PURPLE SEA URCHINS (*STRONGYLOCENTROTUS PURPURATUS*) IN AND OUT OF PITS: THE EFFECTS OF MICROHABITAT ON POPULATION STRUCTURE, MORPHOLOGY, GROWTH, AND MORTALITY

by

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A THESIS

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“Purple Sea Urchins (*Strongylocentrotus purpuratus*) in and out of Pits: the Effects of Microhabitat on Population Structure, Morphology, Growth, and Mortality,” a thesis prepared by Benjamin M. Grupe in partial fulfillment of the requirements for the Master of Science degree in the Department of Biology. This thesis has been approved and accepted by:

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Title: PURPLE SEA URCHINS (*STRONGYLOCENTROTUS PURPURATUS*) IN AND
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Purple sea urchins (*Strongylocentrotus purpuratus*) are common inhabitants of wave-swept rocky shorelines on the Pacific Coast of North America. The effects of microhabitat, inside and outside pits, were investigated in intertidal populations of *S. purpuratus*. Nonpit urchins had significantly larger test diameters and spines, but pit urchins had relatively larger test heights and jaw lengths, indicating possible food limitation in pits. In a tetracycline-tagging study, nonpit urchins grew faster than pit urchins. *S. purpuratus* in both microhabitats are long-lived and seldom moved, though age-frequency distributions suggest that movement out of pits might occur between the ages of five and ten. At South Cove, predation by oystercatchers, raccoons, and the sunflower sea star *Pycnopodia helianthoides* was higher in nonpit microhabitats and is estimated to account for most mortality of *S. purpuratus*. Mortality, growth, and morphology vary between microhabitats, which may have important consequences for populations of *S. purpuratus* and other organisms.

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To my parents, who first introduced me to the wonders of nature.

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CHAPTER I

SEA URCHINS, HOLES IN THE ROCK, AND PUZZLES

Bombarded by waves and the sea
An urchin was speaking to me,
　　"'Tis queer in this storm
　　That I show no alarm.
In this hole, I have all that I need."

When I first arrived at the Oregon Institute of Marine Biology over three years ago, I had never seen a living sea urchin. As far as I was concerned, sea urchins were dangerous, poisonous animals that served as sea otter food and little more. One of the defining moments of my graduate school career came during November 2003 when I visited the tidepools at South Cove of Cape Arago. It was my first chance to see the lower intertidal areas that are usually immersed beneath the waves, and I was astounded to see thousands upon thousands of purple sea urchins (*Strongylocentrotus purpuratus*). They seemed to cover every available surface, inside tidepools and out. More amazing was that many of these creatures resided in small, urchin-sized cavities in the rock. I soon learned not only that pit habitation is a common trait of purple sea urchins, but also that they excavate the pits themselves. I was surprised that such an animal could bioerode the rock, and soon the questions began. Why do they make pits? How long does it take one sea urchin to dig a pit? As a sea urchin grows, does it switch to larger holes like hermit crabs? Is there competition for pits? What are the costs and benefits of inhabiting a pit?

It took a while, but eventually my questions were formulated in such a way that they composed a tight-knit thesis question. The premise of my research is the observation that sea urchins living inside and outside pits are not the same. Chapter II details the morphological and size differences I found between sea urchins living in the two microhabitats. Though the effects of habitat on sea urchins have been studied, pits create a microhabitat on the scale of centimeters whose physical variables are distinctly different from adjacent areas outside pits. Upon finding that the size-frequency distributions of pit and nonpit urchins were different, I asked why it is that nonpit urchins tend to have larger test diameters than pit urchins. Chapters III–V each play a role in answering this question.

I developed several hypotheses that could lead to the observation that nonpit urchins are larger than pit urchins. First of all, nonpit urchins could grow faster than pit urchins. Under this hypothesis, sea urchins might be completely sedentary, but differences in growth rates would translate to significant size differences when accumulated over many years. Second, perhaps pit urchins tend to be younger than nonpit urchins, and when they grow large enough they move outside of their pit. Under this scenario, there would not have to be a difference in growth to account for the difference in size. Third, pit urchins could have higher mortality rates than nonpit urchins. If they died sooner, they obviously would not get to be as big. Finally, sea urchins could recruit to different microhabitats in different years, so that larger nonpit urchins represented an older year class than pit urchins. This fourth hypothesis seemed least likely, and is discussed briefly in Chapter II. The other three hypotheses are each dealt with in their own chapter: differential growth rates in Chapter III, movement (or lack thereof) in Chapter IV, and predation in Chapter V.

When I first became excited about sea urchins and pits, I wanted to answer every question I could think of. Eventually, I realized the impossibility of this task and limited myself to smaller questions that could, in fact, be answered explicitly. However, I soon noticed that my several small questions fit together into a single, overarching question. With each new bit of data, I obtained another puzzle piece; with enough puzzle pieces, a more detailed picture emerged. This manuscript represents my best efforts to arrange those puzzle pieces. The picture may remain incomplete, but it is the nature of science to add and subtract pieces, continually rearranging them until the answers we seek are within our grasp, always directing us to new questions. I have uncovered several interesting pieces of knowledge pertaining to sea urchins, and undoubtedly, another person will pick up where I have left off, adding new pieces to the puzzle.

CHAPTER II

MICROHABITAT-BASED DIFFERENCES IN THE POPULATION STRUCTURE AND MORPHOLOGY OF THE PURPLE SEA URCHIN *STRONGYLOCENTROTUS PURPURATUS*

INTRODUCTION

All organisms are affected by their physical environment. In habitats with seemingly harsh conditions such as hydrothermal vents, arid deserts, or underneath Antarctic ice, plants and animals have specialized adaptations that allow them to survive: chemoautotrophic potential in tube worms (Felbeck 1981), reduced evaporative water loss in desert organisms (Lillywhite & Navas 2006), and glycoproteins that act as antifreeze in fish blood (DeVries et al. 1970). The rocky intertidal can be an extremely harsh environment in which organisms are exposed to powerful wave velocities, rolling boulders and logs, and regular periods of emersion and temperature stress. These physical factors tend to be spatially and temporally variable, and marine ecologists have long been interested in the ways that species distributions (Sebens 1981, Garrity 1984, Mercurio et al. 1985, Williams et al. 1999, Helmuth & Hofmann 2001) and intertidal community structure (Menge et al. 1985, Underwood & Chapman 1996, Davidson 2005, Commito et al. 2006) respond to and reflect this environmental heterogeneity.

The purple sea urchin *Strongylocentrotus purpuratus* inhabits exposed rocky shores from Alaska (O'Clair & O'Clair 1998) to Baja California (McCauley & Carey 1967) and occurs from the shallow subtidal to the mid intertidal, where densities can exceed 400 individuals m^{-2} (personal observation). Intertidal populations of *S. purpuratus* have effects disproportionate to their abundance because of their ability to control algal communities via grazing (Dayton 1975, Sousa et al. 1981). The surf zone continually tests the ability of sea urchins and other intertidal organisms to withstand high water velocities and hydraulic forces (Denny et al. 2003). These powerful hydrodynamic forces are presumed to be the reason behind a common behavior in *S. purpuratus* that contributes to environmental heterogeneity: where the rock is sufficiently soft, urchins excavate and inhabit small, urchin-sized pits or cavities in the substratum (Morris et al. 1980, Kozloff 1983). Urchins are believed to use their Aristotle's lantern to bite off small pieces of rock, and the scraping action of the spines slowly erodes the sides of the pit (Otter 1932). Although it has not been measured, this slow process is certainly possible, since purple sea urchins have been observed to burrow into steel pilings, which are much harder than the sandstone into which they commonly dig (Irwin 1953). Thousands of urchins, each in its own pit, can dominate the intertidal landscape, apparently preventing macroalgal growth or substrate utilization by other organisms (personal observation).

The ability to excavate and inhabit pits means that *Strongylocentrotus purpuratus* can potentially choose among distinct microhabitats with varying biotic and abiotic stressors. A pit microhabitat may dampen the intense hydrodynamic forces of the intertidal easily capable of dislodging a sea urchin (Denny & Gaylord 1996) and reduce the possibility of being crushed by logs or boulders. Living inside pits that contain water might also reduce heat stress and facilitate gas exchange at high tide. Some predators probably experience difficulty capturing a sea urchin that has wedged itself into a pit. Although pits might increase survivorship, there could also be associated trade-offs. In the intertidal, *S. purpuratus* feeds by capturing drift algae with its podia (or tube feet) and passing the food to the Aristotle's lantern (Ebert 1968, Dayton 1975). Successful feeding depends on the ability to grab algae with tube feet or spines in the water, so living inside a pit might decrease feeding and growth rates. Additionally, gonad production might suffer since it is correlated with nutrition (Bennett & Giese 1955). Other echinoids that live in pits (a.k.a., burrows, crevices, cavities) exhibit homing behavior, grazing outside their pits at night and returning before dawn (Nelson & Vance 1979, McClanahan 1999, Blevins & Johnsen 2004). However, the feeding mode of *S. purpuratus* means that it does not have to move to survive, so an individual in a pit could remain there indefinitely, always subjected to a presumably different set of conditions than another urchin outside the pit just 10 cm away. What are the potential implications for this difference in microhabitat? How much of a role does small-scale topography play in the biology and ecology of *S. purpuratus*?

This study begins to address the larger questions surrounding sea urchins and microhabitat by asking whether differences exist in the population structure and morphology of *Strongylocentrotus purpuratus* in tidepools in two microhabitats: inside and outside pits. A change in population structure or morphology might be expected if: 1) abiotic and biotic forces vary between microhabitats, and 2) demographic processes (recruitment, growth, immigration/emigration, mortality) differ between microhabitats, or 3) purple sea urchins are sedentary enough that distinct morphometrics develop as a consequence of long term habitation in a particular microhabitat.

MATERIALS AND METHODS

Study Sites and Sea Urchin Pits

The population structure and morphology of purple sea urchins living inside and outside pits were measured at three sites along the southern Oregon coast (Fig. 1) that differ with respect to geographical orientation, degree of exposure to waves, type of substratum, and community structure. Two sites, Middle Cove and South Cove, are located at Cape Arago (43^{o}18.5'N, 124^{o}24'W) and are characterized by sandstone substratum, large boulders, and abundant cobble. South Cove, oriented to the south, is a protected site that only occasionally experiences large waves, as most large swells arrive from the west or southwest. Middle Cove is situated on the west side of Cape Arago and, therefore, relative to South Cove, is more exposed to strong wave action. It has less cobble than South Cove, but both sites have various sizes of tidepools and profuse macroalgal growth in the intertidal. The bull kelp *Nereocystis luetkeana* forms extensive beds in the subtidal and lower intertidal at both sites, and purple urchins commonly feed on its drifting blades. The third research site was Cape Blanco (42^o 50'N, 124^o 34'W), a rocky headland approximately 50 km south of Cape Arago. The substratum at Cape Blanco is much harder than that at Cape Arago, and is generally metamorphic basalt. Additionally, the tidepools containing sea urchins occur near the point of the cape, which is very exposed to waves and has very little loose cobble. At Cape Blanco, the subtidal kelp beds are composed mainly of *Laminaria setchellii* instead of *N. luetkeana*. The dominant algal species at Cape Blanco near the sampled tidepools is *Postelsia palmaeformis*, which occurs in areas of high wave-exposure (Dayton 1973). It is likely that sea urchins in these tidepools are subjected to greater hydrodynamic forces than those at Cape Arago.

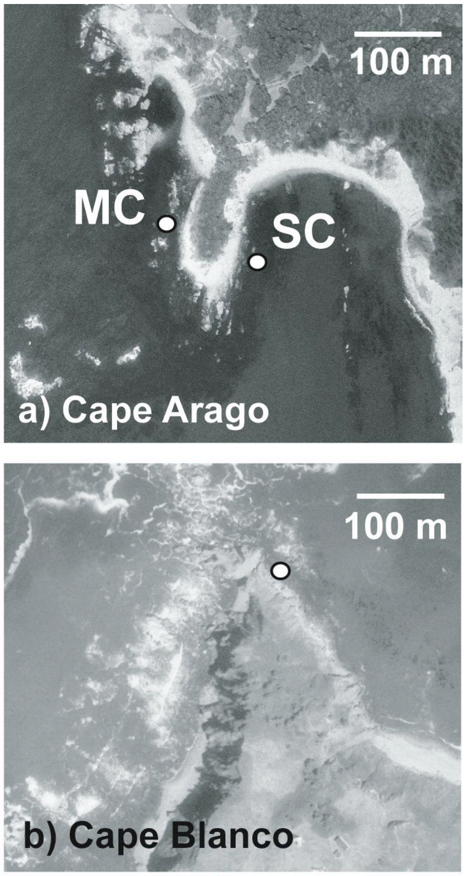


Fig. 1. Location of study sites; a) Middle Cove (MC) and South Cove (SC) at Cape Arago (43°18.5'N, 124°24'W); b) Cape Blanco (42°50'N, 124°34'W); white circles mark approximate locations of tidepools; scale bars are 100 m

Image courtesy of the USGS

Population Structure

The microhabitat-based population structure of *Strongylocentrotus purpuratus* was investigated in three to five different tidepools per site in the springs of 2005 and 2006. No tidepool was surveyed both years. Each pool was –0.2 – 0.5 m above mean lower low water (MLLW) and contained *S. purpuratus* living in both pit and nonpit microhabitats. For the 2005 sampling, sea urchins were systematically removed from a tidepool at low tide, measured, and returned to the tidepool. An attempt was made to sample every individual in the pool if the tide allowed. A sea urchin occupying a shallow depression was determined to be a pit urchin if the substratum covered its ambitus (the widest portion of the test); otherwise it was categorized as a nonpit urchin. Juveniles and recent recruits in large pits were considered pit urchins even if they were much smaller than the pit they inhabited. Knife-edged vernier calipers were used to measure the test diameter and height of each sea urchin to the nearest 0.01 cm. Diameter is defined as the widest distance from one test ambulacrum to the opposite interambulacrum.

In 2006, urchins were collected and sacrificed for a related investigation. The test diameter and height of these animals were measured in the same way, but because the tests were spineless, measurements tended to be slightly smaller. Since the variance associated with repeated measurements of one sea urchin (1 – 2 mm) is similar to the error between identical measurements from a dead and live test (1 mm for a large animal), transformation of the data was unnecessary.

Mean test diameters of *Strongylocentrotus purpuratus* from different microhabitats, tidepools, sites, and years were compared using Student's t-test, and size-frequency distributions were compared using the nonparametric Kolmogorov-Smirnov (K-S) test with the null hypotheses that there are no significant differences in mean size or size-frequency distribution between microhabitats. The K-S test is sensitive to differences in the mean, skewness, and variance, so descriptive methods were used to interpret significant results (Sokal & Rohlf 1995).

Morphology

Morphological comparisons were made in August 2005. At each investigation site, five tidepools were selected that contained sea urchins living inside and outside pits. Six pit urchins and six nonpit urchins between 5 and 8 cm were haphazardly collected from each tidepool for a total of 60 urchins per site. The following parameters were measured on each individual: test diameter and height, total wet mass while intact, peristomial diameter, spine length (average of three primary spines on the ambitus), compression strength, test thickness, length of the demipyramid (hereafter jaw), and the masses of the dissected gonad, gut (including contents), Aristotle's lantern, and skeletal components, which consisted of only the test and spines. Lengths were measured to the nearest 0.01 cm using knife-edged vernier calipers, and masses were measured to the nearest 0.01 g with an electronic balance. The jaw was measured from the shoulder of the esophageal end and the tip of the labial end, and the tooth was not included. Compression strength was measured by gradually increasing the mass resting on the aboral surface of an urchin until its test collapsed. Compression strength was accurate to the nearest 0.5 kg. Test thickness was measured on an equatorial test plate next to the tubercle boss that held a primary spine.

A three-way partially-nested mixed model analysis of covariance (ANCOVA) was used to test the null hypothesis that morphometrics do not vary among sites, tidepools nested within sites, and microhabitats, with total wet mass as the covariate. Tidepools and sites were random factors, while microhabitats was a fixed factor. The height-to-diameter (h/d) ratio was also included as a response variable in the analysis. Because ANCOVA assumes that the covariate has an equal distribution across treatment groups, eleven urchins from Middle Cove and South Cove with mass >150 g were excluded from the analysis. No transformations were necessary to achieve normality or homogeneity of variances. The data were tested for interactions between the covariate and factors, and scatterplots were inspected to ensure that slopes were homogeneous. Error terms of non-significant interactions ($P > 0.25$) were pooled with the residual error following Underwood (1997).

The data collected for population structure analysis were also analyzed with ANCOVA to test whether microhabitat-based morphological differences are detectable across the size range of *Strongylocentrotus purpuratus*. Because site and tidepool interacted significantly with the covariate, one-way ANCOVAs were used to test for the effects of microhabitat on ln-transformed test height within each site. Some sea urchins were excluded so that the range of the covariate, ln-transformed test diameter, was the same at each site. Adjusted means were back-transformed so that values for test height could be compared between microhabitats. Varying ranges of the covariate made comparisons among sites impossible, but the microhabitat-based difference in test heights can be compared within sites. Using test diameter as a covariate, jaw length was examined with a three-way ANCOVA identical to those previously described. Sea urchins with a test diameter >7.2 cm were excluded to maintain equal covariate distributions, and those with a test diameter <2.5 cm were also excluded so that the relationship between the covariate and response variable was linear. Of 1299 measurements, 140 were excluded, yielding a final sample size of 1159. Since sea urchins were collected from five tidepools at Cape Blanco but only three tidepools at the other two sites, the design was unbalanced, but a large sample size increased the robustness of the statistical test. Similar analyses to those already described were performed on ln-transformed test height (2005–2006 data) with ln-transformed test diameter as a covariate, and on jaw length (2006 data) with test diameter as a covariate. Bonferroni pairwise comparisons were used to compare adjusted least square means. The software package SYSTAT 11.0 for Windows was used for all analyses.

RESULTS

Population Structure

In 2005, 697 pit urchins and 848 pit urchins were sampled from eleven tidepools at three sites. In 2006, 648 pit urchins and 654 nonpit urchins were collected and measured from eleven different tidepools at the same three sites. All measurements are contained in Appendix A. The data clearly show that *Strongylocentrotus purpuratus* living outside pits had significantly larger diameters than those inside pits (t-test, $P < 0.001$). The mean (± SD) diameters of nonpit urchins and pit urchins from all sites and sampling dates were 5.5 ± 1.6 cm and 4.9 ± 1.3 cm, respectively. This relationship was found both in 2005 and 2006 (Fig. 2). At all but one site within a given year, *S. purpuratus* was significantly larger when living outside pits (t-test, $P < 0.001$, Fig. 2). In 2006 at South Cove, nonpit urchins had a larger mean diameter than pit urchins, but the difference was nonsignificant (t-test, $P = 0.108$). The difference between test diameters in pit and nonpit urchins was greater at Cape Blanco than at Middle Cove or South Cove (Fig. 2).

The size distribution of *Strongylocentrotus purpuratus* varied significantly between microhabitats (K-S test, $D = 0.260$, $P < 0.001$). The size-frequency distributions of pit and nonpit urchins were significantly different at every site in 2005 and 2006 (K-S test, $P < 0.001$, Fig. 2). Histograms of nonpit urchins have similar shapes to those of pit urchins, with the main difference being that distributions of nonpit urchins are shifted to

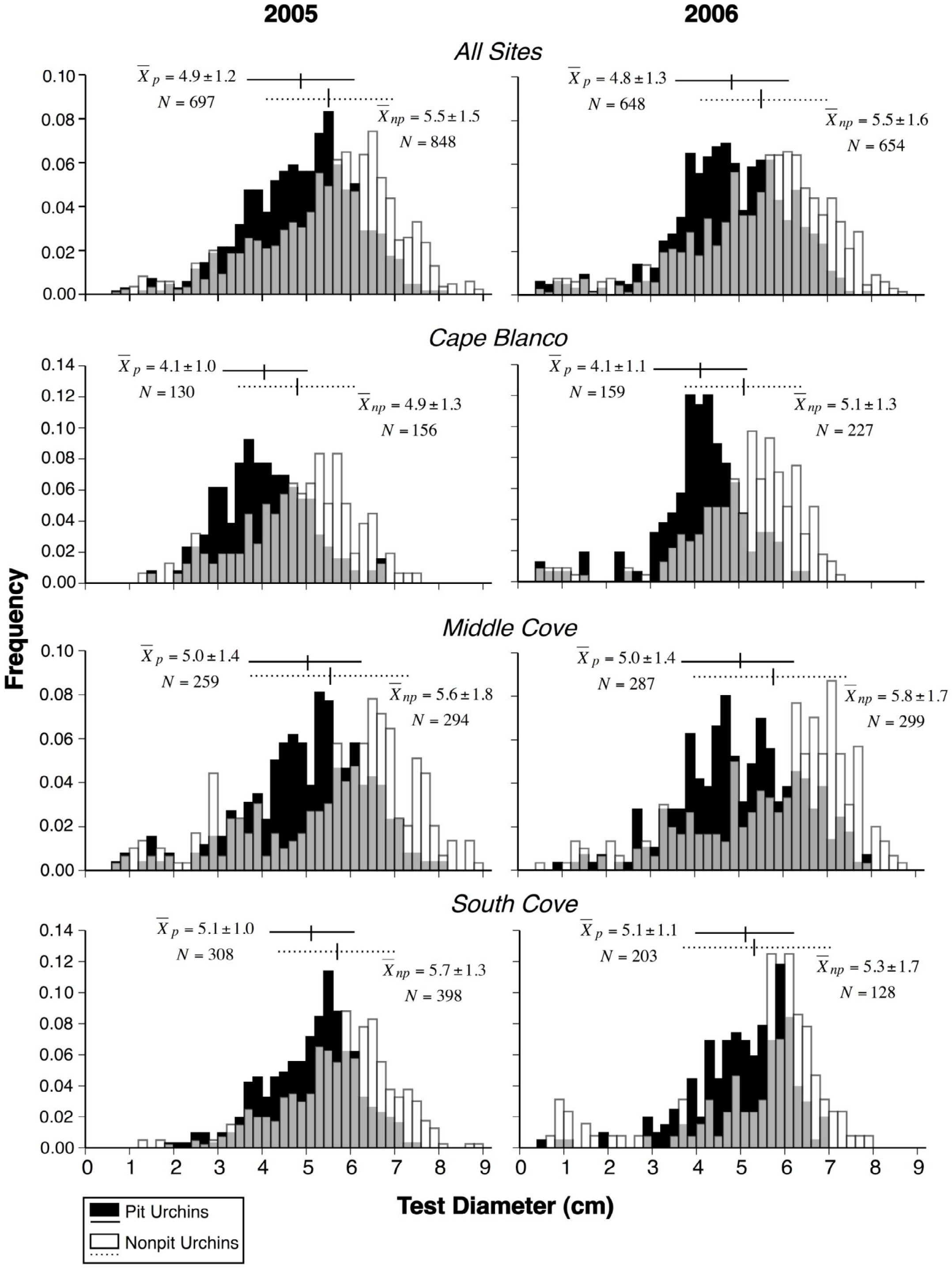


Fig. 2. *Strongylocentrotus purpuratus*. Size-frequency distributions of pit urchins (filled bars) and nonpit urchins (open bars); grey areas indicate overlap of the bars; mean (± SD) test diameter (cm) for each group is denoted by the hashes and bars above each distribution; mean test diameters of pit and nonpit urchins were significantly different (t-test, $P < 0.05$) at every site in both years except for South Cove 2006, and differences in the size-frequency distributions were highly significant in all cases (K-S, $P < 0.001$)

the right (larger) by about 1 cm. Purple sea urchins grow to about 1.5 cm in their first year (Kenner 1992), so the individuals with test diameters <2 cm make up the recruitment class for the year prior to sampling. Weak recruitment pulses were detected in 2005 and 2006 (Fig. 2), but neither abundance nor size distribution of recruits differed between microhabitats (K-S, $D = 0.196$, $P = 0.346$). The size classes of recruits were similar in both microhabitats, but overall, nonpit urchins were generally larger than pit urchins. Thus, the size-frequency distributions of nonpit urchins were skewed to the left more than pit urchins (Fig. 2).

The differences detected in test diameters and size-frequency distributions between pit and nonpit urchins at large scales were also evident at the smaller scales of tidepools (Table 1). Nonpit urchins had a larger test diameter than did pit urchins in 20 of 22 tidepools surveyed (exceptions were South Cove Tidepool B and Middle Cove Tidepool G, of which only nine pit urchins were measured, so the sample mean probably is not indicative of the population mean). Generally, there seemed to be a greater microhabitat-based size difference at Cape Blanco than at South Cove or Middle Cove. At Cape Blanco, nonpit urchins were significantly larger than pit urchins in five of eight tidepools (Hochberg's step-down sequential Bonferroni on Student's t-test, $P < 0.004$). The same can be said for only three of eight tidepools at Middle Cove and two of six tidepools at South Cove. As with the overall site data, K-S tests were significant for most (14 of 22) tidepools, indicating significant differences in population structure on a small spatial scale (Hochberg's Bonferroni, $P < 0.004$).

Table 1. *Strongylocentrotus purpuratus.* Test diameters (cm) in pit and nonpit microhabitats within each surveyed tidepool; Student's t-test was used to detect differences in mean diameters between microhabitats, and the Kolmogorov-Smirnov (K-S) test was used to detect differences in the population structure between microhabitats; the K-S statistic *D* is the maximum difference in frequencies; **bold** indicates significance using a family-wise α = 0.05 and Hochberg's (Hochberg 1988) step-down variation on the sequential Bonferroni procedure

			Pit Urchins			Nonpit Urchins			Student's t-test	K-S Test	
Site	Year	Tidepool	*N*	Range	Mean ± SD	*N*	Range	Mean ± SD	*P*	*D*	*P*
Cape Blanco	2006	A	15	3.0–5.8	4.3 ± 0.7	29	0.9–5.8	4.4 ± 1.1	0.743	0.253	0.533
		B	30	1.4–6.0	3.8 ± 0.9	73	0.5–7.3	5.3 ± 1.0	**<0.001**	0.684	**<0.001**
		C	48	0.6–5.9	4.3 ± 0.9	28	1.2–6.6	5.0 ± 1.1	0.007	0.464	**<0.001**
		D	21	0.8–5.5	3.8 ± 1.2	31	0.7–7.2	5.3 ± 1.8	**<0.001**	0.694	**<0.001**
		E	44	0.4–6.4	4.3 ± 1.3	66	0.6–6.9	5.1 ± 1.4	0.002	0.462	**<0.001**
	2005	F	25	1.6–5.1	3.6 ± 0.8	29	1.4–6.6	5.1 ± 1.2	**<0.001**	0.782	**<0.001**
		G	41	2.2–5.4	3.5 ± 0.8	61	2.0–7.6	4.8 ± 1.2	**<0.001**	0.551	**<0.001**
		H	64	3.0–6.7	4.6 ± 0.9	66	1.6–7.0	4.7 ± 1.3	0.673	0.220	0.090
Middle Cove	2006	A	85	1.5–6.9	4.4 ± 1.1	65	1.9–8.5	4.6 ± 1.6	0.406	0.155	0.355
		B	100	1.0–7.9	5.3 ± 1.4	98	0.5–8.2	6.1 ± 1.4	**<0.001**	0.396	**<0.001**
		C	102	1.3–7.9	5.3 ± 1.4	136	0.7–8.7	6.1 ± 1.8	**<0.001**	0.357	**<0.001**
	2005	D	19	1.3–7.7	5.3 ± 1.7	23	1.2–8.7	6.2 ± 1.9	0.115	0.373	0.093
		E	39	0.9–7.6	5.1 ± 1.6	90	1.2–8.8	6.0 ± 1.9	0.008	0.402	**<0.001**
		F	103	0.7–7.2	4.6 ± 1.2	135	0.9–8.0	5.3 ± 1.7	**<0.001**	0.376	**<0.001**
		G	25	0.9–8.2	5.2 ± 1.7	9	0.9–7.5	4.0 ± 2.6	0.206	0.476	0.091
		H	73	2.5–7.4	5.4 ± 1.1	37	0.7–7.4	5.6 ± 1.7	0.515	0.279	0.038
South Cove	2006	A	60	1.8–6.4	5.1 ± 1.0	48	0.9–7.4	5.7 ± 1.3	0.008	0.408	**<0.001**
		B	54	3.0–6.9	5.3 ± 1.0	33	0.8–7.8	5.2 ± 1.9	0.852	0.305	0.038
		C	89	0.5–7.0	4.9 ± 1.2	47	0.8–7.6	5.0 ± 1.8	0.670	0.272	0.023
	2005	D	128	1.8–7.6	5.5 ± 1.0	152	1.6–8.6	5.7 ± 1.2	0.067	0.201	0.007
		E	133	2.4–6.9	4.9 ± 1.0	119	1.7–7.9	5.8 ± 1.2	**<0.001**	0.407	**<0.001**
		F	47	2.5–6.2	4.7 ± 0.9	127	1.4–8.9	5.6 ± 1.4	**<0.001**	0.376	**<0.001**

Morphological Differences

ANCOVA with wet mass as a covariate

The morphology of *Strongylocentrotus purpuratus* varied significantly between microhabitats for two of the eleven parameters investigated (test height, mass of skeletal components), and microhabitat interactions were significant in three other parameters (test diameter, spine length, jaw length) (ANCOVA, $P < 0.05$, Table 2). Differences in

Table 2. Resulting adjusted means (± SD) for sea urchin morphological parameters in a three-way partially nested mixed model ANCOVA with total wet mass (88.65 g) as the covariate; the random factor tidepool is nested within the random factor site, and microhabitat is fixed; units are centimeters and grams unless otherwise stated; * Microhabitat effect $P < 0.05$; ** Microhabitat x site interaction $P < 0.05$; *** Microhabitat x tidepool (site) interaction $P < 0.05$; [a] compression strength violated the assumption of homogenous slopes and was not analyzed in the ANCOVA model

Parameter	Pit Urchins		Nonpit Urchins
Diameter	5.6 ± 0.2	**	5.7 ± 0.2
Height	3.0 ± 0.2	*	2.9 ± 0.2
Height:Diameter (h/d)	0.54 ± 0.04		0.51 ± 0.04
Peristomial diameter	1.92 ± 0.09		1.90 ± 0.09
Mass of:			
Gonad	8.38 ± 2.52		8.19 ± 2.52
Gut	8.28 ± 2.06		7.98 ± 2.06
Aristotle's lantern	2.50 ± 0.37		2.31 ± 0.37
Skeletal components	44.57 ± 2.80	*	46.47 ± 2.80
Spine length	0.92 ± 0.13	**	1.03 ± 0.13
Jaw length	1.38 ± 0.08	***	1.32 ± 0.08
Test thickness (mm)	1.14 ± 0.09		1.17 ± 0.09
[a] Compression strength (kg)	41.5 ± 10.5		41.0 ± 10.5

the remaining parameters were explained by variation at the tidepool and site levels. The average total wet mass (the covariate) of the 169 purple sea urchins included in the analysis was 88.65 g. Data for all 180 collected sea urchins can be found in Appendix B.

