DIEL VERTICAL MIGRATION OF THE GASTROPOD *NORRISIA NORRISI* ON THE KELP *MACROCYSTIS PYRIFERA*

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ABSTRACT

Norris' top snail, *Norrisia norrisi*, reportedly undergoes a diel vertical migration on *Macrocystis pyrifera* at Santa Catalina Island, climbing up the kelp at dusk and descending at dawn. The influence of irradiance and snail size on the diel behavior and vertical distribution of *Norrisia* on *Macrocystis* has not been studied previously. At Pumpernickel Reef, I made 1,602 observations of snail height and irradiance over a 10 mo period. Mean height above the holdfast was always highest at night for all snail sizes, but snails >17 mm were distributed throughout the kelp during the day. Only snails ≤ 17 mm showed a consistent and significant negative response to irradiance, decreasing their height above the holdfast with increasing irradiance. A 25% increase in the mean number of snails observed at night was due to snails ≤ 17 mm emerging from the holdfast. Diurnal activity was low, with most snails near the holdfast or at the base of blades. At night, snails were more active, moving onto distal portions of the blades and feeding. The diel vertical migration of snails ≤ 17 mm may be an adaptive behavior to avoid diurnal predators and diminishes as snails grow.

Keywords: Diel vertical migration, irradiance, snail size, *Norrisia norrisi*, *Macrocystis pyrifera*.

INTRODUCTION

Studies of diel vertical migrations have focused primarily on marine and freshwater planktonic species (Lampert 1987; Ringelberg 1995), even though diel vertical migrations have been reported in a wide range of taxa (e.g., Thain 1971; Vannini et al. 1995; Takada 1996). Although the proximate and ultimate causes of diel vertical migrations are still under investigation (Ringelberg 1995), such migrations may be either facultative or fixed behaviors that evolved as antipredatory responses by prey to their predators (Sih 1987). Whether the behavior is fixed or not, there are two general sets of cues: exogenous and endogenous. Exogenous cues (e.g., light, gravity, tidal height) typically act as Zeitgebers, setting an endogenous "clock" that drives the behavior (Carthy 1966). Light is generally considered the dominant environmental cue controlling diel vertical migrations (Forward 1976). Recently, researchers have investigated the influence of light in situ on diel vertical migrations (Vannini et al. 1995) and the ontogeny of migratory behavior (Barile et al. 1994; Takada 1996). Despite the evidence that light influences the behavior of vertical migrators and that these behaviors are modified by age and changing selective pressures, the ecological consequences and evolutionary causes of these adaptive behaviors are not well understood.

A common trochid snail in southern California, Norris' top snail (*Norrisia norrisi* Sowerby), has been reported to undertake a diel vertical migration, climbing up *Macrocystis pyrifera* at night, then down the kelp at dawn (Miller 1975), but is rarely found subtidally on the benthic substratum (Ambrose 1984; Schmitt et al. 1983). Miller (1975) suggested that a combination of exogenous (light and gravity) and endogenous (unspecified) stimuli controlled the diel vertical migration of *N. norrisi* on *M. pyrifera*, but Miller did not measure ambient irradiance and could not determine its influence on the behavior of *N. norrisi*.

In a preliminary study, I observed differences in the vertical migratory patterns among *N. norrisi* apparently related to snail size. Since ontogenetic changes in behavior have been reported in veliger larvae (Barile et al. 1994) and post-settlement snails (Takada 1996), I hypothesized that the migratory behavior of *N. norrisi* changed with snail age and size. I made a set of field observations to investigate the relative importance of irradiance and snail size on the vertical migration of *N. norrisi* on *M. pyrifera*, specifically posing the following questions: 1) Do *N. norrisi* have a diel vertical migration on *M. pyrifera*? 2) Do *N. norrisi* of different sizes have different patterns of vertical migration? and 3) Is there a relationship between irradiance, snail size, and vertical migration?

MATERIALS AND METHODS

I observed, measured, and marked *N. norrisi* on tagged *M. pyrifera* plants at various times of the day and night over a 10 mo interval to analyze the vertical distribution and migratory behavior of the snails. By repeatedly observing marked snails of known sizes at different times of the day and night, I reconstructed the diel behavior of snails on kelp without interfering with their behavior.

Study Site

Field observations were made at Pumpernickel Reef (33°26.53´N, 118°28.35´W) on the leeward side of Santa Catalina Island, California, about 1.5 km north of the University of Southern California, Wrigley Institute for Environmental Studies (Figure 1). Pumpernickel Reef extends north from a shallow (1 to 12 m depth) subtidal cove and is partially protected from wave action and strong currents.

