individuals, SD's = 1.4 and 1.0 μm, respectively). I targeted the genus *Navicula* because members of this genus are small (therefore ingestible), and have been employed in postlarval feeding experiments for closely related gastropod taxa (Moss and Tong, 1992; Kawamura et al., 1998; Martinez-Ponce and Searcy-Bernal, 1998).

Both algae were cultured in an incubator at 16.0^{O}C under a 12:12 Light:Dark photoperiod. The 50 ml culture tubes were smashed, immediately prior to running the experiment, such that algal-bearing fragments could be placed in settlement dishes. An adult *Mucus* treatment group was prepared by allowing adult *L. digitalis* to crawl on sanded-glass microscope slides for ~24 hrs. prior to the experiment. The adults were then removed and the slides placed in settlement dishes. In addition to the four treatment groups, positive and negative controls (untreated *High* rock and 0.45μm FSW, respectively) were also run. This experiment was run twice using offspring of two different sets of parents spawned on April 14 and April 25. Larvae spawned on April 14 and April 25 were introduced to the isolates on April 21 and May 2, respectively. Larvae were introduced, sampled and scored in the same manner as explained for the above settlement experiments.

To explore whether or not larvae of *L. digitalis* settle onto *Pollicipes polymerus*, solitary individuals of the latter species were individually placed into six replicate *Pyrex* custard dishes filled with 0.45μm FSW. Since *P. polymerus* were absent from my South Cove site, they were collected from beneath the OIMB pier, which is about 5km north of South Cove, and 1km inside the mouth of Coos Bay. The six barnacle dishes, as well as six replicates of *High* rock (positive control) and a sterile dish (negative control) were

filled with 0.45μm FSW (total dishes = 3 treatments x 6 replicates = 18 dishes), and 50 *L. digitalis* larvae were individually pipetted into each dish. Dishes were sampled and scored as in the above experiments. This experiment was run twice using offspring of two different sets of parents spawned on April 14 and April 25. Larvae spawned on April 14 and April 25 were introduced to the isolates on April 21 and May 2, respectively. Larvae were introduced, sampled and scored in the same manner as explained for the above settlement experiments.

Data Analysis

For all settlement experiments, I compared the percentage of individuals having undergone metamorphosis on each substratum. Although velar shedding and adult shell growth are sequential events during metamorphosis, I only included individuals exhibiting the latter condition in my statistical analysis because: a) they are much more reliably scored, and b) they are more indicative of a successful transition to the postlarval life stage. Statistical comparisons were made for results recorded on day 6, and were analyzed with one-way analyses of variance (ANOVA's) followed by Tukey's Multiple Pairwise Comparison tests ($P < 0.05$). Analyses were run using Statistica (Version 5.1, Statsoft 1996) software. Because data were recorded as percentages, they were arcsine-transformed prior to analysis. In no case did the data violate assumptions of normality (Kolmogorov-Smirnov test, $P > 0.05$) or homogeneity of variances (Cochran's C test, $P > 0.05$).

Juvenile growth rates on *High/Adults* and *Mid/Adults* rock were compared using a repeated-measures analysis of variance design (RM-ANOVA). This data set did not violate assumptions of normality (Kolmogorov-Smirnov test, $P > 0.05$) but did violate assumptions of sphericity (Mauchly's test, $P < 0.05$). Consequently, the appropriate degrees of freedom were adjusted with a Greenhouse-Geisser Epsilon, and a corresponding P value was calculated from a table of F statistics (Girden 1992). Late into this experiment, three of six dishes in the *High/Adults* treatment were intentionally abandoned, and so statistical analysis at all sample intervals employed the remaining three *High/Adults* replicates and three replicates selected randomly from the *Mid/Adults* treatment.

Results

For larvae settled onto *High*, *Mid*, and *CCA* rocky substrata on Februaury 18, metamorphosis (adult shell growth) was most successful on the *High* rock collected from adult *L. digitalis* habitat (Fig. 6B). The percentages of larvae that underwent metamorphosis onto the *High* and *High/Adults* treatment surfaces were 31.0 (SD = 10.4) and 26.6% (SD = 7.0), respectively, and there was no statistical difference between the two (Tukey's, $P = 0.92$). The *Mid/Adults* and *CCA/Adults* treatments induced metamorphosis whereas the *Mid* and *CCA* treatments did not. The percentages of larvae that underwent metamorphosis onto the former two were 10.3 (SD = 3.4) and 8.6% (SD = 3.2), respectively. These percentages were not statistically different from each other (Tukey's, $P = 0.99$), but both were significantly lower than percentages of

metamorphosis onto the *High* and *High/Adults* treatments (Tukey's, all values for P are < 0.001). No metamorphosis occurred in the control dishes. Although one larva initiated shell growth in a *CCA* treatment dish, this was not significantly different from the control (Tukey's, $P = 0.98$).

A repeat of the above experiment, initiated on March 8, yielded very similar results (Fig. 7B). The percentage of larvae that underwent metamorphosis onto the *High* and *High/Adults* treatments were 23.3 (SD = 3.2) and 20.3% (SD = 4.9), respectively, and there was no statistical difference between the two (Tukey's, $P = 0.99$). The *Mid/Adults* and *CCA/Adults* treatments induced metamorphosis whereas the *Mid* and *CCA* treatments did not. The percentages of larvae that underwent metamorphosis onto the former two were 16.3 (SD = 3.6) and 6.3% (SD = 3.1), respectively. These percentages were statistically different from each other (Tukey's, $P < 0.05$). Unlike the February results, percent metamorphosis onto the *Mid/Adults* treatment was not statistically different than percentages onto the *High* and *High/Adults* treatment groups (Tukey's, $P = 0.96$ and 0.93, respectively). No metamorphosis was induced by the *Mid* or *CCA* treatment groups.

Seventy days after settlement on March 8, postlarvae raised on the *High/Adults* substratum were approximately 2mm long and twice the length of siblings raised on the *Mid/Adults* substratum (Fig. 8). The size difference across treatments was highly significant (RM-ANOVA, $P < 0.01$).

In two separate experiments, the macrophytes *Ulva* sp., *Enteromorpha contorta*, *Alaria marginata*, and *Polysiphonia* sp. all failed to induce metamorphosis in larvae of *L. digitalis* (Figs. 9A & B). Percentages of larvae that underwent metamorphosis onto the

positive control (*High* rock) were 26.5 (SD = 2.9) and 34.4% (SD = 4.6), and these percentages mirrored those from the initial settlement experiments.

When larvae were exposed to the isolated components of *High* rock that were suspected as settlement cues, the only isolate upon which they consistently settled and metamorphosed was the filamentous green alga (Figs. 10A-D). Of the larvae settled on April 21, and scored six days later, 33.0 (SD = 8.7) and 26.6% (SD = 8.5) metamorphosed upon the positive control and green alga, respectively. There was no statistical difference in the percent metamorphosis induced by these two treatments (Tukey's, $P = 0.43$). Of the larvae settled on May 2, and scored six days later, 35.0 (SD = 4.5) and 8.7% (SD = 3.2) settled on the positive control and green alga, respectively. During this experiment, statistically fewer larvae metamorphosed upon the green alga isolate than on the positive control (Tukey's, $P < 0.01$). Larvae settling and metamorphosing in the presence of the filamentous green alga grazed upon it (Fig. 11).

There was no statistical difference between the number of individuals that metamorphosed onto *High* rock and *Pollicipes polymerus* (Fig. 12). Of larvae introduced to settlement dishes on April 21, and sampled after six days, 33.0 and 38.0% settled and metamorphosed onto the *High* rock and *P. polymerus*, respectively. There was no statistical difference in the percent metamorphosis induced by these two treatments (Tukey's, $P = 0.50$). No metamorphosis occurred in the sterile control dishes. Of the larvae introduced to settlement dishes on May 2, and sampled after six days, 33.5 and 34.4% settled and metamorphosed onto the *High* rock and *P. polymerus*, respectively.

There was no statistical difference in the percent metamorphosis induced by these two treatments (Tukey's, $P = 0.89$). No metamorphosis occurred in the sterile control dishes.

It is important to note that, at the time larvae were censused in the above experiments (t= 6 days), not all individuals had died or metamorphosed. Hence, it might appear as though subsequent metamorphosis could alter the results of these experiments. However, most unsettled and settled larvae were near death during the day 6 census, and held little promise of survival. Subsamples taken 8 days after introduction confirmed that such larvae died almost invariably.

Discussion

During the course of this study, the only field-collected substrata that induced settlement and metamorphosis of *L. digitalis* larvae were rock fragments collected from adult habitat (*High* treatment group), and mid-intertidal substrata upon which adult *L. digitalis* were allowed to crawl (*Mid/Adults* and *CCA/Adults* treatments). In contrast, neither of the two rocky substrata collected from the intertidal zone below *L. digitalis* habitat (*Mid* and *CCA* treatments), nor any of the four macroalgal species, induced settlement and metamorphosis. These results suggest that, at the site from which I collected adults and substrata, larvae of *L. digitalis* recruit directly into the adult habitat. (Additional settlement and metamorphosis of larvae onto the *High* rock, during experiments in which it was used as a positive control, support this conclusion.) An alternative explanation is that field settlement does indeed occur in the mid intertidal zone, but the target settlement surface(s) was not included in this experiment. This

scenario seems unlikely, because the two substrata collected from the mid intertidal (*Mid* and *CCA* treatments) dominated, almost exclusively, the surface area open to settlement at this tidal level. Furthermore, the role of crustose corraline algae as a settlement surface for larvae of gastropods (Steneck 1982; Morse and Morse 1984; McGrath 1992; Duame et al. 1999) and other taxa (Barnes and Gonor 1973; Rumrill and Cameron 1983; Lambert and Harris 2000) is well documented. Thus, if *L. digitalis* had an evolutionary history of mid-intertidal settlement, this dominant and persistent habitat component would be a likely target surface. This evidence, in concert with the positive results of this study, suggests that recruitment of *L. digitalis* larvae into adult habitat is direct.

A common criticism of experiments such as this one, in which larvae are soaked in standing water with a single settlement surface, is that they are not representative of natural conditions. Critics of this approach contend that settlement in such experiments may be driven by default responses due to the absence of a preferred substratum. This seems especially likely in situations where larvae are maintained in a particular vessel until they exhaust their ability to extend their competent period (see Pechenik et al. 1998) and die. I acknowledge the legitimacy of this line of reasoning, but believe that its logic lends confidence to the interpretations of my results. Specifically, if larvae fail to settle onto a particular substratum during the duration of their competence period, as was the case for the *Mid*, *CCA* and macroalgal substrata, it seems unlikely that they will do so in nature. In contrast, settlement of larvae onto the *High* rock substratum was probably not a default response. This is true because three days after larvae were introduced to settlement surfaces, metamorphosis was well underway or complete among individuals

that ultimately survived as newly settled juveniles. Based on developmental schedules for closely related prosobranchs (Kay, in review; Dodd 1955; Kessel 1964; Koike 1978; Holyoak 1988; Moran 1997), larvae on the *High* rock appear to have settled and initiated metamorphosis within the first day of exposure to this substratum. The results of this study, both positive and negative, do not appear subject to the criticism that default responses might account for the results obtained. Finally, I cannot refute the criticism that water flow can influence settlement patterns in nature (e.g. Boxshall 2000), and that this potential influence was absent during my studies.

Although rates of successful metamorphosis onto the *High* rock substratum might appear relatively low (20-30%), they do not necessarily indicate an inadequacy of the *High* rock as a settlement surface for *L. digitalis*. This is true because stark survivorship bottlenecks at the time of metamorphosis are not uncommon in studies of gastropod settlement. Among Haliotids for example, which are the most closely-related taxon for which there are data regarding metamorphic dynamics, survival rates through metamorphosis are often lower than 35% (Hahn 1989; Moss and Tong 1992; Searcy-Bernal et al. 1992). The apparently low metamorphic rates of *L. digitalis* larvae onto *High* rock during this study do not compromise the credibility of the results.

Differential growth rates of larvae settled onto the *High/Adult* and *Mid/Adult* substrata support the hypothesis that recruitment is direct. Not only did larvae that were settled onto the former surface outgrow their counterparts on the latter surface, but they appeared qualitatively more healthy: their shells were less brittle, they adhered to the surface more tenaciously, and they moved more rapidly when displaying flight behavior.

The direct recruitment pattern hypothesized for *L. digitalis* contrasts with patterns documented for other high intertidal limpet species. Specifically, larvae of some high-intertidal limpet species settle at a low tidal level, where the habitat is distinctly different than that of the adults, and subsequently migrate upward to join their conspecifics (Corpuz 1981; Delany et al. 1998). This indirect recruitment pattern might safeguard young individuals from physical stresses of the adult habitat (e.g. temperature and desiccation) at a life stage when limpets are most susceptible due to their small size (Davies 1969; Wolcott 1973; Chow 1975). In censuses of *L. digitalis* populations, small juveniles are usually most abundant at the lower reaches of the adult range (Frank 1965; Breen 1972). This distribution might be driven by the juveniles' intolerance to physical stresses encountered higher in the adult habitat. In this regard, *L. digitalis* juveniles are similar to limpet species that recruit indirectly into adult habitat. The fundamental ecological difference, however, is that *L. digitalis* occupy a single intertidal habitat type during the benthic stage of their life cycle, whereas indirect recruiters utilize two or more (Corpuz 1981; McGrath 1992; Delany et al. 1998). It is probable that, high within the adult habitat, newly settled juveniles of *L. digitalis* moderate physical stresses by occupying protective microhabitats (Kay, pers. obsv.).

One result yielded by the *High* rock isolate experiments confounds the results of experiments conducted with field-collected substrata. In particular, it is vexing that the adult *Mucus* treatment did not induce settlement during the isolate experiments, whereas *Mid* and *CCA* substrata that had been exposed to adults did induce settlement. One interpretation of this result is that some aspect of the adults' presence other than the

mucus may have triggered settlement onto the *Mid* and *CCA* substrata, but the active agent failed to be imparted to, or retained on, the sanded glass surfaces employed in the isolate experiments. Another possibility is that the adult mucus is only effective as a cue when there is a food source (e.g. diatoms or bacteria) accompanying it at the settlement site. Both of these interpretations are supported by evidence from haliotid research. Specifically, naturally laid mucus trails induce settlement for several species, but Seki and Kan-no (1981) found that mucus isolated from the pedal sole did not induce metamorphosis for larvae of *Haliotis discus-hannai* (reviewed by Davies and Hawkins, 1998). Although the adult *Mucus* isolates did not induce settlement of *L. digitalis* larvae, the results obtained by exposing *Mid* and *CCA* substrata to adults suggests that adults may influence settlement in nature. The role of conspecific adults as a possible settlement cue should not be dismissed.

The failure of the diatom *Navicula* sp. to induce settlement and metamorphosis is not surprising. Although diatoms are abundant and heavily grazed by *L. digitalis* in the high intertidal (Castenholz 1961; Nicotri 1974), they are also ubiquitous throughout the entire inter- and subtidal. Thus, a diatom cue could be a vague and/or potentially misleading indicator of adult habitat. The accuracy of diatoms as a settlement cue could be refined if larvae respond to taxa that are confined to the upper intertidal. It is possible, therefore, that species of diatom other *Navicula* sp. may induce settlement.

The percentage of *L. digitalis* larvae that metamorphosed onto the filamentous green alga (FGA) paralleled the percentage of metamorphosis onto *High* rock from the adult habitat. Although it is true that, during the second *isolate* experiment, significantly

fewer larvae metamorphosed onto the FGA compared to the *High* rock control, this response was probably due to the condition of the algal cultures. The cultures of this slow-growing alga that were employed during this second trial were not as luxuriant as those used in the first trial. The relatively small amount of algal material in the cultures may have failed to induce the same level metamorphosis as their more luxuriant counterparts (Morse and Morse 1984; Krug and Manzi 1999). It should be mentioned that these cultures were not axenic, and so the influence of bacteria in these cultures cannot be dismissed. The possibility of a bacterial cue seems unlikely, however, in light of the fact that other axenic surfaces (e.g. *Mid*, *CCA*, and macroalgal treatment groups) failed to induce settlement.