The ANCOVA for test diameter showed a significant interaction between site and microhabitat ($F_{2,150} = 3.751$, $P = 0.026$, Table 3a). The adjusted mean (± SD) test diameter (cm) of Cape Blanco pit urchins (5.6 ± 0.2) was significantly less than for Middle Cove pit urchins, Cape Blanco nonpit urchins, and Middle Cove nonpit urchins (all groups: 5.7 ± 0.2, $P < 0.001$). No significant differences in test diameter were detected between microhabitats at Middle Cove or South Cove.

Test height was significantly different between microhabitats (ANCOVA, $F_{1,12} = 10.987$, $P = 0.006$, Table 3b) and sites (ANCOVA, $F_{2,12} = 11.983$, $P = 0.001$). Pit urchins were taller than nonpit urchins, with an adjusted mean (± SD) test height (cm) of 3.0 ± 0.2 compared with 2.9 ± 0.2. Site effects were driven by shorter test heights at Middle Cove relative to Cape Blanco ($P = 0.001$) and South Cove ($P < 0.001$).

The h/d ratio was significantly different between sites (ANCOVA, $F_{2,12} = 14.156$, $P < 0.001$, Table 3c); urchins at Middle Cove had a significantly smaller mean (± SD) h/d ratio (0.499 ± 0.039) than South Cove (0.535 ± 0.039, $P < 0.001$) or Cape Blanco (0.531 ± 0.039, $P < 0.001$). Pit urchins (0.535 ± 0.039) had a larger h/d ratio than nonpit urchins (0.508 ± 0.039) but the difference was not significant ($P = 0.148$).

Table 3. *Strongylocentrotus purpuratus.* Three-way partially nested ANCOVAs on (a) test diameter, (b) test height, and (c) height-to-diameter ratio; the covariate was wet mass (88.65 g), and tidepools and sites were considered to be random factors; nonsignificant interactions ($P > 0.25$) were deleted and their error terms were pooled with the residual; **bold** indicates significance at $P \leq 0.05$; Bonferroni pairwise contrasts were used to investigate significant terms, and horizontal lines join similar groups at the listed *P*-value; group codes are CB = Cape Blanco, MC = Middle Cove, SC = South Cove, P = pit, and NP = nonpit

a) Test diameter

Source	d.f.	MS	*F*	*P*
Site	2	0.164	3.962	**0.048**
Microhabitat	1	0.236	2.520	0.253
Site x Microhabitat	2	0.094	3.751	**0.026**
Tidepool (Site)	12	0.041	1.655	0.082
Microhabitat x Tidepool (Site)	12	0.025	0.980	0.471
Residual	138	0.025		
Pooled Residual with *M* x *T* (S)	150	0.025		

$\overline{\text{CBP}\quad\underline{\text{SCP}\quad\text{SCNP}}}\underline{\quad\text{MCP}\quad\text{CBNP}\quad\text{MCNP}}$

$P < 0.005$

b) Test height

Source	d.f.	MS	*F*	*P*
Site	2	0.336	11.983	**0.001**
Microhabitat	1	0.519	10.987	**0.006**
Site x Microhabitat	2	0.059	1.249	0.321
Tidepool (Site)	12	0.028	0.927	0.522
Microhabitat x Tidepool (Site)	12	0.047	1.560	0.110
Residual	138	0.030		
Pooled Residual with *S* x *M*	140	0.030		

$\overline{\text{SC}\quad\text{CB}}\quad\overline{\text{MC}}$

$P < 0.005$

c) Height-to-diameter ratio

Source	d.f.	MS	*F*	*P*
Site	2	2.08×10^{-2}	14.156	**<0.001**
Microhabitat	1	3.17×10^{-2}	5.303	0.148
Site x Microhabitat	2	5.98×10^{-3}	2.522	0.122
Tidepool (Site)	12	1.47×10^{-3}	0.968	0.482
Microhabitat x Tidepool (Site)	12	2.37×10^{-3}	1.567	0.108
Residual	138	1.51×10^{-3}		

$\overline{\text{MC}}\quad\overline{\text{CB}\quad\text{SC}}$

$P < 0.001$

Microhabitat significantly affected the mass of skeletal components (ANCOVA, $F_{1,12} = 14.975$, $P = 0.002$, Table 4a). Nonpit urchins with an adjusted mass of 88.65 g contained skeletal components with a mean (± SD) of 46.45 ± 2.80 g (52.4%) compared to only 44.57 ± 2.80 g (50.3%) in pit urchins. Urchins from different sites ($P > 0.85$) and tidepools ($P > 0.35$) had similar skeletal masses. The microhabitat-based difference in skeletal mass may be related to spine length, for which the interaction between site and microhabitat was significant (ANCOVA, $F_{2,150} = 9.809$, $P < 0.001$, Table 4b). Spines of nonpit urchins were significantly ($P < 0.001$) longer than spines of pit urchins both at Middle Cove (difference of 0.23 cm, 23% longer) and at Cape Blanco (difference of 0.10 cm, 12% longer). The spines of Middle Cove nonpit urchins were significantly longer than the spines of urchins in either microhabitat at any site ($P < 0.001$). At South Cove, there was no significant difference in spine length between pit urchins and nonpit urchins.

The variability in jaw length in *Strongylocentrotus purpuratus* was explained by a significant (ANCOVA, $F_{12,150} = 2.082$, $P = 0.022$, Table 4c) interaction between microhabitat and tidepool. Although pit urchins consistently contained larger jaws than nonpit urchins, the relationship was reversed in three of fifteen tidepools (one at Cape Blanco and two at South Cove). The resulting Site x Microhabitat interaction masked a real effect, which was investigated with a Bonferroni pairwise comparison. Within Middle Cove ($P = 0.028$) and Cape Blanco ($P < 0.001$), the jaw lengths of pit urchins were significantly greater than nonpit urchins.

Table 4. *Strongylocentrotus purpuratus.* Three-way partially nested ANCOVAs on (a) skeletal mass, (b) spine length, and (c) jaw length; the covariate was wet mass (88.65 g), and tidepools and sites were considered to be random factors; nonsignificant interactions ($P > 0.25$) were deleted and their error terms were pooled with the residual; **bold** indicates significance at $P \leq 0.05$; Bonferroni pairwise contrasts were used to investigate significant terms, and horizontal lines join similar groups at the listed *P*-value; group codes are CB = Cape Blanco, MC = Middle Cove, SC = South Cove, P = pit, and NP = nonpit

a) Skeletal mass

Source	d.f.	MS	*F*	*P*
Site	2	1.332	0.155	0.858
Microhabitat	1	147.38	14.975	**0.002**
Site x Microhabitat	2	6.263	0.634	0.547
Tidepool (Site)	12	8.606	1.109	0.358
Microhabitat x Tidepool (Site)	12	9.842	1.268	0.244
Residual	138	7.783		
Pooled Residual with *S* x *M*	140	7.762		

b) Spine length

Source	d.f.	MS	*F*	*P*
Site	2	2.147	31.803	**<0.001**
Microhabitat	1	0.537	3.092	0.221
Site x Microhabitat	2	0.174	9.809	**<0.001**
Tidepool (Site)	12	0.068	3.811	**<0.001**
Microhabitat x Tidepool (Site)	12	0.021	1.183	0.301
Residual	138	0.017		
Pooled Residual with *M* x *T* (*S*)	150	0.018		

CBP SCP SCNP CBNP MCP MCNP

$P < 0.001$

c) Jaw length

Source	d.f.	MS	*F*	*P*
Site	2	0.002	0.451	0.647
Microhabitat	1	0.142	5.946	0.135
Site x Microhabitat	2	0.024	1.831	0.202
Tidepool (Site)	12	0.005	0.786	0.665
Microhabitat x Tidepool (Site)	12	0.013	2.082	**0.022**
Residual	138	0.006		

CBNP MCNP SCNP SCP MCP CBP

$P < 0.001$ for differences between CBP and CBNP
$P < 0.05$ for differences between MCP and MCNP

Although microhabitat was not a significant contributor to the variability in the remaining measured parameters, site and tidepool were. The gut and gonad masses were quite variable, and the Microhabitat x Tidepool (Site) interactions were significant (ANCOVA, gut mass: $F_{12,140} = 2.77$, $P = 0.002$, Table 5a; gonad mass: $F_{12,140} = 2.33$, $P = 0.010$, Table 5b). Pit urchins at Middle Cove appeared to have much heavier guts and lighter gonads than pit urchins at South Cove and Cape Blanco, but significant interactions prevented post-hoc testing.

The Microhabitat x Tidepool (Site) interaction was also significant for the mass of the Aristotle's lantern (ANCOVA, $F_{12,138} = 3.50$, $P < 0.001$, Table 5c). Like jaw length, lantern mass was greater in pit urchins than in nonpit urchins for most, but not all tidepools. Peristomial diameter (ANCOVA, $F_{12,140} = 2.58$, $P = 0.004$, Table 6a) and test thickness (ANCOVA, $F_{12,140} = 2.20$, $P = 0.027$, Table 6b) were significantly different among tidepools, and the latter was significantly different (ANCOVA, $F_{2,12} = 6.68$, $P = 0.011$, Table 6b) among sites, but not microhabitats.

Table 5. *Strongylocentrotus purpuratus.* Three-way partially nested ANCOVAs on (a) gut mass (including contents), (b) gonad mass, and (c) mass of the Aristotle's lantern; the covariate was wet mass (88.65 g), and tidepools and sites were considered to be random factors; nonsignificant interactions ($P > 0.25$) were deleted and their error terms were pooled with the residual; **bold** indicates significance at $P \leq 0.05$; Bonferroni pairwise contrasts were used to investigate significant terms, and horizontal lines join similar groups at the listed *P*-value; group codes are CB = Cape Blanco, MC = Middle Cove, SC = South Cove, P = pit, and NP = nonpit

a) gut mass

Source	d.f.	MS	*F*	*P*
Site	2	108.043	4.414	**0.037**
Microhabitat	1	4.330	0.365	0.557
Site x Microhabitat	2	4.277	59.657	0.707
Tidepool (Site)	12	24.475	5.719	**<0.001**
Microhabitat x Tidepool (Site)	12	11.859	2.771	**0.002**
Residual	138	4.280		
Pooled Residual with *S* x *M*	140	4.280		

b) gonad mass

Source	d.f.	MS	*F*	*P*
Site	2	126.070	15.220	**<0.001**
Microhabitat	1	1.379	0.093	0.765
Site x Microhabitat	2	0.550	0.037	0.964
Tidepool (Site)	12	8.283	1.308	0.220
Microhabitat x Tidepool (Site)	12	14.760	2.331	**0.009**
Residual	138	6.416		
Pooled Residual with *S* x *M*	140	6.332		

$\overline{\text{MC}} \quad \overline{\text{CB} \quad \text{SC}}$

$P < 0.001$

c) lantern mass

Source	d.f.	MS	*F*	*P*
Site	2	0.451	1.560	0.250
Microhabitat	1	1.495	1.238	0.382
Site x Microhabitat	2	1.208	3.243	0.075
Tidepool (Site)	12	0.289	2.714	**0.003**
Microhabitat x Tidepool (Site)	12	0.372	3.495	**<0.001**
Residual	138	0.107		

Table 6. *Strongylocentrotus purpuratus.* Three-way partially nested ANCOVAs on (a) peristomial diameter and (b) test thickness; the covariate was wet mass (88.65 g), and tidepools and sites were considered to be random factors; nonsignificant interactions ($P > 0.25$) were deleted and their error terms were pooled with the residual; **bold** indicates significance at $P \leq 0.05$; Bonferroni pairwise contrasts were used to investigate significant terms, and horizontal lines join similar groups at the listed *P*-value; group codes are CB = Cape Blanco, MC = Middle Cove, SC = South Cove, P = pit, and NP = nonpit

a) peristomial diameter

Source	d.f.	MS	*F*	*P*
Site	2	0.052	3.112	0.082
Microhabitat	1	0.021	2.046	0.178
Site x Microhabitat	2	0.003	0.272	0.766
Tidepool (Site)	12	0.017	2.584	**0.004**
Microhabitat x Tidepool (Site)	12	0.010	1.630	0.090
Residual	138	0.006		
Pooled Residual with *S* x *M*	140	0.006		

b) test thickness

Source	d.f.	MS	*F*	*P*
Site	2	$2.09\text{x}10^{-3}$	6.677	**0.011**
Microhabitat	1	$3.90\text{x}10^{-4}$	1.868	0.197
Site x Microhabitat	2	$4.0\text{x}10^{-5}$	0.191	0.829
Tidepool (Site)	12	$3.13\text{x}10^{-4}$	2.020	**0.027**
Microhabitat x Tidepool (Site)	12	$2.09\text{x}10^{-4}$	1.348	0.198
Residual	138	$1.60\text{x}10^{-4}$		
Pooled Residual with *S* x *M*	140	$1.55\text{x}10^{-4}$		

$\overline{\text{CB}}\qquad\overline{\text{SC}\qquad\text{MC}}$

$P < 0.05$

ANCOVA with test diameter as a covariate

Using the data for all sea urchins with test diameter as a covariate yields slightly different results. A three-way ANCOVA was not used to test ln (test height) because of a significant interaction. Small *Strongylocentrotus purpuratus* at Cape Blanco had large test heights, but large *S. purpuratus* had small test heights relative to Middle Cove and

South Cove. This can be interpreted to mean that at Cape Blanco, juvenile sea urchins had a fat appearance, while older sea urchins were flattened out and widened. In separate one-way ANOVAs for each site, ln (test height) was significantly greater for pit urchins than for nonpit urchins (ANCOVA, $F > 39$, $P < 0.001$ for all sites, Table 7). After the adjusted means have been back-transformed, the difference in test height between pit and nonpit urchins is much greater at Cape Blanco (0.21 cm) than at South Cove (0.11 cm) or Middle Cove (0.09 cm) (Table 14). In addition, *S. purpuratus* at Middle Cove are relatively short compared to Cape Blanco and South Cove.

When test diameter was used as a covariate, microhabitat interacted significantly with tidepool in the ANCOVA for jaw length ($F_{8,1138} = 2.54$, $P = 0.010$, Table 8). The significant interaction is probably attributable to having excessive degrees of freedom (1138) that magnify differences between tidepools and microhabitats. The adjusted mean jaw length was consistently greater in pit urchins than in nonpit urchins for every tidepool. The site ($F_{2,8} = 12.729$, $P = 0.003$) and microhabitat ($F_{1,8} = 52.140$, $P < 0.001$) levels both had significant effects on jaw length in *Strongylocentrotus purpuratus* (Table 8). Differences were highly significant between all sites (Bonferroni pairwise contrast, $P < 0.001$). Sea urchins (adjusted test diameter = 5.00 cm) have adjusted jaw lengths of 1.08 cm at Cape Blanco, 1.06 cm at Middle Cove, and 1.04 cm at South Cove. The adjusted jaw length for pit urchins (1.08 cm) is larger than for nonpit urchins (1.04 cm). The interaction between site and microhabitat was non-significant, and Fig. 3 displays nicely the relationship in jaw length between microhabitats within each site.

Table 7. *Strongylocentrotus purpuratus.* One-way ANCOVAs on ln (test height) between microhabitats by site; separate analyses were run for each site because of heterogeneous slopes; ranges of the covariate (ln test diameter) were selected to meet assumptions of ANCOVA: a) Cape Blanco: 0.0-1.9, b) Middle Cove: 0.0-2.1, c) South Cove: 1.0-2.0; **bold** indicates significance at $P \leq 0.05$; the regression equation giving adjusted least square means is $y_{ij} = \mu + \alpha_i + \beta x_{ij} + \varepsilon_{ij}$; [a]Adjusted least square means are reported as ln (test height) and test height (cm) and are appropriate for a sea urchin with test diameter 5.00 cm

(a) Cape Blanco

Source	d.f.	MS	*F*	*P*
Microhabitat	1	1.089	126.4	**<0.001**
Residual	757	0.009		

(b) Middle Cove

Source	d.f.	MS	*F*	*P*
Microhabitat	1	0.398	56.1	**<0.001**
Residual	1100	0.007		

(c) South Cove

Source	d.f.	MS	*F*	*P*
Microhabitat	1	0.350	39.7	**<0.001**
Residual	944	0.009		

[a]Adjusted Least Square Means

	ln (test height)		Test height (cm)		
Site	Pit	Nonpit	Pit	Nonpit	Difference
Cape Blanco	0.982	0.902	2.67	2.46	0.21
Middle Cove	0.904	0.866	2.47	2.38	0.09
South Cove	0.957	0.918	2.61	2.50	0.11

Cape Blanco: $\mu = -0.8038$, $\beta = 1.0847$, $\alpha_P = 0.0400$, $\alpha_{NP} = -0.0400$

Middle Cove: $\mu = -0.9493$, $\beta = 1.1399$, $\alpha_P = -0.0191$, $\alpha_{NP} = -0.0191$

South Cove: $\mu = -0.9550$, $\beta = 1.1760$, $\alpha_P = 0.0198$, $\alpha_{NP} = -0.0198$

Table 8. *Strongylocentrotus purpuratus.* Three-way partially nested ANCOVA on jaw length data from all 2006 sea urchins; the range of the covariate (test diameter = 2.5–7.2 cm) was selected to meet the assumption of similar distribution across groups; **bold** indicates significance at $P \leq 0.05$; the regression equation giving adjusted least square means is $y_{ij} = \mu + \alpha_i + \beta x_{ij} + \varepsilon_{ij}$; adjusted least square means (cm) are standardized to a sea urchin with test diameter = 5.00 cm

Source	d.f.	MS	*F*	*P*
Site	2	0.096	12.729	**0.003**
Microhabitat	1	0.810	52.140	**<0.001**
Site x Microhabitat	2	0.007	0.802	0.482
Tidepool (Site)	8	0.008	1.963	**0.048**
Microhabitat x Tidepool (Site)	8	0.010	2.541	**0.010**
Residual	1136	0.004		
Pooled Residual with *S* x *M*	1138	0.004		

Adjusted Least Square Means

Factor	Jaw Length (cm)	α
Site		
Cape Blanco	1.080	0.0186
Middle Cove	1.061	0.0001
South Cove	1.042	-0.0187
Microhabitat		
Pit	1.084	0.0231
Nonpit	1.038	-0.0231

$\mu = 0.2541$, $\beta = 0.1614$

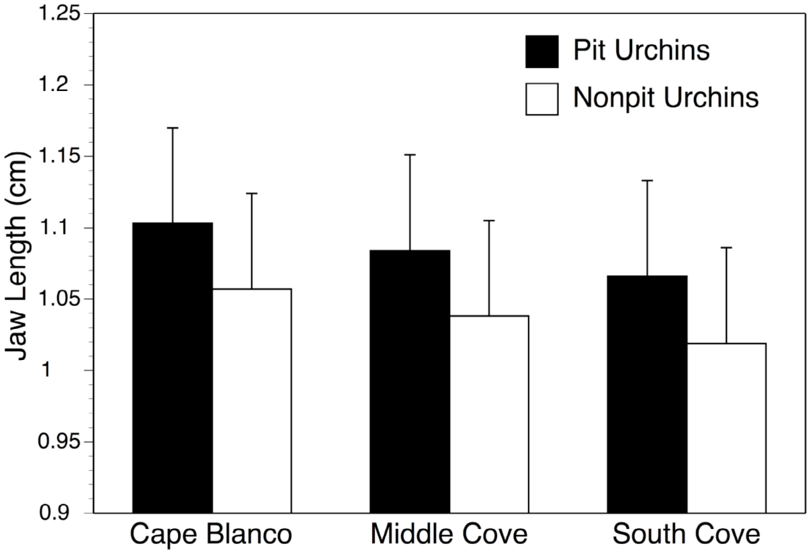


Fig. 3. *Strongylocentrotus purpuratus.* Adjusted jaw lengths (cm) for Site x Microhabitat combinations resulting from three-way ANCOVA; jaw lengths are adjusted to a sea urchin with test diameter = 5.00 cm; error terms are SD

DISCUSSION

This study used field-sampling techniques at three locations on the Oregon coast to test for demographic and morphological differences in *Strongylocentrotus purpuratus* living inside and outside pits. The null hypotheses that the population structure and mean test diameter did not vary between microhabitats were rejected. Microhabitat-based size-frequency distributions were dissimilar within every site and most tidepools, and nonpit urchins were significantly larger than pit urchins. The null hypothesis that pit urchins were not morphologically different from nonpit urchins was also rejected. Purple sea urchins living inside pits had relatively taller test heights, larger jaws, shorter spines, and less skeletal mass than those living in the same tidepools but outside pits.

Morphological differences indicate microhabitat fidelity

I found distinct morphological differences in *Strongylocentrotus purpuratus* from adjacent microhabitats. Is this due to morphological plasticity, with pit urchins and nonpit urchins within centimeters of each other altering their morphology in response to different suites of forces? Plasticity in sea urchins, though widely examined (Ebert 1996) has rarely, if ever been described over such small scales. Rogers-Bennett et al. (1995) found morphological differences in a population of *S. franciscanus*, in which sea urchins living at 5-m depth (incidentally in rock “bowls”) had shorter spines, larger gonads, thicker tests, and smaller Aristotle’s lanterns than those living at 14- or 23-m depth. In the western Pacific, the sea urchin *Anthocidaris crassispina* sometimes inhabits pits created by the sea urchin *Echinostrephus aciculatus*. Yusa and Yamamoto (1994) found that *A. crassispina* in pits had three times heavier gonads than individuals outside pits, though the groups also came from two separate tidepools. Despite the presence of morphological differences on the scales of meters and tens of meters, the effects of smaller scales remain largely unexplored. This study indicates that the microhabitat scale does influence the morphology of *S. purpuratus* in significant ways.

The observed morphological differences of *Strongylocentrotus purpuratus* living inside and outside pits imply some degree of microhabitat fidelity in individuals. If sea urchins were frequent movers within tidepools, one would not expect pit and nonpit urchins to exhibit distinct forms. This possible lack of movement provides a partial explanation for microhabitat-based differences in jaw size. Morphological plasticity in sea urchins is often attributed to food availability [eg. *Strongylocentrotus purpuratus* (Ebert 1980), *S. droebachiensis* (Minor & Scheibling 1997), *Diadema antillaum* (Levitan 1991), *Echinometra mathaei* (Black et al. 1984), and *Paracentrotus lividus* (Fernandez & Boudouresque 1997)]. Sea urchins with little or no food continue to allocate resources to the Aristotle's lantern, making it relatively large compared to well-fed urchins. The larger relative jaw sizes I observed in pit urchins may be due to food limitation. Pit and nonpit urchins occurred in the same tidepools, so why would just one group be food limited? Purple sea urchins in the intertidal tend to be sedentary feeders; drifting algae is trapped by their spines or grabbed by their tube feet (Ebert 1968, Dayton 1975). Pit urchins might be at a disadvantage if their pit is so deep they have difficulty reaching out of it for food. Sedentary sea urchins that do not leave their pits to forage might become food limited.

Other microhabitat-based differences in morphology would not seem to be related to food resources. The relatively short spines of pit urchins at two of three sites suggest that rubbing against the sides of pits wore down their spines. Qualitative field observations indicated that the spines on pit urchins sometimes lack epithelial tissue at the tip and are not as sharp as those on nonpit urchins. That all sea urchins at South Cove had short spines, regardless of microhabitat, is perhaps related to site characteristics. South Cove has much more loose cobble than Middle Cove or Cape Blanco. Here, many sea urchins exhibited a covering behavior in which they held pieces of cobble with their tube feet on top of their test. When waves are breaking on the intertidal habitat, cobble that is held by a sea urchin or loose in a tidepool might rub against or break spines, leading to smaller length spines.

The greater skeletal mass in nonpit urchins is probably not due to their longer spines because the trend is not constant among all three sites. Water velocity and hydrodynamic forces experienced by a sea urchin might affect the thickness of its test. In the absence of protective pits, physical exposure might induce nonpit urchins to allocate more resources to their skeleton (Lewis & Storey 1984, Rogers-Bennett et al. 1995). An alternative possibility is that differences in test shape led to heavier skeletal components in nonpit urchins. Pit urchins tend to be relatively taller and more compact while nonpit urchins tend to be shorter and wider, leading to significant differences in h/d ratio. At all sites, pit urchins had a greater h/d ratio than nonpit urchins. Just as a spherical object contains less surface area than a pancake-shaped object with the same volume, a tall pit urchin might require less skeletal material than a short nonpit urchin of similar mass.

How could a sea urchin's microhabitat affect its shape? The shape of sea urchins has been compared to that of a water droplet; in both, structurally sound forms are created by balancing internal pressure forces (Ellers 1993). In sea urchins, changes in any of the internal pressures (weight, podial forces, coelomic pressure) could alter the forces exerted on the test. The force most likely to be affected by living inside a pit microhabitat is that imposed by the podia as they cling to the substratum. An urchin on a flat surface holds itself in place with its oral podia, creating a downward force. An urchin inside a depression, however, could reduce this downward pull by podia by attaching to the sides of the pit with additional podia. Furthermore, a sea urchin will often wedge its spines against the sides of a pit to hold itself in place, creating an inward force on the side of the test. In pit urchins, perhaps the diminished use of oral podia and the forces created by jamming spines against the rock alter internal pressure forces. These changes in internal forces and the inherent flexibility in sutures between test plates (Johnson et al. 2002) could cause the tests of pit urchins to deviate from the typical water droplet shape.

Nonpit urchins tend to be larger than pit urchins

Strongylocentrotus purpuratus, an echinoid that is ecologically important and common along the North American West coast, has been the subject of numerous population structure studies. The sea urchin populations investigated in this study were similar in size structure to those sampled in 1985 at Cape Blanco and Sunset Bay, Oregon, about five km north of Cape Arago (Ebert & Russell 1988). In both studies, sea urchins with test diameters of 3–8 cm made up the bulk of the population, as recruitment was relatively rare. Ebert (1968) observed similar patterns from 1964–1967 at Sunset Bay with one year of exceptional recruitment in 1963, the only such event over more than two decades (Ebert & Russell 1988). In a latitudinal study, Ebert and Russell (1988) found that at all but one site in California, populations of *S. purpuratus* had smaller mean test diameters than those inside or outside pits in this study. Although pit urchins investigated in the study reported here were significantly smaller than nonpit urchins, the urchins I studied had a larger mean test size than has been observed with most intertidal populations of purple sea urchins.

The present study found clear size structure differences in purple sea urchins between different microhabitats. There is no strict definition for microhabitat, leaving researchers to define it as they see fit. For this research, I have defined microhabitats as the smallest scale at which physical or chemical variables that are relevant to the organism differ (Morris 1987). In the case of pits, hydrodynamic forces certainly are altered relative to a nonpit microhabitat. When the classification of microhabitat is expanded beyond that employed in this study, microhabitat boundaries might be defined by tidepools or substratum rather than microtopography. Using this expanded definition, more studies can speak to the potential impacts of spatial scales smaller than sites on sea urchin population structure. In South Africa, Drummond (1993) investigated the size structure of the sea urchin *Stomopneustes variolaris* in three intertidal areas on the same beach. She found distinct differences in mean size, and the smallest urchins were on an intertidal shelf in which they inhabited “small hollows.” Ebert (1968) also observed size differences in purple sea urchins living in different portions of the same bay, but he attributed them to varying food availability. Growth in *Strongylocentrotus purpuratus* varies among tidepools such that growth rates in pools thousands of kilometers apart might be more similar than between two at the same site (Russell 1987). In Norway, Sivertsen & Hopkins (1995) found large green sea urchins (*S. droebachiensis*) in barrens and kelp beds while smaller urchins dominated areas where the substratum was rocky, shelly, or covered with coralline algae. Unfortunately, data were collected and pooled in a way that prevents determining whether differences among dates, sites, or substrata were related to the observed differences in *S. droebachiensis*. Still, these studies lend evidence to the idea that spatial scales smaller than entire sites can affect the demography of sea urchins. The present study demonstrates that scales smaller than those previously investigated can also affect size structure in *S. purpuratus*.

In *Strongylocentrotus purpuratus*, the microhabitat-based difference in size structure does not seem to apply to juvenile sea urchins. Visual inspection of Fig. 2. reveals that recently recruited (≤2 cm) *S. purpuratus* did not seem to prefer pit or nonpit microhabitats. When recruits were found in either microhabitat, they were usually beneath the spines of conspecifics (Tegner & Dayton 1981, Nishizaki & Ackerman 2001). Small urchins were occasionally found in similarly sized pits, and some small urchins, in the absence of adults, were found attached to clumps of coralline red algae. Since most small sea urchins were found beneath adults, the choice of microhabitat of the adult tended to define the microhabitat inhabited by recruits. Only small recruitment pulses were detected during the study, so it would be worthwhile to investigate juvenile microhabitat following heavy recruitment.

At Middle Cove and South Cove, about 90% of the largest purple urchins (≥7.5 cm) were found outside pits. At Cape Blanco, where the mean test diameter was smaller, almost all of the urchins ≥6 cm were found outside pits. Drummond (1993) described larger sea urchin burrows in sandstone than in a harder substratum, and she proposed that it was easier for urchins to dig large cavities from the softer material. Sea urchins wear away the insides of pits by biting pieces of rock with their Aristotle's lantern and scraping the sides with their spines. Most of the bedrock at Cape Arago, including Middle and South Cove's, is relatively soft sedimentary sandstone. Purple urchins have excavated large, hemispherical pits that can exceed 7 cm in diameter. The metamorphic basalt at Cape Blanco is much harder than sandstone and may limit the bio-erosive capabilities of purple sea urchins.

How can the differences in the population structure of *Strongylocentrotus purpuratus* between microhabitats be explained?

Several hypotheses may explain the difference in size between purple sea urchins inside and outside pits. The separate distributions might be the result of variation in growth; nonpit urchins may grow faster than pit urchins (see Chapter III). Growth could be reduced in two ways. First, the sides of a pit may constrain the growth of its inhabitant. Most pit urchins nearly fill their cavity with little room to spare. Could growth be more difficult or even impossible for a sea urchin closed in on all sides? If an urchin constricted in a pit is to grow, it might be forced to grow upward, which would help explain the larger h/d ratio in pit urchins. Second, a reduced growth hypothesis could be explained by differences in food availability between microhabitats. Since *S. purpuratus* is essentially a sedentary feeder of drift algae, it is possible that more food is accessible to exposed, nonpit sea urchins, which could lead to increased growth rates and larger test diameters. Studies have demonstrated that echinoid populations can display differential growth rates within a site (Ebert 1968, Rowley 1990, Vadas et al. 2002), so it is plausible that the microhabitat scale could also affect growth. Spine damage incurs repair costs that reduce growth in sea urchins (Ebert 1968), and the shorter spines of pit urchins at two sites indicate that they may experience a higher rate of damage (possibly from scraping the sides of the pit) than nonpit urchins.