Individual, non-canopy forming *M. pyrifera* at Pumpernickel Reef were selected using the following criteria: 1) presence of naturally occurring *N. norrisi* on the kelp; 2) relative thickness, height, and overall health of the kelp (a subjective evaluation); and 3) isolation of the study plants from surrounding kelp to reduce the transfer of *N. norrisi* to and from nearby plants. In August 1992, I selected three *M. pyrifera* and tied surveyor's flagging tape to the holdfasts for easy identification at all times of the day or night. Each holdfast was at a depth of six meters and on the edge of a slightly sloped, cobble-filled clearing. Seasonal changes and warm water temperatures, due to a mild El Niño in 1992, caused loss of *M. pyrifera* plants at Pumpernickel Reef, so additional *M. pyrifera* were tagged as previously marked plants disappeared.

Measuring and Marking Snails

After tagging each kelp, I removed all naturally occurring, visible *N. norrisi*. These snails were held for one day in running sea water and measured (greatest shell dimension precise to one mm) using a Monostat Mecanic™ caliper. I marked shell size on the periostracum of each snail using the metal rod of the caliper and markings lasted up to five months. Snails were marked on the first survey of each survey series, making it easy to determine the size of snails without disrupting their natural movement and behavior on the kelp during subsequent surveys. Unmarked snails found after the initial survey were removed from the kelp, measured, marked in situ, then placed at the base of the holdfast if they did not readily reattach to their original position.

Many *N. norrisi* were observed repeatedly over the course of 10 mo, but some were not seen again after the survey series in which they had been initially marked. Because of these losses, several *N. norrisi* were added to each tagged kelp during subsequent survey series. These snails were either emigrants onto the kelp or collected from nearby plants. For *N. norrisi* recovered from a previous survey series, new sizes were scribed alongside the old sizes to reflect the interim growth of the snail.

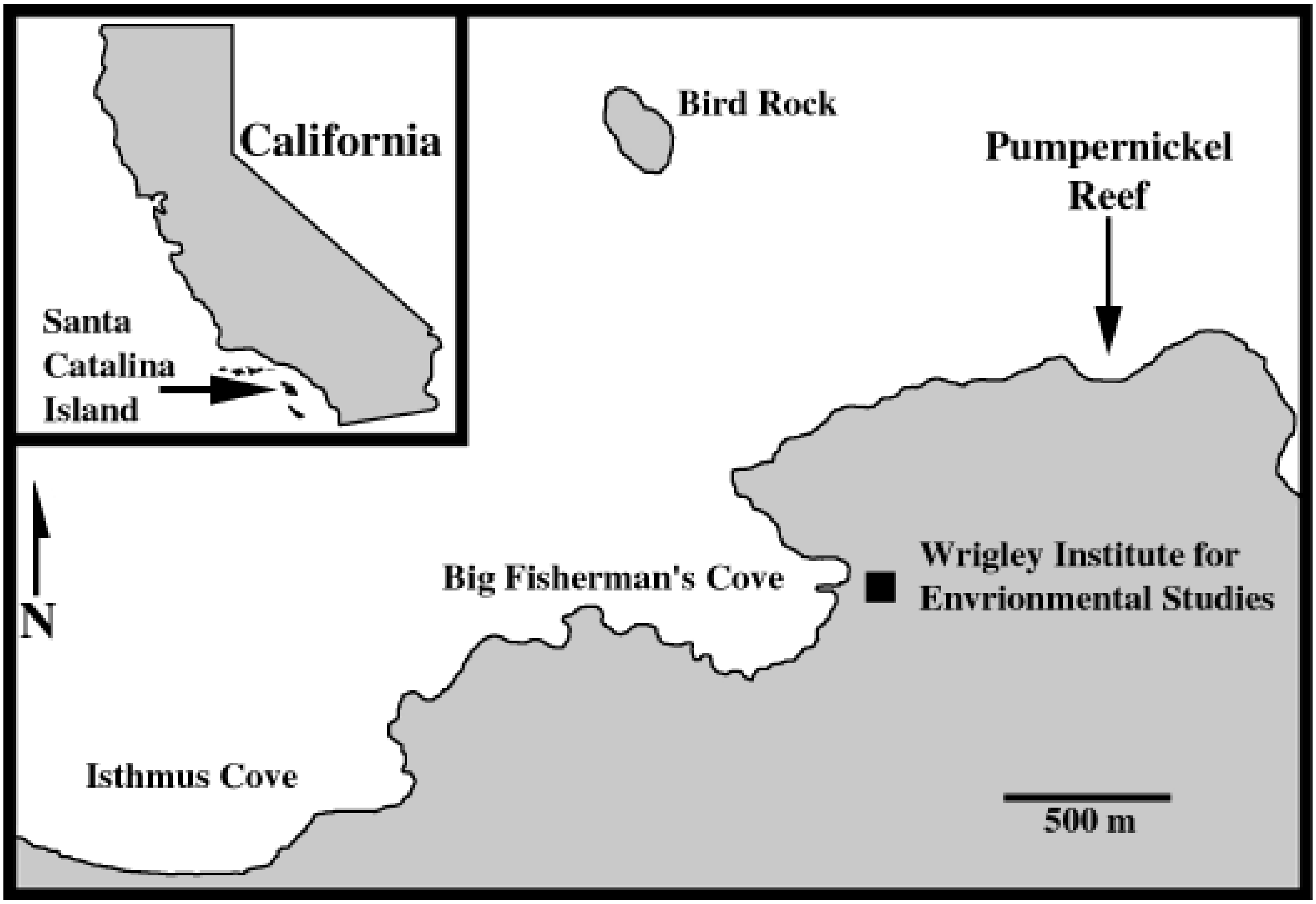

Figure 1. Location of the study site at Pumpernickel Reef, Santa Catalina Island, California.