Larvae that metamorphosed in the presence of the filamentous green alga actively fed upon it. Initial growth was similar to that of *High* rock settlers, but at a size of ~500 μm their shells became brittle, tissues were not as highly pigmented (symptoms of dietary deficiency?), and growth slowed as consumption outstripped algal growth in the settlement dishes. This latter fact is a testament to the apparent impact of grazing upon this alga in the field.

For some species of patellogastropod limpets, the preferential settlement of planktonic larvae onto marine algae is well documented (and is suggested for many others). In all cases that I am aware of, however, the target alga serves not only as the adult food source but also as the adult habitat (Proctor 1968; Fretter and Manly 1977; Steneck 1982; Krug and Manzi 1999). The ecological value of this settlement pattern is quite apparent: the adult habitat is directly associated with the settlement cue. In contrast,

the green alga that induced settlement and metamorphosis of *L. digitalis* larvae during this study was not, by strict definition, an inexorable component of the adult habitat. For the most part, however, the alga was common and abundant in *L. digitalis* habitat along ~ 4 km of rocky coastline near my site at the South Cove of Cape Arago.

With regard to the geographic distribution of the filamentous green alga, and its effectiveness as a settlement cue, certain complications become apparent. For example, if the range of the alga is more restricted than that of *L. digitalis*, or it is locally absent in patches of suitable habitat, then alternative cues must be operative for *L. digitalis* larvae settling in its absence. In a species with a range as extensive as *L. digitalis*, it seems likely that multiple settlement cues might exist throughout the range. Theoretically, multiple settlement cues could be the product genetic adaptation in distant populations. Alternatively, such variation could be physiologically determined by local conditions such as differences in maternal diet. This latter possibility could be readily explored experimentally. Regardless of how multiple cues become established in semi-isolated subpopulations, a potential ecological consequence persists: larvae that are "conditioned" to a particular settlement cue, whether genetically or environmentally, might be limited in their ability to settle and recruit into habitats outside the range of their established cue. The impacts of such limitations in *L. digitalis* larval ecology, if they exist at all, are highly speculative.

The settlement of *L. digitalis* larvae onto *P. polymerus* suggests that, in nature, recruitment onto this host might be direct. Since this host is restricted to the upper intertidal zone, settlement onto *P. polymerus* is consistent with the hypothesis that

recruitment into the high intertidal is direct, and not dependant upon initial settlement at lower elevations on the shore. Unfortunately, I was unable to explore potential specific settlement cues associated with *P. polymerus*. The filamentous green alga (FGA) discussed above was seen on two of the twelve replicate stalks during the course of these experiments, but was minute on these two and entirely absent from the other 10 replicate stalks. At the time of collection, the individual *P. polymerus* stalks that I employed in this experiment bore no adult *L. digitalis*. The possibility of contact with adult *L. digitalis* immediately prior to collection, however, cannot be dismissed. Such contact could have influenced settlement onto this host during my experiments.

Although *L. digitalis* occurs both on rocky substrata and upon *P. polymerus*, individuals that live upon the barnacle host typically have shells that are whiter and more contrastingly tessellate than those that are found on rocky substrata (Test 1945; Byers 1989). It has been suggested that, because the lighter and more tessellate shell pattern enhances crypsis on *P. polymerus*, differential predation by visual predators dictates the morphology of *L. digitalis* that are resident upon *P. polymerus* (e.g. Mercurio and Lowell 1985). Although most authors stop short of proposing any heritable selection for this shell morphology, Giesel (1970) suggests that this dimorphism may indeed be under genetic control. This conclusion has been challenged by the work of Lindberg and Pearse (1990), who discovered that shell morphology in *L. digitalis* changes from the *P. polymerus* morph to the bare rock morph when adults are transplanted from *P. polymerus* to bare rock. These authors conclude that shell dimorphism is a product of plastic responses to habitat type, but is not genetically correlated to habitat type. The fact that

larvae in my study did not settle more strongly onto high intertidal rock than onto *P. polymerus*, even though their parents occupied rocky habitat devoid of *P. polymerus*, indicates that there is no genetic settlement preference with regard to high intertidal rock and *P. polymerus*. Although habitat may influence shell morphology in individuals of *L. digitalis*, the specific morphologies of an individuals' parents appear unrelated to specific habitat preferences at the time of larval settlement.

Results of this study support the hypotheses of Frank (1965) and Breen (1972), which predict that *L. digitalis* larvae recruit directly into adult habitat high in the rocky intertidal. Furthermore, two probable settlement cues have been identified in a rocky intertidal habitat. One is the presence of conspecific adults, although adult mucus alone on a sterile surface did not induce settlement and metamorphosis. The second is a filamentous green alga that is ubiquitous in *L. digitalis* habitat near the site from which adults were collected. This alga appears to be grazed heavily at the South Cove site. The geographic range of this alga, and its relation to that of *L. digitalis*, may be of possible interest for studies of larval dispersal and ecology. Finally, I have demonstrated that larvae of *L. digitalis*, which were progeny of adults inhabiting rocky substrata, settle in equal numbers onto rock from the adult habitat and the stalked barnacle *P. polymerus*.

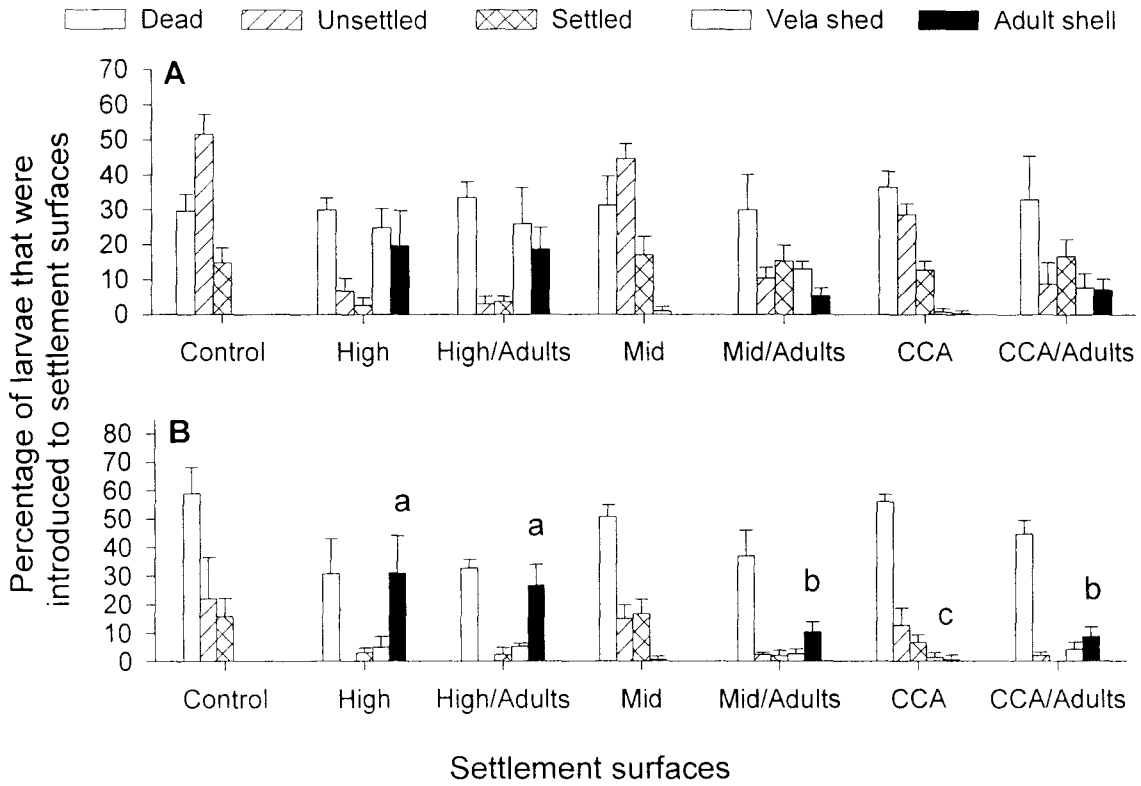

FIGURE 6. Fates of larvae of *Lottia digitalis* 3 days (A) and 6 days (B) after introduction to field-collected settlement surfaces. These larvae are progeny of adults spawned on February 12, and were introduced to settlement surfaces on February 18. Categories on *x-axis* are: Control (negative control; 0.45μm FSW), High (rock from adult *L. digitalis* habitat high in intertidal), Mid (rock from immediately below *L. digitalis* adult range in the mid-intertidal), CCA (pebbles from below adult *L. digitalis* range that were and encrusted by a crustose corraline alga), and "X"/Adults (substratum "X" exposed to adult *L. digitalis* - see materials and methods for detailed description of surfaces). Bars for each treatment group do not sum to 100% because not all larvae were recovered during sample intervals. *Adult shell* bars in Fig. B above which the same letter appears (a,b, or c) are not statistically different (Tukey's, $P < 0.05$). Error bars are 95% confidence intervals.

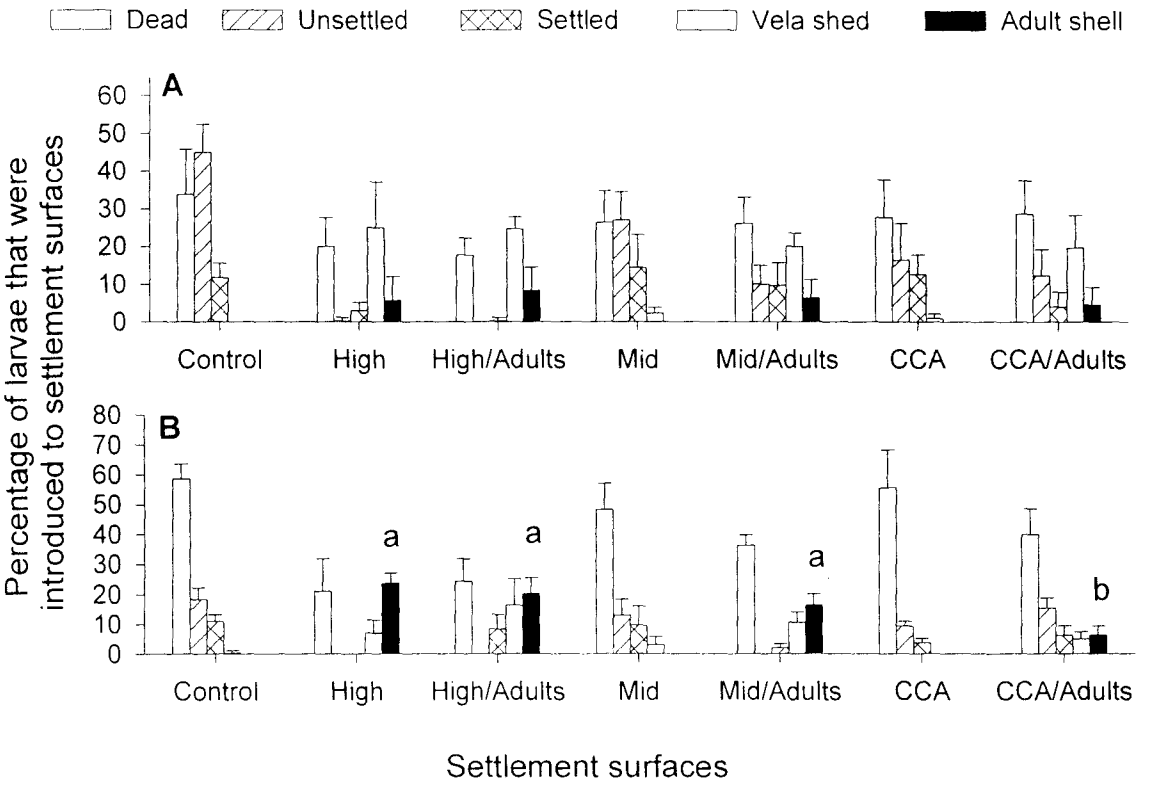

FIGURE 7. Fates of larvae of *Lottia digitalis* 3 days (A) and 6 days (B) after introduction to field-collected settlement surfaces. These larvae are progeny of adults spawned on March 2, and were introduced to settlement surfaces on March 8. Categories on *x-axis* are: Control (negative control; 0.45μm FSW), High (rock from adult *L. digitalis* habitat high in intertidal), Mid (rock from immediately below *L. digitalis* adult range in the mid-intertidal), CCA (pebbles from below *L. digitalis* range, and encrusted by a crustose corraline alga), and "X"/Adults (substratum "X" exposed to adult *L. digitalis* - see materials and methods for detailed description of surfaces). Bars for each treatment group do not sum to 100% because not all larvae were recovered during sample intervals. *Adult shell* bars in Fig. B above which the same letter appears (a or b) are not statistically different (Tukey's, $P < 0.05$). Error bars are 95% confidence intervals.

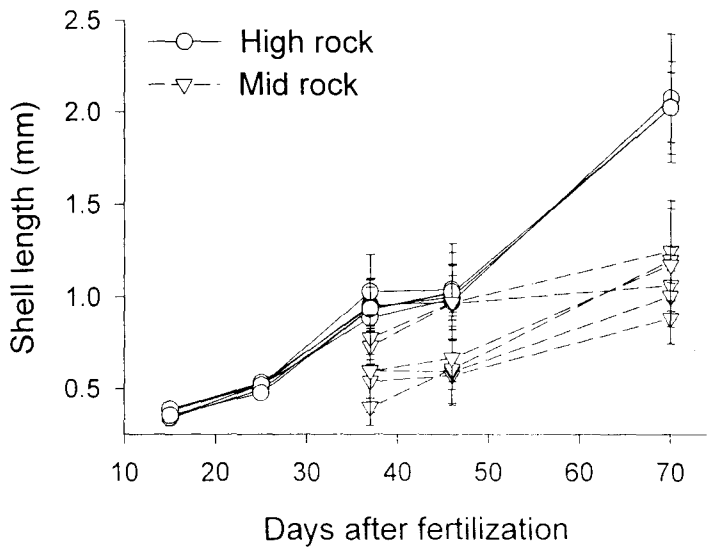

FIGURE 8. Growth of sibling *Lottia digitalis* postlarvae introduced to *High/Adults* and *Mid/Adults* substrata in the laboratory (see materials and methods for substrata descriptions). Each line represents one dish in which there were 5 individuals whose lengths were measured and averaged. Error bars are 95% confidence intervals. Note that three dishes in the *High rock* treatment were abandoned after day 48.

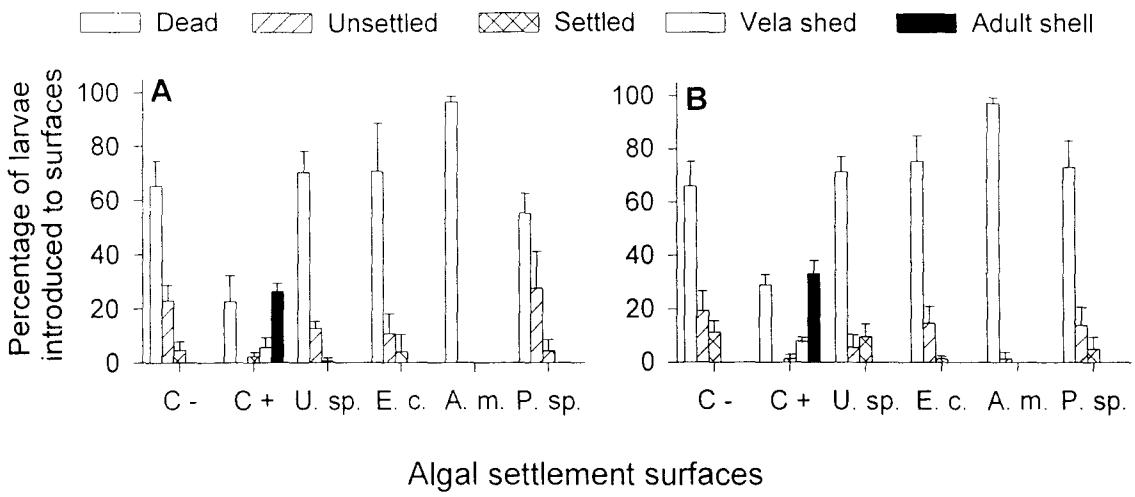

FIGURE 9. Fates of larvae of *Lottia digitalis*, from two different sets of parents, 6 days after introduction to macroalgal settlement surfaces on March 8 (A) and March 12 (B). The categories on the *x-axis* are: C- (negative control; 0.45μm FSW), C+ (positive control-*High* rock from adult *L. digitalis* habitat), U. sp. (*Ulva* sp.), E. c. (*Enteromorpha contorta*), A. m. (*Alaria marginata*), and P. sp. (*Polysiphonia* sp.).

