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The shifting balance of littoral predator-prey interaction in regimes of hydrodynamic stress

Abstract Above lowshore levels of wave-beaten rocky shores, desiccation from tidal exposure and hydrodynamics stresses from wave action are thought to create refuges from predation, allowing concentrations of sedentary prey such as mussel beds. Underwater time-lapse photography on rocky shores in Southern California revealed that dense aggregations of spiny lobsters prey on mussels during nocturnal high tides. In contradiction of the refuge hypothesis, the densest aggregations occurred on midshore levels of the most wave-exposed site, a semi-protected site showed intermediate densities, and a protected site showed only sparse numbers of lobsters. On wave-beaten shores, the lobsters' high mobility and rapid prey handling allowed them to exploit intertidal prey in the brief period at extreme high tide, when both desiccation and hydrodynamic stresses were at a minimum. The spatial differences in lobster densities were, however, positively related to the recruitment rates of juvenile mussels, the preferred prey. A field experiment demonstrated that predation by lobsters within a mussel bed affects the age/size structure of the bed without changing primary percent coverage. Therefore, concentrations of adult prey on some wave-swept sites appear to result from elevated rates of prey recruitment that surpass rates of predation, rather than absolute refuges from predation.

Keywords *Mytilus* · Predation · Recruitment · Refugia · Hydrodynamic stress

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Introduction

A conspicuous seashore phenomenon familiar to both layman and ecologist is the dense concentration of barnacles and mussels where waves break on rocky headlands. The corresponding near absence of mussels in more sheltered areas reinforces a long held tenet of benthic ecology: the occurrence of dense prey populations depends on locally harsh physical conditions that create refuges from predation (Kitching et al. 1959; Lewis 1964; Muntz et al. 1965; Connell 1972, 1975; Menge 1976, 1978a, 1978b). Two gradients of physical stresses determine the bounds of the refuge. Desiccation stress increases vertically up the shore with increasing intervals of low tide exposure, thereby limiting effective foraging of certain intertidal predators to lower shore levels. Wave exposure varies horizontally, along the shore with topography, and wave-generated hydrodynamic stresses may damage predators or hinder their foraging at wave battered extremes of the gradient. Because both types of stresses reach their extreme there, mid to upper shore levels of wave-exposed sites are believed to constitute a spatial refuge from predation, allowing concentrations of adult prey.

Predator type, hydrodynamic stresses, and along shore differences in predation

The spatial refuges were attributed to the adaptive limits of predators. Sea stars and whelks, which served as the models for the original statement of the refuge hypothesis (Connell 1972; Paine 1976), remain within the intertidal zone through all phases of the tides and move slowly as water levels change. Their slow advance and retreat with the tides, coupled with intolerance to prolonged exposure occurring on relatively high shore levels during low tides, limits their ability to exploit prey high on the shore. Because they remain continually within the intertidal zone, they cannot avoid periods of high wave impact on wave-beaten shores. Thus, they are constrained

by both types of physical stress, and on wave-exposed shores their foraging appears to be hampered and confined to relatively low levels. Large mobile aquatic predators, such as large decapods and fishes, enter the intertidal zone at high tide, move quickly with the tides, and kill prey rapidly, so that they are less constrained along the vertical tidal exposure gradient. The apparent absence of prey concentrations on upper levels of some tropical (Menge and Lubchenco 1981) and sheltered temperate (Robles 1987) shores has been attributed to the action of these predators. However, characteristics associated with their high mobility appear to render them vulnerable to hydrodynamic stresses on wave-exposed sites.

Moving water subjects marine organisms to drag and lift (Vogel 1981; Denny 1988), which can damage or dislodge them. Sedentary prey, for example barnacles and mussels, resist these forces by maintaining a firm attachment and low profiles that do not project far into the flow gradients above the substratum (e.g., Koehl 1976, 1982; Denny et al. 1985). Most predators from marine taxa forage only while the shoreline is submerged, and so they too are subjected to hydrodynamic stresses. Like their prey, slow-moving consumers such as stars and whelks maintain low profiles and cling to the rock during wave stress using numerous suckers or a massive flat foot. This makes dislodgement less likely, but as noted above hampers or completely prevents foraging. The large, mobile predators, for example, spiny lobsters and fishes, seem very susceptible to wave stresses because they have little or no attachment and their large frontal areas project further above the rock surface, exposing them to higher, "free-stream" flow speeds. Consequently, foraging by this type of predator was thought to be restricted to comparatively sheltered waters (Muntz et al. 1965; Connell 1972; Howard and Nunny 1983; Menge 1983). Thus, on wave-exposed shores, constraints on the foraging of small, slow-moving predators and the absence of larger, more mobile predators, were presumed to create an absolute prey refuge above midshore levels; while on sheltered shores, predators large and small could extirpate the prey.

Context of the present study

Surprisingly, very little direct evidence supports the hypothesis that hydrodynamic stress provides a refuge from large mobile predators. Indirect evidence included the finding that prey losses within experimental enclosures confining these predators were lower at wave-exposed sites than at protected sites (Menge 1983). Robles et al. (1989) found that on nocturnal high tides, wave-exposed temperate shores had lower densities of the crab *Cancer productus* than sheltered shores nearby. However, no study has provided detailed quantitative estimates of the relationship between the changing densities of large mobile predators and bottom flow speeds for rocky intertidal systems. The density/speed relationship is crucial to

the hydrodynamic stress argument because the hydrodynamic stresses are proportional to the square of the flow speeds (see Howard and Nunny 1983 for a treatment of this in a subtidal habitat). A prey refuge in hydrodynamic stress implies prolonged periods of high bottom flow speeds.

Similarly, possible effects of predators within mussel beds on wave-beaten shores have seldom been tested. Marsh (1986) experimentally demonstrated an effect of avian predators on juvenile *Mytilus* spp. high in the intertidal zone. Wootton (1993) demonstrated that sea stars and birds may reduce the rate at which mussels recolonize midshore levels following experimental removals. Yet no studies expressly tested the refuge hypothesis by looking for effects of large mobile predators within an intact mussel bed.

Snorkeling along the shores of the California Channel Islands, we observed that spiny lobsters, *Panulirus interruptus*, move into the intertidal zone to feed on shelled invertebrates during nocturnal high tides (Robles 1987, 1997; Robles and Robb 1993). The lobsters sometimes foraged within beds of the mussel, *Mytilus californianus*. This observation raised the possibilities that (1) intertidal foraging of large mobile predators was not always suppressed at wave-exposed sites by hydrodynamic stresses, and (2) concentrations of prey do not necessarily occur only in absolute spatial refuges from predation.

For the present study, we deployed on both sheltered and wave-exposed shores underwater time-lapse cameras coupled with electromagnetic current meters, to record the time courses of varying lobster densities and bottom flow speeds as water levels changed over the course of a given tide. As an experimental test of the refuge hypothesis, we conducted a lobster exclosure experiment within a mussel bed. If the results confirmed an effect of lobster predation on mussel population structure – for example changing size frequencies, or the degree of layering and hence density of the mussels – with little or no change in the percent cover, then the refuge hypothesis would be contradicted. We also compared the differences in lobster densities recorded in the time-lapse work with among-site differences in the recruitment of mussels. These data were relevant because possible losses of mussels to predators and other factors could be offset by recruitment. Additionally, previous work suggested that juvenile and young adult mussels are the preferred food of lobsters in this habitat (Robles et al. 1990). Therefore, recruitment rates also might influence differences in lobster abundances. The data from the time-lapse study, recruitment survey, and field experiment are unique and have not been reported previously.