Irradiance Measurements

I used a LI-COR LI-193SB™ submersible spherical quantum light sensor before each survey to measure irradiance ($\mu E/m^2/s$) just above the sea floor (depth of holdfasts). Values ranged from 0 to 750 $\mu E/m^2/s$. During times of the day when irradiance changed rapidly (dawn, dusk), I recorded a second set of measurements after the survey.

If the light sensor did not detect any light at both the start and end of the survey, the survey was defined as nocturnal. The 10 nocturnal surveys began between 2053 and 2257 hr, with at least one nocturnal survey during each of the survey series. Diurnal surveys began between 0505 and 2003 hr and included all dives with light measurements greater than zero at either the start or end of the dive.

Field Surveys

In August 1992, I placed 9 to 18 marked *N. norrisi* on the holdfast of each tagged *M. pyrifera* and subsequently surveyed each kelp at various times of the day and night for the next 17 d. I completed additional survey series during September, October and December 1992, and February, March, April and May 1993. Each series consisted of multiple surveys on two or three consecutive days. All survey series were separated by at least two weeks except for March and April, which were separated by four days; these March/April observations were pooled.

During each survey, day or night, I followed the same search procedure for each tagged *M. pyrifera*. I measured the depth of the holdfast with a Scubapro™ depth gauge (30 cm precision), then circled the base of the holdfast within a radius of 50 cm, searching the substratum for *N. norrisi*. If I found a snail on the surrounding substratum, I placed it on the holdfast. I then began a non-destructive search of the holdfast. If a snail was visible in the holdfast but too difficult to remove, I estimated its size if most of the snail was visible; otherwise the snail was not counted. I continued searching upwards, circling the kelp and gently moving blades aside to ensure a thorough search of the entire kelp. All kelp were surveyed on a single dive. Search procedures on night dives were the same except for the use of flashlights.

Observations

During each survey, I recorded for each *N. norrisi*: snail depth, size, position, and activity. Height of *N. norrisi* above the holdfast was calculated as the difference between the depth of the holdfast and the depth of the snail. If a snail was not marked, I removed it from the kelp, measured it, and scratched its size on the periostracum. Although most *N. norrisi* readily reattached to the kelp after having been handled, those that did not were placed on the holdfast. Position was categorized as: a) not on the kelp but near the holdfast (within 50 cm); b) in or on the holdfast; c) transition zone (where the haptera become stipes); d) sporophyll (reproductive blades of kelp); e) stipe; f) pneumatocyst; and g) blade, which was subdivided into thirds: distal, medial, or proximal to the pneumatocyst. Snail activity was recorded as either inactive, actively crawling up or down, or feeding. Feeding was easily observed in the field through the underside of the nearly transparent blades.

Sampling Error

I was the only diver to survey the *M. pyrifera*, which ensured a relatively constant amount of researcher sampling error. To estimate how many *N. norrisi* were not counted during the day due to the spatial refuge offered by the holdfast, I destructively sampled a *M. pyrifera* plant within the study site in August 1992, using a kelp similar to those included in the study. After a routine survey of the kelp, I collected all three visible snails. I searched the holdfast by cutting away the haptera to expose hidden snails. Five *N. norrisi* (10 to 17 mm) had been concealed within the dense haptera. Therefore, diurnal surveys underestimated the actual number of snails. A similar destructive survey was not done at night, although I suspect the number of individuals within the haptera would be low since most small *N. norrisi* emerged at night and climbed up the kelp (see Results).

Calculations

Statistical analyses were calculated using SAS/STAT®, version 6.03. The significance level of all tests was set with a Type I error = 0.05. Exact *P*-values are given when calculated. Some critical values used are from statistical tables in Daniel (1991).

RESULTS

During seven survey series between August 1992 and May 1993, I conducted a total of 54 surveys at Pumpernickel Reef. Mean survey duration was 58 min, with start times ranging from 0505 to 2257 hr. Over the course of the 10 mo study, I surveyed 19 different *M. pyrifera* plants; most (95%) of the observations were made on six tagged *M. pyrifera*. Only one *M. pyrifera* survived the entire 10 mo study.

Because *N. norrisi* continually climbed onto and off of the tagged *M. pyrifera*, the study population of snails fluctuated. Between 325 and 400 individual snails accounted for 1,602 observations. I could not determine the exact number of individual snails used because shell markings faded with time.