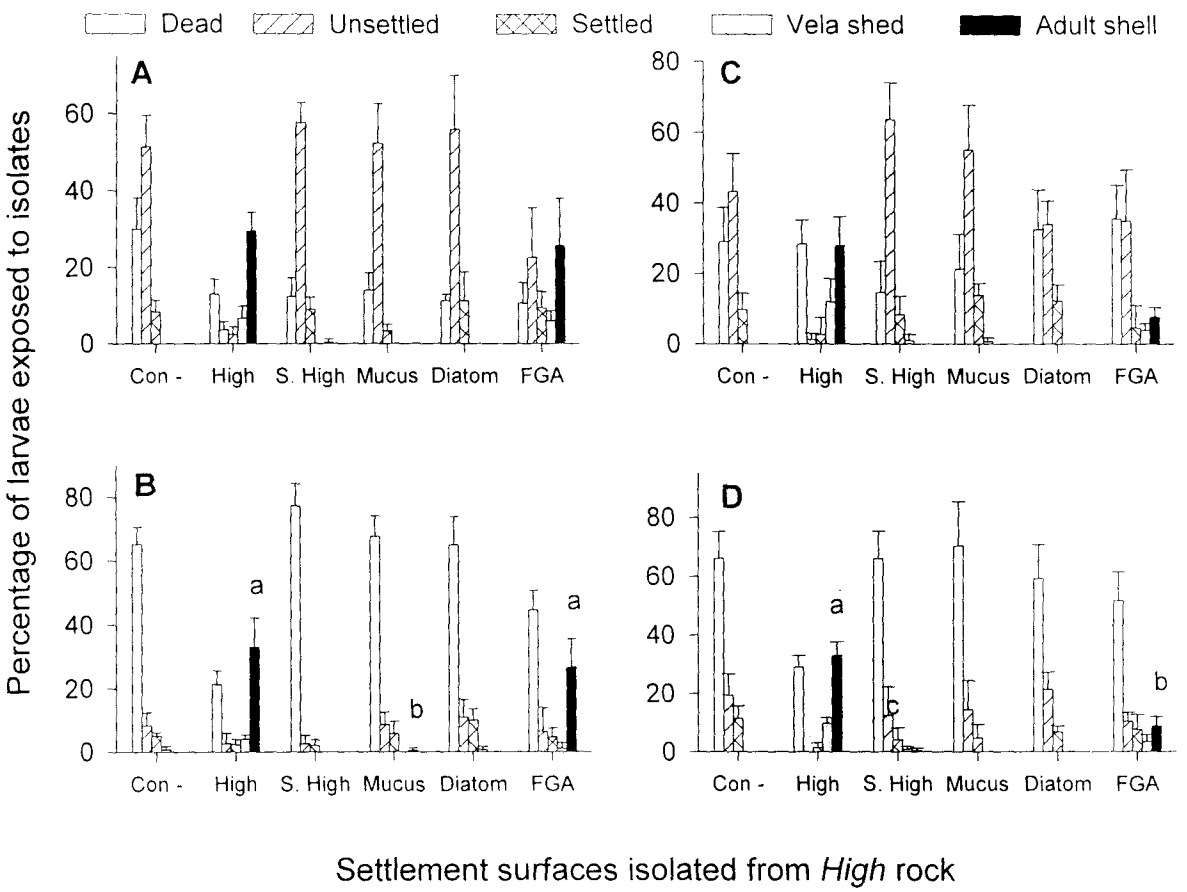

FIGURE 10. Fates of *Lottia digitalis* larvae introduced to isolates of the *High* rock from adult habitat (see materials and methods for description of isolates). Graphs A and B are results 3 days (A) and 6 days (B) after larvae were introduced to isolates on April 21. Graphs C and D are from a repeat of the same experiment in which larvae from a different set of parents were introduced to settlement surfaces on May 2. Graphs C and D are results 3 days (C) and 6 days (D) after larvae were introduced to isolates. *Adult shell* bars in Figs. B and D above which the same letter appears (a,b, or c) are not statistically different (Tukey's, $P < 0.05$). Error bars are 95% confidence intervals.

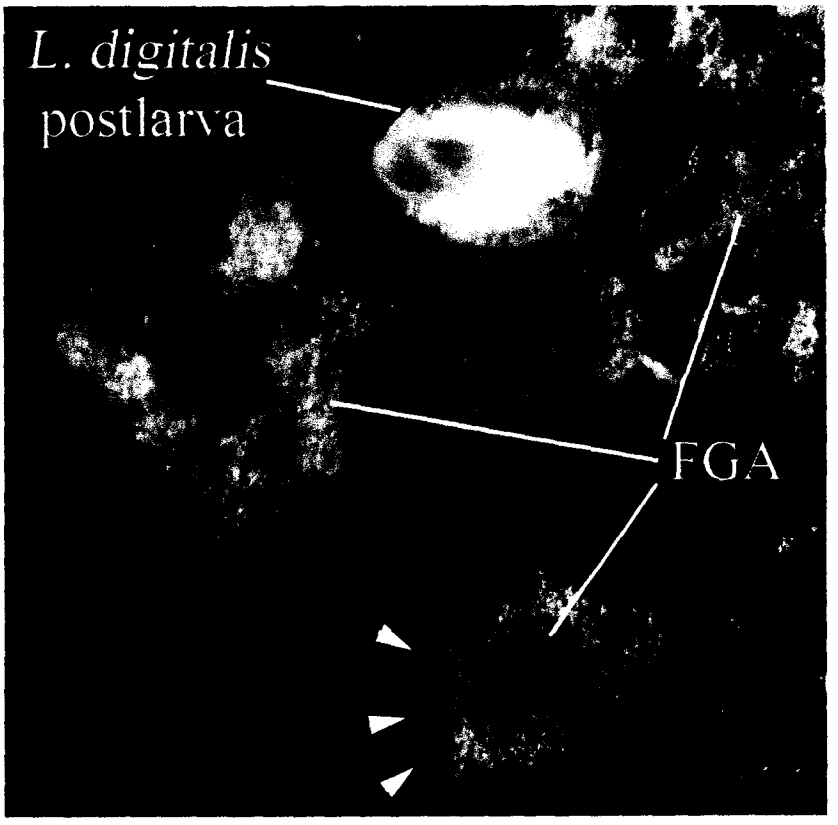

FIGURE 11: A postlarval *Lottia digitalis* that metamorphosed in the presence of, and is actively feeding upon, the filamentous green alga (FGA) isolated from *High* rock collected in adult *L. digitalis* habitat. Arrowheads delineate a "grazing front" around an algal colony recently grazed in this photograph. Scale bar = 200μm.

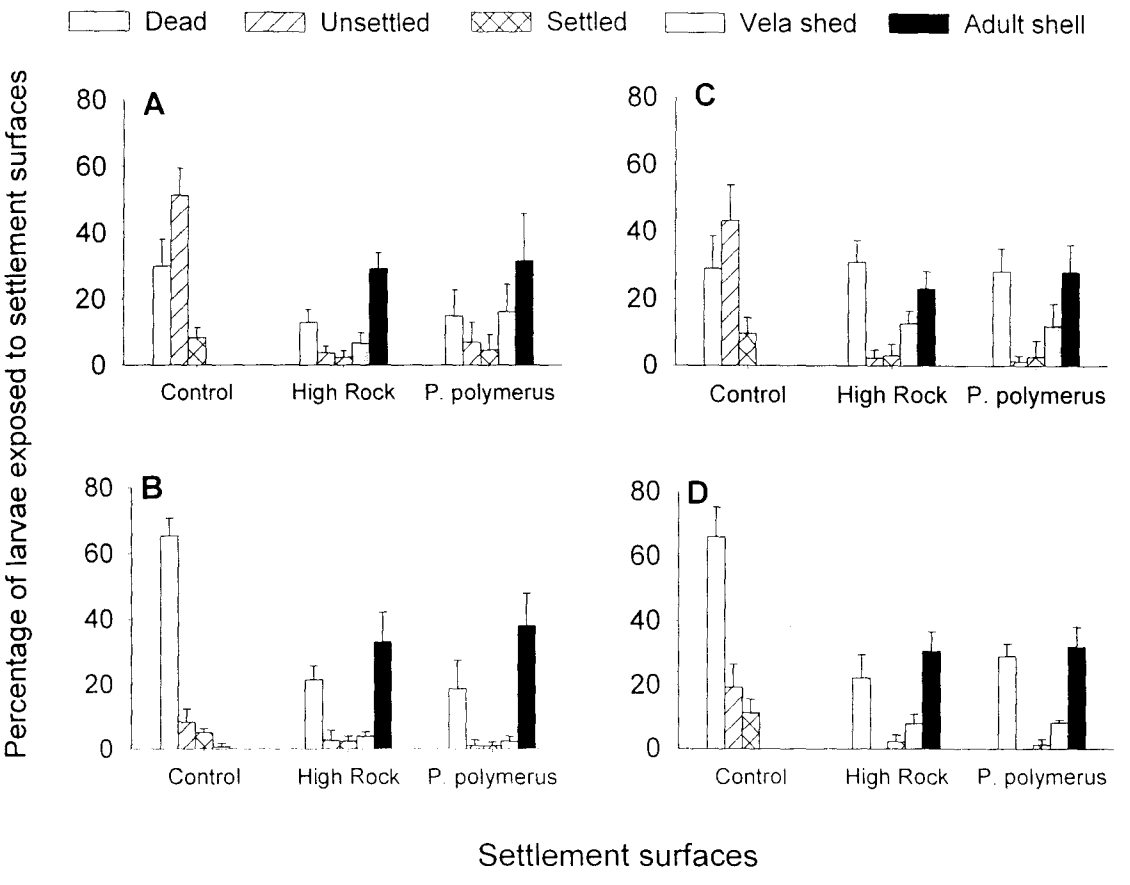

FIGURE 12. Fates of larvae of *Lottia digitalis* introduced to rock collected from adult habitat high in the intertidal (High Rock) and the stalked barnacle *Pollicipes Polymerus*. Control is 0.45 μm FSW. Graphs A and B are results 3 days (A) and 6 days (B) after larvae were introduced to isolates on April 21. Graphs C and D are from a repeat of the same experiment in which larvae from a different set of parents were introduced to settlement surfaces on May 2. Graphs C and D are results 3 days (C) and 6 days (D) after larvae were introduced to isolates. The percentage of individuals that initiated adult shell growth (black bars) upon High Rock and *P. polymerus* was statistically identical in both trials (Tukey's, $P < 0.05$, measured at t = 6 days).

BRIDGE II

The results presented in Chapter III, considered in tandem with observations of Frank (1965) and Breen (1972), suggest that recruitment of *L. digitalis* into adult habitat is driven by settlement rather than post-settlement processes. If *L. digitalis* larvae do indeed settle directly into adult habitat, then juveniles should be present in the habitat at sizes at which they are first visible and identifiable. In order to corroborate the conclusions of Chapter III, I made three censuses, on a quarterly basis, of the habitat from which I removed the adult *L. digitalis* that were spawned in Chapter III. The purpose of this study was to monitor *L. digitalis* recruitment into this habitat and record the presence (or absence), abundance and distribution of new recruits.

Unlike the habitats monitored by Frank (1965) and Breen (1972), which were monolithic slopes openly permissive to vertical migration, the habitat under study in this report is a boulder field habitat. Two observational advantages are inherent to this habitat: A) vertical migration of newly-settled juveniles is probably checked both by isolation of boulders and their large size relative to the tiny (< 250 μm at metamorphosis) settlers, thus maintaining general patterns of initial settlement for a longer period than monolithic habitats, and B) the boulder field permits scrutiny of the importance of substratum directional orientation (e.g. north vs. south facing) in the recruitment of *L. digitalis* into an habitat of ostensibly high physical stress.

CHAPTER IV

ANOTHER ANGLE ON THE RECRUITMENT OF HIGH INTERTIDAL LIMPETS: THE CASE OF *Lottia digitalis* REVISITED

Introduction

The ribbed limpet, *Lottia digitalis* (Rathke 1833), lives high in rocky intertidal habitat throughout its range from British Columbia to Central Mexico (Morris et al. 1980). This dioecious species spawns gametes into the water column where they develop into planktonic veliger larvae, which become competent to metamorphose onto benthic habitat 5-7 days after fertilization (Chapter II of this thesis). During the planktonic life stage, it is likely that wave action and coastal currents disperse larvae, both horizontally and vertically, away from the parental habitat (Shanks 1998). If a larva is to succeed in becoming reproductive, however, it must recruit into a population of adult conspecifics where external fertilization of gametes can occur.

Lottia digitalis population surveys conducted in Oregon (Frank 1965a) and in British Columbia (Breen 1972) revealed that the smallest individuals of a population are typically found low in the adult habitat range, whereas the largest individuals are found higher in the adult habitat. After detailed observations of movement patterns in *L. digitalis* populations, Frank (1965a) hypothesized, and Breen (1972) later concurred, that larvae of *L. digitalis* likely recruit low into adult habitat and subsequently migrate

upwards over the course of seasons and/or years. The fact that newly-settled limpets remain virtually invisible and unidentifiable for many months after initial settlement (Kay, pers. obsv.; Frank 1965a; Parry 1982; Quinn 1988), however, limited the confidence with which Frank was able to elucidate settlement and early recruitment patterns in *L. digitalis*.

I recently conducted a series of simple laboratory settlement experiments, during which *L. digitalis* larvae were exposed to a variety of field-collected substrata (Chapter III of this thesis). The results, considered in concert with Frank's work, indicate that larvae of *L. digitalis* recruit directly into adult habitat. This recruitment pattern contrasts with those of some other high intertidal limpet species, which settle into distinct juvenile habitats and later migrate upward into adult habitat (Corpuz 1981; Delany et al. 1998).

The purpose of this study was to monitor *L. digitalis* recruitment into the habitat from which I collected substrata and adults for previous experiments on settlement (Chapter III of this thesis). Unlike the habitats monitored by Frank (1965a) and Breen (1972), which were monolithic slopes openly permissive to vertical migration, the habitat under study in this report is a boulder field habitat. Two observational advantages are inherent to this habitat: A) vertical migration of newly-settled juveniles is probably checked both by isolation of boulders and their large size relative to the tiny (< 250 μm at metamorphosis) settlers, thus maintaining general patterns of initial settlement for a longer period than monolithic habitats, and B) the boulder field permits scrutiny of the importance of substratum directional orientation (e.g. north vs. south facing) in the recruitment of *L. digitalis* into an habitat of ostensibly high physical stress.

Materials and Methods

Site Description

I monitored *Lottia digitalis* recruitment into a boulder field habitat between 1.0-2.1 meters above MLLW on the south shore of South Cove, Cape Arago, OR. (43^{O} 18' N; 124^{O} 24' W). The shore along this site was exposed, wave swept, and predominantly west-facing. The boulders ranged in size from 0.5-2.0m in diameter, and had a coarse sandstone surface texture similar to 100-grit sandpaper. During winter, a filamentous green alga(e) proliferated on this rock, though lush growth was absent due probably to intense grazing pressure from gastropods. All *L. digitalis* at this site occurred on these sandstone boulders, and the limpets were positioned almost exclusively on vertical surfaces except when they foraged during nocturnal low tides. Very few individuals occurred above or below the vertical range (1.0-2.1m above MLLW) that I surveyed. The limpet *Lottia paradigitalis* was common, but not nearly as abundant as *L. digitalis*, at elevations low in adult *L. digitalis* habitat between 1.0-1.4m above MLLW. One specimen of *Macclintockia scabra* was seen during the entire study, and it was found within the *L. digitalis* habitat range. Boulders at a tidal height of 0.5-1.0 meters above MLLW harbored no *L. digitalis,* but were occupied by *Tectura scutum* (abundant). The limpets *Lottia pelta* and *Tectura persona* were common, but not abundant, from 0.5-2.1 meters above MLLW. Seaward of the boulder field, at a tidal height of 0.0-0.5m above MLLW, a horizontal bench of metamorphic sandstone extended ~20m and was pocked with shallow (<0.25m) tide pools blanketed by crustose corraline algae. Limpet species

found on this bench included *Tectura scutum*, *Lottia asmi* (on *Tegula funebralis*), and *Acmaea mitra* (all three species were common but not abundant, and are listed in decreasing order of abundance).