Materials and methods

Lobster foraging

The lobsters forage in the intertidal zone primarily on nocturnal high tides from May through September (Robles and Robb 1993). In this period, they remain near shore – within the calm, warm
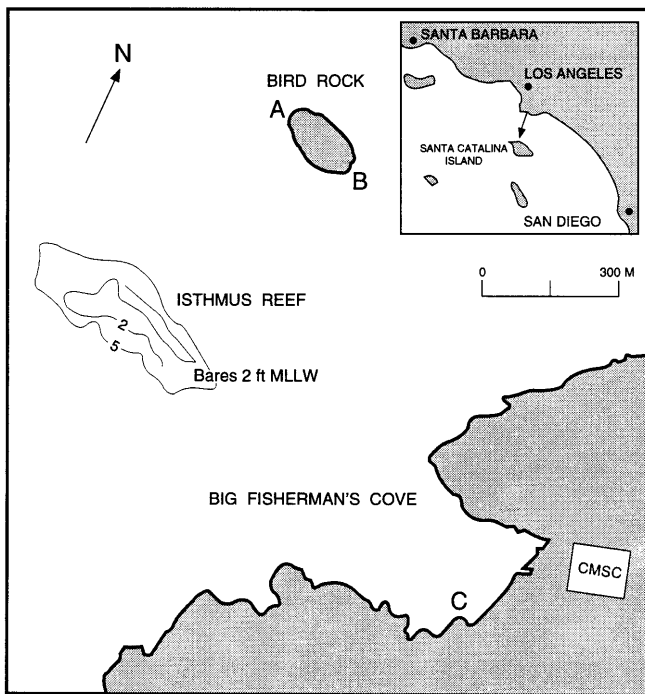
Fig. 1 Map of a portion of Santa Catalina Island showing the location of the time-lapse sites (*A*, *B*, *C*). *Inset* shows the position of the island relative to the mainland. The base of operations, Catalina Marine Science Center (*CMSC*) is also indicated. Predominant swells approach the island from north/northwest

surface waters as they spawn, brood eggs and molt, while periodically preying upon intertidal stocks of shelled invertebrates. The lobsters migrate offshore to deeper water in fall, exploiting subtidal prey species (Mitchell et al. 1969; C.D. Robles, personal observations). The marked seasonality of their occurrence near shore corresponds to seasonal changes in sea surface temperature, wave action, and the diurnal phasing of the tides (Mitchell et al. 1969; Robles and Robb 1993). All three physical factors may have some effect on the seasonal differences in the frequency of intertidal foraging. The higher temperatures of surface water during May–September may promote development of the brooded eggs, favoring residence in very shallow, warmer water (Mitchell et al. 1969). Intertidal foraging is probably dangerous for large mobile predators during fall and winter storms. Regarding diurnal tidal phasing, extreme (spring) high tides, which reach to the highest intertidal levels, occur at night only in spring through summer (April–September). The lobsters, which are strictly nocturnal and aquatic, therefore have access to the greatest extent of the intertidal zone in that period. As a result of the tidal phasing, most of the of time-lapse studies were done on nocturnal spring high tides from May through August.

Study sites

The sites were located on the northwestern coast of Santa Catalina Island (33°25′N, 118°30′W). Numerous spring high tide time-lapse series were run at three sites, hereafter "sites A–C"(Fig. 1). Each site occupied a 15- to 25-m² area on a horizontal bench at +0.6 m mean lower low water (MLLW). Based on topography and current meter records of flow speeds, the sites were subjected to three different wave exposures: site A, on the western tip of Bird Rock, received the full force of prevailing northwesterly swells; site B, on the eastern end of Bird Rock, was semi-protected, and it received northwesterly swells refracting around the rock and occasionally easterly swells that refracted around Catalina itself; and

Table 1 Bottom flow speeds (cm s⁻¹) at sites A–C. Means±1 SE of maximum speed records. Maximum flow speeds were recorded from the nine time-lapse intervals (see Materials and methods) occuring from 1 h before to 1 h after the time of extreme high water for spring tides in spring/summer. The records were then averaged for all runs at a site. Pairwise Mann-Whitney *U*-tests, adjusted for procedure-wise error rate of 0.05 using the Bonferroni correction (Sokal and Rohlf 1981), showed that mean speeds differed significantly

Site	A	B	C
Mean (cm s⁻¹)±1 SE	87.1±3.2	56.9±1.2	27.6±0.8
Number of runs	14	28	13

site C, within Big Fisherman's Cove, was protected from wave action (Fig. 1, Table 1). Further descriptions of topography and biota appear in Robles (1987, 1997) and Robles and Robb (1993).

Mussel recruitment

Mussel recruitment was recorded as the number of mussels <5 mm long per 100-cm² quadrat (randomly placed within a site). A quadrat was processed by removing all the attached life from the stone with a chisel and examining the collection under a magnifying glass. Long-term surveys using this method (Robles 1997) showed large between-site and temporal differences in recruitment, but the sites maintained their relative rankings with respect to recruitment over time (see also Connell 1985). Highest recruitment had been found to occur in winter (Robles 1997; C.D. Robles, unpublished work). Therefore, a winter sampling was used to characterize relative abundances of mussel recruits on the three study sites. In winter 1995, sites A and C each received three random quadrat samples. Site B, which was also part of a separate study of within-site recruitment variation (C.D. Robles, unpublished work), received ten random quadrat samples. Differences in the densities of mussel recruits were tested with ANOVA.

Time-lapse studies

A time-lapse rig consisted of a motorized 35 mm camera in a waterproof housing, synchronized with a powerful underwater strobe. Camera and strobe were mounted 30–40 cm off the substratum on iron frames and focused on a fixed plot in the center of the site. The camera recorded lobster numbers within the plot every 15 min, starting with submergence on the rising evening tide through emergence on the falling tide early the next morning, a period of 5–6 h. A set of 15-min records made over a tide at a site constituted a time-lapse "run". The areas of the plots were adjusted to the topography and visibility of each time-lapse run. Divers observed that the silent operation of the strobe, and the brief duration of the flash did not disturb the lobsters. Numerous time-lapse runs were made during extreme, spring tides at all three sites. To observe lobster foraging during the more shallow high tides of neap tidal series, at least two runs at each site were made on nocturnal neap tides.

During the time-lapse runs, bottom flow speeds 30 cm above the substrate were detected by an electromagnetic current sensor (Marsh-McBirney 510, TM) placed on one side of the fixed plot. The flow speed values were fed to a data logger on shore. A maximum bottom flow speed (cm s⁻¹) was selected for each photo frame from 120 records of speed made at 1-s intervals (time constant =0.02 s) during the 2 min prior to the shutter release. Maximum flow speeds were recorded because extreme hydrodynamic stress occurring just before the shutter release was the factor under consideration, and drag and lift are directly proportional to the square of the flow speeds (Denny 1988). However, using mean flow speeds does not change the outcome of the analysis (C.D.