Determination of Size Classes

Marking each *N. norrisi* on the shell with its size provided a record of growth in the field between survey series. Snail size ranged from 4 to 51 mm. Snails <30 mm grew an average of 1.8 mm/mo (n = 53; SD = 0.71), while snails ≥30 mm grew an average of one mm/mo (n = 11; SD = 0.77). These growth rates were significantly different (t = 3.30; P <0.002), with smaller snails growing more rapidly than larger snails.

To determine if vertical migrations varied with snail size, I grouped snails into four size classes based on estimated annual growth rates from field data. With a slightly conservative growth rate of 1.5 mm/mo, the first size class (≤17 mm) included recruits and snails up to an age of one yr. The second size class (18 to 29 mm) included snails one to two yr old, with an estimated growth rate of one mm/mo after the first year. The third size class (30 to 41 mm) included snails that were probably 2 to 4 yr old, with growth rates less than one mm/mo after the second year. Snails ≥42 mm were seldom seen in successive survey series, and those that were seen had not measurably increased in size.

Vertical Distribution: Day vs. Night

There were marked qualitative differences in snail distribution between nocturnal and diurnal surveys, with more *N. norrisi* visible at night than during the day. Combining data from all tagged kelps, I observed an average of 28 (±1.3 SE) *N. norrisi* per diurnal survey (n = 44) and an average of 35 (±2.3 SE) snails per nocturnal survey (n = 10), a significant increase at night of 25% ($t = 2.21$; $P = 0.03$).

During diurnal surveys, *N. norrisi* tended to cluster among the holdfast haptera. Due to their smaller size, ≤17 mm *N. norrisi* made up the majority (68%; n = 46) of the 68 snails observed within the holdfast haptera during the day, followed by snails 18 to 29 mm (31%; n = 21), and one 33 mm individual. During the day, a higher percentage of *N. norrisi* was found next to, on, or in a holdfast (0 m) than at night. Of the 1253 diurnal observations, 38% (n = 471) were at 0 m; in contrast, only 9% (n = 33) of the 349 nocturnal observations were at 0 m ($\chi^2 = 100.2$; $P < 0.005$). Snails were never observed within the holdfast haptera at night.

Within each survey series, there were at least 24% more *N. norrisi* at 0 m during the day than at night (Figure 2). Using arcsine transformed data, a significantly greater mean percentage (44%) of *N. norrisi* was at 0 m during the day than at night (19%) ($t = 6.69$; $P < 0.001$).

Nocturnal mean height for *N. norrisi* was 0.84 m (±0.039 SE; n = 349), significantly higher ($t = 6.92$; $P < 0.001$) than the diurnal mean (0.52 m ±0.023 SE; n = 1253). Within each survey series, the nocturnal mean height was always significantly greater than the diurnal mean height (Figure 3).

Vertical Distribution: Day vs. Night by Size Class

Significantly more *N. norrisi* were seen at night and were higher on *M. pyrifera* than during the day. On average, almost twice as many ≤17 mm *N. norrisi* were seen at night than during the day ($t = 2.88$, $P = 0.006$) (Table 1). For each of the other three size classes, the difference between average diurnal and nocturnal surveys was not significant (Table 1). The 25% overall increase in the mean number of snails observed at night corresponded almost exactly to the increase in the average number of ≤17 mm *N. norrisi* observed at night (7.3 more snails observed at night). Thus, the increased number of snails observed at night can be explained entirely by the emergence of ≤17 mm *N. norrisi* from the holdfast.

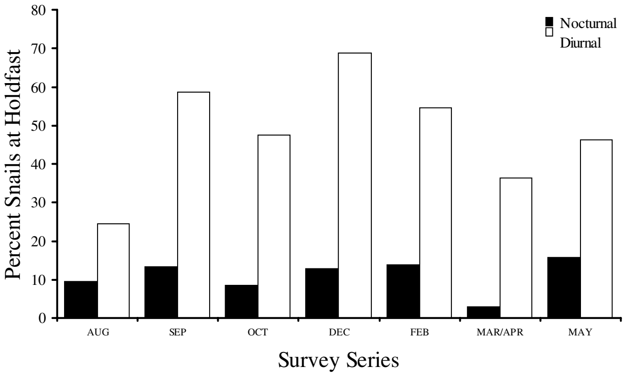

Figure 2. Nocturnal and diurnal percentages of *Norrisia norrisi* at the holdfast (height of 0 m) for each survey series.

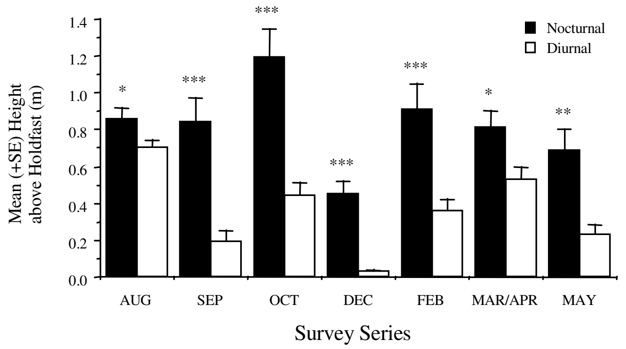

Figure 3. Mean (+SE) nocturnal and diurnal height (m) above the holdfast for *Norrisia norrisi* for all seven survey series. *t*-test; * = *P* <0.05, ** = *P* <0.01, * = *P* <0.001.**

Table 1. Mean numbers of *Norrisia norrisi* observed at night and during the day for each size class. Data pooled for all surveys. Two sample *t*-test statistics and significance values are shown.