A second hypothesis for the observed size-frequency distributions is that pit urchins tend to move between microhabitats as they age (Chapter IV). When sea urchins are smaller, they can inhabit a pit and still have plenty of room for growth. At this stage, the protection of a pit might make it a preferred habitat. In Fiji, sea urchins (*Echinometra* sp.) occur on the crests and flats of reef atolls; crests are much more wave-exposed, but they contain small protective crevices. Appana et al. (2004) found that urchins on the crests of reefs had much smaller mean test diameters than those inhabiting reef flats. They suggested that either larger sea urchins avoid areas of high wave exposure to protect their spines, or predation pressure differs between the two habitats. Movement tends to be rare in recruits of *Strongylocentrotus droebachiensis*, which remain cryptically hidden for the early part of their life (Dumont et al. 2004). Both of these studies cite the need for protection as a reason that smaller urchins might inhabit a hole or crevice until they are better suited to deal with environmental pressures.

However, a sedentary pit urchin will eventually be faced with the dilemma that it cannot erode its pit as fast as it can grow. The cost of remaining in a pit would be the inhibition of growth. Since gonad mass increases with whole body mass, the cessation of growth could be a major disadvantage to a sea urchin. By changing from a pit to a non-pit microhabitat, this inhibition of growth could be avoided, allowing the sea urchin's body and gonads to continue increasing in size. Very large nonpit urchins have test diameters of 8 cm, about 1 cm greater than the largest pit urchins, translating to a nearly 50% larger total mass [for *S. purpuratus*: $m = (0.95 * d^2 * h)/1140$, $R^2 = 0.983$ where m is mass (g), d is test diameter (cm), and h is test height (cm)]. Some large sea urchins, however, have not moved out of their pits. If the nonpit lifestyle was the "right" microhabitat for large sea urchins, then why do some large sea urchins live inside pits? If being in a pit is a disadvantage because growth is inhibited, maybe there are reproductive advantages that come with staying in a pit. One possible advantage to spawning from a pit is that gametes are released into the benthic boundary layer, which can enhance fertilization rates (Yund & Meidel 2003).

Finally, differential mortality rates could lead to the observed size-frequency distributions. Predation has been invoked as the cause of bimodal size distributions in *Strongylocentrotus purpuratus* (Behrens & Lafferty 2004) and other sea urchins (Tegner & Dayton 1981, Cole & Keuskamp 1998, Shears & Babcock 2002). In these studies, predation pressure was strongest on intermediate sizes of urchins; juveniles avoided predation by crypsus and large individuals attained a size refuge. If nonpit urchins have higher survivorship than pit urchins, then, all else being equal, adult nonpit urchins would tend to be older and, hence, larger than pit urchins. Could predation lead to higher mortality rates of pit urchins than nonpit urchins? Of the animals known to consume *S. purpuratus* only sunflower sea stars (*Pycnopodia helianthoides*) (Mauzey et al. 1968), black oystercatchers (*Haematopus bachmani*) (Falxa 1992), and raccoons (*Procyon lotor*) have been seen at the study sites (Carlton & Hodder 2003) (see Chapter V). It is difficult to imagine, however, that any of these predators would preferentially select *S. purpuratus* living inside pits. I have observed oystercatchers and raccoons consume hundreds of nonpit urchins, but have never seen a predator successfully remove an entrenched urchin from its shelter. It seems that *P. helianthoides* could certainly consume a pit urchin, but when one comes upon a sea star with a test in its stomach, it is impossible to know from which microhabitat it came. Preferential predation on pit urchins might arise if the flight response of pit urchins to a starfish is weak or absent, but all purple urchins evacuate some tidepools to escape foraging *P. helianthoides*, regardless of their original microhabitat (personal observation). Microhabitat would not seem to have a significant effect on sea star predation, but pit urchins are much better protected than nonpit urchins from oystercatchers, raccoons, and other predators that must be able to grab or manipulate an urchin in order to consume it. Predation is probably not a cause of the microhabitat-based difference in size because, if anything, it would act to reduce the mean size of nonpit urchins.

Since large relative jaw size is evidence for food limitation in pit microhabitats, perhaps increased mortality could be related to starvation. Starvation is improbable since purple sea urchins can survive for months without food (Meidel & Scheibling 1999), and those animals that are starved tend to become mobile grazers (Mattison et al. 1977, Harrold & Reed 1985). Thus, a starved sea urchin would eventually be expected to leave its pit in search of food. The occasional trapped *S. purpuratus* that has outgrown the opening of its pits is a living testament to the ability to survive despite obligate pit life.

Even if differential mortality were responsible for the high frequencies of large nonpit urchins relative to large pit urchins, it would not explain the reverse relationship where more small urchins live inside pits. Almost half of the pit urchins sampled (626 of 1345, 46.5%) had test diameters ranging from 3 – 5 cm, while only a quarter of nonpit urchins (401 of 1502, 26.7%) fell into the same size class (Table 2). The differential growth hypothesis could explain this trend, because if nonpit urchins grow faster than pit urchins do, they would outgrow size classes faster. The movement hypothesis predicts that small pit urchins would one day move out of pits. Higher relative recruitment to pits could lead to higher frequencies of small pit urchins, but no microhabitat-preference was exhibited within the small recruitment pulses detected in this study. Finally, we must at least consider the possibility that microhabitat does not necessarily result in morphological differences, but rather, that urchins with different morphologies are inclined to select different microhabitats. Under this scenario, certain morphometrics of a sea urchin might increase or decrease its tendency to live in a pit. This explanation seems unlikely considering the range of traits (test shape, jaw length, spine length, skeletal mass) varying with microhabitat. If none of the alternative hypotheses are able to elucidate the relationships between *Strongylocentrotus purpuratus* and microhabitat, the hypothesis of morphology preceding microhabitat might deserve consideration.

Conclusion

The population structure of purple sea urchins *Strongylocentrotus purpuratus* is clearly affected by microhabitat, as urchins that inhabit pits are generally smaller than those outside of pits. The different utilizations of microhabitat lead to different morphologies, with pit urchins having relatively taller tests, larger jaws, shorter spines, and lighter skeletal mass than nonpit urchins. Differences in test shape may be a plastic response to living inside or outside a pit, while larger relative jaw size suggests that pit urchins may be more food limited than nonpit urchins. Microhabitat occupancy may have consequences for reproduction since larger nonpit urchins contain more gonad and reproductive potential than pit urchins. The patterns observed might be explained by differences in growth, movement patterns, or mortality between purple urchins in pit and nonpit microhabitats.

Bridge to Chapter III

In the discussion of Chapter II, I laid out several hypotheses that could explain the larger size of nonpit urchins relative to pit urchins. One of these, the differential growth hypothesis, is the focus of Chapter III. If nonpit urchins have higher growth rates than pit urchins, that might explain the observed bimodal size distributions. If, however, growth rates are similar or pit urchins grow faster than nonpit urchins, then the difference in sizes must be a result of older age in nonpit urchins. While the research detailed in Chapter III was specifically designed to test this hypothesis, it could have application for other invertebrates. In any organism that is sessile or has limited mobility, some individuals are likely to find themselves in undesirable microhabitats. Individuals and species that are best suited to deal with these less-than-ideal conditions will be those most likely to survive and contribute to future generations.

An urchin remained in the gloom,
Protected but finding no food.
        "I'm so tiny," he whined.
        And an adult replied,
"You could grow if you gave yourself room."

"To me you do seem a bit lazy,
Hiding there while I feast. How crazy!
        Come out and you'll grow.
        Believe me, I know.
That burrow was mine as a baby!"

CHAPTER III

DIFFERENTIAL GROWTH RATES OF *STRONGYLOCENTROTUS PURPURATUS* INSIDE AND OUTSIDE PITS

INTRODUCTION

In spatially heterogeneous environments, physical factors can vary greatly across relatively small scales. Every meter of shoreline on a wave-swept coast may appear equally violent, but some microsites on the order of 10 cm^2 experience markedly reduced hydrodynamic forces compared to others (Helmuth & Denny 2003). These microsites, or microhabitats, are biologically important for many organisms. Morris (1987) defines macrohabitats as “distinguishable units…in which an average individual performs all of its bodily functions (home range),” while microhabitats are “physical/chemical variables that influence the allocation of time and energy by an individual within its home range.” Studies considering microhabitat use have shown that environmental heterogeneity at small spatial scales can influence growth and survivorship (Kiesecker & Blaustein 1998, Charles et al. 2002), behavior (Longland & Price 1991, Vanhooydonck & Van Damme 2003), species distributions (Hertz et al. 1994, Koehn et al. 1994, Jones 1999), and community diversity (Guo 1998). Microhabitat studies in the marine environment are not as common as in terrestrial habitats, where an exhaustive body of research exists for rodents, lizards, and other animals [reviews by Smith (2001) and Jorgensen (2004)]. Microhabitat selection would seem to be especially important for marine invertebrates in which mobility is limited or impossible. *Anolis* lizards use sunlight intensity to select a basking location that will raise body temperature quickly (Hertz et al. 1994), but a bryozoan whose growth is inhibited by reduced water flow is unable to move to a more desirable microhabitat (Okamura 1992). The influence of small spatial scales on the population dynamics of marine invertebrates has not been well-studied, so the relative importance of microhabitat is generally unknown.

Secondarily sedentary animals are able to move but do not. Frank (1981) hypothesized that this behavior is characteristic of organisms in patchy environments that are unable to detect differences in mortality risk between patches, in which case the safest strategy is to remain in place. The purple sea urchin (*Strongylocentrotus purpuratus*) is a secondarily sedentary herbivore that occurs all along the Pacific Coast of North America. In past decades, much work on *S. purpuratus* and its congener *S. franciscanus* has focused on their structuring roles as mobile grazers in kelp forests (Mattison et al. 1977, Harrold & Reed 1985). On wave-swept rocky shores, however, *S. purpuratus* tends to adopt a sedentary lifestyle, maintaining its attachment to the substratum and eating drift algae that it catches with its tube feet (Paine & Vadas 1969, Dayton 1975). Where the substratum is sufficiently soft, *S. purpuratus* excavates and inhabits pits, which are protective microhabitats that likely reduce wave exposure and the risk of being crushed by storm-tossed logs and boulders. *S. purpuratus* can occur in densities greater than 400 m^{-2}, but not all are wedged into pits (personal observation). Sea urchins living just outside protective pit microhabitats (hereafter nonpit urchins) have larger mean test diameters and different size distributions than those inside pits (hereafter pit urchins) (see Chapter II). I hypothesized that these differences between sea urchins in the two microhabitats could reflect variation in growth rates, movement, mortality, or recruitment. The differential growth hypothesis is especially promising considering the feeding mode of *S. purpuratus*. Pit urchins cannot extend all of their tube feet or their spines out of a pit, so they might be expected to have a limited ability to capture drift algae compared to nonpit urchins. Pit urchins also have larger jaws relative to nonpit urchins (see Chapter II), a morphological indication of food limitation. If pit urchins are food limited, they would be predicted to allocate more resources to lantern growth and less to test growth, the end result being smaller measured test diameters than nonpit urchins (Ebert 1980b, Black et al. 1984, Levitan 1991). Growth differences in *S. purpuratus* and other sea urchins have been detected in adjacent macrohabitats (Ebert 1968, Andrew & Choat 1985, Russell 1987, Rowley 1990, Russell et al. 1998) but have never been quantified on a microhabitat scale.

The primary purpose of this study was to investigate whether growth rates in pit and nonpit microhabitats could lead to the observed difference in average test diameter in *Strongylocentrotus purpuratus*. I hypothesized that *S. purpuratus* inside pits grow more slowly than those outside pits. This may be due to reduced access to macroalgal drift or the physical constraints to outward test growth presented by the rock sides of the pit. Since this research was carried out in several tidepools at three sites, a second question was asked: which spatial scales should be considered if the growth of *S. purpuratus* is to be modeled properly? If growth in purple sea urchins is sensitive to small scales (e.g., differences in capture rates of drift algae between microhabitats, effects of tidepool size and volume), than large-scale studies need to consider these differences. I hypothesized that small scales (microhabitat and tidepools) do affect growth rates in *S. purpuratus* and can be used to help explain differences among sites.

MATERIALS AND METHODS

Study Sites

Growth of *Strongylocentrotus purpuratus* inhabiting pit and nonpit microhabitats was measured within tidepools at three sites along the Oregon coast (Fig. 1). Two sites, South Cove and Middle Cove, are part of Cape Arago (43^{o}18.5'N, 124^{o}24'W), an exposed headland. Sandstone benches, cobble and boulders, abundant macroalgal growth, and tidepools of various sizes characterize the intertidal at these two sites. The third site, Cape Blanco (42^{o}50'N, 124 ^{o} 34'W) is another headland fifty kilometers south of Cape Arago. Cape Blanco is generally recognized as a biogeographical border that separates northern and southern species on the Pacific Coast (Connolly & Roughgarden 1998, Connolly et al. 2001). Due to its transitional nature, a comparison of growth and demography of *S. purpuratus* between this site and Cape Arago might be revealing. The substratum at Cape Blanco is a metamorphic basalt much harder than the sandstone

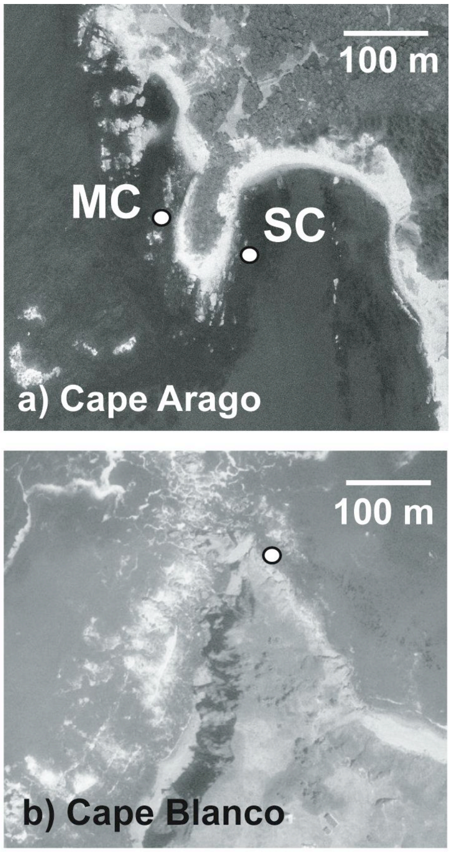


Fig. 1. Location of study sites; a) Middle Cove (MC) and South Cove (SC) at Cape Arago (43°18.5'N, 124°24'W); b) Cape Blanco (42°50'N, 124°34'W); white circles mark approximate locations of tidepools; scale bars are 100 m

Image courtesy of the USGS

substrata at Cape Arago, and cobbles and boulders are absent from the tidepools inhabited by *S. purpuratus* at Cape Blanco. Many boulders and cobble tend to collect, however, about 100 m along the shoreline to the east.

Tidepools provide an excellent intertidal location for mark and recapture experiments with sea urchins, which do not normally leave their pools, resulting in a high recapture rate (Paine & Vadas 1969). Three tidepools at Middle Cove and South Cove and five tidepools at Cape Blanco, ranging from 0.4 – 20 m^2 in area [measured using ImageJ software (Rasband 2006)] and 0.2 – 1.5 m above mean lower low water (MLLW) were selected for study (Table 1). More pools were sampled at Cape Blanco because they tended to be smaller in area with fewer purple sea urchins than those at the other sites. Tidepools were selected haphazardly while keeping in mind the purposes of the growth study. In order to produce accurate growth curves, it was necessary to use tidepools containing a wide size range of *S. purpuratus* living inside and outside pits.

Strongylocentrotus purpuratus often situates itself to maximize the protection it gains from its surroundings. If one is not completely protected in a deep pit, it might be sitting in a shallow pit, squeezed into a crevice, tucked under a boulder, or even wedged between other urchins. For this study, every sea urchins was categorized as either a "pit urchins" or a "nonpit urchin." An urchin was determined to be a pit urchin if its ambitus (the equator, or widest point of the urchin) was level with or below the edge of a pit. Some "nonpit urchins" were situated inside depressions that were shallow enough to be considered nonpit microhabitats; such shallow depressions would not seem to constrain growth or the ability to capture food in these nonpit urchins, compared to pit urchins that are surrounded by rock.

Mark-Recapture Methods

Purple sea urchins were tagged with tetracycline during low tides in the spring of 2005 (Kobayashi & Taki 1969, Ebert 1999a). Tetracycline, which fluoresces under ultraviolet light, is bound along with calcite in the growing tests and lantern parts of sea urchins. Sea urchins were removed from a tidepool and a hypodermic needle was used to inject 0.2 mL of a solution containing 1 mg tetracycline per 10 mL seawater. The

Table 1. Number of *Strongylocentrotus purpuratus* tagged and recovered from research tidepools at each site; columns are Sites (CB = Cape Blanco, MC = Middle Cove, SC = South Cove) and Tidepools, Tidal Height above MLLW, Area of tidepool^{a}, Density of sea urchins^{a}, date sea urchins were injected with tetracycline (Injection Date) and collected (Collection date), time between injection and collection (Growing time), number of sea urchins: Injected, Collected, and collected with visible tetracycline tags (Tagged), and Proportion Recovery of tagged sea urchins per injected sea urchins;
[a] when every sea urchin in a tidepool was not injected and collected, area and density were measured only for the sampled section of the tidepool.
[b] in one tidepool, urchins were collected from a greater area than was injected to maximize the collection of tagged urchins that may have moved.
[c] sea urchins in tidepool MCC were collected over two days because of high surge on 14 April 2006.

Sites	Tidepool	Tidal Height (m)	Area (m^2)	Density (urchins m^{-2})	Injection Date	Collection Date	Growing Time		*Strongylocentrotus purpuratus*			Proportion Recovered
							Days	Years	Injected	Collected	Tagged	
Cape Blanco			2.3	169					325	396	217	0.67
	CBA	0.5	0.36	125	8 Mar 2005	4 Mar 2006	361	0.989	50	45	30	0.60
	CBB	0.5	0.70$^{a\ b}$	157	8 Mar 2005	4 Mar 2006	361	0.989	52	110^{b}	47	0.90
	CBC	0.3	0.30	257	4 Apr 2005	28 Apr 2006	389	1.066	65	77	50	0.77
	CBD	0.1	0.73	71	5 Apr 2005	28 Apr 2006	388	1.063	50	52	33	0.66
	CBE	0.1	0.25^{a}	448	5 Apr 2005	28 Apr 2006	388	1.063	108	112	57	0.53
Middle Cove			13.4	45					684	597	275	0.40
	MCA	0.5	5.2^{a}	29	11 Apr 2005	14 Apr 2006	368	1.008	200	152	77	0.39
	MCB	0.3	1.85$^{a\ c}$	111	12 Apr 2005	^{c}			170	206	98	0.58
	Day 1					14 Apr 2006	367	1.006		109	42	
	Day 2					17 Apr 2006	370	1.014		97	56	
	MCC	1.5	6.3^{a}	38	16 Apr 2005	17 Apr 2006	366	1.003	314	239	100	0.32
South Cove			4.5	74					371	333	147	0.40
	SCA	0.5	0.52	210	28 Mar 2005	1 Apr 2006	369	1.011	131	109	44	0.34
	SCB	0.6	2.34	38	29 Mar 2005	1 Apr 2006	368	1.008	100	88	50	0.50
	SCC	0.6	1.67^{a}	81	1 Apr 2005	1 Apr 2006	365	1.000	140	135	53	0.38
Total			20.2	66					1380	1326	639	0.46

needle was inserted into the peristomial membrane covering the Aristotle's lantern so that the tetracycline solution would remain in the body cavity around the lantern. The sea urchin was then replaced in the position from which it was taken. Visual observations confirmed that sea urchins did not usually move when returned to the tidepool, though pit urchins immediately retreated to the bottom of their pit. An effort was made to mark every sea urchin in one or two tidepools during one low tide. When a tidepool was too large or the sea urchins were too dense to mark every individual, all the sea urchins in one distinct portion of the tidepool were tagged to increase the likelihood of recovery.

In the spring of 2006, one year after tagging, all of the purple sea urchins were collected from the research tidepools. In the cases in which sea urchins in one section of the tidepool were tagged, only animals in that section were collected. It is impossible to tell by visual inspection if a sea urchin has been injected with tetracycline, but because *Strongylocentrotus purpuratus* is largely sedentary in tidepools (see Chapter IV), most of the collected animals had likely been marked. Sea urchins were sexed by removing the peristomial membrane and checking for ripe gonads. They were then placed into individually numbered containers and covered with 6.25% sodium hypochlorite (bleach) to dissolve their soft tissue. After 24 hours, the tests and jaws were rinsed and left to soak in hot water for one more day before being rinsed, air-dried, and stored in individually labeled bags.

The test diameter, height, and demipyramid (jaw) length of each sea urchin were measured with vernier calipers accurate to 0.001 cm, but repeated measures of an individual could vary by as much as 0.1 cm. Jaw length and test diameter are highly correlated in sea urchins (Ebert 1980b), so increments in jaw growth are generally proportional to growth in test diameter. The length of the jaw is defined as the distance between the oral tip (the labial end) and the shoulder at the esophageal end. Growth occurs at both ends of a sea urchin jaw. The labial end is not worn away by scraping because a tooth, held by two demipyramids, contacts food and rock. Jaws were illuminated with ultraviolet light (Blak Ray longwave ultraviolet lamp) in a dark room and inspected for glowing, yellow tetracycline marks. The length of the demipyramid between the tag marks indicates size at the time of injection. Growth increments at the labial and esophageal ends were recorded for each sea urchin using a dissecting microscope (Leica Wild M37) and ocular micrometer with demarcations of 0.0026 cm. The length of the jaw at the time of tagging was measured as the total jaw length minus the two growth increments. All raw data are contained in Appendix C.

Growth in sites and microhabitats

A two-way analysis of covariance (ANCOVA) using the generalized linear model (GLM) provided a statistical comparison of growth between sites and microhabitats for purple sea urchins (Wilkinson 2004). The log transformation of (jaw growth + 0.01 cm) was used as the response variable, because this transformation resulted in the best linear relationship with the covariate jaw length (cm). Site and microhabitat were both fixed factors. Data from South Cove were excluded from the ANCOVA to avoid violating the assumption of homogeneous slopes (Fig. 2A). The regression line for South Cove showed high growth for small sea urchins and low growth for large sea urchins relative to Middle Cove and Cape Blanco. Both microhabitats (Fig. 2B) and two of three sites (Fig. 2A) can be compared, so the ANCOVA was carried out without the South Cove data.

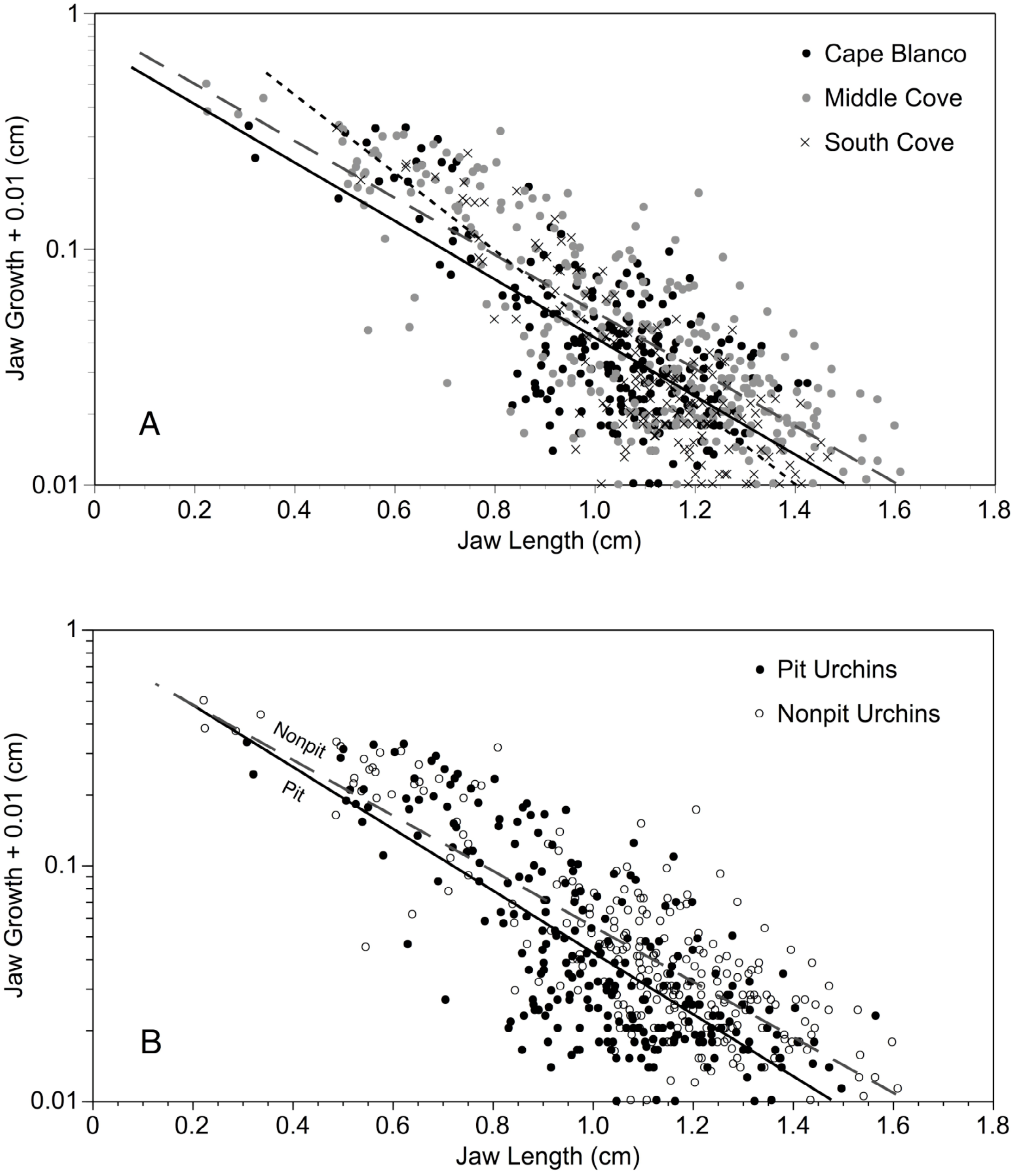


Fig. 2. *Strongylocentrotus purpuratus*. Regressions of growth data tested with a two-way ANCOVA; (A) site and (B) microhabitat were fixed factors, and data from South Cove were excluded because they violated the assumption of homogeneous slopes

Growth model

The Tanaka growth function

Growth in *Strongylocentrotus purpuratus* was modeled with the Tanaka function (Tanaka 1982, 1988). This technique allows the comparison of instantaneous growth rates between sea urchins in different microhabitats, sites, and tidepools. An indiscriminate growth model, the Tanaka function models the growth of organisms characterized by an early lag in growth, followed by a period of exponential growth that soon declines, but never to zero. Ebert (1999b) clearly explained the theory and application of the Tanaka growth function using *S. franciscanus*. Though this model was not developed specifically for any organism, it has been applied mainly to echinoids, including *S. franciscanus* (Ebert & Russell 1993, Ebert 1999a, Ebert & Southon 2003), *S. droebachiensis* (Russell et al. 1998, Russell 2001), and *Evechinus chloroticus* (McShane & Anderson 1997, Lamare & Mladenov 2000), as well as several other taxa, including the ophiuroids *Astrobrachion constrictum* (Stewart & Mladenov 1997) and *Ophiocten hastatum* (Gage et al. 2004) and the bivalve *Nuttalia obscurata* (Dudas 2005). Though sea urchin growth has also been modeled with the Richards (Ebert 1980a, Russell 1987, Kenner 1992), Bertalanffy (Ebert 1977, Barry & Tegner 1990, Morgan et al. 2000), and other growth functions (Jordana et al. 1997, Grosjean et al. 2003), a visual examination indicated that the Tanaka function provided the best fit to the growth data.

In the Tanaka function, the size of an organism at time t (S_t) is defined as:

$$S_t = \frac{1}{\sqrt{f}}\, ln\left|2f(t-c) + 2\sqrt{f^2(t-c)^2 + fa}\right| + d \qquad (1)$$

The four parameters do not all have clear biological meanings, but Tanaka (1988) defines them as such:

a = a measure of the maximum growth rate, which is at $\frac{1}{\sqrt{a}}$,

c = age at which growth rate is maximum

d = a parameter that shifts the body size at which growth is maximum, and

f = a measure of the rate of change of the growth rate (Ebert 1999b)

The Tanaka function can be modified into a three-parameter "difference" equation so that an organism's resulting size after growth (S_{t+1}) can be calculated as:

$$S_{t+1} = \frac{1}{\sqrt{f}} ln\left|2G + 2\sqrt{G^2 + fa}\right| + d \qquad (2)$$

where

$$G = \frac{E}{4} - \frac{fa}{E} + f \qquad (3)$$

and

$$E = e^{\left(\sqrt{f}(S_t - d)\right)}. \qquad (4)$$

By reducing the number of parameters that need to be estimated to three, the difference equation improves the model's ability to create a curve that tightly fits the data.

In the manner of Ebert (1999a), one parameter was varied at a time to get a better sense of how each influences the overall growth curve (Fig. 3A), which is a measure of instantaneous growth rate a given size. Growth curves generated by the Tanaka function can be integrated to calculate overall size as a function of age (Fig. 3B). An increase in the growth parameter *f* accelerates the growth curve's climb to maximum size, but also hastens the subsequent decline in instantaneous growth rate (Fig. 3A). Making *f* small results in slow, steady increases and decreases in growth rate. Because it takes longer for growth to approach 0, organisms attain a larger size when *f* is small (Fig. 3B). Increasing or decreasing the parameter *d* alters the age at which an organism experiences maximum growth, shifting the curve to the right (more time until maximum growth) or left (less time), respectively (Fig. 3A).