Observations

Recruitment of *Lottia digitalis* into the boulder field habitat was monitored on a quarterly basis. The first census took place July 16-18, 2000, at which time I used *Z-Spar* marine epoxy to mark and number fifty haphazardly selected clusters of *L. digitalis* adults. Twenty-five of these marked clusters were selected at random, and I then counted and measured all limpets in a $0.25m^2$ quadrat adjacent to each marker. Limpets were measured to the nearest millimeter using Vernier calipers.

Prior to conducting the next census, which took place October 7-9, 2000, fifty additional *L. digitalis* population clusters were haphazardly marked. From this pool of 100 numbered aggregations (which included the 25 that were censused in July), 25 were again selected at random. Limpets were counted and measured as they were in July. This procedure was repeated again in January 2001 (such that 25 clusters were randomly selected from a pool of 150). The tidal height of each quadrat was measured from its center, and recorded to the nearest centimeter, with a Sears *Craftsman* brand digital contractor's level calibrated to MLLW. This device consists of a stationary base unit, which is left at a known elevation once it is calibrated, and a movable sending unit that measures heights relative to the base unit. In addition to tidal height, the directional

orientation of each quadrat was measured with a compass and reported to the nearest 45^{O} relative to zero (due north).

Identification and Enumeration of Small Individuals

Although spawning in *L. digitalis* is reported to occur in late winter and spring at South Cove (Shanks, 1998), I waited until July to conduct my first census so that all juveniles would be visible and identifiable. Juvenile *L. digitalis* develop longitudinal ridges along their shells, which are characteristic of the species, at a size of 4-5mm. Since no other limpet species present at the study site develops such ridges, I was certain that all ridge-bearing juveniles in my quadrats were indeed *L. digitalis*. In contrast, I was unable to positively identify individuals $\leq$4mm, and so these individuals received special consideration during my censuses. In quadrats that were higher than 1.4m MLLW on the shore, and thus were in a tidal range occupied exclusively by *L. digitalis* (except for very few *Lottia pelta* and *Tectura persona*), all individuals $\leq$4mm were assumed to be *L. digitalis*. This assumption seems safe because *L. digitalis* occurred higher on the shore than any other limpet species at my site, and studies of intertidal limpet recruitment consistently report that newly settled juveniles are restricted to tidal elevations that are well below the upper distributional limit of adult conspecifics (i.e. Frank 1965a; Breen 1972; Parry 1982; Quinn 1988). A more confounding situation was encountered, however, for quadrats that lay within the zone of overlap for *L. digitalis* and *L. paradigitalis* at 1.0-1.4m above MLLW. Typically, both species were abundant in quadrats at that tidal level. To avoid overestimation of *L. digitalis* recruitment at this

tidal level, I censused all limpets ≤4mm that were encountered between 1.0-1.4m above MLLW, but they are reported in my length frequency diagrams as "unidentified" individuals. Furthermore, these individuals were not included in subsequent analyses (see *data analysis* section). The consequence of this approach is that recruitment for *L. digitalis* may have been underestimated at the lower extent of its range. I felt that it was most prudent to err on the side of underestimation, rather than overestimation caused by inclusion of *L. paradigtalis* juveniles in my census, and the exclusion of these individuals had no real impact on the conclusions I drew from this study regarding *L. digitalis* recruitment.

Data Analysis

The results of each census are presented in length frequency diagrams. The distributions for each census were compared in their entirety using a Kolmogorov-Smirnov test ($P < 0.05$). Additionally, the boundaries of the youngest mode (new recruits) in each diagram were defined using probability paper (Ebert, 1999). This technique employs specially scaled graph paper, upon which the cumulative frequencies of size-frequency distribution are graphed. For data that are normally distributed, the data points that are graphed form a straight line. Modes may be identified based on inflection points in the line drawn, which correspond to points at which adjacent modes may be separated. The degree of overlap for adjacent modes was identified as described by Cassie (1954). Unfortunately, I was unable to reliably separate modes comprised of larger size classes (1+ year-olds) from my data set.

In an effort to identify distributional patterns of new recruits in the adult habitat, the tidal height of each quadrat was regressed (least squares linear regression) against: a) the number of new recruits in each quadrat and b) the average size of all individuals in each quadrat. Finally, the number of recruits in each quadrat was regressed against the number of non-recruits (1+ year-olds) in each quadrat. Regression lines and 95% confidence intervals were applied using Sigmaplot (Version 5.0, SPSS Inc, 1999) and were verified using Statistica (Version 5.1, Statsoft, Inc. 1996). The significance of the slope, relative to zero, of all regression lines was calculated as described by Kleinbaum and Kupper (1978, p. 78). These data were considered, in tandem with the directional orientation of each quadrat, in an attempt to elucidate recruitment patterns of *L. digitalis* into the boulder field habitat.

Results

On July 16-18, a total of 4582 *Lottia digitalis* (including unidentified individuals in the 1-4mm size classes) were measured in 25 quadrats that ranged from 1.02 to 2.04 meters above MLLW. Length frequency analysis of this population, whose individuals ranged in size from 1- 25 millimeters, revealed a conspicuous mode centered on 4-5mm (Fig. 13). Probability paper defined the upper limit of this mode at 7mm, with a mean size at 4.40mm (SD = 1.23), and there was only slight overlap between this mode and the 1-2 year-old class. As calculated on probability paper, 33 individuals from the 0-1 year-class (new recruits) were present in the 8mm size class, whereas 34 individuals from the 1-2 year-old class were present in the 7mm size category. Due to the evenness of this

overlap, and in order to simplify subsequent analyses, I exclusively considered all individuals $\leq$ 7mm to be new recruits. The distribution of size classes in this census was significantly different from the distributions in both the October and January censuses (Kolmogorov-Smirnov tests; $P < 0.001$ in both cases).

For quadrats sampled during the July census, there was an inverse relationship between recruit abundance and elevation on the shore, and the latter accounted for 30% of the variation in the number of recruits present in the quadrats (Fig. 14A). The slope of the linear regression in Fig. 14A was statistically different from zero ($\beta \neq 0$, $P < 0.01$). Additionally, there was a trend among quadrats that harbored an unusually large number of recruits. Such quadrats, which lie above the upper 95% confidence interval in Figure 14A, tended to be low or north facing. Similarly, quadrats comprised of limpets with an unusually small mean size (Fig. 14B), tended to also be north facing. There was a positive relationship between height on the shore and the mean size of *L. digitalis* individuals in a given quadrat ($r^2 = 0.28$; $\beta \neq 0$, $P < 0.01$). In July, there was a no relationship between the number of recruits in a given quadrat and the number of non-recruits (1+ year-olds) in that quadrat (Fig. 14C; $r^2 = -0.10$, β not statistically different from zero at the 95% confidence level).

On October 7-9, a total of 2572 *L. digitalis* (including unidentified individuals in the 1-4mm size classes) were measured in 25 quadrats ranging from 1.23 to 2.04 meters above MLLW. The distribution of size classes in the October census was significantly different than distributions for the January census (Kolmogorov-Smirnov; $P < 0.01$). The mode that was centered on 4-5 millimeters in July had, by the time of this census, shifted

to the right where it was now centered on 7-8 millimeters (Fig. 13). Probability paper defined the upper limit of this mode at 9 millimeters, with a mean at 6.5mm (SD = 1.4), and there was considerable overlap between the 0-1 year-class and the 1-2 year-class. Specifically, 80 individuals in the 8 and 9mm size-classes were 1+ year-olds, whereas 48 individuals in the 10mm size-class were from the 0-1 year-class (new recruits). In order to run subsequent regression analysis without overestimation of recruitment, and because I considered individuals $\leq$9mm to be new recruits, I eliminated 32 (80 minus 48) recruits from 9mm size-class. These 32 recruits were subtracted from individual quadrats based on, and in direct proportion to, the total number of recruits in the individual quadrats. As in July, there was an inverse relationship between the number of recruits in a quadrat and that quadrat's height on the shore, and the latter accounted for 33% ($\beta \neq 0$, $P < 0.01$) of the variation in the number of recruits present in the quadrats (Fig. 15A). As in July, there is a trend among quadrats that harbored unusually large numbers of recruits, and such quadrats tended to be low or north facing. Similarly, quadrats comprised of limpets with atypically small mean sizes, which lie below the 95% confidence interval in Figure 15B, tended to be north facing. There was a positive relationship between height on the shore and the mean size of *L. digitalis* individuals in a given quadrat ($r^2 = 0.22$; $\beta \neq 0$, $P < 0.01$). There was no relationship between the number of recruits in a quadrat and the number of non-recruits (1+ year-olds) in that quadrat (Fig. 15C; $r^2 = 0.01$, β not statistically different from zero at the 95% confidence level).

On January 6-7, a total of 2340 *L. digitalis* (including unidentified individuals in the 1-4mm size classes) were measured in 25 quadrats ranging from 1.26 to 2.07 meters

above MLLW. The mode that was centered on 4-5 millimeters in July, and 7-8 mm in October, had, by this time, shifted to the right where it was now centered on 8-9 millimeters (Fig. 13). Probability paper defined the upper limit of this mode at 10 millimeters, with a mean size of 7.4mm (SD = 1.6), and there was considerable overlap of the 0-1 and 1-2 year-old age classes. Specifically, 88 individuals in the 10mm size class were 1 year-olds, whereas 79 individuals in the 11 and 12mm size-classes were from the 0 year-class (new recruits). Due to the evenness of this overlap, and in order to simplify subsequent regression analyses, I exclusively considered all individuals $\leq$10mm as new recruits. Height on the shore accounted for 19% ($\beta \neq 0$, $P < 0.05$) of the variation in the number of recruits present in the quadrats (Fig. 16A). Unlike the July and October data, there is no longer a directional trend (i.e. north-facing) among quadrats that harbored an unusually large number of recruits. Height on the shore accounted for 25% ($\beta \neq 0$, $P < 0.025$) of the variation in mean size of individuals in the quadrats (Fig. 16B). There was no correlation between the number of recruits in a quadrat and the number of non-recruits (1+ year-olds) in that quadrat (Fig. 16C, $r^2 = -0.04$, β not statistically different from zero at the 95% confidence level).

Discussion

Based on growth rates reported by Frank (1965 a, b), Nicotri (1974), and Kay (Chapter III of this thesis) *Lottia digitalis* appear to grow about 1 millimeter/month for the first 6-8 months after settlement. This growth rate, and the length-frequency mode that was centered on 4-5 millimeters in mid-July, implies that spawning of *L. digitalis*

populations in the Cape Arago area probably occurred during February and March 2000. Shanks (1998) monitored the gonad indices of *L. digitalis* at South Cove and determined that spawning occurred once in February of 1995 and twice during April of 1996. This timing is in agreement with my observations, and those of other investigators who have observed winter spawning in northeastern Pacific limpets (Fritchman 1961a, b, c, 1962; Phillips 1981; Koppen et al. 1996).

Although sites of initial settlement cannot be determined from the data presented here, it is probable that recruits settled directly into the adult habitat in which they were surveyed. This appears true for two reasons. First, I have shown that larvae of *L. digitalis* settle and metamorphose upon rock collected from the adult habitat at this site, but do not metamorphose upon rock, nor other dominant substrata, collected immediately below the adult habitat (Chapter III of this thesis). Second, newly-settled juveniles at my site cannot ascend the intertidal by simply moving upwards. This is true because the boulders I sampled within the adult habitat, and those at lower tidal elevation beneath the adult range, typically contacted other rocky subtrata only at their bases. Thus, upward migration in *L. digitalis* at this site requires initial downward movement, and subsequent horizontal migration across habitat in which the many interstices between boulders present barriers to movement. To achieve even slight elevation gains, newly settled juveniles would have had to travel many meters (i.e. ~2-10m) across the boulder field. It seems unlikely that newly settled individuals could have undertaken such a migration in the first few months following settlement. This seems especially true for recruits high in the intertidal, which occurred at heights exceeding 1.6m above MLLW. Rowley

expressed a similar incredulity regarding the migratory potential of newly settled individuals of *Strongylocentrotus* spp. (1989).

The fact that recruit abundance was inversely related to tidal elevation, within the adult habitat, is in agreement with the observations of Frank (1965a) and Breen (1972). Studies of other high-intertidal limpet species show similar recruitment patterns (Fletcher 1984; Quinn 1988). A likely explanation for this pattern is that small individuals are less tolerant, relative to adult conspecifics, of the physical stresses (i.e. desiccation and temperature) encountered high in the habitat zone (Davies 1969; Wolcott 1973; Chow 1975). This line of reasoning is consistent with the now paradigmatic notion, first posited by Connell (1961), that physical factors determine the upper distributional limit of intertidal organisms.

Although physical stresses may have shaped the observed recruitment pattern, in which recruit abundance decreased as height on the shore increased, an alternative explanation warrants mention. Specifically, lower reaches of the adult habitat may have experienced higher settlement because they were submerged, and thus available to settlement, for longer periods of time. Simply put, the pattern could be a function of larval supply (e.g. Roughgarden et al. 1988). High within adult habitat, however, recruits of *L. digitalis* were most abundant in quadrats that faced north. Furthermore, recruit abundance in these quadrats was comparable to lower quadrats (Figs. 14A, 15A). The most logical explanation of this pattern is that north-facing quadrats provided shade, and thus refuge, from the physical stresses that otherwise limit recruitment success at this level. Indeed, shading has been demonstrated to enhance recruitment in high-intertidal

barnacles (Denley and Underwood 1979; Wethey 1984). This explanation lends merit to the notion that physical stresses, rather than larval supply, dictated the inverse relationship between recruit abundance and height on the shore. A second, alternative explanation for the pattern I observed is that waterborne artillery, such as rocks and logs, may have disproportionately eliminated recruits from south facing substrata high in the intertidal (e.g. Shanks and Wright, 1986). A final, though unlikely, alternative hypothesis is that localized and hydrodynamically-driven differences in larval supply delivered disproportionate numbers of settlers to north facing quadrats.

Much of the variation in recruit abundance that I observed, especially among those quadrats with similar tidal heights and/or directional orientations, may have been due to small-scale variations in larval supply. Fine scale (10-100cm^2) spatial variation of settlement events, even at identical tidal elevations, has been observed for barnacles and a bivalve mussel (Raimondi 1990; Menge 1991).

There was no relationship between the number of recruits and non-recruits in the quadrats (Figs. 14C, 15C, 16C). This suggests that fine scale variation in early recruitment patterns do not ultimately influence the adult population structure within the habitat. Although settlement and early recruitment processes appear to dictate the distribution of new recruits within the adult habitat, the mobility of adults obscures the spatial patterns established during early life history. It is for this reason that sessile organisms, such as barnacles, remain model organisms in the study of intertidal settlement and recruitment dynamics.