Size	Night		Day			
(mm)	Mean	No.	Mean	No.	*t*	*P*
≤17	14.9	149	7.6	335	2.88	0.006
18-29	12.6	126	11.5	507	0.42	0.677
30-41	6.5	65	7.7	338	1.06	0.292
≥42	0.9	9	1.7	73	1.10	0.275

Mean height was significantly greater at night for all but the largest size class of *N. norrisi* (Figure 4). The magnitude of differences diminished with increasing size classes. Unlike the other size classes, mean height of ≥42 mm *N. norrisi* was greatest during the day but not significantly different from the nocturnal mean height.

Regression Analyses: Irradiance vs. Height above the Holdfast

I examined the relationship between irradiance and height with 1) pooled data; 2) specific subsets of irradiance values; and 3) size classes. Before performing simple linear regression analyses of irradiance (independent variable) on height (dependent variable), I transformed height data ($\log_{10}(x + 0.01)$).

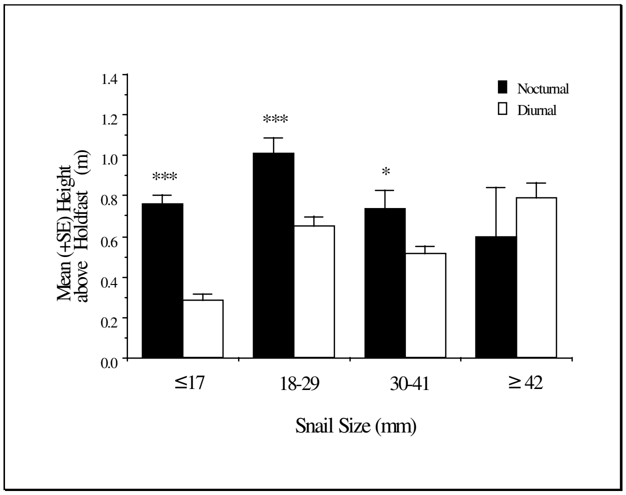

Figure 4. Mean (+SE) nocturnal and diurnal height (m) above the holdfast for four size classes of *Norrisia norrisi*. Means for each size class were pooled from all survey series. *t*-test; * = *P* <0.05, * = *P* <0.001.**

Survey Series Data

For each survey series I used regression analysis to determine trends between log-transformed height above the holdfast and irradiance across all sizes of *N. norrisi*. Except for February, the same significant trend was present in all observation periods: height decreased with increasing irradiance. The correlation for February was also negative, and nearly significant ($P = 0.067$). Since there was no seasonal trend, I grouped all survey series together into a pooled data set for the following analyses.

Pooled Data

There was a small but significant negative relationship between height and irradiance among the pooled data ($n = 1602$; $r^2 = 0.003$; $P = 0.02$); height decreased as irradiance increased. Since *N. norrisi* were reported by Miller (1975) to migrate up the kelp late in the day as sunlight diminished, I compared trends during full sunlight (≥400 µE/m^2/s) and dusk/darkness (after 1600 hr and 0 to 399 µE/m^2/s). Height and irradiance were not correlated during full sunlight ($n = 354$; $r^2 = 0.001$; $P = 0.47$), but were nearly significant during dusk/darkness ($n = 681$; $r^2 = 0.005$; $P = 0.07$).

Irradiance vs. Height within Size Classes

Regression analyses for each size class compared height to 1) all irradiance levels; 2) full sunlight only (≥400 µE/m^2/s); and 3) dusk/darkness only (after 1600 hr and 0 to 399 µE/m^2/s). Regression coefficients and *P*-values are presented for each size class (Table 2). For all irradiance levels, height was negatively correlated with irradiance for ≤17 mm *N. norrisi* (P <0.001), was positively correlated with irradiance for 30 to 41 mm *N. norrisi* ($P = 0.006$), and was not correlated for other size classes. During full sunlight (≥400 µE/m^2/s), height was correlated with irradiance only for *N. norrisi* ≤17 mm and 30 to 41 mm (Table 2): negatively for ≤17 mm *N. norrisi* (Figure 5) and positively for 30 to 41 mm *N. norrisi*. During dusk and darkness (after 1600 hr and 0 to 399 µE/m^2/s), height was correlated with irradiance only for ≤17 mm *N. norrisi* (Figure 5), with height increasing as irradiance decreased, much as it did during the day. Of the four size classes, height and irradiance were significantly correlated for only ≤17 mm *N. norrisi*. During the day, when irradiance was high, ≤17 mm *N. norrisi* were low on the kelp, but as irradiance diminished during dusk, they were the only size class of *N. norrisi* to migrate up the kelp.