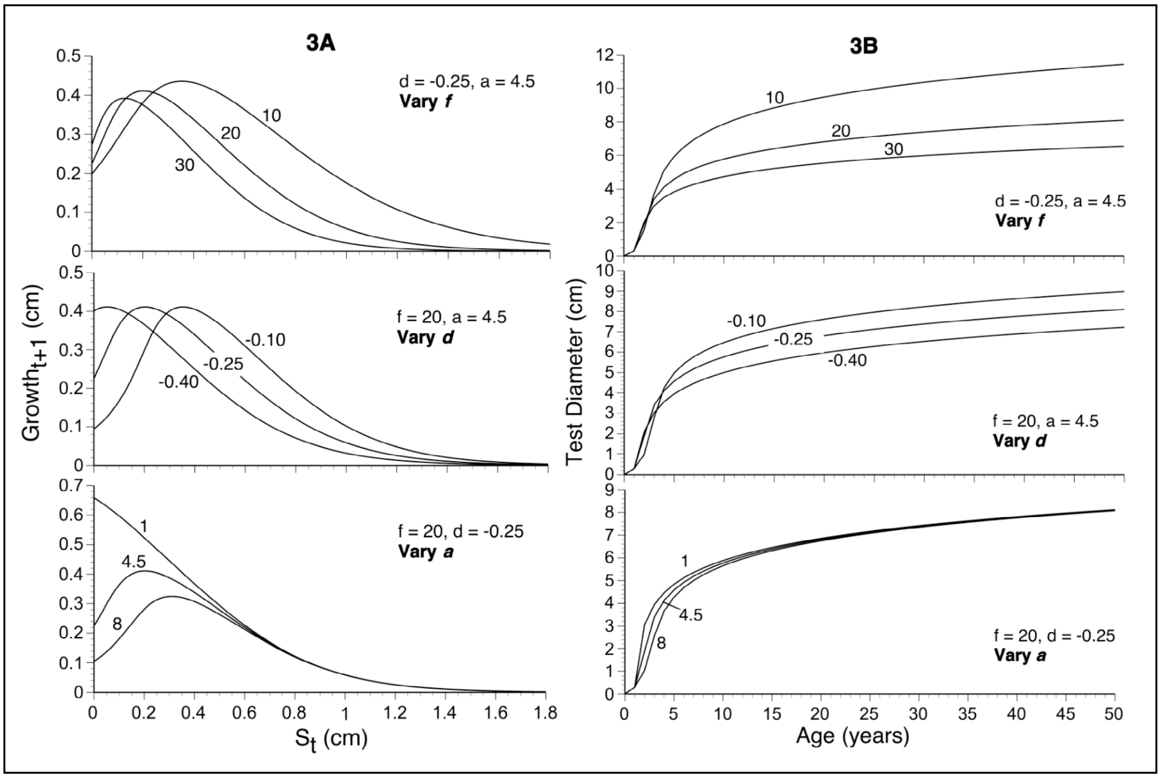


Fig. 3. Effects of variation in Tanaka parameters on growth curves; the parameters *f*, *d*, and *a* were varied individually to demonstrate how each affects the shape of (A) the instantaneous growth curve and (B) the integrated size-at-age curve; Selected parameter values correspond to ranges appropriate for *Strongylocentrotus purpuratus* determined by this study (adapted from Ebert 1999a)

Since the parameter *a* is inversely proportional to maximum growth rate, making it smaller increases the growth rate and vice-versa (Fig. 3A). For an organism that spends a very small proportion of its life in this phase of rapid growth, such as *Strongylocentrotus purpuratus*, changing *a* impacts the overall size less than changing the parameters *d* and especially *f* (Fig. 3B).

Applying the Tanaka function to the growth data

Jaw size at the time of tetracycline tagging (J_t) and final jaw size (J_{t+1}) were used in nonlinear regressions (Systat Software, Wilkinson 2004) to calculate the Tanaka parameters *f*, *d*, and *a*, describing the growth of *Strongylocentrotus purpuratus* from different microhabitats and sites. Growth was also compared between tidepools at Middle Cove, the only site with enough tagged sea urchins within individual tidepools that Tanaka growth curves could be created for each. Instantaneous growth curves ($J_{t+1} – J_t$ plotted as a function of J_t) were generated by inserting the calculated parameters back into the Tanaka model (Eq. 2 – 4).

In nonlinear regression, parameter estimation can be problematic when growth data for some size classes, especially small ones, are missing (Kenner 1992). Small urchins accounted for such a small proportion of the data in some groups that nonlinear regression resulted either in an improper Tanaka curve or the inability to fit any curve to the data. To deal with the general rarity of small *Strongylocentrotus purpuratus*, all individuals from all tidepools with an initial jaw size <0.75 cm (approximately two year-old urchins and younger with test diameters <3.2 cm) were pooled into a single group of sea urchins designated as “young”. These pooled young urchins were used to calculate every nonlinear regression.

Bootstrap methods were applied to the nonlinear regressions to estimate means and confidence intervals of the Tanaka parameters (McPeek & Kalisz 1993). One thousand bootstraps were performed and the bootstrapped parameter estimates (BPE) were obtained by accounting for bias. After sorting the bootstraps from smallest to largest, 95% confidence intervals were calculated as the average of the 25th and 26th samples, and the average of the 975th and 976th samples (Dixon 1993). Differences in Tanaka parameters between treatments were detected by examining the BPEs and confidence intervals.

Age estimation

The difference equation (Eq. 2-4) can be used to create size-at-age curves for each set of Tanaka parameters if size is known for the first-year age group. In this case, J_t was estimated to be 0.1 cm, which is the smallest jaw that was measured in any sea urchin and is the approximate jaw size for a one-year old purple sea urchin (Kenner 1992). Eq. 2 gives J_{t+1}, which is the jaw size at year 1. J_{t+1} is then reentered into Eq. 4 as J_t and so on, until a range of ages and corresponding sizes can be plotted. This method of integrating the Tanaka function over time was used to create size-at-age curves for each set of Tanaka parameters. A power curve was used to describe the allometric relationship between jaw size and test diameter so that test diameter could also be expressed as a function of age. Age was calculated for the jaws of all collected *Strongylocentrotus purpuratus* (tagged and untagged), and age-frequency distributions were created for sites, microhabitats, and Middle Cove tidepools.

RESULTS

Growth in sites and microhabitats

The growth of *Strongylocentrotus purpuratus* living in pit and nonpit microhabitats can be compared in three ways: 1) ANCOVA of the log transformation of growth rate; 2) visual examination of nonlinear regressions fit to the Tanaka function; 3) comparison of the associated Tanaka parameters and confidence intervals. All three techniques demonstrate that *S. purpuratus* grew faster outside of pits than inside pits. Differences in growth rate between sites and microhabitats were tested with a two-way fixed factor ANCOVA on the log-transformed growth increments. The results of the ANCOVA and adjusted least square means are presented in Table 2. The nonsignificant interaction ($P > 0.25$) was removed and its variance was pooled with the residual (Underwood 1997). The growth data from South Cove violated the homogeneous slopes assumption because large sea urchins from that site had very small growth increments (Fig. 2A); these data were excluded from the analysis allowing only a comparison between Cape Blanco and Middle Cove. Jaw growth varied significantly by site and microhabitat. Sea urchins at Middle Cove had significantly larger growth increments than those at Cape Blanco ($F_{1,488} = 41.0$, $P < 0.001$), and nonpit urchins had significantly larger growth increments than pit urchins ($F_{1,488} = 47.9$, $P < 0.001$).

Table 2. *Strongylocentrotus purpuratus.* Comparison of jaw growth for pit and nonpit urchins from two sites using two-way ANCOVA for log (jaw growth + 0.01); initial jaw size was the covariate; South Cove data violated the homogeneity of slopes assumption and were excluded from the analysis; the Size x Microhabitat interaction was nonsignificant and was pooled with the residual error; **bold** indicates significance at $P \leq 0.05$; the regression equation for adjusted least square means is $y_{ij} = \mu + \alpha_i + \beta x_{ij} + \varepsilon_{ij}$; adjusted least square means are for a sea urchin with jaw length = 1.05 cm

Source	d.f.	MS	*F*	*P*
Site	1	2.137	40.96	<**0.001**
Microhabitat	1	2.498	47.88	**<0.001**
Site x Microhabitat	1	0.013	0.252	0.616
Jaw (covariate)	1	46.082	883.18	**<0.001**
Residual	487	0.052		
Pooled Residual with *S* x *M*	488	0.052		

Adjusted Least Square Means

Factor	α	log (growth + 0.01)	growth (cm)
Site			
Cape Blanco	-0.0683	-1.449	0.0255
Middle Cove	0.0683	-1.312	0.0388
Microhabitat			
Pit	-0.0740	-1.455	0.0250
Nonpit	0.0740	-1.306	0.0395

$\mu = -0.04808$, $\beta = -1.2698$ SD = 0.232

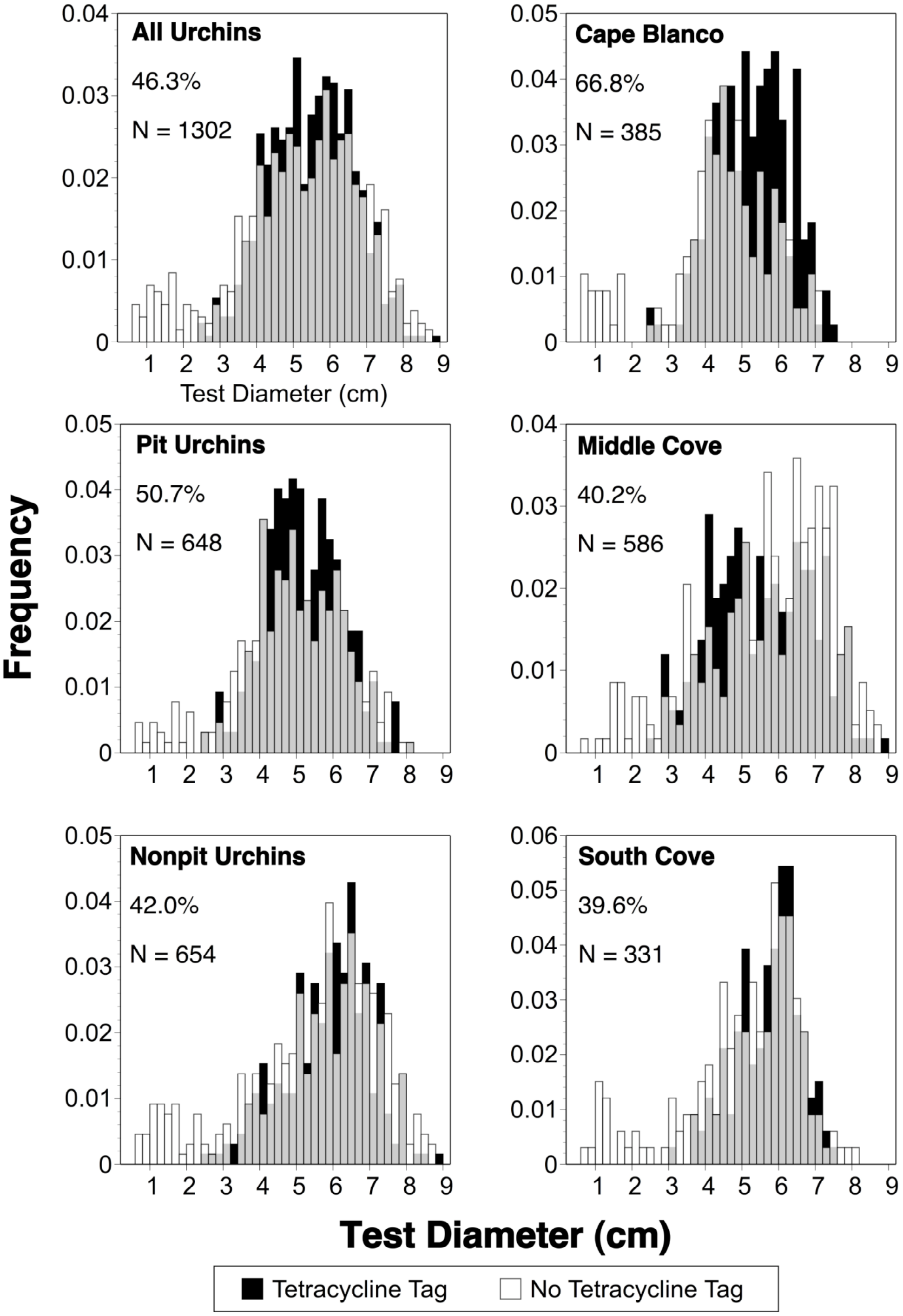


Fig. 4. *Strongylocentrotus purpuratus*. Recovery of tagged *S. purpuratus* from microhabitats and sites; size frequency distributions are for tagged (black bars) and untagged (white bars) jaws; grey indicates overlapping bars; percentage recovery of original sea urchins is noted; the mode between 0.5 and 2.0 cm is made up of sea urchins recruiting after the spring of 2005

Growth model

Tanaka growth function

Of 1380 *Strongylocentrotus purpuratus* injected with tetracycline, 639 (46%) were collected and possessed fluorescent growth marks (Fig. 4, data in Appendix C). Another 687 collected sea urchins were unmarked. Tagging success varied among sites and microhabitats. Cape Blanco had the highest recovery percentage (66.8%), while Middle Cove (40.2%) and South Cove (39.6%) had similar success rates. A higher percentage of pit urchins (50.7%) was recovered than nonpit urchins (42.0%).

The growth of young urchins (jaw length < 0.75 cm) from both microhabitats and all sites was essentially equivalent (Fig. 5). Since none of the grouping factors seemed to have considerable effects on growth of young urchins, pooling them as a group did not compromise the integrity of the growth curves. Since the Tanaka function is inaccurate without a sufficient size range of individuals, the inclusion of young sea urchins as a shared data set allowed the growth curves to take on proper shapes.

Growth rate in *Strongylocentrotus purpuratus* was highest when jaw size was approximately 0.2 cm, after which it decreased rapidly (Fig. 6A-C). At jaw sizes of 0.8 cm and larger, growth rates were greater for nonpit urchins than for pit urchins at all sites. The scatter of data points around the declining section of the growth curves can be seen more clearly in Fig. 6D-F. Large nonpit sea urchins tended to grow slightly more rapidly than large pit urchins. Microhabitat-based differences in growth rate were especially

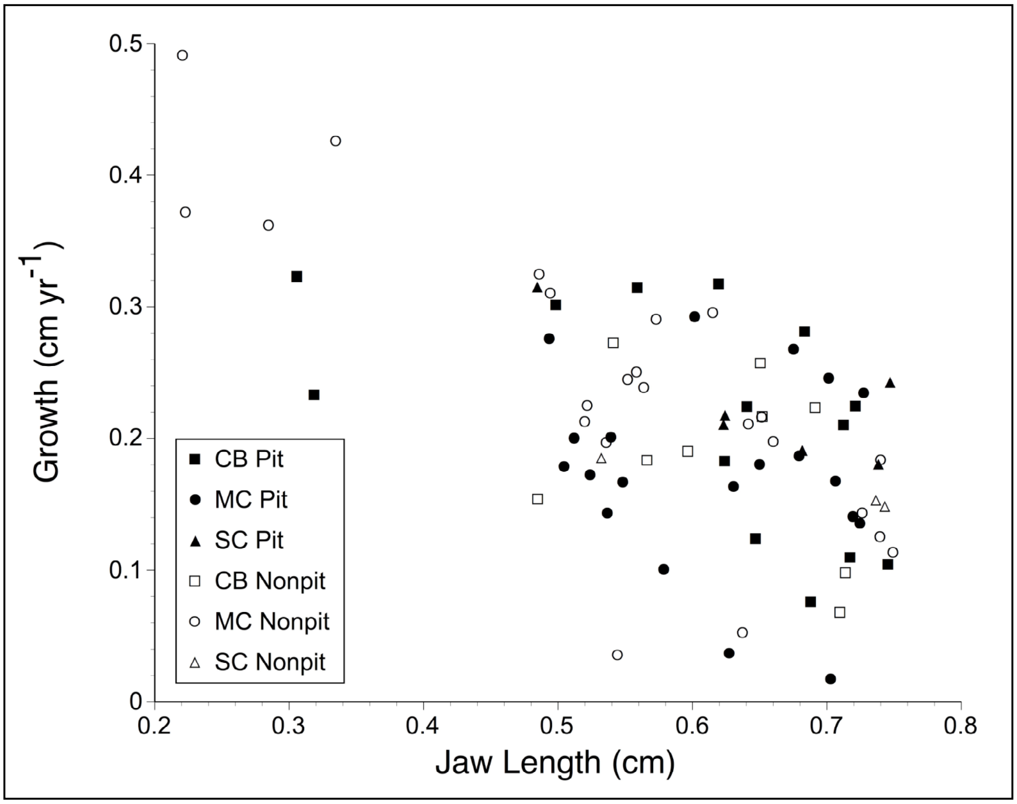


Fig. 5. *Strongylocentrotus purpuratus*. Growth increments over one year as a function of initial jaw length (J_t) for young *S. purpuratus* ($J_t < 0.75$ cm; approximate test diameter < 3.2 cm); sites are denoted by symbol shape, pit urchins are dark symbols, as nonpit urchins are light symbols

apparent at Middle Cove and Cape Blanco, while differences in growth rate were less clear at South Cove.

It should be noted that this analysis was unable to speak toward differences in the growth rates of small sea urchins from different microhabitats or sites. Since the pooled young urchins were included in each nonlinear regression, the early sections of the growth curves are similar. Differences between curves are driven solely by the effects of larger sea urchins and the necessary initial growth lag and sigmoidal shape of the Tanaka function.

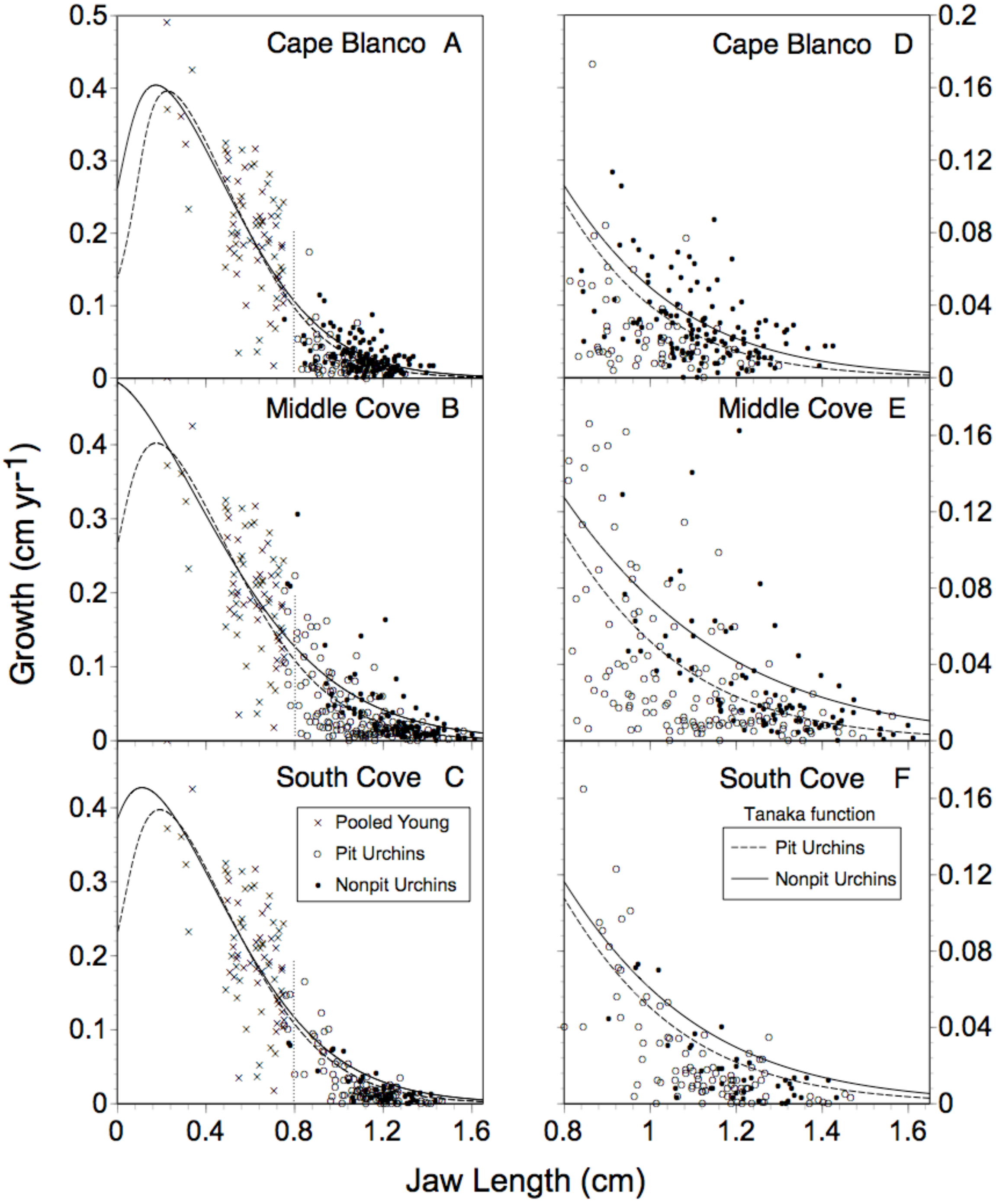


Fig. 6. *Strongylocentrotus purpuratus*. Tanaka function fit to jaw growth data for pit urchins (open circles) and nonpit urchins (filled circles) at three sites; the Tanaka curves are solid for pit urchins and dashed for nonpit urchins; data for young *S. purpuratus* with jaw length <0.75 cm were pooled (x); jaw growth increments are for one year of field growth, and initial jaw length (J_t) is the independent variable; (A–C) instantaneous growth rates for all sizes of *S. purpuratus*, and the dashed line marks the vertical axis for (D–F) where jaw length >0.80 cm

Tanaka function parameters

For the entire data set and individual sites, the Tanaka parameters *f* and *d* are both smaller in regressions fitted to nonpit urchins than to pit urchins (Fig. 7). The bootstrapped 95% confidence intervals of these parameters overlap slightly between microhabitats at Middle Cove, a bit more at Cape Blanco, and extensively at South Cove, indicating that microhabitat's effect on growth was dependent on the site. Of the three parameters, *f* varied the most between microhabitats, as its confidence intervals overlapped less than those of *d* or *a* for each site and overall. Recall that *f* is a measure of the rate of change in growth; nonpit urchins, with lower *f* values than pit urchins, experienced a slower decrease in growth rate, which is demonstrated by the growth curves in Fig. 6A–C. This slower deceleration in growth means that nonpit urchins maintained higher growth rates than pit urchins in all sizes larger than the pooled young urchins.

The effects of pooling the young urchins can be seen in Fig. 7, which reports and displays the Tanaka parameters and confidence intervals for different microhabitats at each site. The parameter *a* did not vary much between groups, and its confidence intervals were almost completely overlapping. When data for all sea urchins are pooled, *a* is 4.62, which corresponds to an approximate maximum growth rate of 0.465 cm year^{-1} ($\sqrt{a}^{-1}$). This maximum growth occurred when sea urchins were less than one year old, and jaw length was about 0.2 cm. While this growth rate is likely an accurate measure for the population, the pooling technique prevents drawing conclusions for any group factors.

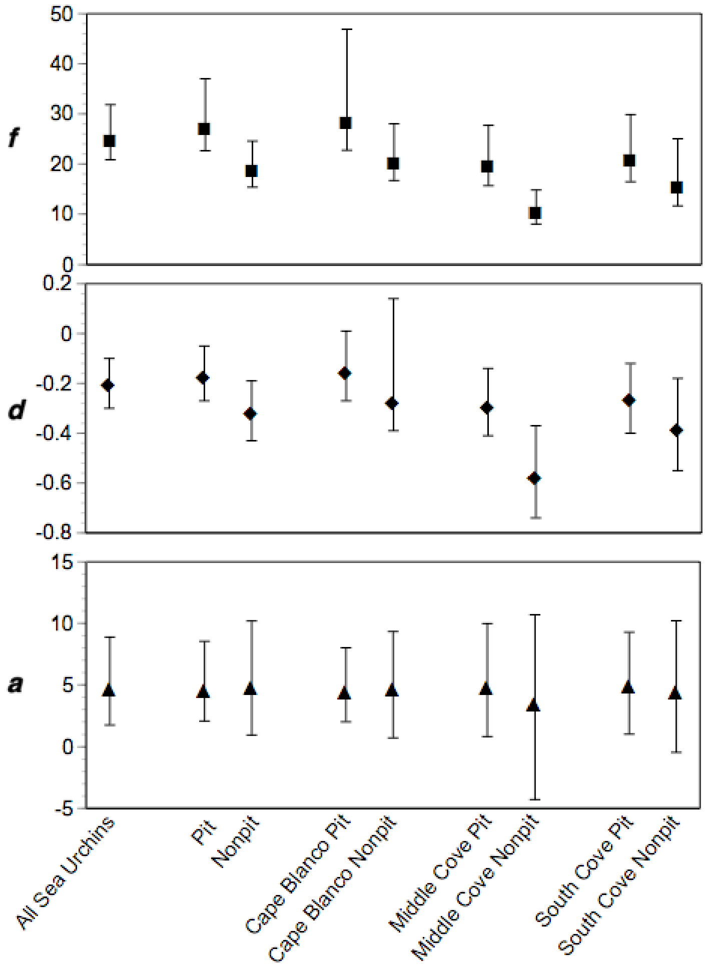


Fig. 7. *Strongylocentrotus purpuratus*. The parameters *f*, *d*, and *a* produced by fitting the Tanaka function to growth of *S. purpuratus* inside and outside pits; error bars are 95% confidence intervals from bootstrapping

Growth data are grouped by microhabitat in Fig. 8, making possible comparisons between sites for sea urchins in each microhabitat. The Tanaka function provides very similar curves for pit urchins at Middle Cove and South Cove, but pit urchins at Cape Blanco grew more slowly. Between sites, the growth curves vary more in nonpit urchins than in pit urchins. Middle Cove nonpit urchins had the highest instantaneous growth rates (Fig. 8) and the lowest *f* and *d* values of any site (Fig. 7). The high growth curve for

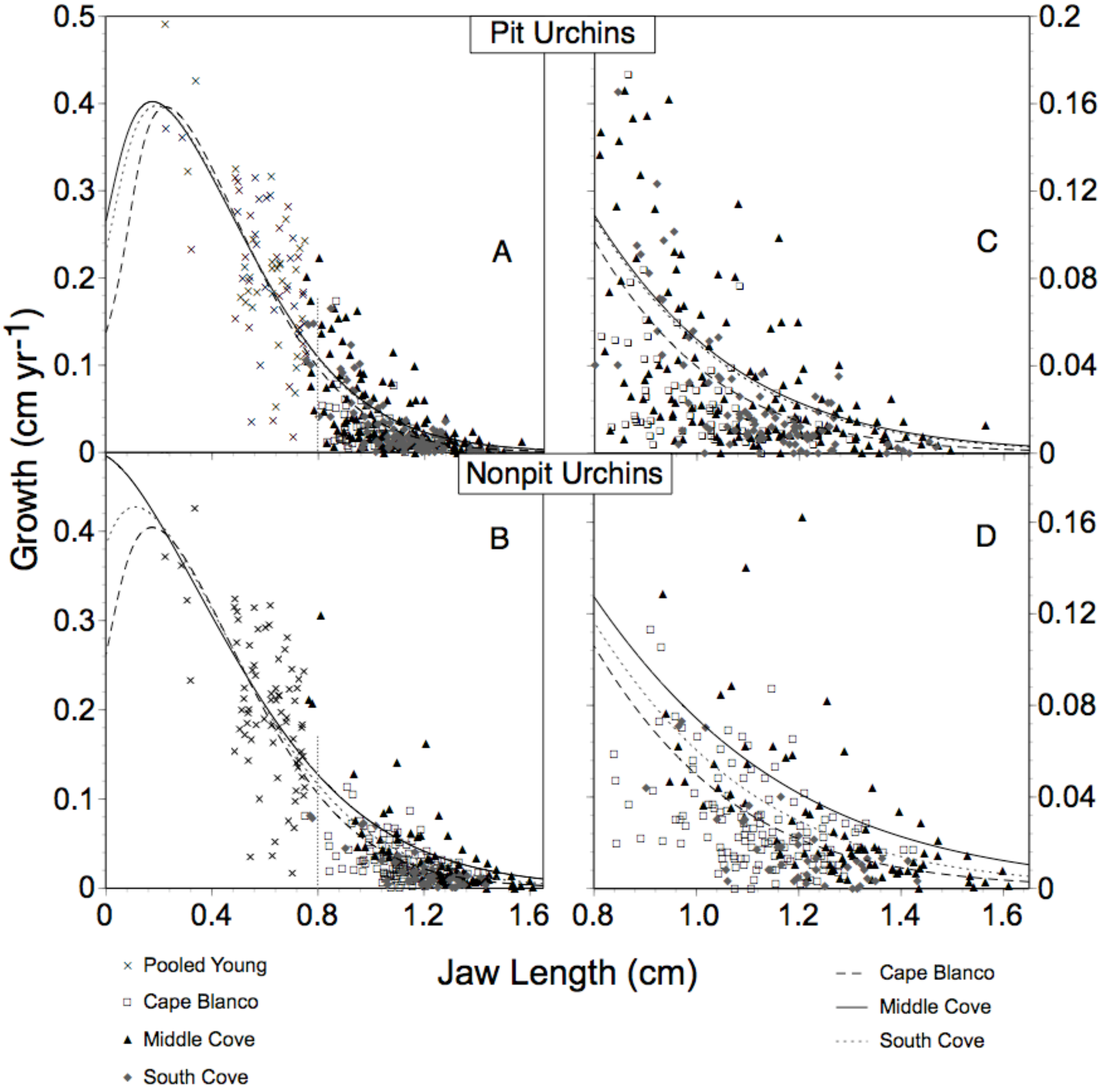


Fig. 8. *Strongylocentrotus purpuratus*. Tanaka function fit to jaw growth data for Cape Blanco (open squares), Middle Cove (filled triangles), and South Cove (filled diamonds) by microhabitat; Tanaka curves are dashes for Cape Blanco, solid for Middle Cove, and dotted for South Cove; data for all *S. purpuratus* with jaw length <0.75 cm was pooled (x); jaw growth increments are for one year of field growth, and initial jaw length is the dependent variable; A-B show instantaneous growth rates for all sizes of *S. purpuratus*, and the vertical dashed line marks the vertical axis for C-D where jaw length >0.80 cm

Middle Cove is driven in particular by the low f value, which slows the deceleration in growth rate relative to the other sites. In nonpit microhabitats, the growth rate of large sea urchins at Middle Cove was twice that of large sea urchins at the other sites. Nonpit urchins at Cape Blanco, on the other hand, grew more slowly that at any other site.

Age estimation

The Tanaka growth functions were integrated over time to predict jaw size at given ages. Additionally, overall size in sea urchins can be estimated from the growth model, as test diameter (D) is tightly coupled ($R^2 = 0.96$, Fig. 9) to jaw length (J), where

$$D = \alpha(J^{\beta}). \tag{5}$$

This allometric relationship is similarly strong for sea urchins in microhabitats within sites (R^2 varies between 0.95 and 0.98), so jaw length was converted to test diameter using the proper α and β for each site-microhabitat combination. Using these equations in the Tanaka function allowed for the creation of growth curves showing test size at a given age.