Robles, unpublished work). The current sensors do not record accurate velocities in highly aerated water. The changes in speed and abundance reported here occurred during full submergence, not during the swash (the turbulent wave wash producing high aeration at the times of initial submergence and emergence). The number of runs available to characterize speed differences among sites (Table 1) is greater than the number of runs available to determine speed/density relationships because some daytime records were used for the former and the cameras sometimes malfunctioned.

If hydrodynamic stresses inhibit intertidal foraging, one would expect a negative relationship between bottom flow speeds and lobster densities. Accordingly, we made graphical analyses of the time courses of lobster abundances and bottom speeds over individual tidal sequences. To determine whether the speed/density relationships seen in individual time-lapse runs were general, all runs at a site were pooled. The records of speed were divided into quartiles, and the frequencies of lobster densities within in each quartile were represented with box plots (Cleveland 1993). This provided a visualization of how frequently different values of speed and density were associated.

The graphical analysis indicated that within a given time-lapse run on wave-exposed sites, lobster densities were negatively correlated with bottom flow speeds. In contrast, speeds and densities did not appear to be correlated on the sheltered site. Over the course of a high tide, wave-exposed sites displayed flow speeds ranging from only slightly higher than those occurring on the sheltered site to speeds many times greater, exceeding the speeds presumed to inhibit the foraging of other lobster species (Howard and Nunny 1983). The sheltered site showed uniformly low bottom speeds throughout the course of a run. Therefore, a statistical confirmation that the correlations were in fact significantly negative on the wave-exposed sites and not significantly different from zero on the sheltered site would be consistent with the interpretation that hydrodynamics stresses inhibit, but not completely suppress, lobster foraging.

A method was devised to test whether the speed/density correlations from individual runs differed significantly among the sites. The raw data were not normally distributed; both the speed and density estimates showed markedly different variances among sites; and the individual records were time-dependent, not independently and randomly sampled within a run. A Spearman correlation coefficient was calculated for each time-lapse run. The coefficients were then grouped by site. Formally, S_{ijt}=speed, D_{ijt}=density at time t of run j, r_{ij}=sample correlation of S_{ijt} and D_{ijt} over t, r_i=average of r_{ij} over runs, j. The null hypothesis that the values of the Spearman correlation coefficients did not differ among the sites was tested with one-way ANOVA (Sokal and Rohlf 1981). The subgroups (by site) of coefficients were normally distributed and homoscedastic.

Field experiment

We conducted a lobster exclosure experiment to test whether lobster predation affected the mussel beds. Confirming predator effects would constitute a contradiction of the hypothesis of an absolute refuge. Mussel densities in plots set within a mussel bed and covered by cages (treatment) were compared with those on otherwise similar plots covered by open-ended, "sham" cages (control) or open plots (control). (The lobster exclosure experiments reported previously by C.D. Robles, e.g., Robles and Robb 1993; Robles 1997, were conducted in areas completely covered by algae and were arranged as a test of the keystone predator hypothesis, Paine 1966, 1974).

The cages and sham cages were fashioned of heavy gauge 1-inch-square (2.5-cm-square) galvanized wire mesh coated with epoxy. Each enclosed an area slightly larger than the sub-area of 20×40 cm used as a sample plot. Treatment and controls were assigned by lot to the three plots within a replicate. Five replicates were placed within the mussel bed on the east end of Bird Rock along a line at +0.6 m MLLW, the furthest approximately 10 m windward of site B. The replicates were installed and an initial census of mussels was made in April 1986. In spring, mussel larvae that settled during the winter peak become conspicuous, and
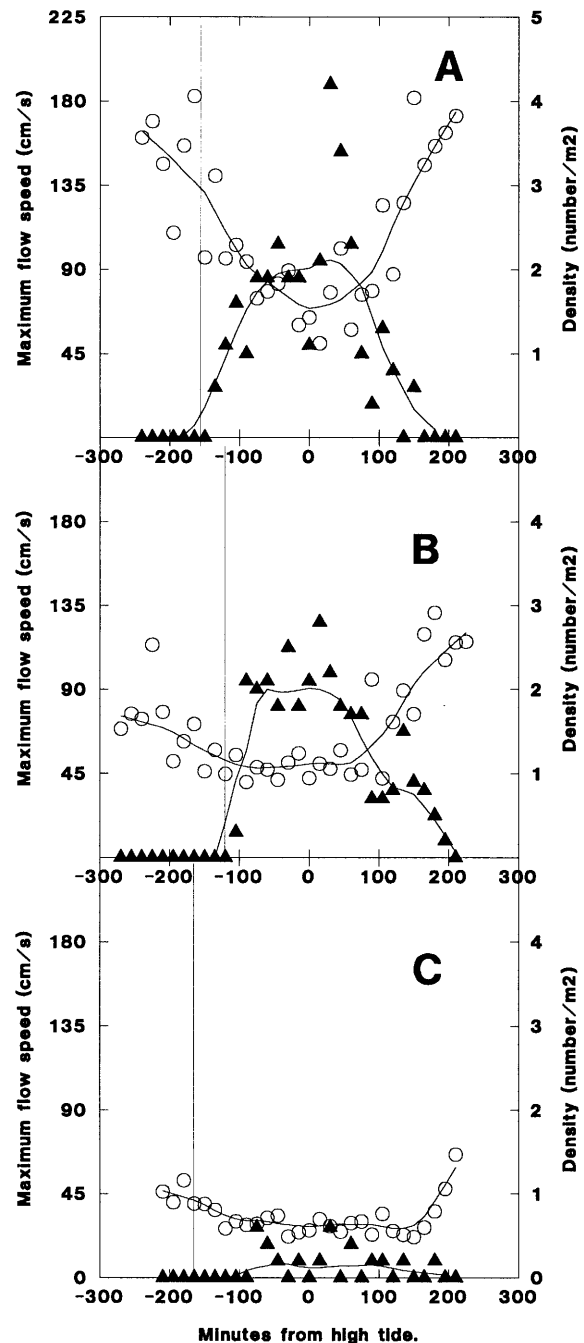