Table 2. Linear regression analysis of log-transformed height above the holdfast for three irradiance categories by each size class of *Norrisia norrisi*. *P*-values are shown for the regression equation.

Irradiance (E/m^2/s)	Size (mm)	No.	r^2	Slope	*P*-value
All values	≤17	484	0.1492	-0.0015	<0.001
(0-750)	18-29	633	0.0002	<-0.0001	0.708
	30-41	403	0.0185	0.0001	0.006
	≥42	82	0.0005	<-0.0001	0.844
Full sunlight	≤17	84	0.0757	-0.0024	0.011
(≥400)	18-29	95	0.0032	0.0006	0.585
	30-41	134	0.0475	0.002	0.011
	≥42	41	0.0005	0.0002	0.885
Dusk/darkness	≤17	253	0.1234	-0.0033	<0.001
(0-399 and	18-29	274	0.0043	0.0009	0.278
> 1600 hr)	30-41	133	0.0170	0.0011	0.135
	≥42	21	0.0600	0.0018	0.285

Position of *N. norrisi* on *M. pyrifera*

The diurnal and nocturnal positions of *N. norrisi* on *M. pyrifera* differed. Of the 1253 snails observed during the day, 31% (n = 383) were in, on, or near the holdfast and 28% (n = 348) were on blades. In contrast, 70% (n = 244) of the snails observed at night were on blades, and only 4% (n = 14) were on or near the holdfast. During the day, 66% (n = 120) of *N. norrisi* on stipes were climbing, whereas only 93% (n = 37) of *N. norrisi* on stipes were climbing at night. In general, snails were more active at night.

During the day, the position of *N. norrisi* on blades (n = 348) was significantly biased towards the center of the kelp, with 49% (n = 170) at the base of the blade near the pneumatocyst, 39% (n = 136) in the middle of the blade, and only 6% (n = 20) on the exposed, distal end of the blade ($\chi^2 = 206.9$; P <0.005). The distribution of snails on blades changed markedly at night, with 24% (n = 59) on the basal third of the blade, 49% (n = 120) on the medial third, and 22% (n = 53) on the distal third ($\chi^2 = 97.5$; P <0.005). Using blade positions and day vs. night as categories, I determined that position of *N. norrisi* on *M. pyrifera* blades was not independent of day and night ($\chi^2 = 56.12$; P <0.005). Not only were more *N. norrisi* observed on *M. pyrifera* at night, but they were more conspicuous due to increased activity and movement onto more exposed, distal portions of kelp blades.

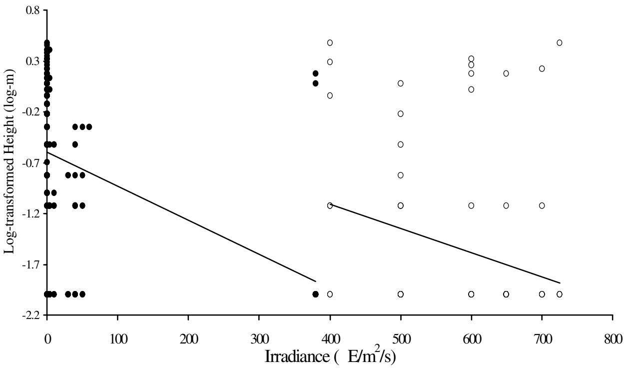

Figure 5. Regression of transformed height ($\log_{10}$ (x+0.01)) above the holdfast on irradiance (μE/m^2/s) for $\leq$17 mm *Norrisia norrisi* during dusk/darkness (>1600 hr and 0 to 399 μE/m^2/s; *n* = 253; filled circles) and full sunlight ($\geq$400 μE/m^2/s; *n* = 84; open circles). Regression equations were significant for both dusk/darkness ($y = -0.0033x - 0.599$; $r^2 = 0.1234$; $P < 0.001$) and full sunlight ($y = -0.0024x - 0.153$; $r^2 = 0.0757$; $P = 0.011$).

Feeding Observations

Although four times as many diurnal surveys were conducted, eight of the 14 feeding *N. norrisi* were seen at night. During the day, I observed six snails feeding; one snail was feeding on a pneumatocyst, the others were eating blade tissue. All eight of the *N. norrisi* observed at night fed only on blade tissue. Nocturnal feeding events were probably undersampled because extended and direct lighting from dive lights caused some of the feeding snails to stop and slightly withdraw into their shells.

DISCUSSION

In general, *Norrisia norrisi* can be active at all times of the day and distributed throughout the entire thallus of *Macrocystis pyrifera* at Santa Catalina Island (Bakus 1974; Miller 1975; Schmitt et al. 1983; Hartman 1983; Stebbins 1986). In this study, at any time of the day or night, 69% of the *N. norrisi* observed on kelp at Pumpernickel Reef were above the holdfast and 31% were next to, on, or in the holdfast.