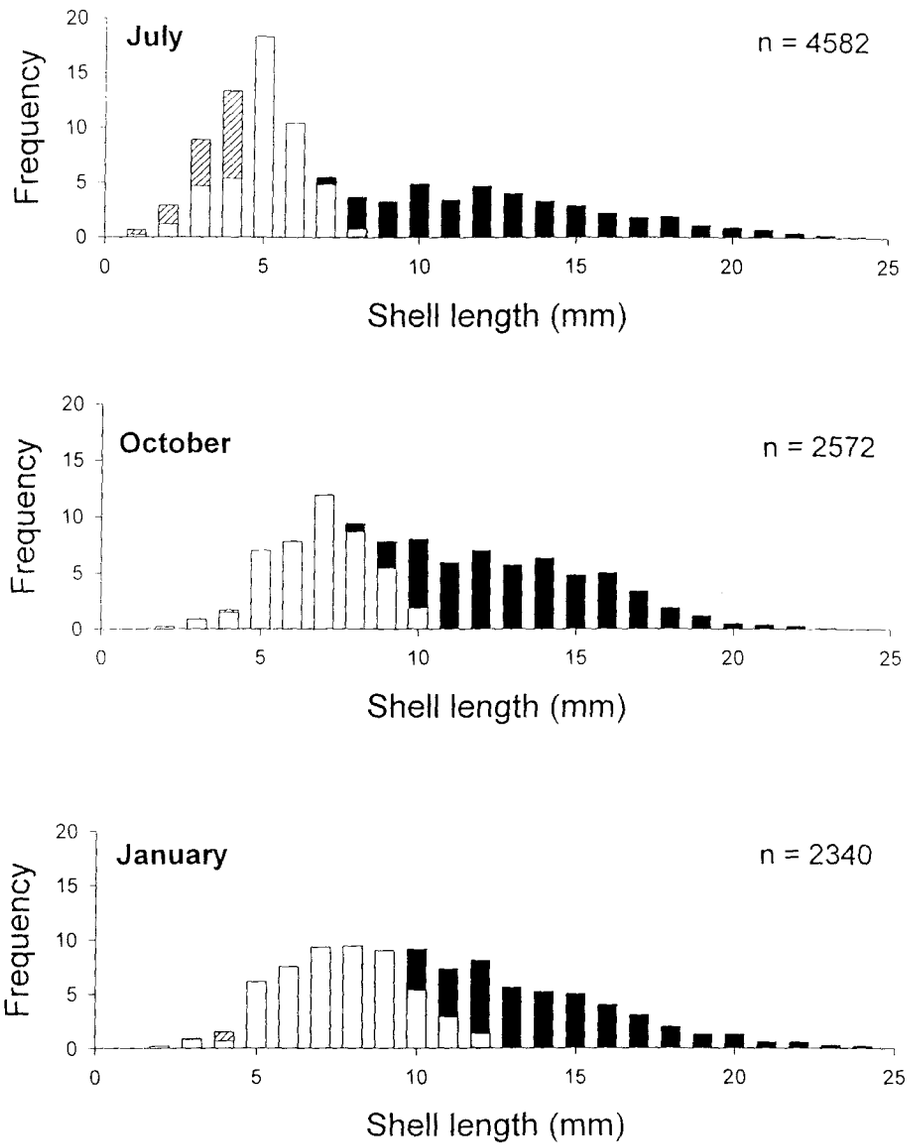

FIGURE 13. Composite results for censuses of *Lottia digitalis* from 25 different $0.25m^2$ quadrats within an adult habitat. Twenty-five quadrats were selected independently for each of the censuses, which took place during July 2000, October 2000, and January 2001. Open bars represent new recruits, solid bars represent 1+ year-olds. Hashed bars represent the number of recruits 1-4mm in length that were censused in the zone where populations of *L. digitalis* and *Lottia paradigitalis* overlapped. The identity of these individuals was considered to be unknown, and they were not included in subsequent analyses (i.e. figures 2-4). The "n's" reported are the total number of individuals measured during each census.

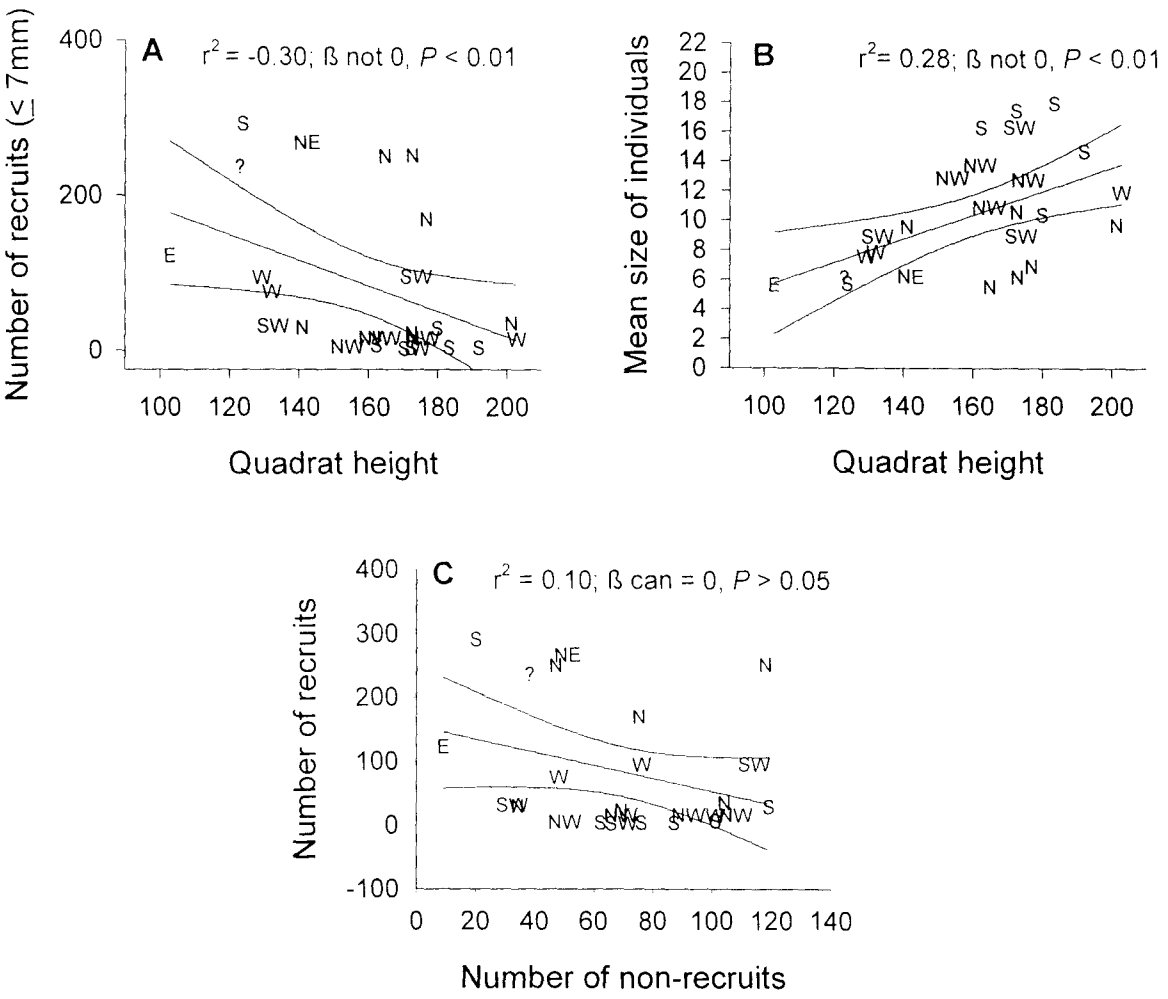

FIGURE 14. Least squares linear regressions for various features of the 25 quadrats sampled in July 2000. Each letter in figures A-C is a data point that represents a quadrat, and the letter corresponds to the directional orientation of the quadrat (N = north; NW = northwest, etc...). The question mark symbol (?) represents a quadrat whose numbered tag was dislodged by heavy surf before the orientation could be measured. The features regressed were: A) the number of recruits in a quadrat versus that quadrat's tidal height, B) the mean size of individuals in a quadrat versus that quadrat's tidal height, and C) the number of non-recruits (1+ year olds) in each quadrat versus the number of recruits in that quadrat. Curved lines are 95% confidence intervals. The significance of the slope (β) of each regression line, relative to zero, was measured at the confidence level reported in each graph.

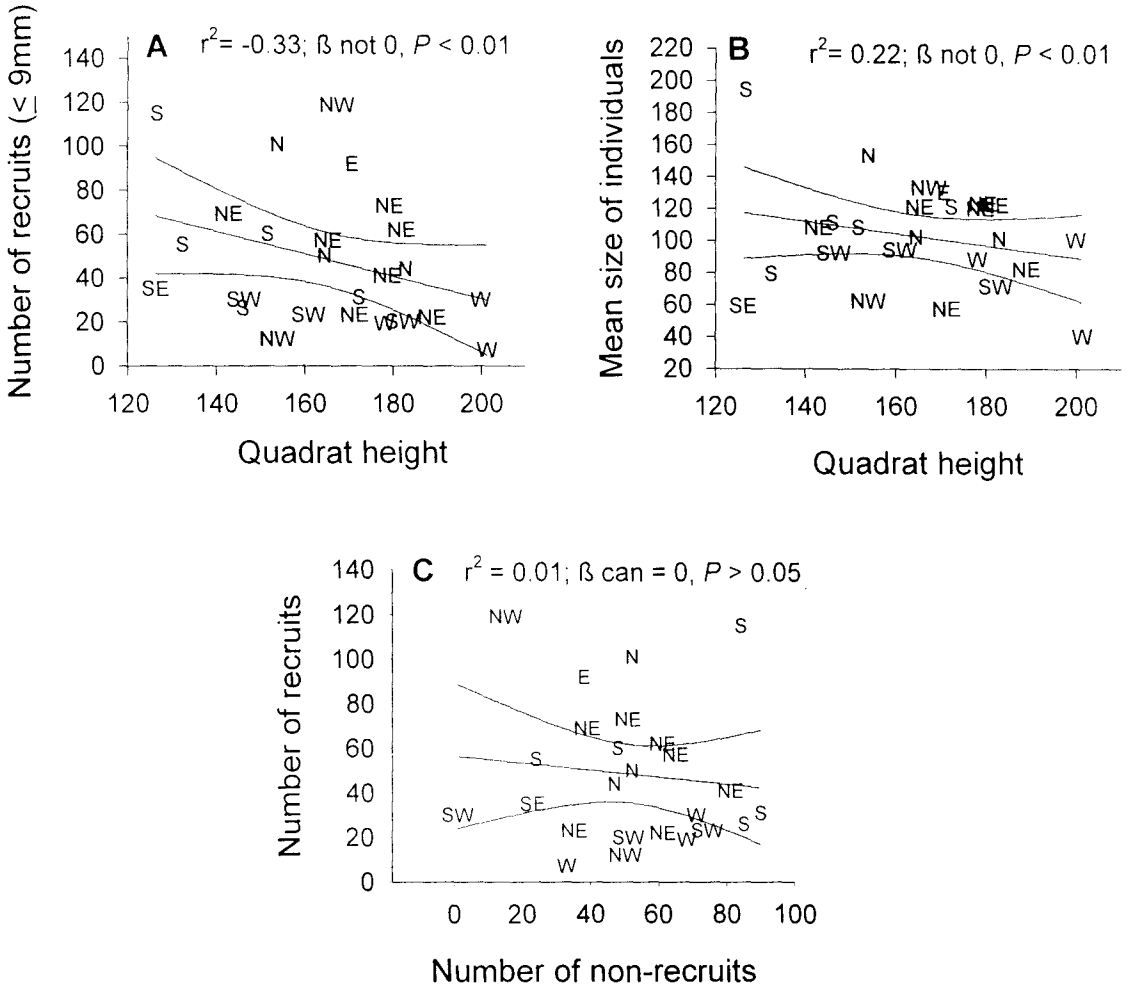

FIGURE 15. Least squares linear regressions for various features of the 25 quadrats sampled in October 2000. Each letter in figures A-C is a data point that represents a quadrat, and the letter corresponds to the directional orientation of the quadrat (N = north; NW = northwest, etc...). The features regressed were: A) the number of recruits in a quadrat versus that quadrat's tidal height, B) the mean size of individuals in a quadrat versus that quadrat's tidal height, and C) the number of non-recruits (1+ year olds) in each quadrat versus the number of recruits in that quadrat. Curved lines are 95% confidence intervals. The significance of the slope (β) of each regression line, relative to zero, was measured at the confidence level reported in each graph.

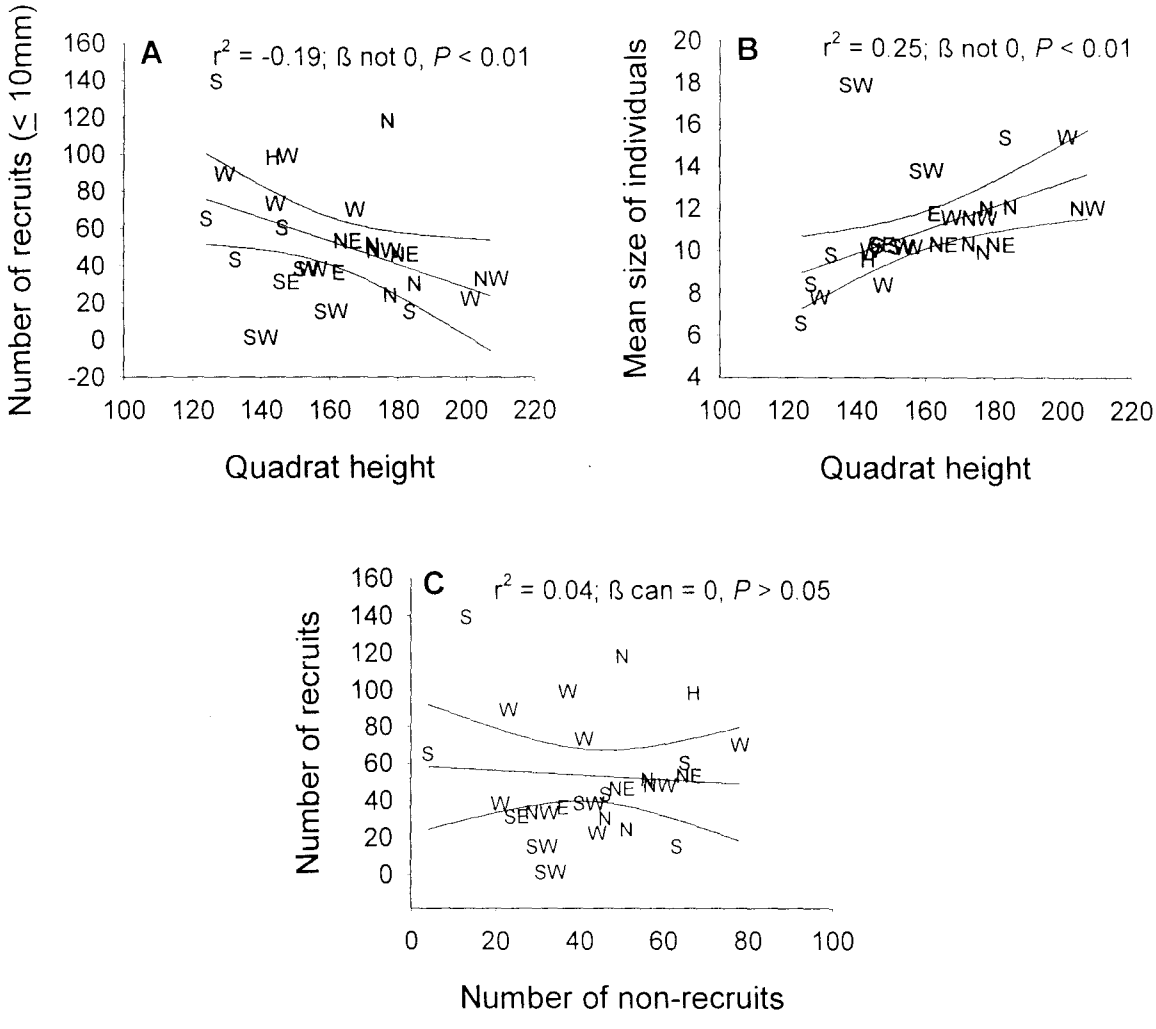

FIGURE 16. Least squares linear regressions for various features of the 25 quadrats sampled in January 2000. Each letter in figures A-C is a data point that represents a quadrat, and the letter corresponds to the directional orientation of the quadrat (N = north; NW = northwest, etc...). The letter "H" represents a quadrat with an angle of orientation that was *Horizontal*. The features regressed were: A) the number of recruits in a quadrat versus that quadrat's tidal height, B) the mean size of individuals in a quadrat versus that quadrat's tidal height, and C) the number of non-recruits (1+ year olds) in each quadrat versus the number of recruits in that quadrat. Curved lines are 95% confidence intervals. The significance of the slope (β) of each regression line, relative to zero, was measured at the confidence level reported in each graph.