Fig. 2A–C Representative runs made on spring nocturnal high tides. Sites are listed *from top to bottom* in order of decreasing wave exposure. *Abscissa* marks time (min) from extreme high water; *left ordinate*, maximum bottom flow speeds (*circles*) and *right ordinate*, lobster densities (*triangles*). *Curves* drawn with the LOWESS procedure, tension=0.3 (Cleveland 1993, SYSTAT software). *Vertical lines* indicate the time of sunset

the lobsters begin migration towards shore to feed on these and other shelled invertebrates (Mitchell et al. 1969; Robles and Robb 1993). A follow-up census was made in late summer (3 September 1986), at which time the lobsters had reached maximal abundance near shore, just before their migration back to deeper water. For both censuses we recorded the species and sizes of mussels within the plots. Adult mussels (>3 cm long) occurred as a monolayer,
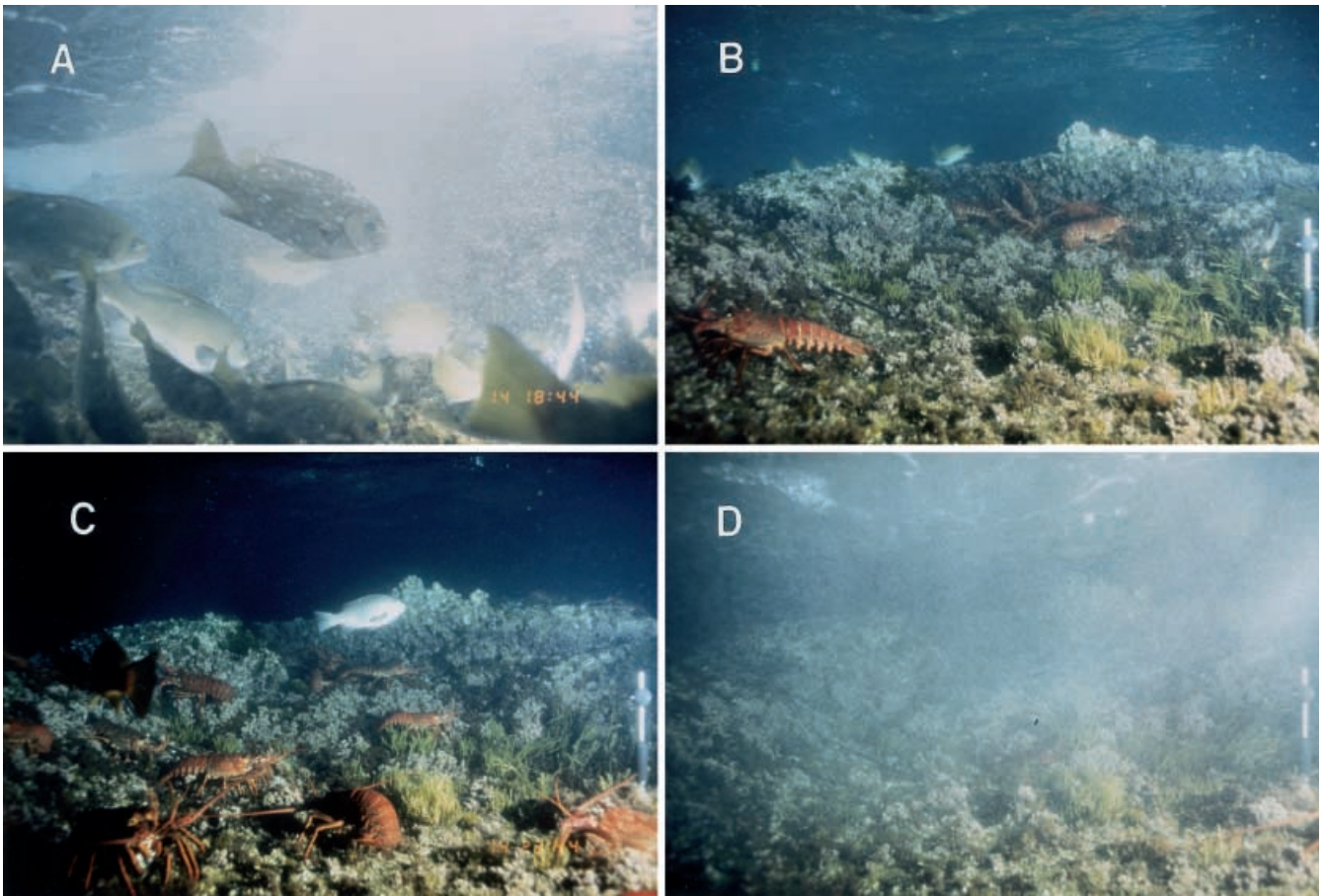
Fig. 3A–D Photos from a time-lapse run at the most wave-exposed site during a nocturnal spring tide in summer. **A** At sunset, diurnal herbivorous fish forage in turbulence immediately following submergence. **B** After sunset, tidal depth increases, speeds diminish and lobsters begin to accumulate. **C** At extreme high water, lobsters reach peak densities. **D** Most lobsters have left the site, coinciding with high bottom flow speeds of lower water levels

Table 2 Recruitment of *Mytilus* spp. (mean number, ±1 SE, of newly settled mussels <5 mm long) tabulated by site and species. ANOVA for means of *M. californianus* density, data transformed to ranks to achieve homoscedasticity: $F=15.97$, $df=3,13$; $P=0.000$

Site	A	B	C
M. californianus	208.3±99.7	18.1±4.3	1.0±1.0
M. galloprovincialis	0.3±0.3	0.4±0.2	0.0±0.0
Total small mussels	208.7±99.5	18.5±4.2	1.0±1.0

and all mussels >1 cm long could be counted. Smaller mussels, which occurred underneath as well as on the sides of the adults, were not counted. *M. californianus* recruits grow to 3–5 cm long in their first year (Seed and Suchanek 1992; C.D. Robles, personal observations). Thus, the timing of this brief experiment allowed us to record the appearance and survivorship of a cohort of *Mytilus* spp. that constituted the "young of the year" as they grew out to conspicuous sizes in the mussel bed.

Initial densities of mussels, and percent changes of densities from initial to final dates, were examined in separate two factor ANOVAs with experimental treatments and blocks (replicates) as factors. Where necessary, the raw data were rank transformed to achieve homoscedasticity.

Results

Mussel recruitment

The quadrat survey showed significant differences in the densities of recruits among the sites (Table 2). As in other studies (Robles 1997; C.D. Robles, unpublished work) recruitment of *M. californianus*, the species that made up most of the recruits, increased over progressively more wave-exposed sites. The abundances of adult mussels also differed among the sites. A continuous bed of *M. californianus* lay just above (+0.9 m MLLW) and to the windward of the camera's field of view on site A. Clumps of *M. californianus* interspersed with red algal turfs occurred within the camera's field of view, and a continuous bed occurred to the windward, on site B. Site C was covered by a red algal turf with no adult mussels (Robles 1997). Thus, both prey abundances and their rates of replenishment appeared to increase with wave exposure.

Time-lapse studies

Individual time-lapse runs often revealed a striking correspondence between maximum bottom flow speeds and

Table 3 Differences among sites in the strength of speed/density relationship during spring high tides. Mean±1 SE of Spearman correlation coefficients (S_p) for speed/density records of individual time-lapse runs are tabulated by site. ANOVA of means: $F=4.58$, $df=2,25$, $P=0.02$

Site	A	B	C
Mean $S_p \pm 1$ SE	−0.42±0.08	−0.25±0.10	+0.11±0.11
Number of runs	8	15	6

lobster densities. For reasons presented in the Discussion, the bottom flow speeds depend on the mean depth and the height of the waves. Therefore, over the course of a tide, speeds varied with the changing water levels and with the wave exposure of the site. On the most wave-exposed site (A), maximum bottom flow speeds were slowest about the time of extreme high water; speeds occurring at other times were far greater (e.g., Fig. 2A). Most importantly, dense aggregations of lobsters occurred during the brief period of minimal speeds that occurred as the tide crested. The lobsters left the area and retreated to deeper water as water levels fell and bottom flow speeds increased (Fig. 3). Their departure preceded the intermittent emergence of the swash period. The semi-protected site (B) showed a similar, inverse relationship between flow speed and densities, but peak speeds and densities were not as great as at the exposed site (e.g., Fig. 2B). On the sheltered site (C), although flow speeds were low for prolonged periods, lobsters were scarce, and the few present left at the beginning of the swash period (e.g., Fig. 2C).