Slight differences in growth rates accumulate over time to result in large differences in eventual size (Fig. 10). Consider a purple sea urchin with a jaw length of 1.33 cm, the largest collected from a pit at Cape Blanco. Based on the Tanaka function for all Cape Blanco pit urchins, it would have a test diameter of 6.02 cm and a predicted age of 25 years (Table 3). A Cape Blanco nonpit urchin with the same jaw length would have a test diameter of 6.61 cm and a predicted age of 19 years. Since growth rates are

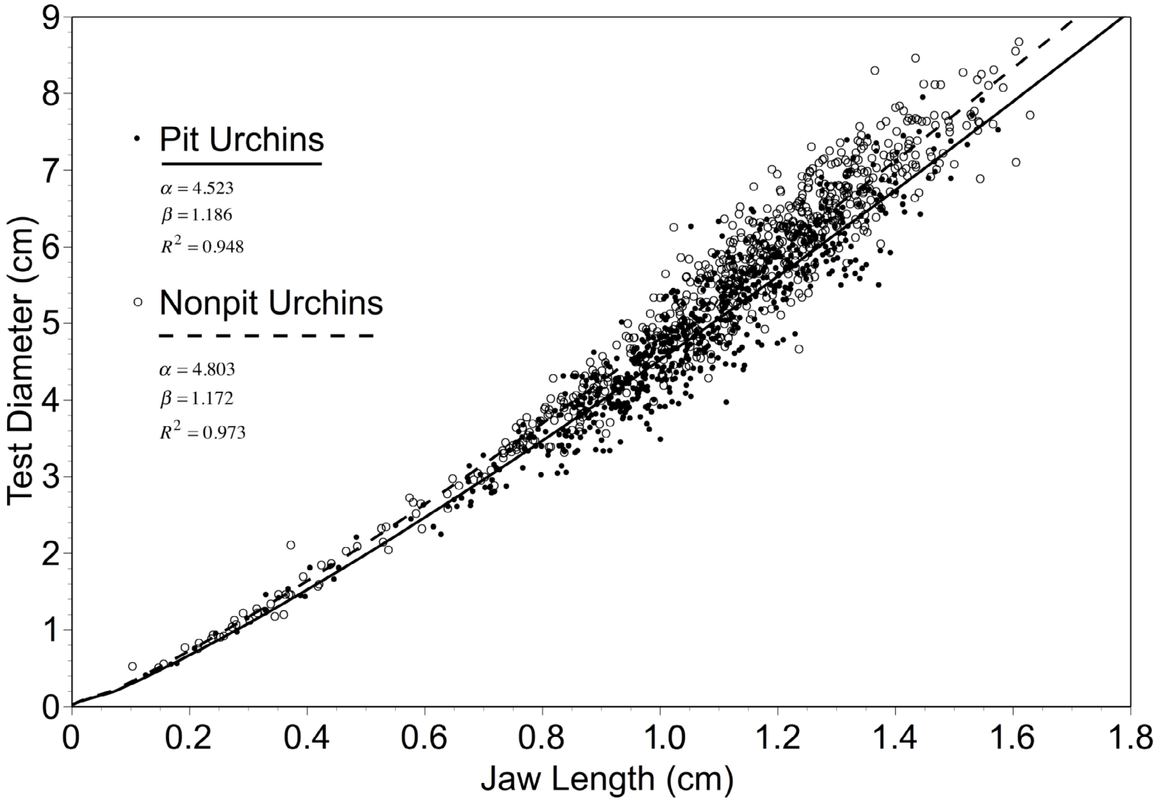


Fig. 9. *Strongylocentrotus purpuratus*. Power relationship between jaw length and test diameter in pit and nonpit urchins; high R^2 values allow size to be expressed in terms of test diameter in Fig. 10, 13, and 15

higher at Middle Cove, a pit urchin with the same jaw length is predicted to be 18 years old with a test diameter of 6.37 cm, while a nonpit urchin might be just 11 years old with a test diameter of 6.75 cm. At each site, this pattern becomes more pronounced with older sea urchins. At the age of 30, nonpit urchins have test diameters approximately 1 cm greater than do pit urchins at all sites, and the difference is 1.5 cm at Middle Cove. The

Table 3. *Strongylocentrotus purpuratus*. The effects of differential growth rates on large, old *S. purpuratus*; data in the first table are standardized to a jaw length of 1.33 cm, and data in the second table are standardized to a 30-year old sea urchin; all lengths are in cm

Jaw length = 1.33 cm	Test Diameter		Age	
Site	Pit	Nonpit	Pit	Nonpit
Cape Blanco	6.02	6.61	25	19
Middle Cove	6.37	6.75	18	11
South Cove	6.48	6.80	19	15

Age = 30 years	Test Diameter		Jaw Length	
Site	Pit	Nonpit	Pit	Nonpit
Cape Blanco	6.03	7.09	1.33	1.41
Middle Cove	6.93	8.41	1.43	1.61
South Cove	7.10	7.96	1.44	1.52

growth curves from the fitted Tanaka functions indicate that *S. purpuratus* grows faster and attains much larger sizes outside of pits than inside pits (Fig. 10B).

The largest age classes of pit urchins are between three and seven years at each site, compared to eight to twelve years for nonpit urchins (Fig. 10). The differences in these modes are very distinct at Cape Blanco and Middle Cove. At Cape Blanco, pit urchins outnumber nonpit urchins from ages one to seven, after which nonpit urchins clearly dominate the distribution. At Middle Cove, similar frequencies of sea urchins occupy pit and nonpit microhabitats for most ages, but pit urchins predominate for ages four to six, and nonpit urchins make up the majority of the one to two and nine to twelve year old age groups. At South Cove, sea urchins from ages two to eight tend to live inside pits, and nonpit urchins do not seem to dominate any age classes.

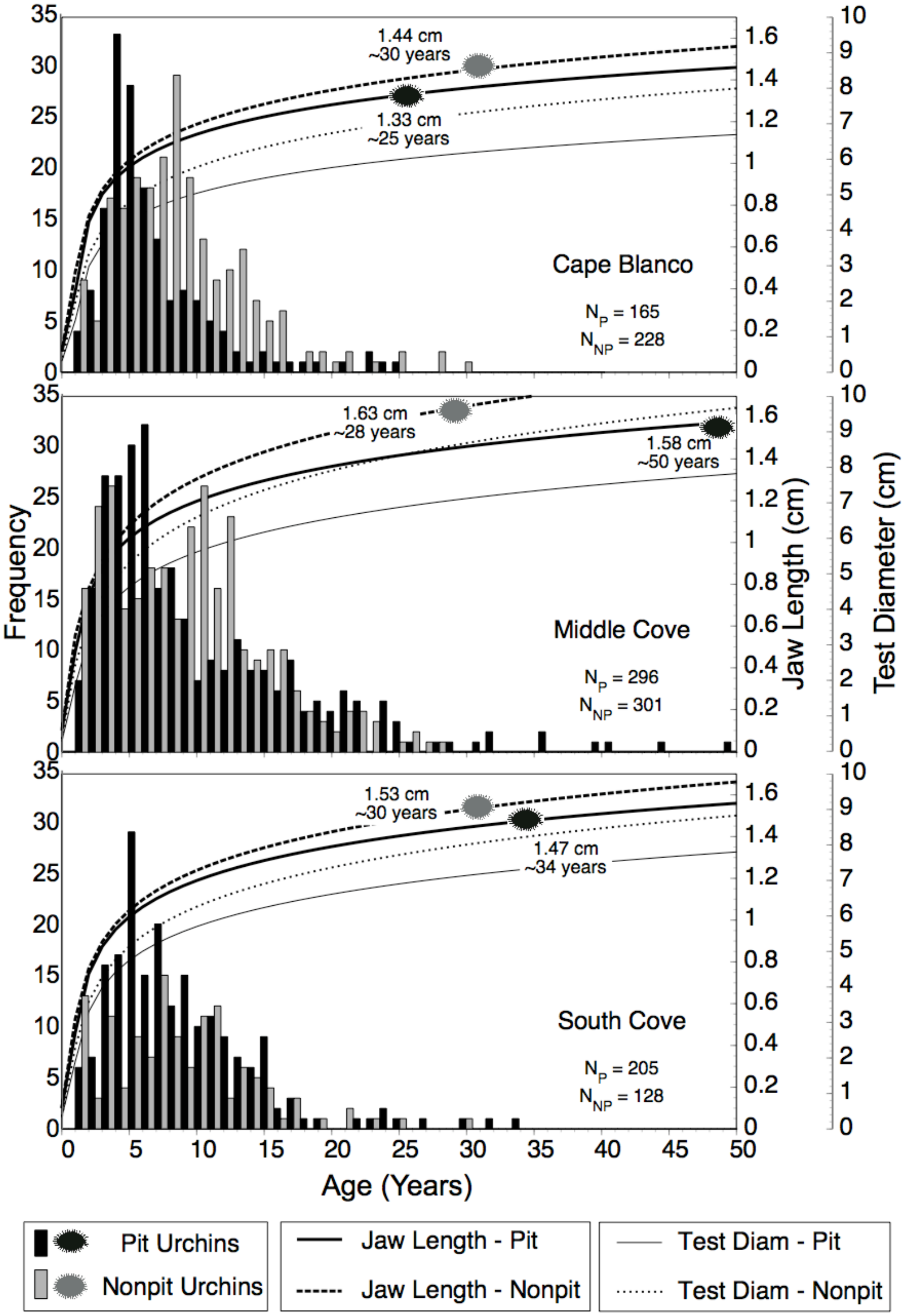


Fig. 10. *Strongylocentrotus purpuratus*. Age-frequency distributions and size-at-age curves for pit and nonpit urchins at each site; histograms were created by inserting the jaw lengths of all urchins into the Tanaka function to acquire estimated age; the calculated oldest pit and nonpit urchin at each site, corresponding to the largest jaw, is denoted by the sea urchin image on the growth curve

Growth differences between sites and tidepools

Site differences were apparent when microhabitat was ignored and nonlinear regression was used to fit the Tanaka function to the data from each site. Consistent with the ANCOVA results, the fastest growth occurred at Middle Cove and the slowest at Cape Blanco (Fig. 11). The Tanaka growth parameters and bootstrapped 95% confidence intervals for data pooled by site and tidepool are presented in Fig. 12. The age-frequency distributions, created from inserting jaw lengths into the growth curves integrated over time (Fig. 13), show several modal age groups of *Strongylocentrotus purpuratus*. At Cape Blanco, these modes occur at 4, 10, and 17 years, suggesting high recruitment pulses in 2002, 1996, and 1989. Middle Cove has similar modes at 3 – 5, 12 – 13, and 17 years, suggesting especially successful recruitment in 2001 – 3, 1993 – 4, and 1989. The distribution at South Cove is less clear, although there appear to be modes at 5- and 12-years as in Middle Cove. Each population of *S. purpuratus* is long-lived, with the oldest individuals close to 50 years old (Fig. 13).

Middle Cove was the only site with enough data to construct growth curves for individual tidepools. Sea urchins in tidepool MCC grew much faster than those in MCA or MCB (Fig. 14). This discrepancy in growth rates is reflected in extremely low values for the Tanaka parameters *f* and *d* for MCC (Fig. 12). The 95% confidence intervals for *f* and *d* do not overlap, suggesting that the growth of sea urchins in MCC was significantly higher than in the other pools. Enough *Strongylocentrotus purpuratus* were collected from MCC that the growth of pit and nonpit urchins could be evaluated separately in this one tidepool. Differences between the Tanaka parameters were small, indicating very

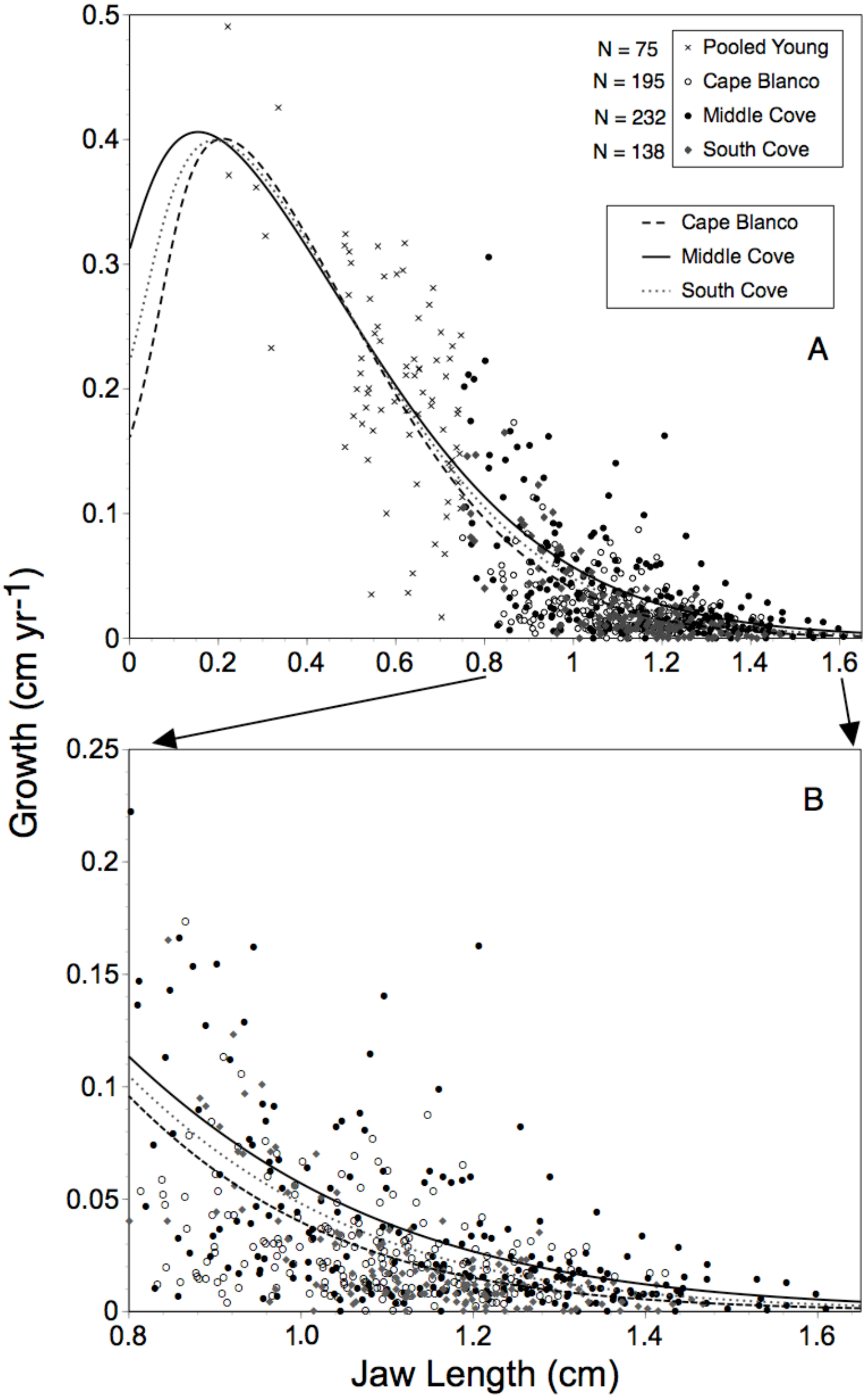


Fig. 11. *Strongylocentrotus purpuratus*. Tanaka function fit to jaw growth data over one year for *S. purpuratus* at Cape Blanco (open circles), Middle Cove (filled circles), and South Cove (filled diamonds); data for all *S. purpuratus* with jaw length <0.75 cm was pooled (x); A is the entire data set and B has been zoomed in to focus on the majority of the data;

little variation between the microhabitat-based growth curves in MCC (Fig. 12). Growth in *S. purpuratus* living both inside and outside pits in MCC was high relative to MCA and MCB, which is depicted in the size-at-age graph (Fig. 15). Associated with the rapid growth rate of sea urchins in MCC are small estimations of maximum age (20 – 22 years) compared to MCA (34 years) and MCB (40 years).

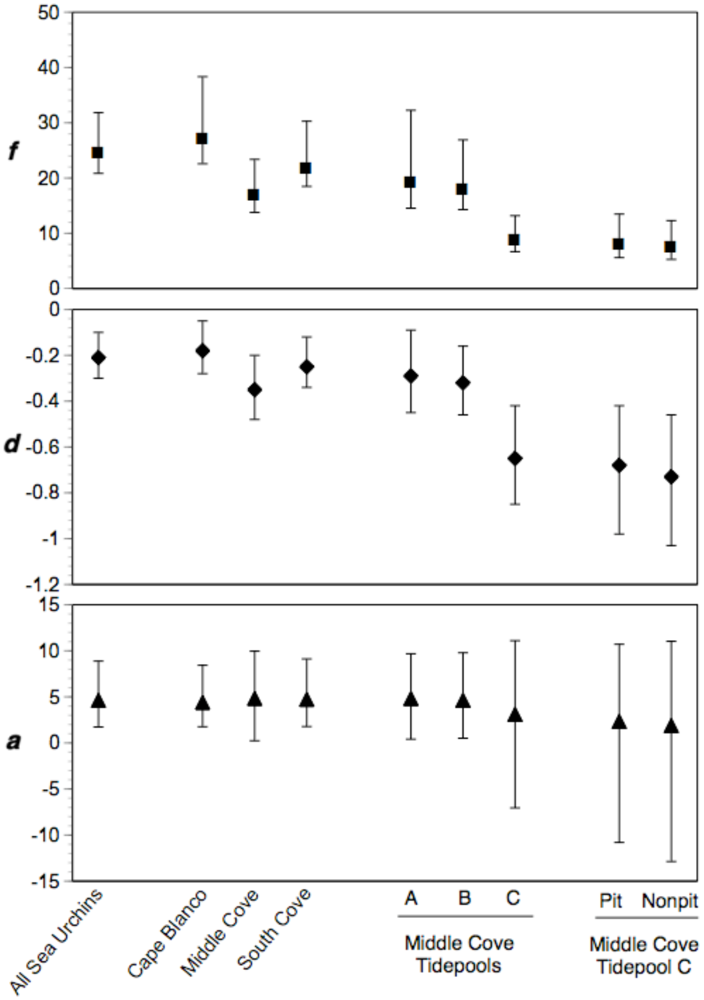


Fig. 12. *Strongylocentrotus purpuratus*. The parameters *f*, *d*, and *a* produced by fitting the Tanaka function to growth of *S. purpuratus* from different sites, tidepools, and microhabitats within Middle Cove tidepools; error bars are 95% confidence intervals from bootstrapping

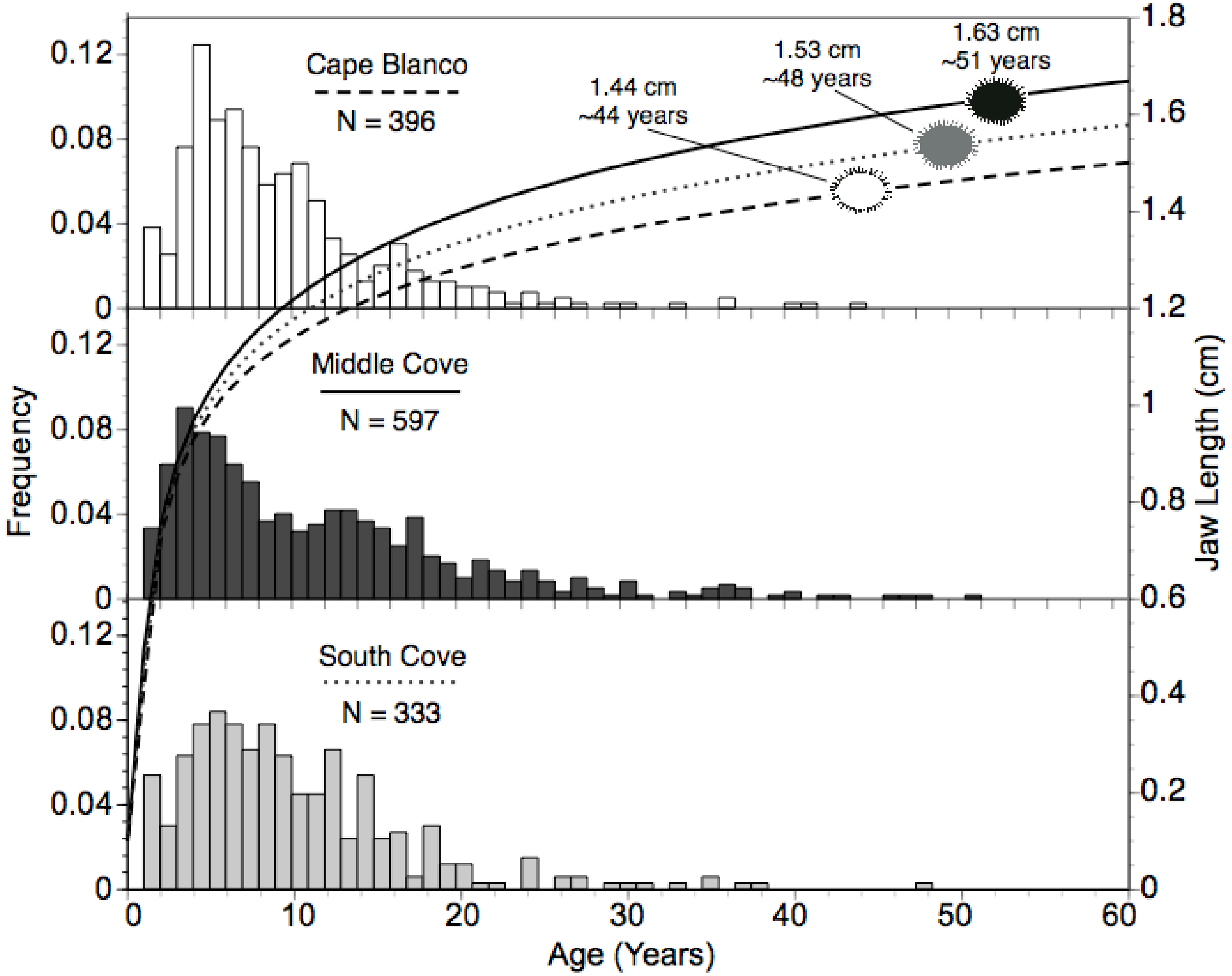


Fig. 13. *Strongylocentrotus purpuratus*. Age-frequency distributions and size-at-age curves for *S. purpuratus* at three sites; histograms were created by inserting the jaw lengths of all urchins into the Tanaka function to acquire estimated age; the oldest sea urchin at each site, corresponding to the largest jaw, is denoted by the sea urchin image on the growth curve

Visual inspection of Fig. 15 indicates that the age-frequency distributions in the tidepools are different. MCA had high frequencies of *S. purpuratus* younger than five years. MCB contained few sea urchins of these small size classes, and the modal age appears to have been about 14 years. The data from MCC repeat the patterns seen at the site level; the modal age of pit urchins is four to six years, and beyond eight years, nonpit urchins were more numerous than pit urchins.

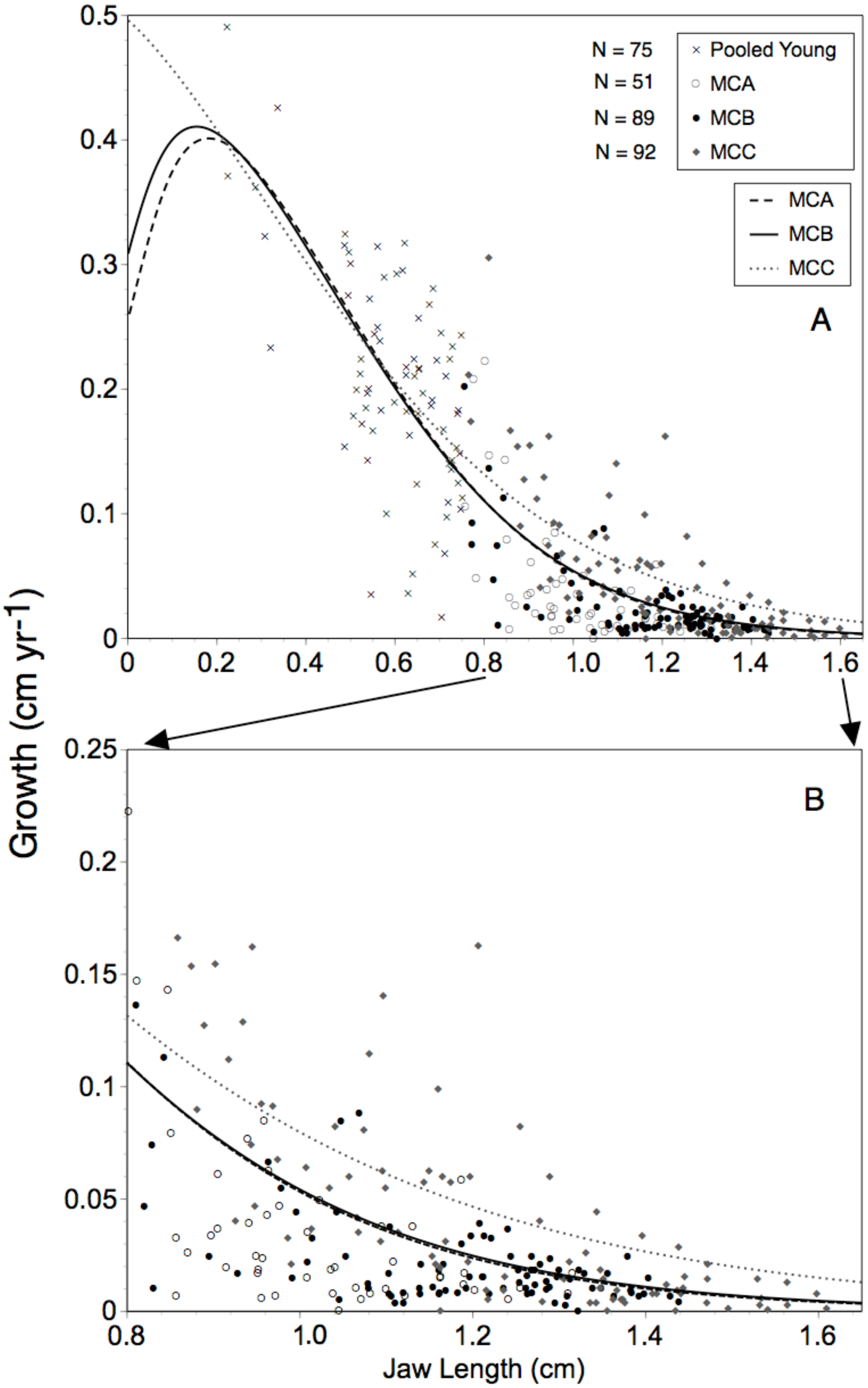


Fig. 14. *Strongylocentrotus purpuratus*. Tanaka function fit to jaw growth over one year for *S. purpuratus* from tidepools MCA (open circles), MCB (filled circles), and MCC (filled diamonds); data for all *S. purpuratus* with jaw length <0.75 cm was pooled (x); A is the entire data set and B has been zoomed in to focus on the majority of the data points

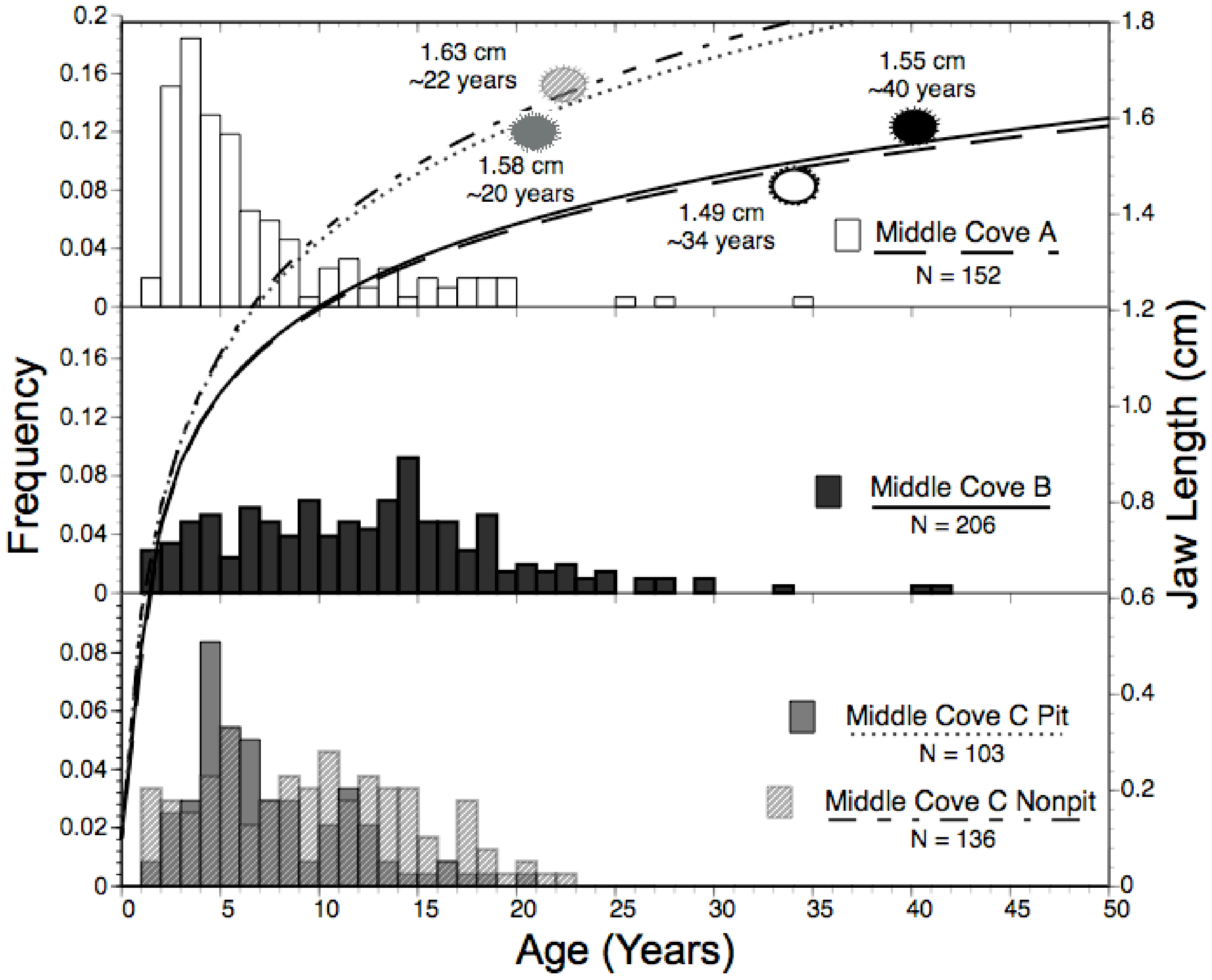


Fig. 15. *Strongylocentrotus purpuratus*. Age-frequency distributions and size-at-age curves for *S. purpuratus* in Middle Cove tidepools; MCC is split into pit and nonpit urchins ; histograms were created by inserting the jaw lengths of all urchins into the Tanaka function to estimate age; the oldest sea urchin at each site, corresponding to the largest jaw, is denoted by the sea urchin image on the growth curve

DISCUSSION

Lack of small sea urchins

All of the spatial scales investigated, microhabitats, tidepools, and sites, had substantial effects on the growth of *Strongylocentrotus purpuratus*, despite several shortcomings in the data. First, the nonlinear regressions were complicated by an unavoidable lack of data in first-year *S. purpuratus*. No tetracycline-tagged sea urchin had a test diameter <3 cm, corresponding to a two- or three-year old individual. Inspection of the size-frequency distributions in Fig. 4 indicates that the first-year size class was made up of untagged sea urchins with a test diameter less than 2 cm; in the spring of 2005, these individuals were either cryptically hidden or had not yet recruited to the tidepools. Thus, the data set did not include any sea urchins less than one-year old. Yamaguchi (1975) pointed out that this lack of data in the youngest size classes limits the ability of many studies to properly model growth in benthic invertebrates, which was true in this case. In Fig. 16A, the Tanaka function has been applied to the data from Cape Blanco without the pooled young urchins. The resulting exaggerated lag in growth of juvenile *S. purpuratus* displays maximum growth to occur when jaw size is 0.4 – 0.5 cm; at these growth rates, the size of maximum growth would not be reached until six to eight years, which is a severe underestimation based on other studies (Ebert 1968, Rowley 1990, Kenner 1992). The best solution for this data set was to pool all juveniles with initial jaw length less than 0.75 cm into a single group of data. My intention was to properly model the growth of adults, not juveniles, and pooling the smallest sea urchins allows for accurate comparisons of growth in most size classes. Fig. 16B contains the same data as Fig 16A with the addition of the young urchins, and the Tanaka function matches observed growth in juvenile *S. purpuratus* much more closely.