Although Miller (1975) reported a diel vertical migration (up at night), this was true in the present study only for ≤17 mm *N. norrisi*, and not for larger individuals. During the day, ≤17 mm *N. norrisi* were most frequently in or near the holdfast of the kelp, tightly clustered among the holdfast haptera and the dense, thickened pre-stipes. Snails ≤17 mm were more common at night, significantly increasing the number of visible snails on the kelp by 25%. I often observed these small snails emerge from the holdfast haptera at dusk, then climb rapidly up the kelp onto the sporophylls and blades. Snails ≤17 mm were the only size class to consistently, and significantly, climb up the kelp in response to decreased light levels (Table 2).

The diurnal and nocturnal distributions of *N. norrisi* on *M. pyrifera* differed significantly. During daylight hours, 38% of all snails observed were associated with the holdfast (0 m); this was reflected in a low diurnal mean height (0.52 ±0.023 m).

These observations are consistent with those of other researchers studying *N. norrisi* on Santa Catalina Island: Bakus (1974) reported that smaller *N. norrisi* tend "to be located in or around the holdfast;" Schmitt et al. (1983) did not include *N. norrisi* <20 mm in their study on the consequences of shell fouling because they "usually inhabit kelp holdfasts;" and Stebbins (1986) studied the density, distribution, and feeding habits of *N. norrisi* on *M. pyrifera*, but did not observe any "juvenile" *N. norrisi* (<15 mm), presumably because holdfasts were not searched.

Factors Influencing Vertical Distribution

Diurnal Predators

Norrisia norrisi ≤17 mm remain in the protective shelter of the haptera during the day, while those that cannot fit disperse throughout the kelp, often clinging to stipes and pneumatocysts. Remaining in the holdfast haptera during the day could be an effective means of avoiding diurnally active benthic predators such as the sea stars *Pisaster giganteus*, *P. ochraceus*, *and Astrometis sertulifera* (Leighton 1971), and the whelk *Kelletia kelletii* (Schmitt et al. 1983). *Norrisia norrisi* displayed escape and avoidance responses, along with increased escape velocity, following tactile stimulation by these four predators (Schmitt 1981).

Although most *N. norrisi* clung vigorously to *M. pyrifera*, any dislodged from the kelp dropped to the rocky substratum, and immediately began crawling back toward the kelp (Schmitt et al. 1983; Lonhart 1996). Schmitt et al. (1983) reported *N. norrisi* that fell off *M. pyrifera* or *Eisenia arborea* moved relatively rapidly along the bottom until another kelp was encountered, then climbed it. The daily per capita mortality rate for *N. norrisi* tethered to rocky substrata was 17-times greater than for snails tethered to adjacent *M. pyrifera* (Schmitt et al. 1983). Thus, diurnally active, benthic predators could exert a strong selective pressure on *N. norrisi*.

Nocturnal Predators

At night, fewer than 10% of the *N. norrisi* observed were near the holdfast, and most of these were actively crawling upwards, contributing to a significantly higher nocturnal mean height (0.84 ±0.039 m). The increase in nocturnal mean height and the 25% increase of snails seen on the kelp can be attributed to the emergence of ≤17 mm *N. norrisi* from cryptic refugia within the holdfast and their upward migration. In the early evening (1600 hr) and into the night, ≤17 mm *N. norrisi* were the only size class to consistently and significantly climb the kelp. Only *N. norrisi* ≤17 mm had a diel vertical migration; this was not a general behavior of the entire population.

The upward migration of ≤17 mm *N. norrisi* at night could be a strategy to avoid nocturnally active benthic predators such as *Panulirus interruptus* (spiny lobster) and *Octopus bimaculatus* (two-spotted octopus)(Davis 1984; Stebbins

1986). Except for the smallest snails in large holdfasts, the holdfast is probably not an effective refuge against the prehensile tentacles of an octopus or the probing maxillipeds of a lobster. Foraging lobsters were common at Pumpernickel Reef at night and they are known predators of *Norrisia* (Engle 1979; Schmitt 1981; Schmitt et al. 1983). While only a few *Octopus bimaculatus* were seen foraging at night, Ambrose (1984) reported that *O. bimaculatus* at Santa Catalina Island most commonly consumed gastropods (71.5%), and 12% (by number) of the *O. bimaculatus* diet was *N. norrisi*. Both lobster and octopus forage primarily on the sea floor, and snails migrating up the kelp at night could effectively reduce the encounter rate with these nocturnally active benthic predators.

Small *N. norrisi* that fall off the kelp should be especially vulnerable to attack (presumably much more so than larger snails) from a variety of benthic predators. The relatively thin shell of ≤17 mm *N. norrisi* is a weak defense against many predators. If benthic predators are the main selective pressure influencing the evolution of vertical migration in these snails, then predation must have been (or still is) most intense during the day, when snail inactivity and hiding reduce dislodgement and exposure to benthic predators. At night, when risk of predation is relatively low, snails become more active and migrate up, presumably to forage.