The speed/density relationships in the separate runs depicted in Fig. 2 were typical for all runs made in similar conditions. Combining data from all nocturnal high tide runs of summer revealed a strong inverse relationship between the extreme flow speeds and lobster density at the wave-exposed site, a moderately negative relationship for the semi-protected site, and no relationship between the smaller range of flow speeds and low densities at the sheltered site (Fig. 4A–C). Differences in the Spearman correlations of speed and density were statistically significant, and the means of the correlations were progressively more negative with increasing wave exposure (Table 3).

Time courses recorded during neap tide runs showed that some intertidal foraging occurred under those conditions. The data also suggest that overall lobster densities decrease on wave-exposed sites and increase on sheltered sites as nocturnal tides advance from spring to neap levels, although more runs must be made to confirm this trend (Fig. 5). *Panulirus interruptus* is strictly nocturnal (Mitchell et al. 1969), and the effect of sunlight was evident in individual time-lapse runs that spanned the time of predicted sunset (e.g., Fig. 2B, vertical line indicates time of sunset). Moonlight did not stop intertidal foraging (Fig. 6), but knowing whether there are more subtle relationships between moonlight and shallow water foraging would require more sampling.
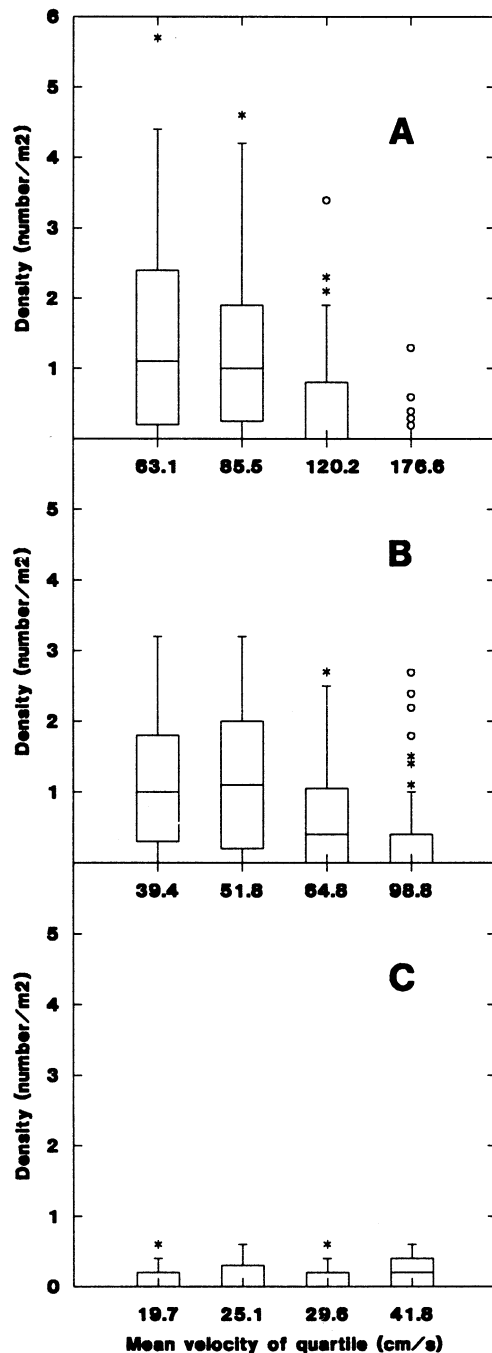

Fig. 4A–C Relationship between frequencies of maximum flow speed and densities of foraging lobsters. Speed records are divided into *quartiles* and the corresponding distributions of densities represented with *box plots*. The boxes were ranked along the *x*-axis according to the mean bottom flow speed of that quartile. The *line* transecting each *box* indicates the median density; *upper and lower sides* at the first and third quartiles; and *gates, asterisks, and circles* at progressively more extreme ranges from the medians

Field experiment

The ANOVA of initial mussel densities indicated no differences among treatment groups at the outset of the experiment (Table 4). By chance assignment of the experimental plots, the sham cage group showed a higher mean

Fig. 5 Comparison of representative time-lapse runs between nocturnal spring (*left*) and neap tides (*right*) at sites A, B, and C. *Axes, symbols, and curves* as in Fig. 2. *Vertical lines* mark time of sunset
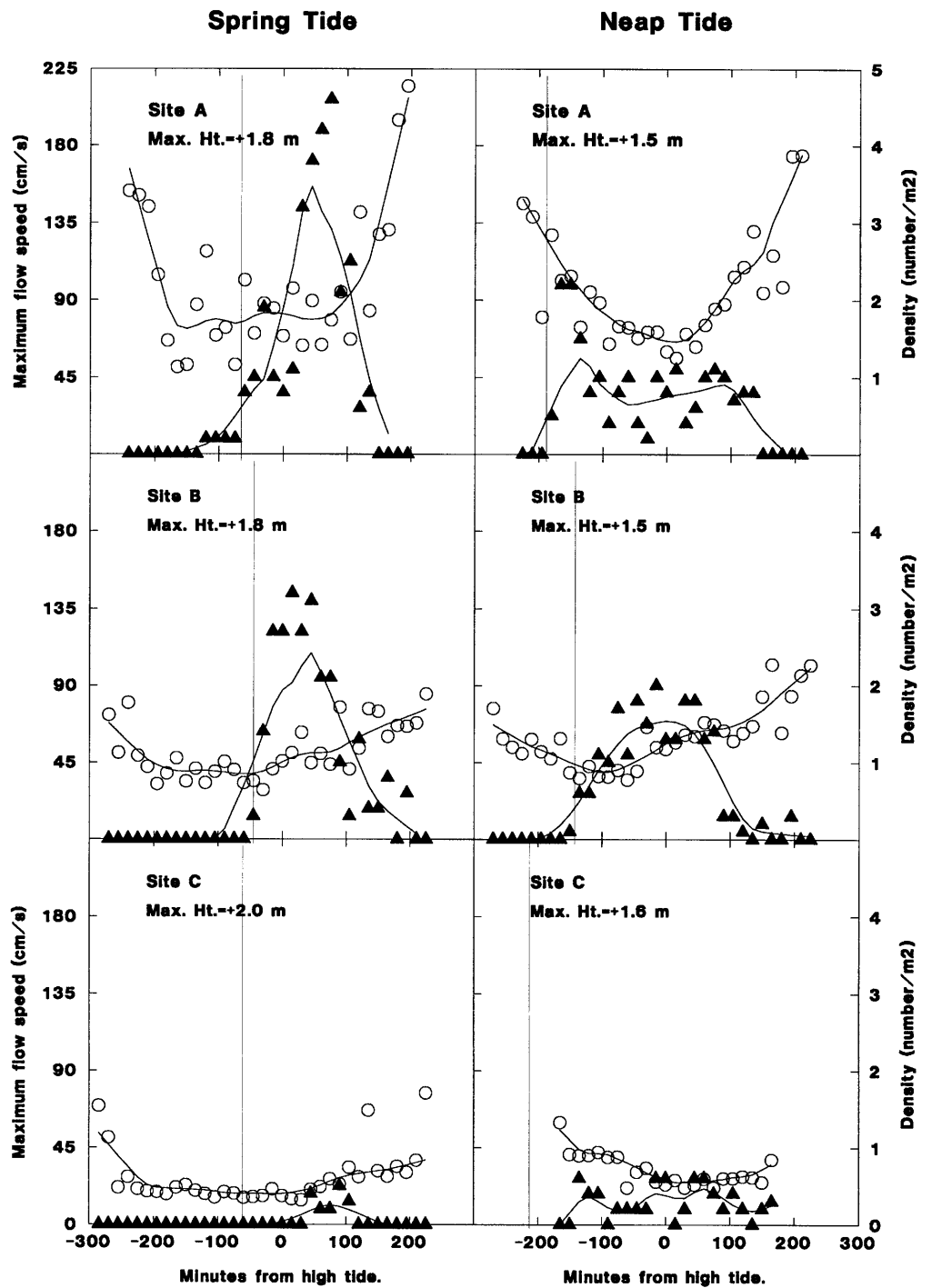