BRIDGE III

As demonstrated with *Lottia digitalis* in Chapters III and IV, marine gastropod larvae and newly-settled juveniles can exhibit settlement preferences and postlarval distributional patterns, respectively, during their recruitment into high intertidal adult habitat. These patterns indicate that successful recruitment is related to the ability of larvae to occupy favorable locations during settlement and recruitment processes. Although this is true, marine invertebrate larvae, like all organisms, exist not only in space but also in time. The following chapter explores a pattern in the timing of development in larvae of the flat abalone *Haliotis walallensis.*

Chapter V of this thesis, in addition to describing larval development of *H. walallensis,* reports on the postlarval effect of a five-day extension of metamorphic *competence* (the stage at which larvae are morphologically and metabolically able to metamorphose and inhabit benthic habitat) in larvae of *H. walallensis*. The significance of this research, and relevance to this thesis, is as follows. Since larvae of benthic marine invertebrates are weak swimmers, and readily become entrained in currents, they have limited spatial control over their return trip to adult habitat (Shanks 1995). However, they might exert some temporal control by extending their competence periods, thereby increasing the probability that they will encounter suitable settlement surfaces (Morgan 1995).

CHAPTER V

SPAWNING, LARVAL DEVELOPMENT AND THE EFFECT OF AN EXTENDED METAMORPHIC COMPETENCE PERIOD IN LARVAE OF THE FLAT ABALONE, *Haliotis walallensis* STEARNS

Introduction

Benthic marine invertebrates with planktonic larval stages impose an apparently critical challenge on their progeny. Not only must offspring survive various perils of the plankton, they must also return to suitable adult habitat if they are to recruit into reproductive populations. If settlement is to be successful, furthermore, the arrival of a larva at a favorable site must occur while it is *competent* (morphologically and metabolically able) to metamorphose into the benthic habitat.

Laboratory studies of larval development reveal that many marine invertebrates are able to forgo metamorphosis well beyond initial metamorphic competence, and as a consequence retain their larval morphology and remain in their pelagic environment (reviewed by Pechenik 1990). This phenomenon has been studied in a number of taxa, and has been variously referred to as *developmental arrest* (Miller & Hadfield 1990), *delay of metamorphosis* (Birkeland et al. 1971; Pechenik 1986, 1990; Wendt 1996, 1998), and *extension of the metamorphic competence period* (Kempf and Hadfield 1985). This paper employs the latter terminology. Despite the difficulty of gathering field evidence

that larvae in nature extend their metamorphic competence periods, a handful of studies suggest that this phenomenon does indeed occur (Bayne 1965; Emlet 1986; Pechenik 1986). The ecological significance of the ability to undergo an extended competence period may be related to larval dispersal in marine invertebrate taxa. Since larvae of benthic marine invertebrates tend to be weak swimmers, and readily become entrained in currents, they have limited spatial control over their return trip to adult habitat (Shanks 1995). However, they might exert some temporal control by extending their competence periods, thereby increasing the probability that they will encounter suitable settlement surfaces (Morgan 1995).

The ecological benefit of an extended competence period could be negated if the extension were to impose energetic or physiological stress on a larva (Wendt 1998). This is especially true for non-feeding larvae with a finite supply of endogenous nutrition (Pechenik et al. 1998). The ways in which an extended competency period can compromise postlarval performance are manifold. The most severe repercussion is the inability of a larva to successfully undergo metamorphosis once an appropriate surface is encountered (Woollacott et al. 1989; Pechenik and Cerulli 1991). When larvae that have experienced prolonged larval periods do successfully undergo metamorphosis, they often experience suppressed juvenile growth rates (Pechenik et al. 1993; Woollacott et al. 1989). Retarded growth, no matter what the cause, has ostensibly grave implications for organisms that must secure resources (i.e. space) in highly competitive environments. A more subtle physiological consequence of extended larval period, which has yet to be thoroughly researched, is the ability of newly-settled juveniles to endure physical and

biological stresses (Pechenik et al. 1998). A final consequence of lengthened larval period is that individuals remain in the plankton where instantaneous mortality rates are extremely high (Rumrill 1990; Morgan 1995; Lamare and Barker 1999). The extension of competence periods in marine invertebrate larvae, although ecologically adaptive, is not always an inconsequential event.

Members of the genus *Haliotis* produce lecithotrophic larvae that spend 7-14 days in the plankton (Strathmann, 1987). Veligers of the flat abalone *Haliotis walallensis* Stearns, reared at 12.5^{O}C, reach competence 9-10 days after fertilization, but survive in culture for 10 days after competence (Kay, pers. obsv.). This study describes an experiment that explored the postlarval effects of a five-day extension of the metamorphic competence period in larvae of *H. walallensis*.

In addition to the experimental results presented in this paper, I include observations of spawning and larval development for *H. walallensis*. Although the genus *Haliotis* has been the subject of intensive larval culture and has inspired many superb accounts of development (see particularly Crofts 1937; Seki & Kan-No 1977: and see Hahn 1989 for a summary of described species) there is no published description of spawning and larval development for *H. walallensis*. Knowledge of larval development in *H. walallensis* is of interest because many of its congeners are raised aquaculturally, and because this species is the most abundant haliotid in coastal waters off Oregon, USA (pers. obsv.). Furthermore, a brilliantly colored cytoplasmic pigment is precisely segregated during the development of this species, which makes it a prime candidate for studies focused on cellular partitioning during embryogenesis. From a broader

perspective, accounts of larval development are valuable because larval life-history influences the ecology (Roughgarden et al. 1988), dispersal capacity (Mileikovsky 1971; Johannesson 1988), evolutionary persistence (Jablonski & Lutz 1983; Jablonski 1986;) and genetic structure of marine taxa (Strathmann 1986).

Materials and Methods

Collection and Spawning

Gravid *Haliotis walallensis* adults were collected by SCUBA diving at Norton's Gulch and Gregory Point near Charleston, OR., and at Tichner's cove, near Port Orford, OR. during spring and summer 1999 (Table 4). All animals were transported to flow-through seawater tables at the Oregon Institute of Marine Biology (OIMB) in Charleston, OR., where they were held until spawning was induced. Although most culturists endorse *dry* transport of adult abalone (e.g. animals are wrapped in dampened cotton cloths), abalone collected during this study were transported in seawater to avoid stresses (e.g. desiccation and/or temperature fluctuation) that might induce spawning. For the duration of their holding period at OIMB, the abalone were fed *ad libitum* on the macroalga *Nereocystis leutkeana*.

Adults of *H. walallensis* were induced to spawn by immersion in a weak solution of hydrogen peroxide (see Hahn 1989). Specifically, each liter of seawater was buffered with 6.6ml of 2M Tris(hydroxymethyl)aminomethane (Tris-base), allowed to equilibrate for 15 minutes, then 3ml of a freshly prepared 6% H_2O_2 solution was added. Animals were soaked in this solution for 2.5 hrs, after which time the vessels were rinsed and

refilled with isothermal 0.45 μm filtered seawater (FSW). Individual animals were spawned in separate 2L vessels, which required frequent water changes but allowed for prompt and hygienic collection of freshly shed gametes. Immediately upon release, eggs were siphoned through a 300 μm sieve to occlude any large debris (i.e., feces and mucus), and were then allowed to settle in 1L beakers filled with 0.45 μm FSW. The water in these settling chambers was repeatedly decanted, such that eggs were rinsed a total of three times. Sperm were rinsed one time through a 50 μm nitex sieve. A stock solution was then prepared and sperm density calculated with a hemacytometer.

Fertilization and Larval Culture

Rinsed eggs were settled into monolayers (~1400 eggs/cm^2) on the bottom of 1L beakers filled with 0.45 μm FSW. Sperm were then stirred into the beakers to yield a final concentration of ca. $3.0x10^5$ sperm ml^{-1}. After 10 minutes, the eggs were rinsed of excess sperm using the decanting procedure described above. The cultures were then placed in dark incubators at temperatures that were isothermal to the adult holding tanks (8.0-9.0^{O}C or 12.5-13.5^{O}C, depending on season).

Development was monitored at regular intervals with the use of a light microscope. All size measurements were made to the nearest 4.4 μm with an ocular micrometer. Cultures were maintained in the dark until trochophores hatched, at which time larvae in the upper half of the vessels were decanted and diluted to a concentration of 2 larvae ml^{-1}. When larvae had completely formed their protoconchs and operculae, they were diluted in 2.5L jars to a concentration of 1 larva per 2ml FSW, and they were

stirred gently for the remainder of the larval period at 12 beats $min.^{-1}$ (described in Strathmann 1987). Veligers were rinsed and restored to isothermal 0.45μm FSW once daily. Metamorphosis was observed in the context of the experiment detailed below.

Extension of Competence Period Experiment

This experiment was conducted with *H. walallensis* larvae from adults collected, and spawned on June 29, 1999, and it was performed at 12.5-13.5^{O}C. Larvae were reared to competence using the techniques described above, and were deemed competent to metamorphose when they had formed 3+ tubules on their cephalic tentacles (Seki and Kan-no 1977). I was able to see these tubules most easily by settling larvae onto a cover slip, and then mounting them foot-side-up on a microscope slide. At this morphological stage, larvae also demonstrated behavioral competence by loosely adhering and gliding across laboratory glassware (described by Morse and Morse 1984). When larvae were introduced to settlement surfaces at this stage, they settled immediately and oriented their vela and cephalic tentacles downward such that they contacted the substratum.

Upon reaching competence, 10 larvae from each of 5 culture vessels were individually introduced into six replicate dishes (total larvae per dish = 50; times 6 dishes = 300 larvae total). These dishes contained pebbles that were covered with an unidentified species non-geniculate crustose coralline alga (CCA) from the Corallinaceae. These algae are preferred settlement and growth surfaces for haliotid juveniles (Morse and Morse 1984; Shepherd and Duame 1996; Duame et al.1999). These pebbles were collected from the field, and so variation among them was inevitable. However, the size

of each replicate pebble, and the condition of the CCA upon them, was held consistent to the best of my ability.

Using an identical procedure, a second group of larvae were introduced to settlement dishes five days after the first treatment group. For four days after the introduction of larvae, all dishes in both treatment groups were monitored every 12 hours. The total number of larvae settled and metamorphosed on each rock was recorded. Two events were used as evidence of metamorphosis: the shedding of velar lobes and initiation of adult shell growth. These events are sequential, as velar shedding always precedes the initiation of adult shell growth. The advantage of monitoring two indices of metamorphosis was that, aside from lending confidence to my observations, I was able to more clearly resolve the timing of metamorphosis in both treatment groups.

In addition to scoring metamorphosis, I followed growth rates of all post-larvae at 5-day intervals. I recorded growth in units of adult shell surface area, rather than shell length, because measurements of surface area provide higher resolution of growth than length measurements. To record the surface area of juveniles, individuals were videotaped through a dissecting microscope. The video tape was replayed on a monitor and paused on each individual, at which time acetate outlines of the image of these individuals were drawn and cut to fit. To calculate the surface area of individual juveniles, the weights of individual outlines were compared to an acetate standard of known mass and surface area.

Data Analysis

All statistical tests were conducted on both Systat (version 9.0, SPSS Inc. 1999) and Statistica (Version 5.1, Statsoft 1996) software. The effect of an extended competence period, on the timing of both velar shedding and initiation of adult shell growth, was compared with a repeated measures analysis of variance design (RM-ANOVA). For each replicate dish in both treatment groups, the number of individuals with shed vela and/or adult shell growth was recorded as a percentage of the total larvae introduced to settlement surfaces (some larvae were unaccounted for after censuses). Because data were recorded as percentages, they were arcsine-transformed prior to analysis. Neither of these data sets violated assumptions of normality (Kolmogorov-Smirnov test, $P > .05$). For data describing velar shedding, I tested for violations of sphericity using Mauchly's test. When sphericity was violated, I adjusted the corresponding degrees of freedom using the calculated Huynh-Feldt epsilon value (Girden 1992). Subsequently, from these adjusted degrees of freedom, an adjusted P value was derived. For data describing adult shell growth, I used a Cochran's C test to test for heterogeneity of variances. I used the Cochran's C test in lieu of Mauchly's because the latter is not employable in situations where two (or fewer) levels (points in time at which data are recorded) are reported.

To compare the size of juveniles, both across treatment groups and over time, I used a nested ANOVA with repeated measures. Because each settlement dish contained many individuals (measurements), dish was a nested term within treatment (extension vs.

no extension). Dish was considered a random factor, whereas treatment was a fixed factor. Data from the dishes did not violate assumptions of normality (Kolmogorov-Smirnov test, $P < 0.05$). I tested for violations of sphericity with Mauchly's test, and corrected for violations using the Huynh-Feldt epsilon as described above. All P values reported are adjusted values (where necessary).

Results

Collection and Spawning

Adult *Haliotis walallensis* were found most consistently at depths of 7-20 meters, although one individual was found under a boulder in the low intertidal. The abalone were almost exclusively associated with spatially heterogeneous habitat, such as boulder fields or deeply contoured rock reefs. Throughout the project, no transportation-related spawning or mortality occurred.

Whereas 3 of the16 collected females spawned lightly in their holding tables, and in the absence of intentional induction, immersion in hydrogen peroxide reliably induced spawning in both sexes (Table 4). It was not unusual for treated animals to climb to the water's surface and torque their shells prior to spawning, and typically they were much more active than untreated animals. No mortality occurred as a result of this spawning protocol.

Brilliantly colored grass-green eggs were released individually in large pulses, and sperm were extruded in cloudy puffs that readily dissipated in gently agitated water. Gamete release typically lasted 2-3 hours among males and 1.5 hours among females, but

some females continued to spawn lightly up to 24 hours after treatment. Gametes were released through two or more of respiratory pores 3-7. The total number eggs spawned varied greatly among females, but two females shed at least 5.0 x 10^6 (Table 4). Eggs were negatively buoyant.

Early Development and Pigment Partitioning

Larvae cultured at 12.5-13.5^{O}C were successfully reared to metamorphosis on two occasions. Two spawns at 8.0-9.0^{O}C failed to produce larvae that developed normally beyond the pre-torsional stage. The first symptoms of abnormality surfaced when larvae were halfway through torsion. At this stage they swam in tight spirals with no net directional movement. In most cases, larvae remained on the bottom of culture vessels. This behavior contrasts that of healthy larvae, which swim directionally and stay in suspension. Larvae never developed beyond this stage, and ultimately died with a "half-torted" morphology.

The timing of larval development in *H. walallensis* is presented in Table 5 for cultures reared at 12.5-13.5^{O}C and 8.0-9.0^{O}C (through initiation of larval shell growth). Timing presented below refers to rearing events at the higher temperature. Development within cohorts was always synchronous.

Eggs from three females had average diameters of 195 (SD=3.8, n=10), 202 (SD=2.3, n=15), and 198 μm (SD=4.1, n=20), and were surrounded by egg membranes which measured 230 (SD = 4.3), 234 (SD = 3.7) and 230 μm (SD = 4.7) in total diameter, respectively (Fig. 17A). The egg membrane did not expand after fertilization. The

brilliant color of *H. walallensis* eggs is due to a pigment that is precisely segregated during embryogenesis. In unfertilized ova, the pigment was distributed throughout the surface of the egg except for a small beige area associated with the vegetal pole. The size of the beige patch ranged from ~10 to 25% of the egg surface area, and varied across spawns but not among ova from a single female.

First cleavage in *H. walallensis* was holoblastic, equal and meridional. In the two-cell stage, the green egg pigment is contained equally in the animal portion of both blastomeres (Fig. 17B). Second cleavage was holoblastic, equal and spiral. In the resulting four-cell stage, the green pigment is partitioned equally in the animal half of all four blastomeres (Fig. 17C). Third cleavage was unequal, dexiotropic, and horizontal. Consequently, micromeres of the eight-cell stage were densely pigmented and shifted clockwise (when viewed from above) relative to the macromeres (Fig. 17D).

At the eight-cell stage, a small amount of green pigment was still present in the animal end of the macromeres. However, at fourth cleavage the macromeres divided unequally and laeotropically, such that the cleavage plane was located nearer the animal end of the cells (Fig. 17D). As a result, the parent macromeres gave rise to four daughter macromeres and four daughter micromeres, the latter of which inherited most of the parental green pigment. Meanwhile, the animal micromeres of the eight-cell stage divided laeotropically and gave rise to eight daughter micromeres. As a result, fourth cleavage yielded a 16-cell stage in which 12 darkly pigmented micromeres are above (closer to the animal pole) four beige macromeres, which are only slightly pigmented at their animal end (Fig. 17E).

During the fifth cleavage, at which time divisions were no longer synchronous, each blastula was comprised of four beige macromeres that remain vegetal to the 16-32 darkly pigmented micromeres. In this manner, the green pigment was localized to the animal micromeres. This conspicuous morphology persisted through subsequent asynchronous divisions, until at least the 64 cell-stage.