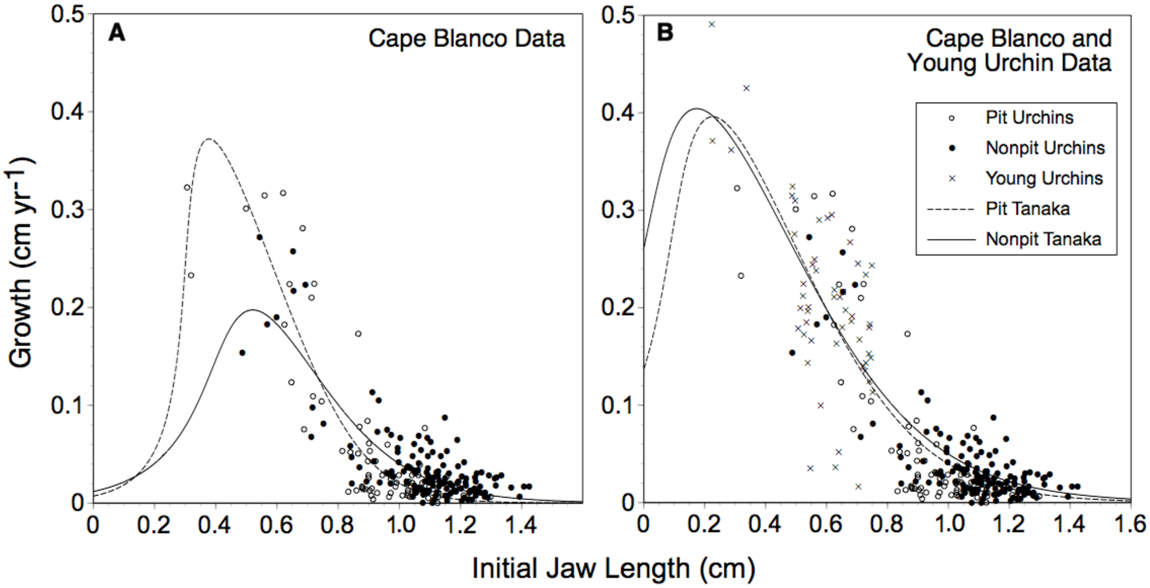


Fig. 16. *Strongylocentrotus purpuratus*. Effect of pooling young urchins on Tanaka growth functions for pit urchins and nonpit urchins at Cape Blanco; A contains only data from Cape Blanco, while B contains the same data as A plus pooled young sea urchins from Middle Cove and South Cove; the growth lag is too severe in A and maximum growth is not reached until 6 – 8 years; juvenile *S. purpuratus* complete their exponential growth phase very quickly, so the Tanaka function better represents biological reality when young urchins are included in the dataset

Incidentally, the six smallest sea urchins with fluorescent marks on their jaws were either pit urchins at Cape Blanco or nonpit urchins at Middle Cove. Although these two site-microhabitat combinations displayed the lowest and highest growth rates, respectively, the tagged juveniles all contained similarly large growth increments. This is too small a sample size from which to generalize, but the lack of distinct patterns in the growth of small, tagged sea urchins increases the legitimacy of the pooling-the-young technique. The diet of sea urchins changes as they age, so adults and juveniles could be subjected to varying levels of food availability in the same tidepool (Breen et al. 1985, Rowley 1990, Nishizaki & Ackerman 2004).

In most nonlinear regressions, plotting instantaneous growth rate against size resulted in predicted maximum growth at a jaw length of 0.2 cm, equivalent to a juvenile sea urchin less than one year old. The temporal resolution of this study is one year, and upon recovery, no tagged sea urchin was determined to be younger than two years, so at least the entire first year of growth is missing from the data. To increase the accuracy of the Tanaka curve, the growth of juvenile *S. purpuratus* needs to be investigated in detail over much shorter time intervals. Such small urchins cannot survive the puncture of their peristomial membrane. Tagging post-settlement size classes usually involves submergence in a calcein solution, which is incorporated into the skeleton and fluoresces just like tetracycline (Russell & Urbaniak 2004).

Low recapture rate of tagged sea urchins

Given 1380 sea urchins were injected with tetracycline, the recapture of just 639 tagged animals seems low at first. This recapture rate of 46%, however, compares well with success rates in other studies (Rowley 1990, McShane & Anderson 1997, Russell 2001). In the laboratory, tagging success is usually 100%, so why are field percentages lower? Either the tetracycline did not tag all sea urchins, or some individuals moved or died during the course of one year, so that half of the collected sea urchins had not been tagged. The more probable explanation is that tetracycline was not bound into the jaws of every sea urchin that was administered an injection. When viewed under ultraviolet light, not all tagged jaws fluoresce equally. The brightest growth marks are seen on small jaws, while large jaws from old individuals often possess very faint, almost undetectable growth marks. This is because the faster a sea urchin grows, the more calcite – and therefore, tetracycline – bound in its skeletal elements. Animals that are growing slowly tend to incorporate less tetracycline, and if they not growing at all they will show no growth mark. In this study, marking took place in the early spring when the intertidal was relatively devoid of fleshy macroalgae, and many sea urchins likely had empty stomachs and were not growing. Although the timing of injections resulted in the capture of the entire growing season (summer and fall), delaying until later in the spring or summer when macroalgal biomass is greater might have increased the tagging success.

If food limitation reduces tetracycline incorporation in the jaw, how can the relatively high recapture rate at Cape Blanco be explained in light of the food limitation in that population (see Chapter II)? One reasonable explanation is that sea urchins at Cape Blanco incorporated more tetracycline simply because they were growing faster at that particular time. Site differences between Cape Blanco and Cape Arago could result in different food sources available to populations of *S. purpuratus* at different times, and sea urchins display bursts of growth when they are fed after a period of starvation (Minor & Scheibling 1997).

The second possibility for low recapture rates, mobility of *Strongylocentrotus purpuratus*, cannot be ruled out. The tidepools at Cape Blanco were small so it was easy to find all of the sea urchins during a low tide. The tidepools also had steep sides and were mostly contained, with very few surge channels that a sea urchin might use as an exit. In contrast, the tidepools at Middle Cove and South Cove tended to be much larger (see Table 1), and had more surge channels. Only two of the six tidepools at these sites could be considered contained (MCA and SCB), so it is possible that sea urchins could have emigrated from the other tidepools. However, this explanation is unlikely because recovery rates were not much greater in MCA or SCB than the less contained tidepools. Russell et al. (1998) found a size difference between tagged and untagged *S. droebachiensis* in tidepools, and they argued that large sea urchins exhibit a greater degree of sedentary behavior than small sea urchins, resulting in higher recapture rates. This conclusion was probably correct for that study because they were able to tag very small individuals (<3 cm diameter) that could display greater mobility than adults. Observations of *S. purpuratus* at South Cove, discussed in Chapter IV, indicate that movement is somewhat uncommon in adults.

Selection of the Tanaka function

The Tanaka function created the best fit for the data, despite the difficulties presented by small sample sizes and a lack of juveniles. Many biologists have used the Richards (Richards 1959, Ebert & Russell 1992, Kenner 1992, Lamare & Mladenov

2000) or Bertalanffy (Bertalanffy 1938, Jordana et al. 1997, Morgan et al. 2000) growth functions to model sea urchin growth, but neither was appropriate in this case. The Bertalanffy function was deemed inappropriate because it assumes that growth decreases at a constant rate, whereas the decline of the Tanaka function's instantaneous growth curve (e.g., Fig. 6) slows with increasing jaw size (Knight 1968). Additionally, growth rate in *Strongylocentrotus purpuratus* never reaches zero, which is assumed by both the Bertalanffy and Richards functions. Growth increments were detected in at least half of the largest jaws of *S. purpuratus* collected at each site, a recovery success rate equivalent to other size classes, so the assumption of asymptotic size is biologically inappropriate. This indeterminate growth and the early growth lag observed in other studies (Yamaguchi 1975, Nichols et al. 1985, Rowley 1990, Middleton et al. 1998, Lamare & Mladenov 2000) make the Tanaka function (Tanaka 1982, 1988) the best growth model for these data.

Scales of variation in growth

The growth study reported here demonstrated that, over most of the size range of *S. purpuratus*, nonpit urchins grow faster than pit urchins. When the Tanaka growth function is fit to jaw data, instantaneous growth rates are higher in nonpit urchins than pit urchins when jaw size is larger than 0.75 cm (jaw size at three years), the Tanaka parameters *f* and *a* are significantly different between microhabitats, and ANCOVA analysis found growth to vary significantly by microhabitat. Previous comparative growth studies in sea urchins have not focused on the scale of tens of centimeters, so these findings are the first to indicate that microhabitat at the scale of the organism plays a significant role in the population dynamics of sea urchins. According to Morris' (1987) definition of microhabitat, varying physical or chemical variables between pit and nonpit microhabitats produced the observed differences in growth. Physical factors are the more likely choice to affect *Strongylocentrotus. purpuratus*, as a pit likely alters the hydrodynamic forces to which a resident sea urchin is exposed. Rock walls abrade against spines, shortening them and possibly decreasing overall growth (Ebert 1968, Lewis et al. 1990). Perhaps most importantly, a pit urchin sits in a depression that places its aboral surface near or below the substratum. A nonpit urchin is more exposed, which should result in a greater ability to catch food (drift algae) that is delivered to the intertidal by waves. Increased access to food in nonpit urchins should result in higher growth rates, which is the conclusion I draw from this portion of the study.

The hypothesis of higher growth in nonpit urchins than pit urchins was supported, further strengthening my previous supposition (see Chapter II) that pit urchins are food-limited based on their relatively large jaw size. Food availability has a major impact on growth in *S. purpuratus* (Ebert 1968, Edwards & Ebert 1991), and other sea urchins are known to depend heavily on food availability [e.g., *Evechinus chloroticus* (McShane & Anderson 1997), *Lytechinus variegata* (Beddingfield & McClintock 1998), *S. droebachiensis* (Minor & Scheibling 1997), and *S. franciscanus* (Morris & Campbell 1996)], so if pit urchins are food-limited, they would be expected to grow more slowly than nonpit urchins. Of course, it is also possible that the physical constraints imposed on sea urchins by the sides of pits were responsible for reducing growth, and without experimental manipulation, it is impossible to attribute the growth effects to one factor.

In a study in which size differences were explained by growth rates, Vadas et al. (2002) attributed bimodal distributions in populations of *Strongylocentrotus droebachiensis* in Maine, USA to markedly different growth rates. They did not tag sea urchins, but instead obtained age and growth data from bands on the test plates. The authors detected two modes in the size-at-age data, corresponding to distinctly different growth patterns. Using a mixture model based on the Bertalanffy growth function, Vadas et al. identified slow-growing and fast-growing morphs of *S. droebachiensis*, leading to a greater difference in size than was observed for *S. purpuratus* in the present study. The case of *S. droebachiensis* is especially pertinent to this study because in both cases, sea urchins with different growth patterns occur side-by-side. This lack of spatial separation means that individuals subjected to the same physical conditions exhibit different growth rates. Vadas et al. suggests that genetic variation or differences in recruitment of *S. droebachiensis* may drive the observed patterns, while microhabitat caused small-scale growth differences in *S. purpuratus*. Like *S. purpuratus*, many other echinoids occupy burrows, crevices, or holes, but most of these species are mobile grazers that exhibit homing behavior (Nelson & Vance 1979, Carpenter 1984, Blevins & Johnsen 2004). Microhabitat might affect other secondarily sedentary species that remain inside protective crevices in a similar manner as *S. purpuratus* inhabiting pits in rocky intertidal habitats.

Microhabitats may be defined by environmental variables, but the larger macrohabitat scale encompasses the entire area in which an organism performs its biological functions (Morris 1987). This definition is quite applicable for highly mobile rodents, but for a benthic organism with limited mobility such as *Strongylocentrotus purpuratus*, it is perhaps more appropriate to think of macrohabitat as the contiguous home range of a population. In this study, tidepools, and perhaps sites, fall under the auspices of this adapted definition. A mobile sea urchin could easily leave a mirohabitat, but might be unlikely to move out of its macrohabitat (see Chapter IV). Environmental heterogeneity resulted in growth effects at both of these scales.

At Middle Cove, the growth patterns in tidepool MCC were dramatically different from MCA and MCB, which supports previous studies documenting within-site variability in tidepool growth rates (Ebert 1968, Russell 1987, Russell et al. 1998). In one of these studies, growth patterns of *Strongylocentrotus purpuratus* in a southern California tidepool were less similar to another tidepool at the same site than to a tidepool on Vancouver Island, approximately 3000 km to the north (Russell 1987). Russell (2001), however, did not find growth differences between macrohabitats for *S. droebachiensis* in intertidal and subtidal habitats, nor did Ebert and Russell (1992) for *S. franciscanus* in tidepools separated by less than 1 km. Macrohabitat scales seem to be a determining factor in growth some of the time, but not all of the time, so what might explain its importance at Middle Cove? Several characteristics of MCC might have led to the high growth rates observed. First, it was a very large, one-meter-deep tidepool with a low density of *S. purpuratus* (Table 1). At 1.5 m above MLLW and protected by a large rock outcrop, MCC is wave-protected and supports profuse macroalgal growth, including the bull kelp *Nereocystis luetkeana*, whose drift is commonly consumed by *S. purpuratus* (Lawrence 1975). Compared to MCA and MCB, sea urchins in MCC almost certainly have greater food resources and experience less spine damage, which is caused by waves and is associated with reduced growth (Edwards & Ebert 1991). Tidepool MCC has a macrohabitat much more similar to subtidal kelp forests than the other tidepools at the site (personal observation). Forty years ago, in another study of *S. purpuratus* five kilometers north of Cape Arago at Sunset Bay, Ebert (1968) found similar growth differences between three macrohabitats: a boulder field, tidepools in the *Postelsia palmaeformis* zone, and tidepools in the eelgrass zone. The potential effects of growth differences on small-scales should make researchers wary of pooling site data before investigating potential differences within a site. Local scale differences are often the most important factors to consider and can outweigh differences between sites.

The growth curves fit to the Tanaka function were highest for Middle Cove and lowest for Cape Blanco, and ANCOVA confirmed the descriptive analysis. Though *Strongylocentrotus purpuratus* appeared to grow faster at Middle Cove than South Cove (Fig. 11), this may be an illusion resulting from within-site differences. Inspection of Fig. 12 reveals that the Tanaka parameters for South Cove are nearly identical to those for MCA and MCB, and the effects of MCC skew the overall results from Middle Cove. It is difficult, therefore, to compare sea urchin growth between Middle Cove and South Cove, though growth is certainly higher at Middle Cove than at Cape Blanco, 50 km south. The community compositions of these sites are highly variable, and differences in growth could easily be related to food availability or quality. The dominant kelp at Cape Blanco is *Laminaria setchelli,* and *Nereocystis leutkeana*, which forms extensive subtidal beds all around Cape Arago, is absent. In laboratory experiments Vadas (1977) found that *S. purpuratus* did not seem to exhibit strong grazing preferences but had adsorption rates of 85% for *N. leutkeana* (the highest of seven algae) compared to 64% for *L. saccharina*, which is slightly less woody than *L. setchelli*. If *N. leutkeana* represents a food source of higher quality than other algae such as laminarians, one would naturally expect to find higher growth rates in *S. purpuratus* at Cape Arago than at Cape Blanco. Jaw allometry indicated that *S. purpuratus* at Cape Blanco are food-limited compared to Middle Cove and South Cove (see Chapter II), further supporting the hypothesis that observed growth differences at these sites is related to the macroalgal communities.

Do higher growth rates explain the larger size of nonpit urchins relative to pit urchins?

Tanaka growth curves, the associated function parameters, and ANCOVA provide conclusive evidence that jaw growth for *Strongylocentrotus purpuratus* was greater in nonpit urchins than in pit urchins. *S. purpuratus* found inside pits were significantly smaller than those outside pits, and the microhabitats were characterized by significantly different size distributions (see Chapter II). Differential growth rates between microhabitats likely contribute to these observed differences in size, but can growth exclusively account for the observed differences in size-frequency distributions? Based on estimated age-frequencies, it does not appear that they do. The data in Fig. 10 suggest that microhabitat use probably changes with age. If differential growth rates were solely responsible for the microhabitat-based size differences, similar modal ages would be predicted in each microhabitat. At Middle Cove and Cape Blanco, the five-year mode tends to be made up of pit urchins, but the ten-year mode is mostly nonpit urchins. THis suggests that many of the nonpit urchins were pit urchins at some point in the past. The faster growing nonpit urchins are also older than pit urchins, so growth and movement may both contribute to size differences.

Emigration out of pits by *Strongylocentrotus purpuratus* could be responsible for this pattern. As was discussed previously, movement of purple sea urchins in the intertidal seems to be rare (Paine & Vadas 1969, personal observation, Dayton 1975). Given five years, however, a growing sea urchin might leave a pit, and finding no larger pit to occupy, become a sedentary nonpit urchin. Alternatively, pit urchins could be subject to higher mortality than nonpit urchins. These hypotheses are explored further in Chapters IV and V. In some regions, the recruitment of *S. purpuratus* is known to be highly variable, so it is likely that the presence of modal ages indicates past years of better-than-normal recruitment (Pearse & Hines 1987, Ebert & Russell 1988, Rowley 1989). If different cohorts of sea urchins exhibited different microhabitat preferences, it could lead to the differences seen in microhabitat occupancy in the 1996 and 2001 recruitment classes. Juvenile sea urchins in the study tidepools occurred fairly evenly inside and outside pits and seemed to be associated with large adults more so than any particular microhabitat. It may be noteworthy to mention that no *S. purpuratus* with a test diameter less than 2 cm was found inside a large (>5-6 cm) pit unless it was underneath the spine canopy of an adult. Outside of pits, recently recruited juveniles seemed less likely to be associated with adults. Associations between juvenile sea urchins and adult spine canopies were described by Tegner and Levin (1983), though the relationship has been described as stronger in *S. franciscanus* than *S. purpuratus*. Based on the few observations in these data, it is difficult to formulate juvenile- or recruitment-based hypotheses because heavy recruitment pulses do not appear to have occurred at the study sites within the past five years.

Estimation of age in *Strongylocentrotus purpuratus*

The growth curves obtained by fitting the Tanaka function to jaw growth data indicate that purple sea urchins are long-lived animals on the order of decades. When sea urchins were grouped by site and microhabitat, maximum age was estimated to be 30 years for nonpit urchins and 25-50 years for pit urchins, depending on the site (Fig. 10). The use of microhabitat-specific growth curves, however, implies microhabitat fidelity that may or may not be reality for *Strongylocentrotus purpuratus*. When sea urchins were injected and replaced in a tidepool, they were not observed to move from the spot to which they attached, though pit urchins retreated as far as possible into their pit. Still, it was impossible to know at the time of collection whether a sea urchin had remained in the same microhabitat since it was injected with tetracycline. The age of a sea urchin could be severely underestimated if it spent almost an entire year living inside a pit that it evacuated one day prior to collection. For the purposes of characterizing growth by microhabitats, movement was assumed minimal by necessity. Differences in microhabitat-based growth provide some validation for this conjecture, as do the morphological differences described in Chapter II, but the question remains: how likely is it for a sea urchin to spend its entire life, or at least the year of tagging, in the same microhabitat?

Field observations on the dates sea urchins were collected provide support for the assumption of minimal movement. Where *S. purpuratus* that were surrounded by a common red coralline alga, *Lithothamnium*, were pried from the substratum, a small patch of bare rock usually was usually observed underneath them. Both pit and nonpit urchins revealed rock scars upon removal. *Lithothamnium* covered much of the substratum in all of the tidepools, especially those at Middle Cove and Cape Blanco. Rhodoliths such as *Lithothamnium* sometimes grow less than 1 mm year^{-1}and have been aged to 86 years, though larger individuals are probably over a century old (Frantz et al. 2000). Whether a grazing or shading effect, the continuous rock coating of *Lithothamnium* and lack of algae underneath *S. purpuratus* is evidence for sedentary behavior. If the sea urchins were mobile grazers, they would be expected to create bare patches in the *Lithothamnium* faster than it could grow back.

The assumption of minimal movement emphasizes the potential importance of differences in growth rates between microhabitats, but what is the likelihood of a sea urchin spending its entire life in one place? Since the age-frequency data in Fig. 10 suggest that movement between microhabitats may occur, most *Strongylocentrotus* *purpuratus* probably do not spend their entire lives in the same microhabitat. The microhabitat-based growth curves, then, are extreme boundaries, between which lies the true growth curve for the population. To obtain accurate age estimates for *S. purpuratus* in tidepools, it is probably more appropriate to apply the Tanaka function to pooled data from a tidepool or site, macrohabitats from which individuals are unlikely to leave.

The site-specific growth curves (Fig. 13) yield maximum age estimates of 45 – 50 years for *Strongylocentrotus purpuratus* at each site. These estimates seem reasonable in light of other studies. In the western Atlantic Ocean, another study used the Tanaka function and tetracycline-tagged sea urchins to age *S. droebachiensis* to at least 30 years (Russell 2001). *S. franciscanus*, which grows to be much larger than *S. purpuratus*, is known to live over 160 years (Ebert & Southon 2003), measurable because detectable radiocarbons were incorporated into test plates during the nuclear testing era in the late-1950s. Middleton et al. (1998) found growth in the deep-sea echinoid *Echinus affinis* to be linear with respect to volume, and they estimated ages of 30 years for individuals with 5 cm test diameters. The authors applied their aging technique to four congeners to achieve ages of 10 – 20 years (Nichols et al. 1985, Gage et al. 1986). An age estimate of 50 years for *S. purpuratus* may well be an underestimation for at least two reasons. First, the largest sea urchin collected had a test diameter of 8.67 cm, but individuals at Middle Cove and South Cove can exceed 9 cm in test diameter. If larger sea urchins had been collected, age estimates may have been higher. The second reason stems from the inability of the tetracycline-tagging technique to measure zero growth. The very edge of the esophageal end on some jaws showed very faint fluorescent lines, indicating that these animals were growing very slowly and therefore undergoing minimal calcification at the time of tagging. Certainly, growth in some sea urchins was nonexistent or so slight that tetracycline was not incorporated into their jaws or tests, which was one of the explanations for lower than expected recapture rates. Non-growing individuals administered injections would have been misclassified as untagged sea urchins, and their exclusion from the Tanaka function resulted in the possible upward skewing of growth curves and the underestimation of ages.

The Tanaka parameters and age estimates vary based on how the data were grouped for nonlinear regression. Table 4 displays six different estimates of age for the collected sea urchin with the largest measured jaw (1.63 cm). It is apparent that as the Tanaka model is used to fit fewer and fewer data points, growth rate increases, and the estimation of maximum age decreases. When data from each site are included in the Tanaka function, the estimated age of this sea urchin is 100 years, but when the data are trimmed to just tidepool MCC nonpit urchins, the estimated age plummets to 22 years. The lack of consistency in age estimates using Tanaka parameters from different data groupings might be an artifact of including the pooled young urchins (jaw < 0.75 cm) in every nonlinear regression. As sample size decreases in the data groupings, the 75 young urchins make up a greater proportion of the sample for nonlinear regression, potentially overweighting the left side of the growth curve. The growth curve comparisons remain valid, but maximum ages calculated from incremental size data should be considered nothing more than estimates.

Table 4. *Strongylocentrotus purpuratus*. Variation in age estimation using the Tanaka function; Grouping refers to the particular set of growth data from which the Tanaka function was fit, *N* is number of sea urchins per dataset including pooled young, and Max Age is the age estimated by inserting the largest jaw measured (1.63 cm) into the integrated Tanaka function used to create size-at-age curves; parameters *f* and *d* are also shown; MC = Middle Cove, MCC = Middle Cove Tidepool C

Grouping	*N*	Max Age	*f*	*d*	R^2
All *S. purpuratus*	640	100	24.64	-0.21	0.753
Nonpit	382	59	18.49	-0.32	0.799
MC	307	51	16.97	-0.35	0.862
MC Nonpit	221	28	10.15	-0.58	0.775
MCC	167	25	8.73	-0.65	0.758
MCC Nonpit	121	22	7.48	-0.73	0.723

Conclusion and application

The growth of *Strongylocentrotus purpuratus* was affected by microhabitats, tidepools, and sites, representing scales spanning five orders of magnitude. Differences in growth rate can possibly be explained by food availability or quality. *S. purpuratus* living inside pits had slightly lower growth rates than those outside pits, but compounded over time, these slight differences result in big differences in size. Still, differential growth rates alone are insufficient in explaining the larger test diameters of nonpit urchins compared to pit urchins. Analysis of age-frequencies based on rates of jaw growth show a modal size of pit sea urchins at about five years age and a modal size of nonpit urchins at about ten years age. Mortality, movement, or other factors are at least partially responsible for the difference in the size structures between microhabitats.

Other marine invertebrates that utilize multiple microhabitats may also display differential growth rates, but few investigations have tested this hypothesis. Species that tend to be partially or fully sessile have the greatest potential to show microhabitat-based differences in growth, because mobile species are more easily able to choose a desirable habitat. In immobile organism might be relegated to one particular microhabitat, and so any microhabitat-based effects are likely to be compounded over time. Shellfisheries might be most suited to take advantage of species-microhabitat interactions. As one example, *Strongylocentrotus purpuratus* is one of many sea urchins harvested for its roe, and the knowledge that nonpit urchins experience accelerated growth would be useful information to a fishery manager who is either setting an age limit for harvesters or seeding juveniles where they will quickly reach minimum size. In South Africa, the sea urchin *Parechinus angulosus* serves as essential microhabitat for juveniles of the abalone *Haliotis midae*, which decline precipitously when sea urchins are removed. Day and Branch (2002) suggest that exploitation of the predators of *P. angulosus* has artificially increased the number of sea urchins, which subsidizes an extremely valuable abalone fishery. If juvenile *H. midae* were to be seeded, the knowledge of microhabitat use emphasizes the advantage to releasing them in an area of high sea urchin density. Additional knowledge of the effects of microhabitat on the growth and survival of economically valuable species will increase the ability to manage fisheries in an efficient and ecologically sound manner.

Bridge to Chapter IV

Though nonpit urchins grew faster than pit urchins, the differential growth hypothesis was only partially supported. The differences in growth rates could not solely account for the size differences in sea urchins from pit and nonpit microhabitats, so another factor must be contributing to the observed patterns discussed in Chapter II. The movement hypothesis is considered in Chapter IV. If pit urchins emigrated from their pits at a certain size or age, the result would be nonpit urchins that tend to be larger (as described in Chapter II) and older (as indicated in Chapter III) than pit urchins. I monitored 21 marked plots for one year to investigate the movement of sea urchins. The study admittedly would have been more effective if individuals were distinguishable, but purple sea urchins, with their small spines, are notoriously difficult to mark. However, despite some ambiguous conclusions, some interesting findings presented in this chapter help elucidate the overall questions of this study.

There once was an urchin named Zot
Who refused to move out of his spot
Though he seemed pretty bored
He knew his rewards
Were the kelp that he caught from his spot.

CHAPTER IV

SEDENTARY HABITS OF THE PURPLE SEA URCHIN

INTRODUCTION

As common benthic grazers, sea urchins have a profound influence on the algal composition of temperate and tropical nearshore habitats (reviewed by Lawrence 1975; Dayton 1975, Breen & Mann 1976, Harrold & Reed 1985, Fletcher 1987, Andrew 1991, Tegner et al. 1995, Benedetti-Cecchi et al. 1998). Among the best-known examples of sea urchins playing the role of dominant grazers are the red and purple sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus*. Both species occur in kelp forests on the North American Pacific coast. Normally, sea urchins are fairly sedentary and are sustained by adequate amounts of drift algae. When drift algae becomes limiting, however, their movement increases and they graze on live kelp stands, turning kelp beds into urchin-dominated barrens with no macroalgae (Mattison et al. 1977, Dayton 1985, Harrold & Reed 1985).

Unlike *Strongylocentrotus franciscanus*, *S. purpuratus* is common in intertidal areas of wave-swept rocky shorelines. In these habitats, purple sea urchins are not mobile grazers, but acquire food by catching drift algae with their modified podia (tube feet)

(Ebert 1968, Paine & Vadas 1969). Where the rock is sufficiently soft, sea urchins excavate and inhabit small, urchin-sized cavities or pits in the substratum (Morris et al. 1980, Kozloff 1983). *S. purpuratus* digs pits presumably by the combined actions of biting small pieces of rock with the Aristotle's lantern and scraping the rock with its spines. Thousands of sea urchins, each in its own pit, often dominate the intertidal landscape, apparently preventing macroalgal growth or substrate utilization by other organisms (personal observation). Sea urchins occur in one of two microhabitats often in the same tidepools: outside and inside pits (hereafter nonpit and pit urchins, respectively). Nonpit urchins grow faster than pit urchins and have larger test diameters (See Chapters II & III). The two groups are morphologically distinct; nonpit urchins have longer spines and greater skeletal mass than pit urchins, which have relatively larger test heights and demipyramid (jaw) lengths. If the growth and morphology of *S. purpuratus* are related to microhabitat, then individuals must remain in the same microhabitat for long periods to develop distinctive morphological traits. If sea urchins frequently move between microhabitats, it is less likely that the observed differences in growth and morphology are microhabitat-related.

I investigated the frequency of movement in *Strongylocentrotus purpuratus* living in different microhabitats and tidepools at South Cove. I was particularly interested whether *S. purpuratus* displayed sedentary behavior, if sea urchins in either microhabitat display a greater propensity for movement, and if one microhabitat seems to be preferred over the other. I hypothesized that sea urchins would display long-term habitation of microhabitats and that movement would be infrequent. These questions were addressed with a one-year field monitoring study and a short manipulation of microhabitat.