Table 4 Initial densities in the exclosure experiment. Mean number±1 SE of mussels in the 800-cm² plots are tabulated with respect to treatment group, species, and size class. *P*-values for block effect (replicates) and treatment effect in the ANOVAs are tabulated with respect to mussel species and size class

Species and size class	Open	Sham	Cage	P_{block}	$P_{treatment}$
M. californianus <5 cm	16.2±2.6	20.0±6.5	23.6±6.5	0.418	0.572
M. californianus >5 cm	30.8±3.6	40.4±4.8	29.4±1.9	0.186	0.074
M. galloprovincialis total	5.4±1.6	4.8±1.9	3.2±1.0	0.027	0.345

Fig. 6 Comparison of time-lapse runs made on new and full moon spring tides. *Axes, symbols, and curves* as in Fig. 2. *Vertical lines* mark time of sunset

FULL MOON　　　　**NEW MOON**
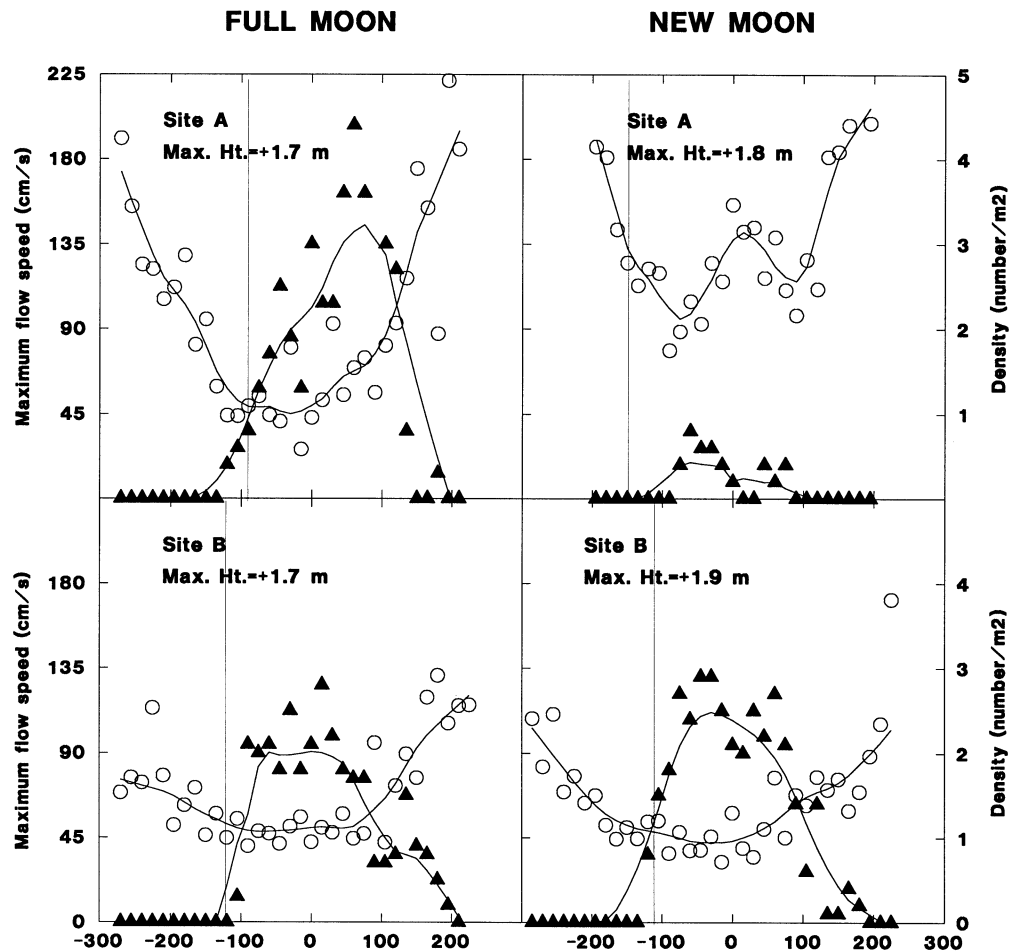
density of large *M. californianus* than either the control and cage treatment, but these differences were not statistically significant. Initial densities of *M. galloprovincialis* differed among the replicates (significant block effect, Table 4). Patchy, gregarious recruitment is characteristic of the very similar species *Mytilus edulis* (Petersen 1984; discussion in Pawlick 1992), and this factor may have been responsible for the significant block effect.

During the experiment, divers observed lobsters feeding on mussels throughout the uncaged portion of the mussel bed, including the control plots. Mussels dominated the cover of experimental plots during the experiment; the small changes in percent covers did not differ among the treatment and control groups (Table 5). However, the composition of the mussel clumps did change, including a significant increase within exclosure plots, and a corresponding decrease in control plots, of juvenile and small adult *M. californianus* (Table 6). *M. galloprovincialis,* which did not exceed 5 cm in length, also showed a significant increase in treatments relative to controls (Table 6). The lobsters prefer to consume small *M. californianus* and *M. galloprovincialis* over large *M. californianus* (Robles et al. 1990). In the field experiment, the lobsters decreased the densities of the "young of the year" *M. californianus* and *M. galloprovincialis*

Table 5 Percent covers of mussels at beginning and conclusion of the mussel bed exclosure experiment. Mean percent *Mytilus* spp.±1 SE are tabulated with respect to treatment group. Cover of mussels on any given plot consisted of >90% *M. californianus*. ANOVA of change in percent covers for each plot compared among experimental groups: $F=0.466$, $df=2,12$; $P=0.639$

	Open	Sham	Cage
Beginning	87±3	87±4	88±4
Conclusion	82±3	85±6	87±6

without significantly affecting the total percent cover of mussels. The seeming contradiction of changes in density without changes in percent cover results from the arrangement of individuals within the clumps. The juvenile mussels >1 cm were often attached on the sides of the larger mussels, contributing little to the primary cover. The mussels grow and change orientation, offsetting declines in percent cover resulting from predation (discussion in Petraitis 1995; Reusch and Chapman 1997).