At 15 hours after fertilization, gastrulae bore cilia at the apical tuft and along the rudimentary prototrochal girdle. At this stage, the embryos began rotating slowly within their egg membranes. The rate of rotation steadily increased to a maximum of ~ 1 rotation15 sec^{-1}. immediately prior to hatching. At 22 hours after fertilization, the egg membranes appeared distended, and the trocophores emerged by 23.5 hrs.

Later Development

Newly hatched trochophores swam to the surface of their culture vessels, even when they were maintained in complete darkness. Two hours after hatching, trochophores averaged 243 μm in length and 185 μm in width (SD = 7.1 and 4.3, respectively; n = 15 from each of two females; width measured at the protrochal girdle).

In newly hatched trochophores, green pigment was most concentrated around the stomodaeum and shell gland, in addition to the prototrochal girdle (Fig. 17F & G). During initial larval shell secretion, pigment disappeared from the shell gland, and the stomodeum migrated anteriorly along the ventral surface. The maternal green pigment in pretorsional veliger larvae became concentrated in and around the still-forming velum and foot rudiment (Fig. 17H). The pigment becomes increasingly restricted to the velum

as veligers approach competence (Fig. 17G). Settling competence was reached at 10.0-11.0 days after fertilization, at which time larval shells averaged 240.4 μm long, as measured from the tip of the aperture to the extreme posterior end (SD=18.5, n=10 each from 2 females). The fully formed velum in *H. walallensis* is slightly bilobed, but most often appears circular, and it bears compound prototrochal cilia that are ~100 μm (+/- 10 μm) long at competence.

When competent larvae were exposed to the non-geniculate CCA that was employed as a settling surface, they typically crawled across the substratum and moved their cephalic regions in a lateral motion. Frequently, settled larvae swam upwards from the substratum, then "landed" on it in a nearby location, and repeated the crawling behavior. Another typical behavior exhibited by settled larvae was a forward rearing of the protoconch. Seki and Kan-no (1977) have described these behaviors for *Haliotis discus-hannai*. Larvae of *H. walallensis* shed their vela as soon as 24 hours after introduction to settlement surfaces, and they initiated adult shell growth as soon as 48 days after settlement. The timing of these metamorphic events varied between treatment groups form the *extension of competence period experiment*, as detailed in the following section.

Extension of Competence Period Experiment

Twenty-four hours after introduction to settlement dishes, 32.5% of larvae that had their competence period extended had shed their vela (Fig. 18). In contrast, larvae that were introduced upon reaching initial competence didn't shed their vela until 48 or

60 hours after introduction. For all data recorded on, and after, the *48hr* sample interval, there was no overall effect of extended competence period on the number of individuals that had shed their vela ($F = 0.73$, $P = 0.416$; Table 6). During this time interval, however, there was a significant difference across treatment groups in the interaction between treatment and time ($F = 20.170$, $P < 0.001$). This significant interaction (time vs treatment) difference is due to the fact that individuals in the *no-extension* treatment showed a large increase in the percentage having shed vela between the 48 and 60hr. sample intervals.

Individuals in the *extension* treatment group initiated growth of the adult shell as soon as 48 hours after introduction to dishes, whereas non-delayed larvae did not initiate growth until 96 hours after introduction (Fig. 19). For data recorded on the *96hr* and *7day* sample periods, extension of competence period had no effect on the number of individuals that initiated adult shell growth ($F = 1.512$, $P = 0.252$; Table 7). Similarly, for these two sample periods there was no significant interaction effect between treatment and time ($F = 0.081$, $P = 0.783$).

Fifteen days after introduction to settlement dishes, individuals experiencing a five-day extension of their competence period were significantly larger in shell area than those individuals who experienced no extension (Fig. 20) ($F = 592.8$, $P < 0.001$; Table 8). As a consequence of this higher initial growth rate, individuals from the *extension* treatment "caught-up" in size to individuals in the no-extension treatment soon after settling (Fig. 21). Specifically, there was no overall effect of an extended competence

period, after the 20-day interval following initial competence, on the size of individual *H. walallensis* juveniles ($F = 0.093$, $P > 0.768$; Table 9).

Discussion

Spawning and Larval development

The maximum number of eggs released by an individual was similar to numbers recorded for *Haliotis kamtschatkana* (Caldwell 1981). Instances of less prolific egg release during this study were partial spawns, rather than evidence of lower fecundity, as many females that spawned lightly had bulging and unquestionably ripe gonads after gamete release. Partial spawning has also been noted in *H. kamtschatkana* (Caldwell 1981) and *Haliotis rufescens* (Giorgi and DiMartini 1977). Due to this behavior, averaging the number of eggs released by all females in this study will underestimate fecundity in *H. walallensis*.

Early cleavage patterns in *H. walallensis* were typical of other haliotids (Van Den Biggelaar 1993). Similarly, later larval development paralleled that of *Haliotis discus hannai*, as described and illustrated in detail by Seki and Kan-no (1977). Despite the vast literature on haliotid larval development, however, I have not encountered a description of egg pigment partitioning for a member of this family. Precisely segregated embryonic pigments have been observed in larvae of *Tegula funebralis* (Moran 1997) and *Haliotis sorenseni* (Leighton 1972), but the specific patterns of their partitioning during cleavage were not described. In both *T. funebralis* and *H. sorenseni*, as in *H. walallensis*, the dark green pigment was segregated ultimately into vela of precompetent veligers. It is

difficult to know whether the pigment I observed in *H. walallensis* simply acts as a marker during development, or whether it has some intrinsic value (e.g. UV protection) for the cells to which it is destined. This developmental feature lends itself to further study.

The schedule of early development at 8.0-9.0^{O}C, when compared to the 12.5-13.5^{O}C schedules, indicates a temperature effect that is typical among haliotids (Hahn 1989). My inability to raise larvae to competence at 8.5-9.5^{O}C was unexpected, and may have resulted from culture complication(s) unrelated to temperature. This conclusion seems likely because 8.0-9.0^{O}C falls within the range of summer ocean temperatures in southern Oregon, and because many species of abalone have been cultured over a wide range of temperatures (Hahn 1989). Alternatively, low temperature may have induced developmental abnormality in larvae reared at 8.0-9.0^{O}C. This notion is bolstered by the observations of Leighton (1974), who reported that torsion was frequently arrested after 90^{O} among larvae of *Haliotis* spp. reared at "subnormal" temperatures. This is the same condition that I observed in larvae of *H. walallensis*.

As mentioned above, with regard to developmental time, it is typical for individual haliotid species to show a plastic response to temperature. Considering this phenomenon, one might predict a geographical trend whereby developmental periods for warm water species are shorter in duration than those of cool water species. This pattern holds in many cases, but enough exceptions exist to dismiss it as a rule (Table 10). In no case is larval period in haliotids shorter than 4 days. This lower limit may be dictated by larval physiology, since rapid growth and differentiation might, at some critical rate,

compromise developmental accuracy (Arendt 1997). An additional physiological constraint on developmental rate is the availability of energy and materials that are required for growth and differentiation. This constraint has been implicated in species that feed during development. Thus, if haliotids are strictly lecithotrophic, as the conventional wisdom holds, then this constraint is probably not operative. Recent evidence suggests, however, that abalone larvae might depend upon absorption of dissolved organic nutrients to meet their developmental and metamorphic energy budgets (Jaeckle and Manahan 1989a, b; Shilling et al. 1996). If this is the case, then the ability of abalone larvae to absorb nutrients during development might influence their developmental rate.

Extension of Competence Period Experiment

My results suggest that older competent larvae of *H. walallensis* settle, and metamorphose, more quickly than competent younger larvae. This observation is consistent with results reported by Rumrill and Cameron (1983) for the black chiton *Katharina tunicata*. Similarly, larvae of *Haliotis iris* allowed to develop beyond initial competence settle more quickly, and in higher numbers, than those settled at initial competence (Tong and Moss 1992). Aside from postmetamorphic survivorship, which is addressed in both of these studies, neither compared postlarval performance across treatment groups.

The affect of an extended competent period on postlarval performance, in marine invertebrates, has received considerable attention of late (reviews by Pechenik 1990;

Pechenik 1998). In previous studies focused on lecithotrophic larvae, measurable effects of delay are consistently deleterious. Contrary to this pattern, my results indicate that a 5-day extension of the competence period beyond initial competence in *H. walallensis* accelerates initial juvenile growth rates, such that any size setback resulting from the extension is shortly overcome. There is probably a time threshold, beyond which a larva subjected to an extended competence period displays retarded growth or dies. Unfortunately, I did not have time to explore this threshold. Consequently, the length of time that a larvae of *H. walallensis* can extend the metamorphic competence period, without suffering any obvious deleterious consequences, remains to be elucidated.

One possible explanation for the postlarval growth data is that, immediately after metamorphosis, larvae having experienced a 5-day extension of their larval period are better equipped to harvest and/or process food than their counterparts settled at initial competence. Moss and Tong (1992) report that the number of radular teeth in *Haliotis iris* larvae continues to increase after initial competence is reached. This morphological development might allow for superior grazing ability in older larvae.

Aside from grazing more voraciously, young juveniles with many radular teeth may be able to rupture diatom frustules more efficiently than larvae with relatively few teeth. Because newly-settled haliotids cannot digest the siliceous cell walls of diatoms, the ability to rupture frustules with their radulae enhances the nutritional value of diatoms (Kawamura 1996). Additionally, older larvae might also have a more developed digestive enzymatic capacity, for it has been shown that digestive enzyme activities increase with age in postlarval *Haliotis discus hannai* (Takami et al. 1998).

Evidence from the literature suggests that, for juvenile fish starved over short periods of time and then reintroduced to full food rations, brief intervals of stunted growth are often compensated by subsequent periods of accelerated growth (Russell & Wootton 1992; Nicieza & Metcalfe 1997). It is possible that the growth compensation I observed in delayed *H. walallensis* larvae is a common response among marine organisms that experience periods of food limitation. If this is true, then the compensation may not have been facilitated solely by morphological developments (e.g. radular teeth, digestive enzyme capacity) within the *extension* treatment group. Clearly, the accelerated growth (and all growth) that I observed was physiologically mediated. The extent to which morphological developments enhanced or facilitated this response, however, is not evident.

Although the above considerations might account for the accelerated growth rate that I observed in *H. walallensis* larvae experiencing an extended competence period, they do not do so irrefutably. The reader should bear in mind that the experiment described herein was not repeated. The results should be interpreted cautiously. Given that these results contradict the general trend among studies focused on extension of competence periods (also referred to as "delay of metamorphosis") in marine invertebrates, a cautious interpretation seems especially warranted.

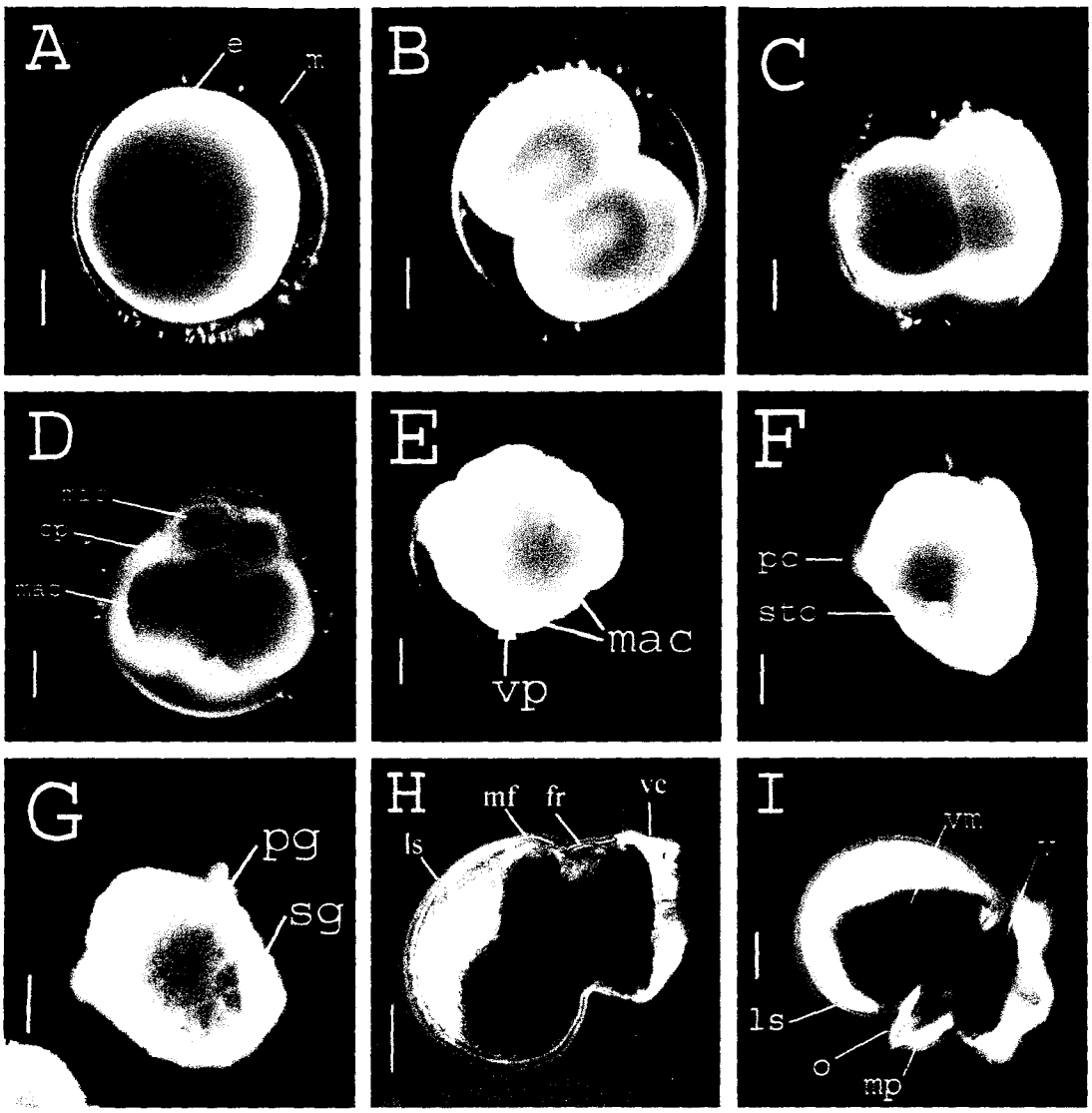

FIGURE 17. (A) Uncleaved egg (e) of *Haliotis walallensis*, surrounded by its egg membrane (m). Sperm can be seen adhering to the membrane. (B) Two cell stage (2.25 hrs. post fertilization). Note concentration of green pigment at animal pole. (C) 3.0 hr. old embryo at four-cell stage. (D) 4.5 hr. old embryo in eight-cell stage, comprised of four micromeres (mic) and four macromeres (mac). Also visible is cleavage plane (cp) along which a single macromere will be divided into one micromere and a persistent macromere. (E) lateral view of a 16-cell stage of *H. walallensis* at 6.0 hrs., with 12 micromeres above (nearer the animal pole) four maromeres. vp, vegetal pole. (F) 24hr. old trochophore in which the stomodeum (sto) is visible. pc, prototrochal cilia. (G) 24hr. old trochophore in which the shell gland (sg) is visible. pg, prototrochal girdle. (H) Pretorsional veliger at 50hrs. mf, mantle fold; fr, foot rudiment; ls, larval shell; vc, velar cilia. (I) Post torsional veliger at 75hrs. mp, metapodium; o, operculum; v, velum; vm, visceral mass. All scale bars = 40 μm.