MATERIALS AND METHODS

Study Sites

The study was conducted in tidepools at South Cove, Cape Arago (43^o18.5'N, 124^o24'W), a prominent rocky headland on the southern Oregon Coast (Fig. 1). South Cove is a well-protected site at Cape Arago that is subjected to heavy surf only when large swells originate from the south in the winter. The intertidal zone is a gently sloping, sandstone bench with abundant cobble and boulders. Tidepools range widely in size and are scattered about the east and west sides of the cove. *Strongylocentrotus purpuratus* is extremely abundant within their habitat with average densities of 60–72 m^{-2}, though aggregations can exceed 400 m^{-2}. The lower distributional limit is 0.3 m below mean lower low water (MLLW). When in tidepools, sea urchins occur as high as 1 m above MLLW, but are otherwise limited to 0.5 m and below. Many sea urchins inhabit pits that have been excavated from the sandstone. Macroalgal growth begins in late March or early April and quickly accelerates; a diverse group of seaweeds dominates the mid and lower intertidal by late spring. The most prominent members of this group are *Nereocystis luetkeana, Alaria marginata,* and *Egregia menziesii* in the low intertidal, and

Iridaea cordata , *Fucus distichus, Hedophyllum sessile, Ulva* sp., *Sargassum muticum,* and *Cystoseira geminata* in the mid intertidal (ca. 0.5 – 1.5 m above MLLW). South Cove is a popular public area that experiences thousands of annual visitors.

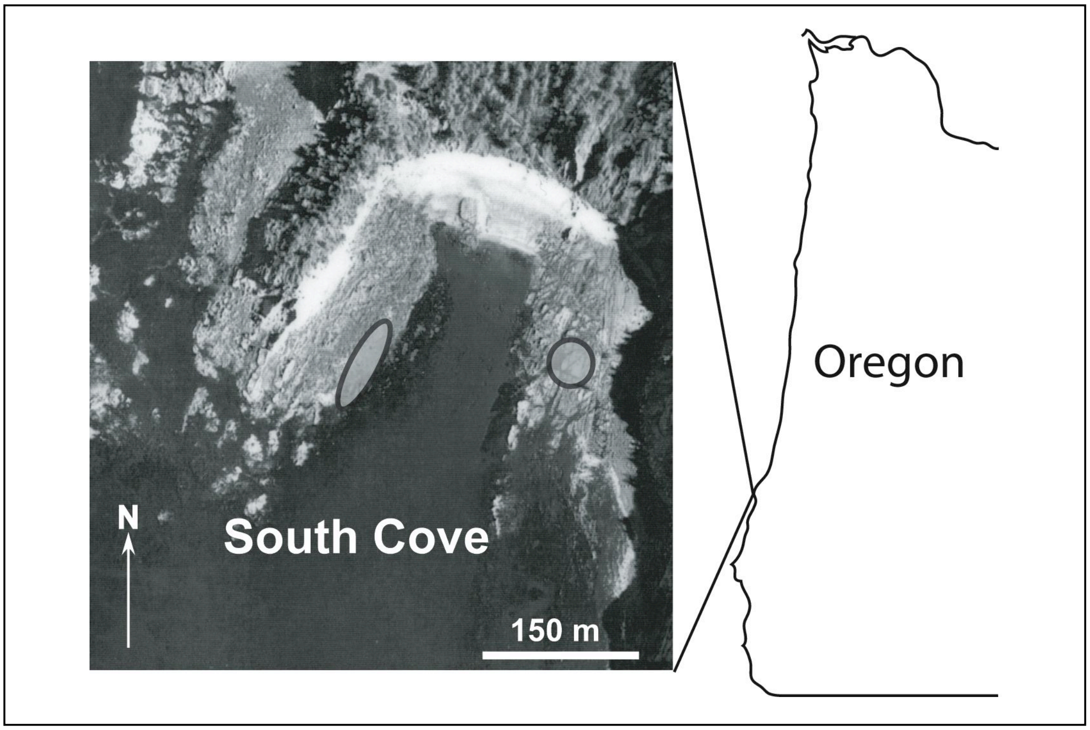


Fig. 1. Location of study site: South Cove, Cape Arago. Study plots were located in tidepools on the east side (the sphere) and the west side (the ellipse) of South Cove

Movement experiment

A manipulation was designed to test whether disturbed sea urchins display a microhabitat preference and how microhabitat affects a disturbed urchin’s propensity for movement. During a falling low tide, three tidepools approximately 0.5 m above MLLW were selected for the experiment. Tidepools ranged from 0.5–3 m^2 and contained

Strongylocentrotus purpuratus living inside and outside pits. Two tidepools were completely contained, and one was located in a surge channel, but the tide was low enough during the experiment that the water was still. Ten haphazardly selected pit urchins in each tidepool were randomly divided into two treatments: “Inside” and “Outside”. The sea urchins were disturbed removed from their pits by carefully using a wide knife as a lever to pry them out. To distinguish between Inside and Outside urchins, spines were clipped into distinctive patterns with wire-cutters. A large patch of spines was clipped from one randomly selected treatment group, and two small patches were clipped from the other treatment group. In case the clipping patterns varied in their effects on the sea urchins, the treatment groups received each clipping pattern at least once. Sea urchins were handled for no more than a minute, and then were returned to the tidepool. Sea urchins in the Inside treatment were returned to their pits, and sea urchins in the Outside treatment were haphazardly placed in nonpit locations, with the stipulation that they were at least 10 cm from the nearest empty pit. A sketch made in the field was used to indicate the position of each sea urchin at the outset of the experiment. After two hours, before the rising tide reached the pools, the locations of the sea urchins were noted. The distance of displacement was measured for sea urchins that moved. Three days later, the tidepools were rechecked and the final microhabitats were noted for sea urchins in each treatment. Displacement was not measured since I could not distinguish among the five sea urchins within a treatment.

A chi-square test for a single variable was used to test the H_0 that disturbed sea urchins occurred in a 50:50 ratio in pit and nonpit microhabitats. Rejection of the H_0

would indicate that one microhabitat was preferred over the other. A two-way contingency table was used to test the H_0 that there is no relationship between treatment (Inside or Outside) and the occurrence of movement after two hours. Fisher's Exact Test was used to correct for small cell counts (Sokal & Rohlf 1995).

Field monitoring of marked plots

At South Cove, a tidepool field monitoring study was used to investigate the frequency of movement in *Strongylocentrotus purpuratus*. Its usefulness as a measuring tool for mortality became apparent as the research was carried out. In June 2005, I haphazardly selected 21 locations in tidepools to be permanent study plots. To mark the plots, holes were drilled in the rock and were filled with cylindrical pieces of turquoise plastic. An original intention of the study was to quantify the number of sea urchins that evacuate their pits, so while all of the plots had ca. 20–60 pit urchins, they did not necessarily contain equal numbers of nonpit urchins. Only 3 out of 21 plots initially contained more nonpit urchins that pit urchins.

The plots were categorized by location in South Cove: East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES). I refer to these three areas as macrohabitats containing pit and nonpit microhabitats (for definitions see Chapter II and (Morris 1987). On the east side of South Cove, six ESTP plots were selected for monitoring. The east side of South Cove is noticeably flatter than the west side, as it lacks a large boulder and cobble field. Surge channels cut through the sandstone bench, creating many intertidal “islands” that are covered on top with surfgrass (*Phyllospadix scouleri*) and are pocketed with small tidepools. Sand accretes in the surge channels and to a lesser extent the tidepools during the summer months. The plots were in tidepools about 1 m above MLLW, and plots #5 and #6 were in the same tidepool, separated by 1 m. Eleven WSTP plots were selected from 0 to 1 m above MLLW. Seven of these plots were situated in three sections of a very large tidepool. Plots in the same section (#16–17, #18–20, and #21–22) were spaced 1 m from each other. Rocks emerging from the tidepool were assumed to reduce the likelihood of movement between sections. Four WSES plots were not in tidepools, but on rocks projecting from tidepools that were 10–30 cm above the water level at low tide. Plots #9 and #10 were on the same rock, separated by 1 m.

Field monitoring of *Strongylocentrotus purpuratus* involved multiple observations and digital photographs (Canon Powershot S70) of each plot during low tide. Seaweed obscuring the sea urchins was removed while the photo was taken and subsequently replaced. I attempted to maintain an identical frame of view in the photos by orienting the view frame according to the blue plot markers. I made note of any significant changes in or around the tidepools, including the presence of potential predators (especially *Pycnopodia helianthoides*), apparent changes in boulder position, changes in urchin appearance, etc. The plots could usually be checked in one hour or less.

All plots except two were monitored semi-regularly from 8 June – 23 August 2005 (Summer), and from 27 January – 11 June 2006 (Winter & Spring). Field monitoring of Plot #2 ceased after 261 days because the plastic markers disappeared and incorrect photos were taken, and field monitoring of Plot #14 ended after 295 days when the sea urchins were collected for a related growth study. Like most of the North American Pacific coast, Oregon experiences mixed semi-diurnal tides, and it is only during spring tidal series that the plots were accessible. Data do not exist for fall 2005 because nighttime low tides, heavy winds, and rain interfered with data collection. During most tidal series, I made an effort to visit the plots on several consecutive days to increase the temporal resolution of the study.

The digital photos were downloaded onto a personal computer and viewed with Adobe Photoshop (Adobe Systems Incorporated 2002). The contrast, brightness, and color of photos were adjusted so that sea urchins were easily visible. Photos from consecutive dates were compared and the following data were recorded: 1) the frequency of each possible change in location (To or From a Pit or Nonpit microhabitat); 2) the number of sea urchins that had not moved since the beginning of the study; and 3) the change in the number of sea urchins since the previous photo. The situation sometimes occurred in which there was a new sea urchin present in a photo, but a sea urchin was missing from some location in the previous photo. Distinctive rocks and algae held by the podia, scars, and test diameter were clues that allowed me to determine whether these were the same or different sea urchins.

The number of pit urchins, nonpit urchins, and empty pits were counted in the first and final photographs, and a paired student's t-test was used to test the H_0 that there were no significant differences in these counts between June 2005 and June 2006 (Systat

Software, Wilkinson 2004). The paired student's t-test was also used to compare the proportion of sea urchins in each microhabitat at the beginning and end of the study.

Changes in the location of sea urchins (To a Pit, From a Pit, To a Nonpit, From a Nonpit) were summed and expressed as a frequency of movement per urchin per tidal cycle (urchin changes)(urchin^{-1})(tidal series^{-1}). Standardization to tidal series (i.e., 28 days) resulted in equivalent units for the Summer (75 days of monitoring) and Winter&Spring (136 days). Movement frequencies were compared within different seasons and macrohabitats. Separate analyses included only observations taken when 24 hours had elapsed since the previous observation, with the hypothesis that changes in location on a short time scale were more likely to be due to movement as opposed to mortality.

RESULTS

Movement experiment

When *S. purpuratus* were spine-clipped, individuals sometimes appeared distressed, waving their spines and sometimes displaying pedicillariae. Upon being returned to the tidepool, the Inside treatment group quickly wedged themselves into the bottom of their pit, with one exception. Sea urchins in the Outside treatment group, however, began moving immediately. Within two hours, nine had settled into pits or shallow depressions, two were wedged into crevices in the rock, and only four remained on flat substrate. After three days, twelve sea urchins Outside pits had moved, but only one sea urchin Inside pits moved. Results of the field manipulation are displayed in Table 1. The two H_0 were rejected. *Strongylocentrotus purpuratus* in tidepools showed a preference for pit microhabitats after being disturbed by breaking spines ($P < 0.001$, $\chi^2 = 15.38$, df = 1). Sea urchins placed outside pits showed a propensity for movement, while those inside pits remained in place ($P < 0.001$, $\chi^2 = 16.43$, df = 1).

Field monitoring of marked plots

I photographed *Strongylocentrotus purpuratus* in the permanent intertidal plots thirteen times each from 9 June – 23 August 2005 and 27 January – 11 June 2006. Field monitoring occurred on consecutive dates seven times in the Summer season and six times in the Winter & Spring period. The average number of days between visits was 18 in the Summer and 20 in the Winter & Spring. As few as 9 and as many as 41 days passed between tidepool visits, in addition to the sampling hiatus between August and January (155 days).

Table 1. *Strongylocentrotus purpuratus*. The influence of microhabitat on movement of spine-clipped *S. purpuratus*. Only the three-day results are displayed, but the two-hour patterns were similar

	Pit	Nonpit
Observed	23	3
Expected	13	13

$\chi^2 = 15.38$, df = 1, $P < 0.001$

The H_0 that disturbed *S. purpuratus* occurs in a 50:50 ratio in pit and nonpit microhabitats was rejected.

	Inside	Outside
Moved	1	12
Stayed	14	3

$\chi^2 = 16.43$, df = 1, $P < 0.001$

The H_0 that there is no relationship between microhabitat and propensity for movement was rejected.

Sedentary sea urchins and total abundance

Sedentary urchins were those that did not move after field monitoring began. I did not observe any changes in location for most *Strongylocentrotus purpuratus;* 637 (93%) sea urchins were sedentary during the Summer (75 days), and 549 (80%) sea urchins remained sedentary through the Winter & Spring (367 days). *S. purpuratus* in WSES plots were most likely to be sedentary (97% after 75 days; 95% after 367 days). For the sea urchins present in the plots at the end of the study, I calculated the percentage that had been sedentary for the previous year ("Sedentary Survivors" in Table 2). About 94%

of the sea urchins photographed on 11 June 2006 had not changed position since 9 June 2005. This percentage was similarly high in the three microhabitats, even though abundances varied greatly.

In June 2005, the 21 intertidal plots contained 688 *Strongylocentrotus purpuratus*. One year later, the same plots contained just 583, a decline of 15.3% (Table 2). Sea urchin abundance decreased at a high rate in ESTP (–25.4%) and WSTP (–14.8%), but was virtually unchanged in WSES (+1%) (Fig. 2). Some plots experienced a much greater decline than others in the same macrohabitat. In ESTP, 31 sea urchins disappeared from Plot #1, while the other five plots had a net loss of 16 urchins. The ESTP plots were not checked between 25 February and 19 April 2006, during which time 22 urchins in shallow pits disappeared from Plot #1. In WSTP, 44 of 59 missing sea urchins came from Plots #17 and #18. The decrease in Plot #17 was especially dramatic; it contained 24 urchins at the beginning of the study and two at the end. Nine urchins disappeared from this plot during the summer, and another thirteen went missing before the end of February. The abundance of *S. purpuratus* in the WSES macrohabitat did not fluctuate by more than two urchins in any plot (Fig. 2, Table 2).

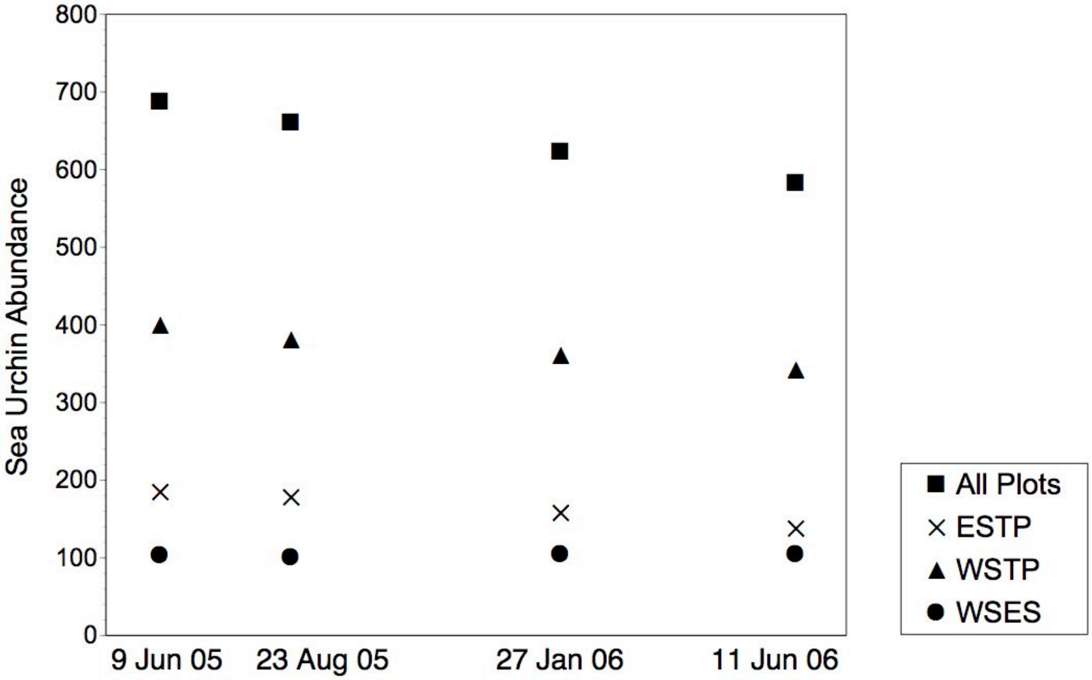


Fig. 2. *Strongylocentrotus purpuratus*. Total *S. purpuratus* in 21 plots from 9 June 2005 – 11 June 2006; Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); no observations were made during 23 August 2005 – 27 January 2006

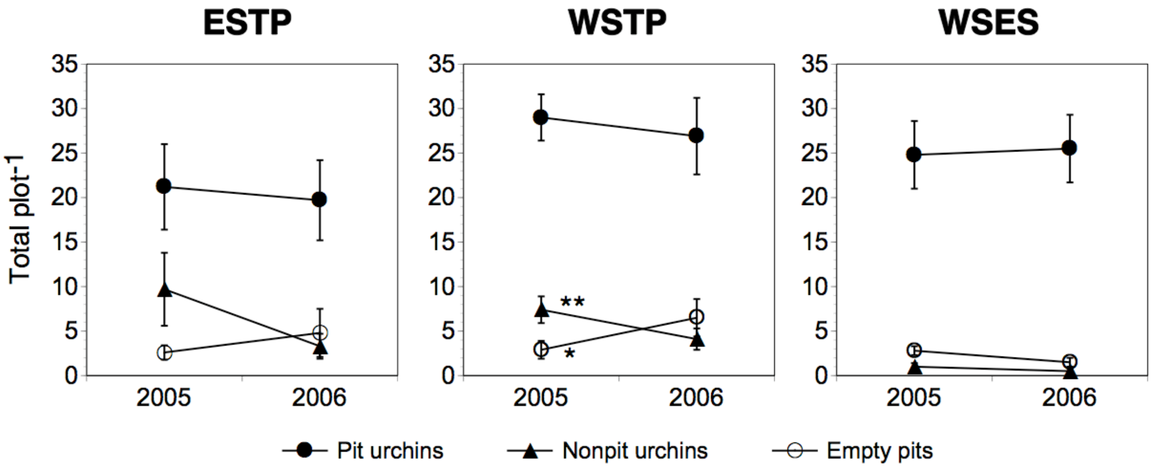
Microhabitat distribution

The distribution of *Strongylocentrotus purpuratus* inside and outside pits is reported for plots in Table 3, and the means (± SE) by macrohabitat are reported in Table 4 and Fig. 3. These tables illustrate two important trends. First, between 2005 and 2006, there was significant decrease in the number of nonpit urchins (*P* < 0.01, paired student's t-test) but there was no significant difference in the abundance of pit urchins. Second, although the frequency of pit urchins increased or did not change in every case except Plot #6 (Table 3), the number of empty pits increased in most plots and was significantly

Table 2. *Strongylocentrotus purpuratus*. Changes in tidepool population of *S. purpuratus* after 75 days and 1 year; Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); displayed is the initial, final, and change in total urchins for each plot, percentage of *S. purpuratus* that were sedentary for 75 days and 1 year, and the percentage of surviving *S. purpuratus* that had been sedentary for one year; sedentary urchins appeared in the same location in every photo

		Total *S. purpuratus*				Sedentary for 75 days		Sedentary for one year		Sedentary Survivors
Macrohabitat	Plot #	9 June 2005	11 June 2006	Change	%	Total	%	Total	%	
ESTP	1	52	21	-31	-60	47	90	21	40	100
	2	18	14	-4	-22	14	78	13	72	93
	3	17	13	-4	-24	15	88	12	71	92
	4	28	23	-5	-18	27	96	22	79	96
	5	34	31	-3	-9	34	100	31	91	100
	6	36	36	0	0	35	97	32	89	89
WSTP	10	33	34	+1	+3	29	88	29	88	85
	12	64	60	-4	-6	62	97	59	92	98
	14	30	26	-4	-13	26	87	26	87	100
	15	19	19	0	0	18	95	17	90	89
	16	46	49	+3	+7	46	100	43	93	88
	17	24	2	-22	-92	15	63	1	4	50
	18	53	31	-22	-42	46	87	27	51	87
	19	28	24	-4	-14	26	93	24	86	100
	20	41	40	-1	-2	40	98	38	93	95
	21	34	33	-1	-3	32	94	32	94	97
	22	28	23	-5	-18	25	89	22	79	96
WSES	8	26	28	+2	+8	26	100	26	100	93
	9	36	36	0	0	35	97	35	97	97
	11	22	23	+1	+5	21	96	21	91	91
	13	19	17	-2	-11	18	95	17	89	100
All plots		688	583	-105	-15.3	637	92.6	549	79.8	94.2
ESTP		185	138	-47	-25.4	172	93.0	131	70.8	94.9
WSTP		400	341	-59	-14.8	365	91.3	318	79.5	93.3
WSES		103	104	+1	+1.0	100	97.1	99	96.1	95.2

higher in 2006 (4.8 ± 2.7 pits) than in 2005 (2.6 ± 0.8 empty pits) ($P < 0.01$, paired student's t-test). The ratio of pit-to-nonpit urchins increased not because the number of pit urchins rose, but because the number of nonpit urchins fell. These trends are generally repeated within each macrohabitat (Fig. 3). ESTP had the largest increase in frequency of pit urchins because so many nonpit urchins left Plot 1. Total empty pits decreased in WSES, but only by two.



*$P < 0.01$, ** $P < 0.001$ using Hochberg's (1988) family-wise correction

Fig. 3. *Strongylocentrotus purpuratus*. Change in plot means (±SE) of *S. purpuratus* inside and outside pits and empty pits from 2005 to 2006 (Table 4 data); Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); the paired student's t-test was used to test for significant differences between 2005 and 2006

Table 3. *Strongylocentrotus purpuratus*. Initial and final microhabitat distribution of *S. purpuratus* and empty pits; Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); plots were monitored for one year except: [a]Plot 2 was monitored 261 days through 25 Feb 2006, and plot 14 was monitored 295 days through 1 April 2006

		9 June 2005					11 June 2006				
		Total count		Frequency			Total count		Frequency		
Macrohabitat	Plot	Pit	Nonpit	Pit	Nonpit	Empty Pits	Pit	Nonpit	Pit	Nonpit	Empty Pits
ESTP	1	24	28	0.46	0.54	5	20	1	0.95	0.05	18
	2[a]	6	12	0.33	0.67	1	5	9	0.36	0.64	3
	3	10	7	0.59	0.41	0	12	1	0.92	0.08	4
	4	19	9	0.68	0.32	0	17	6	0.74	0.26	1
	5	33	1	0.97	0.03	2	30	1	0.97	0.03	2
	6	35	1	0.97	0.03	0	34	2	0.94	0.06	1
WSTP	10	21	12	0.64	0.36	0	27	7	0.79	0.21	2
	12	54	10	0.84	0.16	0	51	9	0.85	0.15	5
	14[b]	12	18	0.40	0.60	0	13	13	0.50	0.50	0
	15	18	1	0.95	0.05	0	19	0	1.00	0.00	2
	16	40	6	0.87	0.13	4	47	2	0.96	0.04	4
	17	23	1	0.96	0.04	7	2	0	1.00	0.00	21
	18	46	7	0.87	0.13	7	30	1	0.97	0.03	18
	19	24	4	0.86	0.14	8	21	3	0.88	0.12	10
	20	34	7	0.83	0.17	0	35	5	0.88	0.12	2
	21	26	8	0.76	0.24	2	30	3	0.91	0.09	3
	22	21	7	0.76	0.24	4	21	2	0.91	0.09	4
WSES	8	25	1	0.96	0.04	2	27	1	0.96	0.04	1
	9	35	1	0.97	0.03	0	35	1	0.97	0.03	1
	11	22	0	1.00	0.00	2	23	0	1.00	0.00	1
	13	17	2	0.89	0.11	3	17	0	1.00	0.00	3
Total		545	143	0.79	0.21	47	516	67	0.89	0.11	106

Table 4. *Strongylocentrotus purpuratus*. Initial and final plot means (±SE) and frequency of *S. purpuratus* inside and outside pits and empty pits per plot; Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); the paired student's t-test was used to check for significant differences between 2005 and 2006

	9 June 2005					11 June 2006				
	Total count		Frequency			Total count		Frequency		
Macrohabitat	Pit	Nonpit	Pit	Nonpit	Empty Pits	Pit	Nonpit	Pit	Nonpit	Empty Pits
ESTP	21.2 ± 4.8	9.7 ± 4.1	0.69	0.31	2.6 ± 0.8	19.7 ± 4.5	3.3 ± 1.4	0.86	0.14	4.8 ± 2.7
WSTP	29.0 ± 2.6	7.4 ± 1.5	0.80	0.20	2.9 ± 1.0	26.9 ± 4.3	4.1 ±1.2	0.87	0.13	6.5 ± 2.1
WSEP	24.8 ± 3.8	1.0 ± 0.4	0.96	0.04	2.8 ± 0.5	25.5 ± 3.8	0.5 ± 0.3	0.98	0.02	1.5 ± 0.5
Total	26.0 ± 2.6	6.8 ± 1.5	0.79	0.21	2.1 ± 0.6	24.6 ± 2.7	3.2 ± 0.8	0.89	0.11	5.0 ± 1.4
Paired t-test between years	*NS*	*	**	*	*					

**P* < *0.01,* ** *P* < *0.001* using Hochberg's (1988) family-wise correction

Movement frequency by microhabitat

Changes in the location of sea urchins could be categorized four ways: To a Pit, From a Pit, To a Nonpit, or From a Nonpit. The frequencies of each change in location for macrohabitats and seasons are displayed in Fig. 4. Sea urchins tended to move From a location more frequently than To a location in a plot, agreeing with the general decline in sea urchin abundance between plots. The location of sea urchins in the WSES macrohabitat changed least frequently (Fig. 4). There were more than 0.1 changes From a Pit (urchin^{-1})(plot^{-1}) during Winter & Spring in ESTP, and during both seasons for WSTP. The only other instance in which there were at least 0.1 changes in location (urchin^{-1})(tidepool^{-1}) was To a Pit during Winter & Spring in ESTP.

More changes in location were detected when more days elapsed between observations (Fig. 5). Changes in urchin location plot^{-1} and urchin^{-1} were about four times higher after more than nine days compared to one day. After one day, there was a mean (± SE) of 0.008 ± 0.002 changes in location urchin^{-1}, which is equivalent to 0.231 ± 0.047 changes (urchin^{-1})(tidal series^{-1}). This means that during a given tidal series, about one of four sea urchins would be expected to show a change in location. Fig. 6 displays the frequencies of changes in location within each macrohabitat when sea urchins were observed on consecutive days. The amount of movement in and out of pits was about twice as great as the movement to and from nonpit locations.