The ANOVA for percent changes (Table 6) also revealed significant block effects. The causes of the differences between replicates remain unknown, but some factor varying with location within the mussel bed – such as

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Table 6 Percent changes in mussel densities in the exclosure experiment. Mean percentages±1 SE are tabulated with respect to treatment group, species, and size class. *P*-values for block effect (replicates) and treatment effect in the ANOVAs are tabulated with respect to mussel species and size class

Species and size class	Open	Sham	Cage	P_{block}	$P_{treatment}$
M. californianus <5 cm	−36.3±19.1	−45.6±4.6	+108.2±110.7	0.089[a]	0.002[a]
M. californianus >5 cm	−8.3±7.4	−15.2±5.2	−3.3±10.1	0.045	0.362
M. galloprovincialis total	−6.3±48.1	+57.3±95.4	+296.7±90.8	0.031	0.010

[a] Data for ANOVA rank transformed to achieve homoscedasticity

possible differences among the replicates in their accessibility to the lobsters – is implicated.

Discussion

Hydrodynamic regimes and lobster foraging

The combined force of lift and drag is directly proportional to the square of the bottom flow speed (Denny 1988). Acceleration reaction is probably negligible, because velocity differentials over the length of a lobster are small (Denny 1995; M.W. Denny, personal communication). The comparatively large drag coefficients of the "shrimp-like body form" (Daniel and Meyhofer 1989; Denny 1995) suggest that even moderate flow speeds may exert a significant burden to movement, if not cause dislodgement. Howard and Nunny (1983) present experimental evidence, quantitative observations of Atlantic clawed lobsters (*Homarus gammarus*) in flume tanks, that suggests foraging may be suppressed by flow speeds as low as 45 cm s⁻¹. They also found a negative correlation between flow speed and lobster abundance over comparatively large spatial scales in surveys of the shallow subtidal zone (*Homarus* is not known to enter the intertidal zone). We found spatial differences in the strength of the association between bottom flow speed and the densities of spiny lobsters. On wave-exposed sites, which showed the greatest range in both flow speeds and lobster densities, significant negative correlations developed over a temporal scale of hours.

The short time courses of the speed/density relationships are most interesting because the changing lobster densities cannot be explained by fluctuations of prey abundance, lunar phase or other comparatively long period phenomena. Abundances of small mussels on the sites decline gradually, over successive weeks under the influence of predation (Robles 1987, 1997). Comparing time-lapse runs between new and full moons gave no indication of an effect of lunar phase, apart from its relation to water levels and flow speeds (see below). Potential predators of the lobsters, octopus (*Octopus bimaculoides*) and leopard sharks (*Triakis semifasciata*) were seldom observed in the intertidal zone; nor did we see, whether in the time-lapse or in our numerous dives on or below the sites, periodic abundances or activities in these species that might account for the patterns of *Panulirus* movements. Thus, patterns of water motion alone suggest themselves as the factor constraining short term patterns of lobster abundance.

The changes in maximum bottom flow speeds over the course of a tide (e.g., Fig. 2) arise from the hydrodynamics of shallow water waves. The profiles of the bottom seaward of the sites are steep enough that wave heights do not change as they approach the shoreline. The recordings were made when the sites were continually submerged and not within the swash (see Denny 1995 for discussion). Therefore, linear wave theory applies, and bottom flow speeds will be inversely proportional to the depth (Denny 1995). One would expect maximum bottom flow speeds, and hydrodynamic stresses, to follow a U-shaped curve, inverse to the changing tidal levels. This pattern might be confounded if significant wave heights changed over the course of a run. However, surface waves in the spring/summer period originated from long duration winds far to the south and significant wave heights remained relatively constant for prolonged periods (Coastal Data Information Program 1985–1995). Bottom flow speeds at wave-exposed sites followed the expected, U-shaped pattern, with minimum speeds occurring at extreme high tide. On sheltered shores, variation in bottom speeds was comparatively low. As predicted, the time courses of lobsters densities roughly traced mirror images of the flow speed curves (e.g., Fig. 2).

The time-lapse findings appear to be part of a general pattern. Snorkeling at high tide along other shorelines of the California Channel Islands we have observed that lobsters forage most frequently on spring high tides from May to September. Lobster aggregations apparently occur at exposed locations in the least stressful hydrodynamic circumstances found there: extreme high water during spring tides in the months of least wave energy (Coastal Data Information Program 1985–1995).

While patterns of water flow may shape some aspects of the periodicity of lobster foraging, prey abundance appears to influence the magnitude of peak lobster densities. At nightfall the lobsters trek from their subtidal dens into the intertidal zone, where they feed almost exclusively on mussels (Robles 1987; Robles et al. 1990; Robles and Robb 1993). Adult *M. californianus* were more abundant, and the densities of newly recruited juveniles higher, on more wave-exposed sites. Thus, the highly mobile lobsters were able to exploit a brief window of opportunity provided by the hydrodynamic regime, forming the densest aggregations in areas with the highest densities and replenishment rates of their prey.

Prey concentrations and the concept of refugia

It cannot be said, by any rigorous definition, that the mussel beds resided in a spatial refuge from predation generated by hydrodynamic and desiccation stresses. In hydrodynamically favorable periods, the lobsters crawled over the beds, preying on smaller mussels, sometimes pulling up large mussels to gain better purchase on the shell before attempting to crush it, or to gain better access to smaller ones (Robles et al. 1990). Although strictly aquatic, the lobsters forage across the complete vertical range of the tides, and the mussel bed on the experimental site fell completely within the lobsters' foraging range (Robles 1987; Robles et al. 1990). The exclosure experiment demonstrated an effect of predation in an area that might otherwise have been viewed as a spatial refuge. Therefore, lobster predation has been found to affect mussel abundances at midshore levels over the entire wave exposure gradient (Robles 1997), and both inside (this study) and outside (Robles and Robb 1993; Robles 1997) the mussel beds.

Other exceptions to the refuge hypothesis have been reported. Shortly after the original statement of the refuge hypothesis (Connell 1970; Paine 1974), Paine (1976) published observations of subtidal sea mounts (pinnacles of rock that do not break the surface at low tide). He found massive beds of large mussels (*M. californianus*) persisting despite predation by very large sea stars (*Pisaster ochraceus*). Similarly, Reusch and Chapman (1997) describe the persistence of shallow subtidal beds of the mussel *M. edulis* exploited by the sea star *Asteria rubens*. These subtidal examples are relevant because they involve some of the same prey species cited in reference to intertidal prey refuges, but desiccation stress was not a factor protecting these prey concentrations. Furthermore, the sea stars were large enough to kill most, if not all, of the mussels present in the beds. Within the intertidal zone of rocky shores in the Pacific Northwest, beyond the northern distribution limit of the spiny lobsters, observations by divers at high tide revealed that *P. ochraceus* sometimes forages above the lower boundary of beds of *M. californianus* (C.D. Robles and R.A. Desharnais, unpublished work), suggesting that here too mussel beds do not occur in inviolable refuges.

