Asterina* that moved (A,B) and distance moved by those that did (C,D) between sampling periods at addition and control plots during day and night. Data are mean \pm 1 se. Day: n=3, Night: n=2. Seven bat stars were each followed in one control and one addition plot. Distance moved is straight line distance calculated from x,y coordinates. Lack of error bars indicates no bat stars moved between sampling periods during one of the two night replicates.

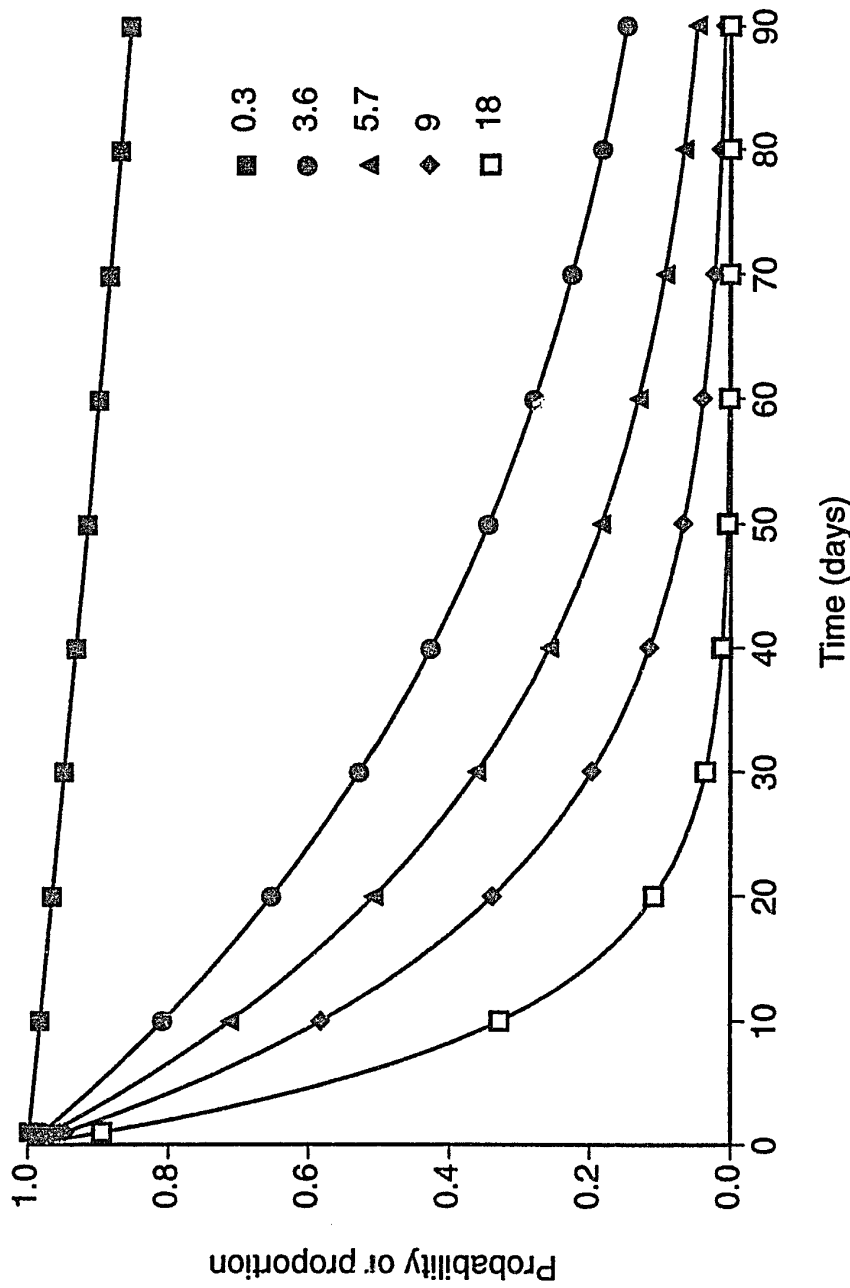


Fig. 5. Probability of not being grazed or proportion of the population not grazed as a function of time using parameters in Table II. Each curve represents a different bat star density from 0.3 to 18.0 per square meter. Thirty days is the time over which visible recruitment was seen during the field experiment. Ninety days was the duration of the experiment.