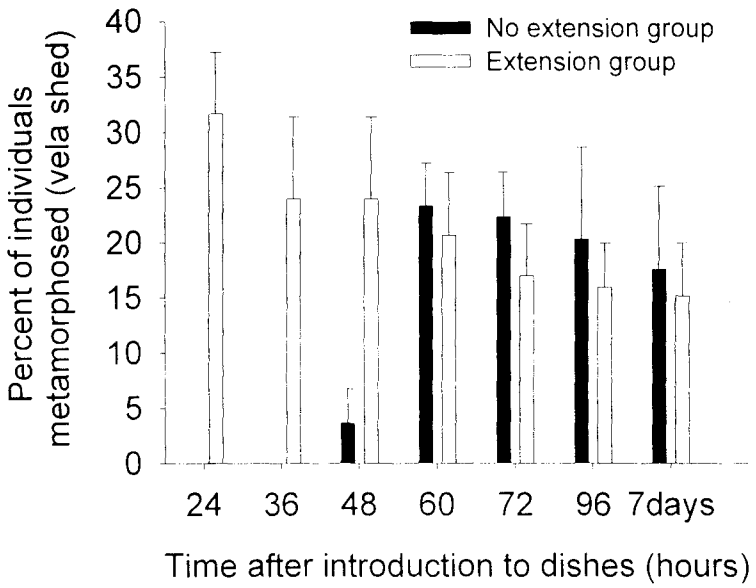

FIGURE 18. The percentage of *Haliotis walallensis* larvae having shed their vela at given sample intervals (x-axis). Each data bar represents the mean of five settlement dishes (one percentage reported for each dish). Error bars are 95% confidence intervals, see Table 6 for statistical analysis.

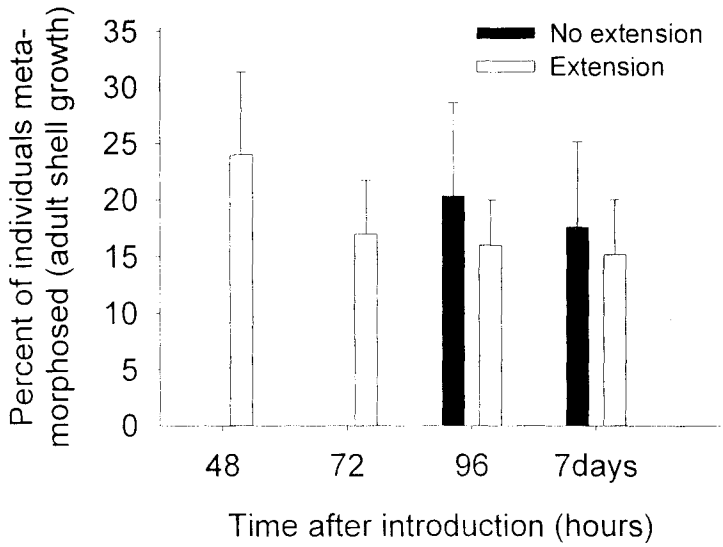

FIGURE 19. The percentage of *Haliotis walallensis* larvae having initiated adult shell growth at given sample intervals (x-axis). Each data bar represents the mean of five settlement dishes. Error bars are 95% confidence intervals, see Table 7 for statistical analysis.

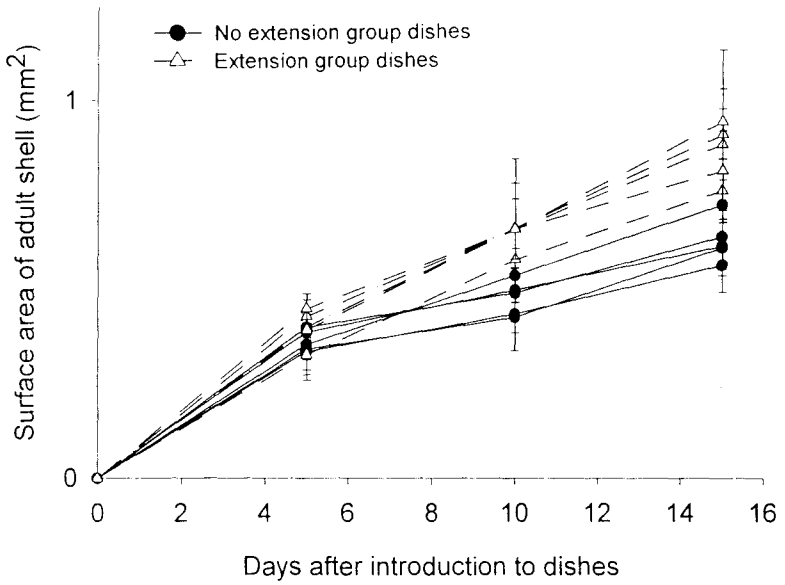

FIGURE 20. Size of postlarval *Haliotis walallensis* after introduction to settlement dishes. Each line represents average growth for individuals in a single settlement dish. In order to balance the data for statistical analysis, I measured all individuals in a given dish, then randomly selected five of these size values for each dish at each interval. Error bars are 95% confidence intervals, see Table 8 for statistical analysis.

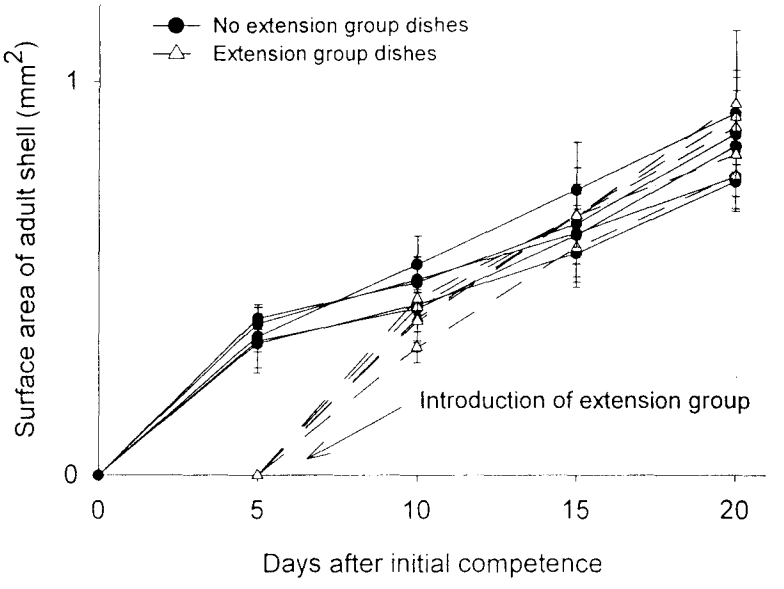

FIGURE 21. Size of postlarval *Haliotis walallensis* after initial competence. Each line represents average growth of individuals in a single settlement dish. In order to balance the data for statistical analysis, I measured all individuals in the dish, then randomly selected five of these size values for each dish at each interval. Error bars are 95% confidence intervals, see Table 9 for statistical analysis.

TABLE 4. Summary of laboratory spawing events in *Haliotis walallensis*.

Date collected,site*	Date spawned	# spawned/ # attempted	# eggs released, ♀ length (mm)
4/15/99, N.G.	4/17/99	1/2 ♂	
		0/2 ♀	-
	4/19/99	2/4 ♂	
		1/4 ♀	$1.5x10^5$, 112
5/20/99, G.P.	5/27/99	1/4 ♂	
		6/6 ♀	$2.2x10^6$, 120; $2.2x10^6$, 160
			$2.4x10^6$, 135; $2.4x10^6$, 143
			$5.0x10^6$, 128; $5.2x10^6$, 148
6/26/99, T.C.	6/27/99	1/2 ♂	
		0/2 ♀	-
6/29/99, T.C.	6/29/99	1/5 ♂	
		2/8 ♀	$1.0x10^5$, nr; $4.0x10^4$, nr
	7/22/99	2/5 ♂	
		2/3 ♀	$1.0x10^6$, nr; $5.5x10^5$, nr
	8/5/99	2/2 ♂	
		2/3 ♀	$2.5x10^5$, nr; $5.0x10^4$, nr

* sites are Norton's Gulch (N.G.), Gregory Point (G.P.) and Tichner's Cove (T.C.). See text for more specific location descriptions.
nr = sizes of females were not recorded.

TABLE 5. Summary of development in *Haliotis walallensis* at 12.5-13.5^{O}C and 8.0-9.0^{O}C.

Developmental event or stage	Time since insemination	
	12.5-13.5^{O}C *	8.0-9.0^{O}C**
1st cleavage	2.0 hr	3.5 hr
2nd cleavage	2.75 hr	5.25 hr
3rd cleavage	3.75 hr	7.5 hr
4th cleavage	4.5 hr	9.5 hr
32 cell stage	6.0 hr	15.5 hr
64 cell stage	10.5 hr	19.0-21.0 hr
Prototrochal cilia visible	16.0 hr	< 39.0 hr
Trochophore hatch-out	24.0 hr	50.5 hr
Larval shell initiated	30.5 hr	65.0 hr
Larval shell completed	48.0 hr	-***
Operculum formed	67.5 hr	-
Eye spots visible	< 91.0 hr	-
Propodium formed	97.75 hr	-
Cilia on propodium	< 4.8 d	-
Snout protrusion formed	< 6.9 d	-
Cilia on mantle cavity	< 8.0 d	-
3+ tubercles on cephalic tentacles	10.0 d	-
Larvae adhere to glassware	11.0 d	-
Larvae introduced to settlement surfaces	12.0 d	-
Vela shed	14.0 - 15.0 d	-
Adult shell growth	15.5 - 16.5 d	-
Suface area of adult shell = 1mm^2	30.0 - 34.0 d	-

* Times are averaged from two rearing events on 4/17/99 and 7/22/99
** Times are averaged from two rearing events on 8/5/99 and 1/17/00
*** Development failed at this time – see text for description

TABLE 6. Repeated measures ANOVA on the effect of an extended competence period on time to velar shedding in larvae of *Haliotis walallensis* (with introduction to settlement surfaces as t = 0). Only data for larvae 48 hours and older are included in this analysis. See Fig. 18.

Source*	Sum-of-squares	df	Mean-square	F	P
Between subjects					
Treatment	27.841	1	27.840	0.73	0.416
Error	304.092	8	38.0114		
Within subjects					
Time	251.403	4	62.850	6.223	0.002
Time x Treatment	814.805	4	203.701	20.170	<0.001
Error	323.165	32	10.099		

*All sources violated the assumption of sphericity (Mauchly's test). Therefore, the degrees of freedom corresponding to each *F*-ratio were multiplied by the Huynh-Feldt epsilon (0.847), and an adjusted *P* value was obtained. The adjusted *P* values are reported.

TABLE 7. Repeated measures ANOVA on the effect of an extended competence period on time to initiation of adult shell growth in larvae of *Haliotis walallensis* (with introduction to settlement surfaces as t = 0). Only data from the 96hr. and 7-day sample period were included in this analysis. See Fig. 19.

Source[†]	Sum-of-squares	df	Mean-square	*F*-ratio	*P*
Between subjects					
Treatment	27.966	1	27.966	1.512	0.253
Error	147.916	8	18.490		
Within subjects					
Time	1.941	1	1.941	0.086	0.776
Time x treatment	1.830	1	1.830	0.081	0.783
Error	179.674	8	22.459		

[†]Data at all sample intervals displayed homogeneity of variances as determined by Cochran's C test ($P > 0.05$ in all cases).

TABLE 8. Repeated measures, nested ANOVA on the effect of an extended competence period on the size of *Haliotis walallensis* postlarvae 5, 10, 15 days after introduction to settlement dishes. See Fig. 20.

Source*	Sum-of-squares	df	Mean-square	*F*-ratio	*P*
Between subjects					
Treatment	2.964	1	2.964	592.8	<0.000
Replicate (treatment)	0.040	8	0.005	3.023	0.008
Error	0.074	45	0.002		
Within subjects					
Time	6.121	2	3.061	1912.466	<0.001
Time x treatment	5.478	2	2.739	1711.597	<0.000
Time x replicate (treatment)	0.070	16	0.004	2.730	0.008
Error	0.144	90	0.002		

*All sources violated the assumption of sphericity, (Mauchly's test.) Consequently, the degrees of freedom corresponding to each *F*-ratio were multiplied by the Huynh-Feldt epsilon (.6320), and an adjusted *P* value was obtained. The adjusted *P* values are reported.

TABLE 9. Repeated measures, nested ANOVA on the effect of an extended competence period on the size of *Haliotis walallensis* postlarvae 5, 10, 15 and 20 days after initial competence. See Fig. 21.

Source*	Sum-of-squares	df	Mean-square	*F*-ratio	*P*
Between subjects					
Treatment	0.001	1	0.001	0.093	>0.768
Replicate (treatment)	0.065	8	0.008	3.831	0.002
Error	0.091	43	0.002		
Within subjects					
Time	25.253	3	8.418	3978.616	<0.001
Time x treatment	0.031	3	0.010	4.839	0.024
Time x replicate (treatment)	0.167	24	0.007	3.288	0.002
Error	0.273	129	0.002		

*All sources violated the assumption of sphericity (Mauchly's test). Consequently, the degrees of freedom corresponding to each *F*-ratio were multiplied by the Huynh-Feldt epsilon (.4208), and an adjusted *P* value was obtained. The adjusted P values are reported.

TABLE 10. Developmental periods for haliotids from a wide geographic range.

Species	Larval period (days)*	Temp. reared (^{O}C)**	Location of Study	Source
H. sorenseni	10.0	15.0-16.0	So. Calif., USA	(Leighton, 1972)
H. walallensis	10.0	12.5-13.5	Oregon, USA	(This study)
H. kamtschatkana	8.0	11.0	Washington, USA	(Caldwell, 1981)
H. corrugata	8.0	16.0	So. Calif., USA	(Leighton, 1974)
	6.0	18.0		
H. iris	7.0-9.0	13.0-15.0	Wellington, N.Z.	(Moss and Tong, 1992)
	4.5	18.0	New Zealand	(Tong and Dutton, 1981)
H. rufescens	7.0	15.0	So. Calif., USA	(Morse and Morse, 1984)
	5.0	20.0		(Leighton, 1974)
H. sieboldii	6.0-7.0	16.0-17.0	Japan	(Ino, 1952, in Hahn, 1989)
H. tuberculata	4.5-5.0	17.2	Brest, France	(Koike, 1978)
H. discus hannai	4.2	20.0	Tohoku, Japan	(Seki and Kan-no, 1977)
H. scalaris	4.1	20.0	South Australia	(Kay, unpublished)

* Larval period defined as time from fertilization to settling competence.

** All temperatures are representative of ambient conditions during the reproductive season at each study location.

CHAPTER VI

CONCLUDING SUMMARY

The objective of this thesis, and the research described herein, was to achieve a better understanding of how marine gastropod larvae make the transition from a plankton benthos. Since adults of marine invertebrates with planktonic larval stages are not randomly distributed in nature, one might predict *a priori* that the process of settlement and recruitment is not a random process. Chapters III, IV and V of this thesis confirm the validity such a prediction, and processes by which larvae of *Lottia digitalis* and *Haliotis walallensis* achieve success as recruits.

Results of chapter III support the hypotheses that *L. digitalis* larvae recruit directly into adult habitat high in the rocky intertidal. Furthermore, two probable settlement cues were identified in a rocky intertidal habitat. One was the presence of conspecific adults, although adult mucus alone on a sterile surface did not induce settlement and metamorphosis. The second was a filamentous green alga that is ubiquitous in *L. digitalis* habitat near the site from which adults were collected. The geographic range of this alga, and its relation to that of *L. digitalis*, may be of possible interest for studies of larval dispersal and ecology. Finally, I have demonstrated that larvae of *L. digitalis*, which were progeny of adults inhabiting rocky substrata, settle in equal numbers onto rock from the adult habitat and the stalked barnacle *P. polymerus*. One possible future direction of this research is to determine whether or not larval

settlement cues are determined by maternal diet. The ubiquity of the filamentous green alga I isolated, and the improbability of a range for this alga that is as broad as the range for L digitalis, suggests that diet might be an important determinant of larval settlement cues. I am not aware of any research that has been conducted to address this question.

The observations of Chapter IV suggest that the distribution of new recruits in an adult *L. digitalis* habitat were dependant upon height on the shore and directional orientation of the substratum. The importance of directional orientation could readily be assessed experimentally, though the mobility of *L. digitalis* would require an engineering solution to the confounding effects of emigration. Although *L. digitalis* may recruit directly into the high intertidal, distributional patterns within a given habitat are far from uniform.

Chapter V revealed that larvae of *Haliotis walallensis* may improve their odds of encountering appropriate settlement sites by prolonging the amount of time they can spend in the plankton while capable of undergoing metamorphosis. When the results of Chapter V are viewed in the context of experiments that I conducted with *L. digitals*, it becomes apparent that marine gastropod larvae operate in both space and time to maximize the probability of an encounter with sites that are favorable for settlement. Further exploration of this topic awaits at the seashore.

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