Diet of *Norrisia norrisi*

Kelps, especially *M. pyrifera*, are preferred by *N. norrisi* over all other potentially available algae (Wakefield and Murray 1998). Stebbins (1986) and Hartman (1983) hypothesized that feeding preferences of *N. norrisi* for certain portions of *M. pyrifera* may partially explain the distribution of the snails on the kelp. Except for sea urchins, few macroherbivores feed on *M. pyrifera* haptera; and, when provided with equal amounts of blade, sporophyll, stipe, and haptera tissue, *N. norrisi* preferred haptera least, consuming only 6% relative to the other tissues (Leighton 1971). Stebbins (1986) reported *N. norrisi* in the lab preferred *M. pyrifera* sporophyll tissue to mature or apical blades. Like Stebbins (1986), Leighton reported *N. norrisi* had the strongest preference for sporophyll (51%) and blade (32%) tissues. Stebbins (1986) suggested that, if the distribution of snails depended on feeding preferences, most snails should be concentrated at the sporophylls. Neither his data nor the present study support this hypothesis. At Pumpernickel Reef, snails were spread throughout the kelp thallus during the day (31% holdfast; 28% blade; 14% stipe; 14% sporophylls), while at night only 3% of the snails were on sporophylls and 70% were concentrated on blades, especially on the middle and distal portions. Feeding was more common at night; and, in all but one case, the snails were feeding on mature blades. Sporophylls do not appear to be preferred and probably do not influence the migration behavior.

Wakefield and Murray (1998) reported *N. norrisi* significantly preferred *M. pyrifera* blades vs. all other available kelps and macroalgae. For small, vulnerable snails, remaining in the safety of the holdfast during the day and climbing at night to feed on blades may lower the risk of predation. Because of the increased activity of ≤17 mm *N. norrisi* at night on *M. pyrifera* and their movement onto the middle or distal portions of blades, I hypothesize that nocturnal feeding on blade tissue is an important factor determining their vertical distribution and migration. Furthermore, I propose that ≤17 mm *N. norrisi* do not consume haptera tissue during the day, presumably because haptera tissues are more costly to process or have low caloric value. Future research exploring these hypotheses would focus on the caloric value of *M. pyrifera* blade, sporophyll, and haptera tissue, the amount of time snails spend feeding on each tissue, and the growth rate of juveniles fed a diet of each tissue.

If migratory behavior of *N. norrisi* on *M. pyrifera* is an adaptive trait, how do snails behave on other erect macroalgae? I also observed (but did not quantitatively study) the distribution of *N. norrisi* on *Eisenia arborea* at Pumpernickel Reef. During the day, snails of all sizes (but especially snails ≤17 mm) tended to cluster at the bifurcation of the stipe and among the proximal ends of the blades. At night, snails emerged from their diurnal refugia and moved onto the central and distal regions of the blades, presumably to feed. It appeared *N. norrisi* on *E. arborea* were relatively inactive during the day and fed on the blades at night, much like their behavior on surrounding *M. pyrifera*.

Irradiance and Diel Vertical Migration

Hartman (1983) suggested that large snails (upper 10% of snails collected) are positively phototactic but small snails (lower 25%) are not influenced by light. In this study, ≤17 mm *N. norrisi* appeared to be negatively photoresponsive, but this behavior diminished with size. Although most of the activity and 14 feeding observations were at night, all six *N. norrisi* observed feeding during the day were large (≥18 mm); a diminished negative response to light and increased energetic requirements would cause large snails to distribute themselves throughout the kelp during the day.

As *N. norrisi* grow larger, the snails are excluded from hiding in the holdfast since they become too large to crawl among the densely packed haptera. Increased size, escape speed, and a thicker shell all provide increased protection from diurnally active predators, which may allow *N. norrisi* to exploit other portions of the kelp during the day, resulting in a wider distribution on the kelp. Since escape velocity is strongly correlated with size (Schmitt 1981), the risks to larger *N. norrisi* of exploiting other portions of the kelp and becoming dislodged may be lower than the risks to smaller snails. Once dislodged, larger snails may have a better chance of avoiding benthic predators and returning to the safety of the kelp than smaller snails.

Unlike the migration by all sizes of *N. norrisi* on *M. pyrifera* reported by Miller (1975), this study detected differences among size classes, with only ≤17 mm *N. norrisi* having consistent diel vertical migrations. Snails ≤17 mm remained close to the holdfast during the day, then steadily increased their mean height above the holdfast as dusk approached, climbing up the stipes and onto the blades. I propose that diminishing irradiance at dusk provides a cue for ≤17 mm *N. norrisi* to emerge from the holdfast and climb up the kelp to feed on blade tissue. Conversely, increasing irradiance at dawn may trigger their return to the lower portions of the kelp and refugia within the holdfast. As snails age and increase in size, I propose the negative photoresponse diminishes, enabling larger snails to forage throughout the kelp during the day and at night.

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