Without recourse to absolute spatial refugia, mussel densities and size frequencies within the bed are influenced by the dynamics of size-dependent predation and varying prey recruitment. Regarding size-dependent predation, laboratory electivity trials (Robles et al. 1990) show that the mussels gain resistance to crushing as they grow larger, and, when given a choice, lobsters kill smaller mussels more frequently. Although kill rates in the field probably diminish greatly with increasing mussel size, direct observations by divers and shell collections bearing characteristic damage marks show that the largest lobsters do sometimes kill the largest mussels on the shore (Robles et al. 1990). The decrease in the numbers of large (>5 cm long) *M. californianus* evident in the controls (Table 6) did not represent a significant change in the survivorship of this size class. However, power analysis (Cohen 1988) shows that given the small sample size (5 replicates), a type I error rate of 0.05, and the observed sample variability, a 20% discrepancy between controls and treatment in the survivorship of *M. californianus* >5 cm long would be confirmed only 30% of the time. Therefore, it seems plausible that an effect of predation on all size classes was present, but that a relatively low rate of consumption, coupled with the low power of the test, made an effect of predation on larger sizes difficult to confirm.

Regarding recruitment, the progressive increase from the sheltered to wave-exposed sites in the densities of mussel recruits (Table 2) represents a general spatial trend for *M. californianus*. Previous surveys of the natural substrata show higher rates of recruitment of *M. californianus* at relatively wave-exposed sites (Robles 1997). Investigations using artificial spat collectors in Southern California and the Pacific Northwest show similar differences between protected and wave-beaten shores in the recruitment of *M. californianus* (Menge 1992; Menge et al. 1994; C.D. Robles, K. Johnson, A. Martel, and B. Chesney, unpublished work). All the prior work either examined similar natural substrata, or deployed identical artificial collecting surfaces, over all values of wave exposure. Therefore, varying wave action itself, rather than differences in the substratum, is implicated in the consistent spatial differences in recruitment. In the present study, spatial differences in wave action appears to have influenced both rates of prey loss and replacement.

For species with pelagic larvae, a dense intertidal population can persist only if losses to predators and other factors are recouped by recruitment from planktonic larval stocks. In the *Mytilus-Panulirus* system, predation appears to be the primary source of morality of small mussels on midshore levels at all points along the wave exposure gradient (Robles and Robb 1993; Robles 1997; this study). Therefore, the sum of the evidence suggests that concentrations of mussels on the wave-exposed shores owe their existence to a shift in the balance of the predator-prey interaction. The shift does not arise from the suppression of effective predation, although hydrodynamic stresses and tidal emergence do appear to weigh in the balance. Rather, along the gradient from sheltered to wave-exposed sites, a point is reached beyond which rates of prey recruitment surpass the corresponding rates of predation, supporting dense populations.

References

Cleveland WS (1993) Visualizing data, 1st edn. Hobart, Summit, New Jersey, pp 25–28

Cohen J (1988) Statistical power analysis for the environmental sciences. Lawrence Erlbaum, Hillsdale

Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of Thais. Ecol Monogr 40:49–78

Connell JH (1972) Community interactions on marine rocky intertidal shores. Annu Rev Ecol Syst 3:169–192

Connell JH (1975) Some mechanisms producing structure in natural communities. In: Cody ML, Diamond J (eds) Ecology and evolution of communities. Belknap, Cambridge, pp 460–490

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J Exp Mar Biol Ecol 93:11–45

Daniel TL, Meyhofer E (1989) Size limits in escape locomotion of carridiean shrimp. J Exp Biol 143:245–265

Denny MW (1988) Biology and the mechanics of wave-swept environments. Princeton University Press, Princeton

Denny MW (1995) Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. Ecol Monogr 65:371–418

Denny MW, Daniel TL, Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. Ecol Monogr 55:69–102

Howard AE, Nunny RS (1983) Effects of near-bred current speeds on the distribution and behavior of the lobster, *Homarus gammarus* (L.). J Exp Mar Biol Ecol 71:27–42

Kitching JA, Sloane JF, Ebling FJ (1959) The ecology of Lough Ine. 8. Mussels and their predators. J Anim Ecol 28:331–341

Koehl MAR (1976) Mechanical design in sea anemones. In: Coelenterate ecology and behavior. Plenum, New York, pp 23–31

Koehl MAR (1982) Interaction of moving water and sessile organisms. Sci Am 247:124–134

Lewis JR (1964) The ecology of rocky shores. English University Press, London

Marsh CP (1986) Rocky intertidal community organization: the influence of avian predators on mussel recruitment. Ecology 67:771–786

Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. Ecol Monogr 46:355–393

Menge BA (1978a) Predation intensity in a rocky intertidal community: Effect of algal canopy, wave action, and desiccation on a predator feeding rates. Oecologia 34:17–35

Menge BA (1978b) Predation intensity in a rocky intertidal community: relation between predator foraging activity and environmental harshness. Oecologia 34:1–16

Menge BA (1983) Components of predation in the low zone of the New England rocky intertidal region. Oecologia 58:141–155

Menge BA (1992) Community regulations: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765

Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol Monogr 51:429–450

Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol Monogr 64:249–286

Mitchell CT, Turner CH, Strachan AR (1969) Observations on the biology and behavior of the California spiny lobster, *Panulirus interruptus* (Randall). Calif Fish Game 55:121–131

Muntz L, Ebling FJ, Kitching JA (1965) Predatory activity of large crabs. J Anim Ecol 34:315–329

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–76

Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120

Paine RT (1976) Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858–873

Pawlick JR (1992) Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr Mar Biol Annu Rev 30:273–335

Petersen J (1984) Larval settlement behavior in competing species: *Mytilus californianus* Conrad and *M. edulis* L. J Exp Mar Biol Ecol 82:147–159

Petraitis PS (1995) The role of growth in maintaining spatial dominance by mussels *(Mytilus edulis)*. Ecology 76:1337–1346

Reusch TBH, Chapman ARO (1997) Persistence and space occupancy by subtidal blue mussel patches. Ecol Monogr 67:65–87

Robles CD (1987) Predator foraging characteristics and prey population structure on a sheltered shore. Ecology 68:1502–1514

Robles CD (1997) Varying recruitment in constant species assemblages: implications for predation theory of intertidal communities. Ecology 78:1400–1414

Robles CD, Robb J (1993) Varied carnivore effects and the prevalence of intertidal algal turfs. J Exp Mar Biol Ecol 166:65–91

Robles CD, Sweetnam DA, Dittman D (1989) Diel variation in intertidal foraging of *Cancer productus* L. in British Columbia. J Nat Hist 23:1041–1049

Robles CD, Sweetnam DA, Eminike J (1990) Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. Ecology 71:1564–1577

Seed R, Suchanek TH (1992) Population and community ecology of *Mytilus*. In: Gosling EM (ed) The mussel *Mytilus*. Elsevier, Amsterdam, pp 87–169

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, New York

Vogel S (1981) Life in moving fluids. Princeton University Press, Princeton

Wootton JT (1993) Size-dependent competition: effect on the dynamics vs. the end point of mussel bed succession. Ecology 74:195–206