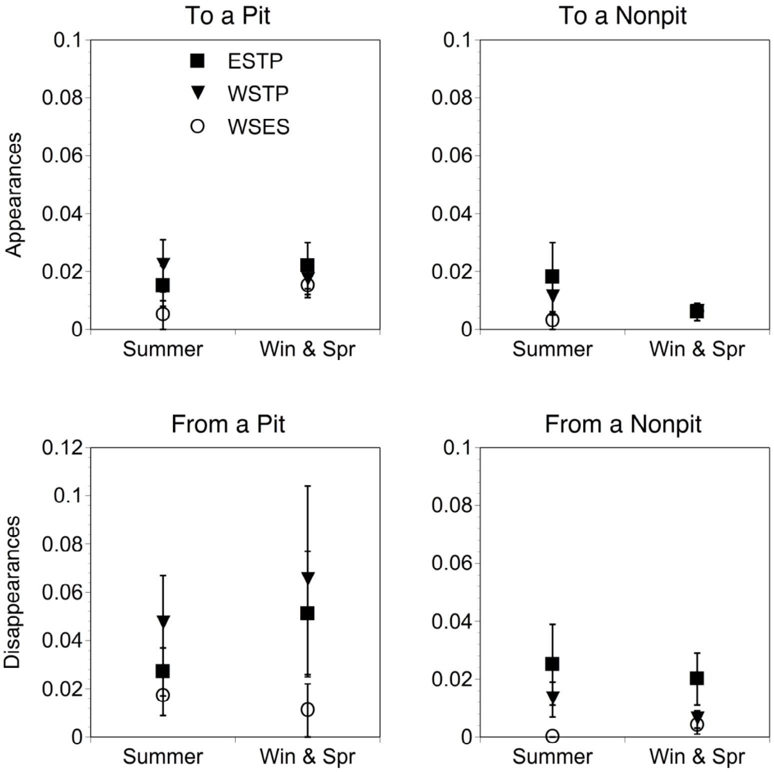


Fig. 4. *Strongylocentrotus purpuratus*. Microhabitat-specific changes in urchin locations during Summer (9 June – 23 August 2005) and Winter & Spring (27 January – 11 June 2006); units for appearances and disappearances are (changes in location)(urchins^{-1})(tidal series^{-1}); Macrohabitats are East Side Tidepools (ESTP), West Side Tidepools (WSTP), and West Side Exposed Substrata (WSES); error terms are SE

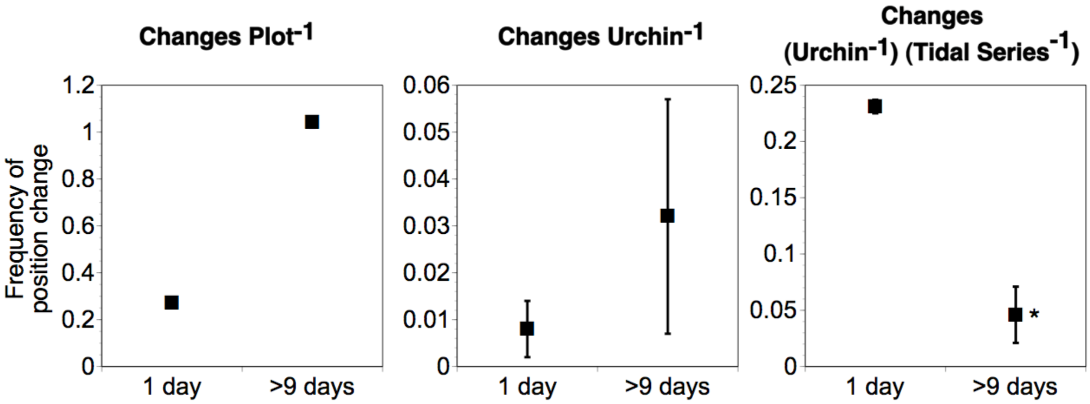


Fig. 5. *Strongylocentrotus purpuratus.* Mean (± SE) changes in sea urchin location when checking plots after 1 day or >9 days; sea urchins observed to change locations were 68 after 1 day and 197 after >9 days; units for change in location is in bold type above figure; >9 days group had a range of 9 – 41 with mean 19.4 days; *this value is severely underestimated because temporal resolution for the >9 day group is so low; these data were collected after an average of 19 days, so many instances of urchin movement may have gone undetected

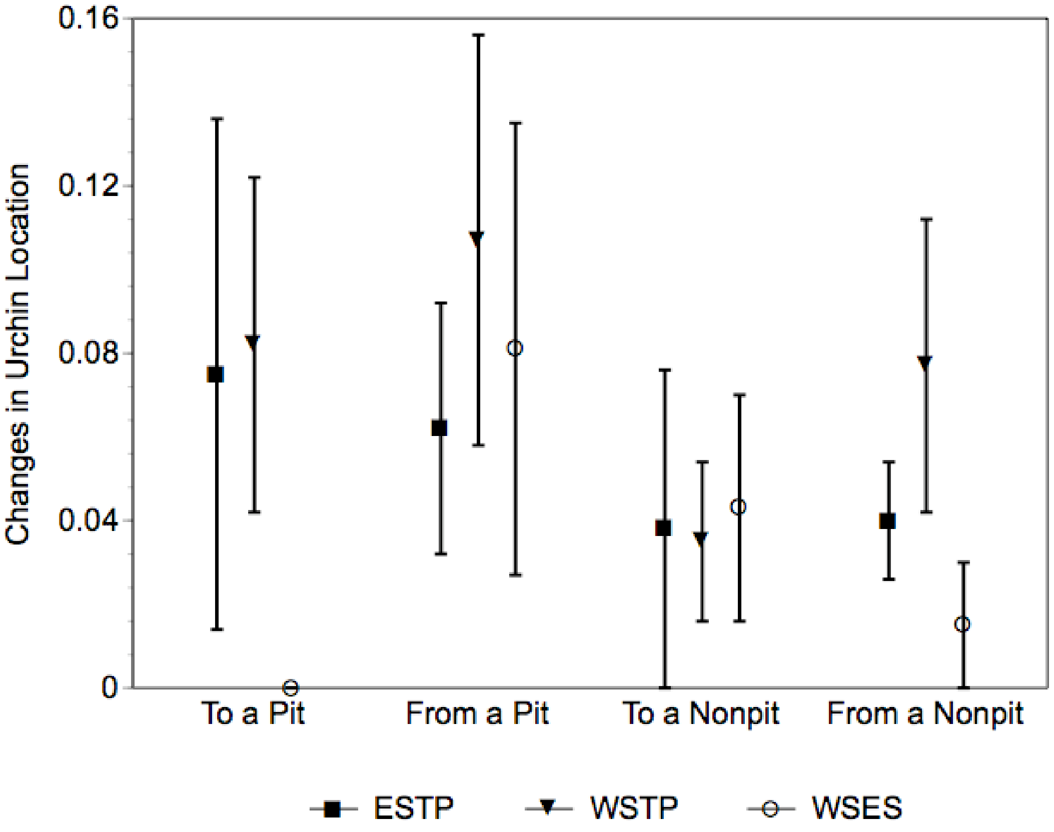


Fig. 6. *Strongylocentrotus purpuratus.* Movement frequency in *S. purpuratus* when plots were checked after 24 hours; units are (movement frequency)(urchin^{-1})(tidal series^{-1}); Macrohabitats are East Side Tidepools (ESTP-squares), West Side Tidepools (WSTP-triangles), and West Side Exposed Substrata (WSES-open circles); error terms are SE

DISCUSSION

A sedentary lifestyle in *Strongylocentrotus purpuratus*

The major limitation of this study is my inability to accurately distinguish movement from mortality. The presence and subsequent absence of a sea urchin in a series of photos could mean that the animal moved or died. However, I can deduce that a sea urchin had not moved when its location was unchanged. In every set of photos, most individuals appeared in the exact same location repeatedly. Often, unmoving sea urchins in successive photos even held the same rocks and pieces of algae for days at a time. Over the course of this study, most sea urchins were never observed to move. An astonishing 94% of the sea urchins appearing in the final set of plot photos had been sedentary for the length of the one-year study. The data provide overwhelming evidence that *Strongylocentrotus purpuratus* tends to live a sedentary lifestyle at South Cove.

This finding adds weight to my previous conclusions concerning morphology and growth in *Strongylocentrotus purpuratus*. At three sites, morphological distinctions were made between sea urchins living in different microhabitats (see Chapter II). Pit urchins had relatively taller tests and larger Aristotle's lanterns, while nonpit urchins had greater test diameters, spine length, and skeletal mass. Nonpit urchins also had higher growth rates than pit urchins (see Chapter III). The interpretation that microhabitat-use leads to the observed differences in morphology and growth inherently assumes that most sea urchins do not frequently switch microhabitats. This study, which detected extensive sedentary behavior in *S. purpuratus*, supports the hypothesis of consistent microhabitat-use and validates the partitioning of pit urchins and nonpit urchins.

Despite the high frequency of sedentary behavior displayed by intertidal sea urchins, some individuals in the plots obviously moved. Observation of the presence followed by the absence of a sea urchin in a photo could be the result of movement or mortality, but how can the two be distinguished? The most accurate measure of movement frequency comes from the data collected on successive days. If I was present at South Cove during low tide, terrestrial predators were unable to forage on sea urchins. The sunflower sea star (*Pycnopodia helianthoides*), the only known marine predator that consumes sea urchins at South Cove, could still forage at high tide, but then I probably would have seen them near the plots during the following low tide. Since I only observed *P. helianthoides* a few times near Plots #17 and #18, I presume that when the location of sea urchins changed after one day, movement was the cause. There were 12 – 14 plot observations made one day after the previous observation (depending on the plot). In these instances, there was a mean of 0.231 ± 0.047 movements (urchin^{-1})(tidal series^{-1}) (Fig. 5). Therefore, after four tidal series (16 weeks), one would expect approximately one occurrence of movement per urchin.

Fig. 6 indicates that movement frequency was greater for pit urchins than for nonpit urchins. Since pit urchins were much more numerous than nonpit urchins (Table 3), individual movement rates were actually greater in nonpit microhabitats. A manipulation demonstrated that pits were the “preferred” microhabitat when the spines of a sea urchin had been clipped. These results that individual behavior may be related to microhabitat; sea urchins inside pits are less likely to move than those outside pits.

Yusa and Yamamoto (1994) also reported a difference in echinoid movement related to microhabitat. They investigated *Anthocidaris crassispina*, which, like *S. purpuratus*, occurs inside and outside of pits in tidepools. *A. crassispina* inside pits never moved, but outside pits they were highly mobile. When sea urchins were switched into the opposite microhabitat, they altered their movement patterns accordingly; urchins outside pits still moved much more than those inside pits. In the present study, the conclusion of a sedentary lifestyle is appropriate for pit urchins, which account for most of the individuals observed. More data are needed to demonstrate the same for nonpit urchins. A field observation involving *Lithothammnium* sp., a coralline encrusting algae, lends some support to the sedentary lifestyle hypothesis for sea urchins in both microhabitats. In tidepools with high urchin densities, substratum between urchins is often covered with *Lithothamnium*. Removing a nonpit urchin from the rock reveals a bare patch, identifying that position as a home scar that the sea urchin has scraped clean of algae. If nonpit urchins were mobile, additional bare patches and scrapes of the algae would indicate their grazing activity. The unbroken algal crust in some tidepools may be a sign of sedentary behavior in *Strongylocentrotus purpuratus* in different microhabitats.

Habitation of pits (also “crevices,” “cavities,” or “burrows”) is a common behavior in various species of sea urchins in temperate (Otter 1932, Lissner 1980, Kawamata 1998) and tropical regions (Grünbaum et al. 1978, Carpenter 1984, Neill 1988, Schoppe & Werding 1996). Many echinoids move out of their burrows at night to forage and return to their protective microhabitats before dawn (Grünbaum et al. 1978, Nelson & Vance 1979), while other studies did not observe movement out of burrows (Otter 1932, Maier & Roe 1983, Tsuchiya & Nishihira 1985, Yusa & Yamamoto 1994, Schoppe & Werding 1996). Predation has been implicated as a cause for homing behavior in sea urchins that forage outside their pits (Carpenter 1984, Neill 1987), and McClanahan (1999) used tethering experiments to show that predators restrict *Echinometra viridis* to crevices during daylight hours. The lack of observed movement in *Strongylocentrotus purpuratus* does not preclude nocturnal foraging as a common behavior, but considering the high densities of sea urchins in many tidepools (>100 m^{-2}), it seems highly unlikely that each individual could move around at night and manage to reoccupy its own pit during the day. The ability to home precisely in such high densities would be quite an unexpected discovery.

The lack of mobility in *Strongylocentrotus purpuratus* is likely related to the habitat in which they are found. The risk of dislodgement is at least 50% when water velocity is greater than 17 m s^{-1} (Denny & Gaylord 1996), and velocities have been measured in excess of 25 m s^{-1} on exposed rocky shorelines (Denny et al. 2003). Several studies have demonstrated that movement in sea urchins is negatively correlated with water velocity. Kawamata (2001) reported that movement rates were reduced by half when water velocity was 0.4 m s^{-1}, and movement became nearly impossible when water velocity was increased to 0.7 m s^{-1}. Likewise, under calm ocean conditions, the sea urchin *Centrostephanus coronatus* always emerges from its burrows at night at depths of 5 m (Lissner 1980). It was only when seas became rough that many sea urchins became sedentary. Though aggregations of mobile grazing *S. purpuratus* have been observed in the subtidal (Harrold & Reed 1985), the extreme wave velocities and hydrodynamic forces that assail the shoreline might prevent similar behavior in intertidal populations of *S. purpuratus*.

Frank (1981) described the conditions that might make a sedentary lifestyle adaptive in an organism capable of mobility. While observing oystercatchers forage on limpets in Middle Cove of Cape Arago, 1 km from the site of this study, he discovered that most limpets on horizontal surfaces were eaten (Frank 1982). Meanwhile, limpets on vertical surfaces were still abundant, having been restricted to locations inaccessible to the oystercatchers. While the limpets studied were mobile grazers, their foraging paths led them back near their original starting place (imperfect homing), so from the perspective of a terrestrial predator, they were essentially unavailable. Frank (1981) proposed that sedentary or homing behavior might be adaptive when: 1) food is locally available; and 2) there are long-lasting, significant differences in survivorship between patches, so that an organism is benefited by remaining in its habitat patch permanently. In this study, *Strongylocentrotus purpuratus* displayed secondary sedentary behavior, meaning that although capable of moving, they stay in one place. As feeders of drift algae, they fulfill the first of Frank's criteria for adaptive sedentary behavior. To fully test his hypothesis, mortality would need to be clearly linked to movement, which this study was not designed to accomplish. However, one year of field-monitoring led to several findings related to mortality.

Movement or mortality?

Mortality was a confounding factor that sometimes made it impossible to infer movement when a sea urchin disappeared from a plot photo, as it could have moved or died. A change in abundance (as measured by the sum of sea urchins in all plots) could be due to recruitment, immigration into or emigration out of plots, or mortality. If recruitment of *Strongylocentrotus purpuratus* had been heavy in recent years, juveniles increasing in size and becoming more visible may have confounded the results. Since recruitment has been weak at South Cove for at least four years (see Chapter III), hard-to-see small urchins were not problematic. If immigration and emigration rates were not equal for the study plots, my counts of total abundance would be affected. Assuming that habitat inside and outside plots is comparable, there is no reason that moving urchins should be more likely to immigrate to or emigrate from the plots, so I would not expect movement to influence overall abundance. This study suggests that mortality in the tidepools was approximately 15%, equal to the proportion of sea urchins that went missing from the marked plots during the year of field monitoring. This rough estimate, based on the disappearance of about 100 sea urchins from plots covering a fraction of South Cove, agrees nicely with data from other populations of *S. purpuratus*. Russell (1987) measured z (mortality rate) to range from 0.12–0.33 in San Diego, California and from 0.10–0.16 on Vancouver Island. Of the two locations, the climate and oceanographic conditions in Oregon are more similar to Vancouver, and my estimate for mortality falls in line with Russell’s maximum estimate.

Decreases in abundance of *Strongylocentrotus purpuratus* were detected in nearly every plot and varied greatly between plots. Specifically, sea urchins in plots #1, #17, and #18 were most likely to move or die, and together these plots accounted for 71% of the total decrease in abundance. A possible explanation for higher movement/mortality in these plots comes from extensive field observations. From January–August 2006, I observed considerable predation on sea urchins by *Pycnopodia helianthoides*, American black oystercatchers (*Haematopus bachmani*), and raccoons (*Procyon lotor*) (discussed in detail in Chapter V). The east side of South Cove, where Plot #1 was located, was the central foraging area of at least six oystercatchers and two raccoons. Both predators are able to consume over 35 sea urchins during a single low tide, so it is not hard to believe that they would eventually forage in the monitoring plots. Additionally, two months after the monitoring period ended, the remaining thirteen sea urchins in Plot #3 went missing. Plots #1 and #3 are shallow pools on tall sandstone benches surrounded by the surfgrass *Phyllospadix scouleri*. It is more probable that these plots were discovered by foraging raccoons or oystercatchers than every urchin evacuated the tidepools and moved into the surfgrass (Laur et al. 1986).

Plots #17 and #18 were located in a large, mid intertidal pool on the west side of South Cove. Though the tidepool contained hundreds, if not thousands of *Strongylocentrotus purpuratus*, I never observed any terrestrial predators near it. One *Pycnopodia helianthoides*, however, was observed in August 2005 and on several occasions thereafter, usually at the deepest part of the tidepool underneath surfgrass. This sea star, which has been observed to specialize on *S. purpuratus* in the rocky intertidal

(Mauzey et al. 1968, Dayton 1975), is likely responsible for the missing sea urchins in Plots #17 and #18, which were closest in proximity to the *P. helianthoides*. Unlike oystercatchers and raccoons, *P. helianthoides* only eats one sea urchin per day, but *S. purpuratus* usually reacts to its presence by moving away from it relatively quickly (Dayton 1975). If many of the sea urchins that disappeared from these plots were chased away instead of eaten, then I may be overestimating predation in my estimate based on urchin abundance in study plots.

The number of nonpit urchins decreased more than the number of pit urchins, which were much more common. Nonpit urchins could be more susceptible to predation than pit urchins, but other sources of mortality might be more likely to kill nonpit urchins without harming pit urchins. During winter storms, strong surges produce acceleration forces strong enough to move boulders and slam cobble into the substratum with enough force to influence the distribution of barnacles, limpets, and other species (Dayton 1971, Shanks & Wright 1986, van Tamelen 1996). Some of these wave-borne projectiles may collide with and damage the tests of sea urchins. At South Cove, about 9% of tests from sacrificed sea urchins had damage marks, indicating that living sea urchins underwent recalcification to repair dents or breaks in their test plates. Sea urchins lacking protective pits would seem especially subject to damage from wave-borne projectiles, which probably leads to mortality more often than successful test repair. Even deadlier than a flung cobble would be a rolling boulder. In one tidepool at South Cove, a large (ca. 0.5 m^3) boulder was found to have moved several meters during the winter, narrowly avoiding the sea urchins in Plot #14. Using a crowbar as a lever, I lifted the boulder to find sea urchins underneath it that survived, protected inside their pits. This anecdotal evidence suggests that survivorship in intertidal *Strongylocentrotus purpuratus* is enhanced by protective pits in the substrata.

Conclusion

One year of field monitoring and a short-term manipulation study were used to investigate movement and mortality in *Strongylocentrotus purpuratus*. The primary finding was that movement was very infrequent in an intertidal population of *S. purpuratus* at South Cove, Cape Arago. About 94% of the sea urchins present at the end of the study were not observed to move during the year; thus they were sedentary. A field manipulation indicated that disturbed *S. purpuratus* utilize pit microhabitats as refuges, and observations of movement suggested that nonpit urchins might be more likely to move than pit urchins. Extreme water velocities encountered in the intertidal might present a high risk of dislodgement that is ameliorated in when a sea urchin remains sedentary inside a pit. The total abundance of *S. purpuratus* was observed to decline by 15% during the year, from 688 to 583 individuals. A large part of this decline was probably due to mortality resulting from predation. Movement out of plots may also have contributed to the change in abundance, but most individuals were sedentary, reducing the likelihood that emigration from pits played a significant role. Nonpit urchins decreased more than pit urchins, suggesting that microhabitat use affects mortality. A positive trade-off associated with living in a more dangerous environment outside a pit could be an increased growth rate (see Chapter III). Nonpit urchins grow faster than pit urchins and attain a larger size, so although they might be more likely to perish, nonpit urchins may have greater reproductive output than pit urchins.

Bridge to Chapter V

Though this chapter focuses on the sedentary habits of *Strongylocentrotus purpuratus*, it is the infrequent observations of movement that actually address the major question at hand. Technically, if each sea urchin moved only once in its life, but tended to move out of pits, then nonpit urchins would be larger than pit urchins, as indicated in Chapter III. If sea urchins live an average of 16 years, and 6% of the population moves once in a year, then each urchin would move on average one time during its life. These averages are quite similar to the observations from South Cove. So while I have not proven that movement out of pits accounts for the microhabitat-based difference in size structure, I also cannot reject the hypothesis. Combined with the effects of differential growth, movement seems a likely mechanism to produce the bimodal distribution.

However, one hypothesis remains, that dealing with differential mortality. Chapter V is the result of diligence and nature's serendipity. One cannot truly understand a habitat until he has experienced it frequently and seasonally. Over the past two years, I feel I have just begun to understand the ecology of South Cove and particularly its sea urchins. In 2006, a unique predation event occurred at this site, and the resulting unequal microhabitat effects contributed another piece to this puzzle.

There once was an urchin named June
Who crawled out of a tidepool at noon.
She thought she was safe
Far from stars and big waves,
But she just didn't count on raccoons.

CHAPTER V

STAMPEDING SEA URCHINS AND INDIRECT EFFECTS IN AN INTERTIDAL FOOD WEB

INTRODUCTION

Ecologists characterize interspecific relationships based on changes in the abundances or densities of species resulting from interactions. Direct effects such as predation, competition, grazing, and mutualisms involve only two species. When one species influences another by interacting with a third species, the interaction is said to be one of indirect effects (Menge & Branch 2001). For example, on New England's rocky shores, the snail *Littorina littorea* is an important grazer that structures tidepool algal communities (Lubchenco 1978). When the predatory green crab *Carcinus maenas* reduces the density of *L. littorea*, positive indirect effects are passed on to the algae that are released from grazing pressure. Predation alone is not responsible for reducing snail density, as was first believed. When *L. littorea* detects the presence of *C. maenas,* it moves away from the predator evacuating the tidepool. This fleeing response reduces grazing pressure more than the direct effects of the predator, which in this case may be negligible (Trussell et al. 2004). The indirect effects of *C. maenas* on the tidepool algae are trait-mediated, that is, they result from *L. littorea* changing its behavior in response to a detected predator (Schmitz et al. 2004). Brown (1999) suggested that understanding the role of "fear" should be central to the study of species interactions. In an effort to avoid predation, herbivores may flee predators as in the case of *Littorina littorea*, resulting in reduced density.

A shift in behavior can also produce cascading effects in the community. Two species of sea urchins (*Strongylocentrotus droebachiensis* and *S. franciscanus*) altered their grazing rates when exposed to the chemical cue of a predatory sea star (*Pycnopodia helianthoides*) (Freeman 2005). Like *C. maenas*, simply the presence of *P. helianthoides* may benefit the algal community by causing the herbivores to flee. Trait-mediated interactions cannot always be measured by trophic cascades. Kiesecker and Blaustein (1998) used experimental pools to expose larval red-legged frogs (*Rana aurora*) to different combinations of predators. No predator by itself had a significant effect on the tadpoles; when bullfrogs were added to the pools, *R. aurora* moved deeper, and when smallmouth bass were added to the pools, *R. aurora* moved into the shallows. When both predators were placed in the pools, however, *R. aurora* experienced significant mortality. *R. aurora*'s trait-mediated response to one predator made it more susceptible to the other.

The effects of multiple predators on a population of purple sea urchins (*Strongylocentrotus purpuratus*) were investigated in Oregon. The predators included one invertebrate, the sunflower sea star *Pycnopodia helianthoides* (hereafter *Pycnopodia*) and two terrestrial predators, the raccoon (*Procyon lotor*) and the American black oystercatcher (*Haematopus bachmani*). Of the three, *Pycnopodia* is the best-known predator of sea urchins (Mauzey et al. 1968, Dayton 1973, 1975, Moitoza & Phillips

1979, Tegner & Dayton 1981, Duggins 1983, Lafferty & Kushner 2000), while the behavior is less common in raccoons (Carlton & Hodder 2003) and oystercatchers (Falxa 1992, Wootton 1997).

Oystercatchers, especially the European species (*Haematopus ostralegus*) have been the subjects of many studies investigating foraging behavior (O'Connor & Brown 1977, Wanink & Zwarts 1985, Meire & Ervynck 1986, Leopold et al. 1996). Several studies have demonstrated that oystercatchers display aspects of optimal foraging behavior, in which energy gain is maximized and energy loss is minimized (Stephens & Krebs 1986). Oystercatchers select prey that is larger than what is most commonly available (Hartwick 1976, Goss-Custard 1996), and they make economic decisions when foraging, selecting prey that offer the most energy per unit effort (Wanink & Zwarts 1985, Meire & Ervynck 1986).

Thirty years ago, Dayton (1973, 1975) described a combination of direct and indirect interactions that resulted from several years of field observations in rocky intertidal regions of Washington. At one particular site, Dayton noted that a *Pycnopodia* occasionally entered a tidepool densely packed with purple sea urchins. The urchins immediately responded to the presence of *Pycnopodia* by exposing defensive pedicillariae and moving away, often over the backs of their neighbors. Within weeks to a few months, tidepools were completely cleared of sea urchins, and the bare substrate was soon colonized by algal settlers. Dayton called this phenomenon “urchin stampeding.” The stampeding urchins, now holding onto the spines of other urchins instead of rocks, were not able to maintain their grip when exposed to strong waves, and after being swept into the surf, many were caught and consumed by the giant green anemone *Antheopleura xanthogrammica*. The number of sea urchins consumed by the sea anemones was probably an order of magnitude greater than those consumed by *Pycnopodia*, which eats only one urchin per 24–48 hours (Dayton 1973). In this example, the indirect effects (urchin stampeding) of *Pycnopodia* are greater than its direct effects (predation). *Pycnopodia* can eat at most one sea urchin per day, but it caused hundreds of sea urchins to stampede out of tidepools to their death. *A. xanthogrammica* benefited from the trait-mediated behavior displayed by the sea urchins, since they obtained much more food when *Pycnopodia* was foraging nearby (Dayton 1973).

Beginning in early 2006, at Cape Arago in southern Oregon, I observed a similar situation in which the presence of *Pycnopodia* resulted in large stampedes of purple sea urchins. The primary beneficiaries of *Pycnopodia*'s indirect effects in this scenario, however, were black oystercatchers and raccoons. I describe the foraging behaviors of all three predators and estimate the overall effect on the local sea urchin population. An opportunity was presented to compare interspecific direct effects when each predator was observed foraging in the same area at South Cove. Finally, I compare the sea urchin population structure to the death assemblages preyed on by oystercatchers and raccoons. The various abundances, behaviors, and foraging strategies of the predators necessitated the utilization of different methods of data collection for *Pycnopodia*, oystercatchers, and raccoons. Descriptions of field observations, foraging behaviors, and data are contained in the results.

MATERIALS AND METHODS

Study site

All observations and data were collected at South Cove of Cape Arago (43°18.5’N, 124°24’W) (Fig. 1), a prominent headland in southern Oregon, USA. Cape Arago is exposed to large swells and strong winds associated with winter storms, but South Cove is otherwise fairly protected. The U-shaped cove has a sandy beach flanked by two intertidal sandstone benches. The west side of South Cove (hereafter: West Side) is a cobble- and boulder field that gradually slopes toward the water. Near the opening of the cove (the black outline in Fig. 1A), the intertidal becomes slightly more exposed, macroalgal growth is profuse in the growing season (e.g., *Nereocystis luetkeana, Alaria marginata, Iridaea cordata, Fucus distichus, Hedophyllum sessile, Egregia menziesii, Ulva* sp., *Sargassum muticum, Cystoseira geminata*), and purple sea urchins occur in large tidepools and on sandstone benches. This extensive population of sea urchins covers most available surface from approximately 0.75 m above mean lower low water (MLLW) to 0.3 m below MLLW. Many of the sea urchins are situated inside depressions they excavate from the rock (see Chapter II). Special attention was given to four large tidepools, denoted H, I, J, and K, where urchin stampeding in 2006 was first observed. Tidepool H was approximately 5 m^2 in area, tidepool J was approximately 8 m^2 in area, and tidepools I and K were approximately 15 m^2 in area. Tidal height was 0 MLLW for each tidepool except J, which was approximately 0.4 m above MLLW. Although these tidepools are not representative of the West Side, their patterns are valuable in elucidating the extent of *Pycnopodia*'s effects at South Cove, since data were not collected in other areas during most of the study.

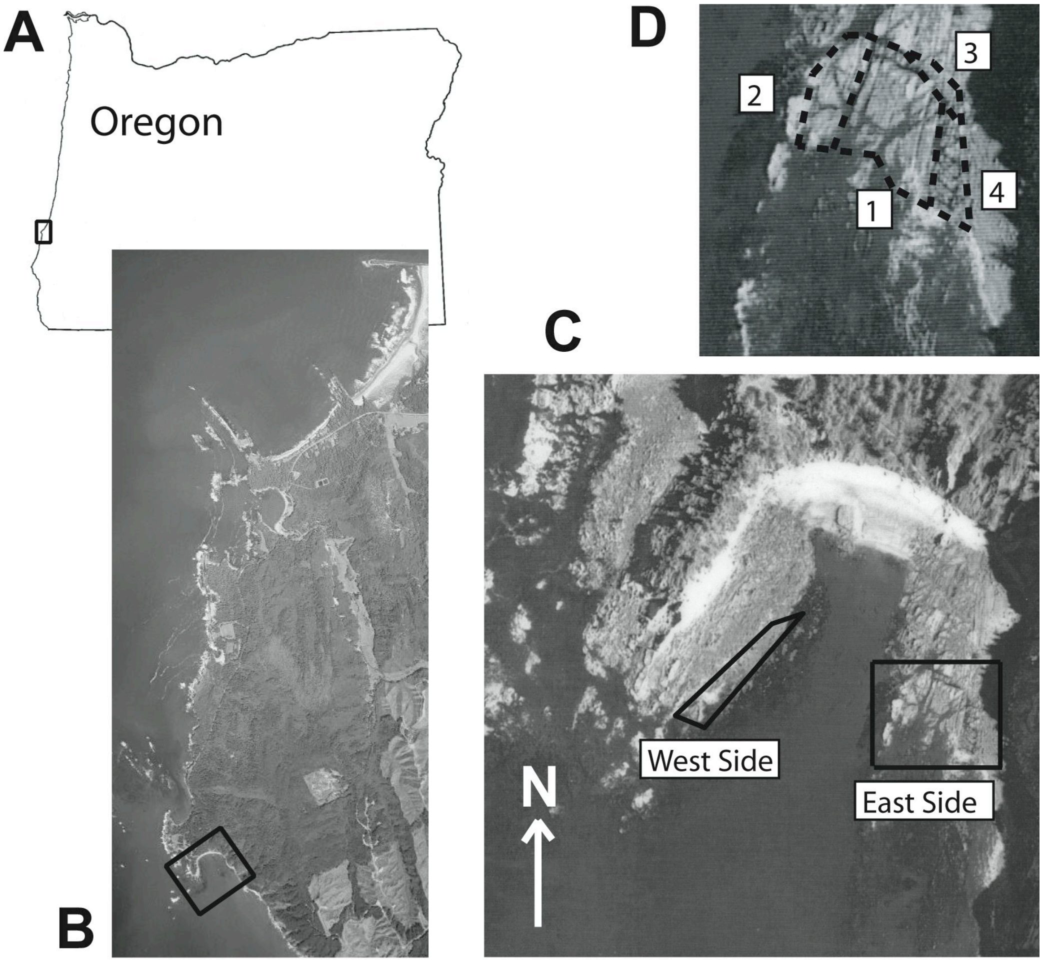


Fig. 1. The location of the study site; (A) Oregon, with a box around Cape Arago expanded in (B); a box around South Cove is expanded in (C); a polygon marks the West Side study area, and a box around the East Side is expanded in (D); sections of East Side referred to in the text are: (1) sandstone benches, (2) low islands blocked by deep surge channels, (3) sandy, protected area, and (4) boulder field; Photograph B courtesy of NOAA, Photograph C/D courtesy of Oregon Department of Geology and Mineral Industries

The east side of South Cove (hereafter East Side), lacking a large boulder and cobble field, has a markedly flatter topography than the West Side. Intertwining surge channels cut the sandstone bench into intertidal "islands" about 1 m above MLLW that are pocketed with tidepools and covered on top by the surfgrass *Phyllospadix scouleri*. High densities of sea urchins are found on shorter benches up to 0.5 m above MLLW, but they are most abundant at or below MLLW. Many of the urchins are wedged inside excavated pits (see Chapter II), especially those on the sides of surge channels, which in which sand accretes during the summer. The lower distributional limit for sea urchins seems to be about 0.5 m below MLLW. The low benches do not contain surfgrass, but brown, filamentous algae (*Sargassum muticum* and *Cystoseira geminata*) are common on vertical surfaces and adjacent to tidepools packed with sea urchins. The macroalgal community on the East Side is not as dense or speciose as the west side. *Laminaria setchelli* is well established throughout surge channels and the shallow subtidal, and *Egregia menziesii* is common below MLLW. On both sides of South Cove, where sea urchins cover extensive portions of the substrate, macroalgal growth is restricted to the tops and sides of rocks. An intertidal boulder field begins on the landward side of the benches and follows the coastline south out of the cove.

Sea urchin density

The frequency of data collection depended on the tidal cycles; Oregon and most of the North American West Coast experience mixed semidiurnal tides, so it was only during daylight low tides below 0 m MLLW that study areas were emergent. During a particularly low tide in May 2006, the density of sea urchins was measured with belt transects. On the West Side, I counted all the sea urchins in three random transects 1 m wide and 20–25 m long, extending from approximately 0.3 m below MLLW, the lower boundary for sea urchins at that location, to the upper boundary 0.75 m above MLLW. On the East Side, urchins in three transects with random origins along the northern edge of the sandstone benches were counted (see Fig. 1D). Transects were 1 m wide and extended 24, 29, and 49 m across the benches and surge channels. Density was calculated as total sea urchins divided by the total transect area, including surge channels. The total area of the sites (black polygons in Fig. 1C) was calculated using overhead aerial photographs (Oregon Department of Geology and Mineral Industries) and ImageJ (Rasband 2006). In addition, the size structure of the sea urchin population was sampled by measuring the test diameters to the nearest 0.1 cm of all the sea urchins in 24 randomly placed quadrats.

Predation by *Pycnopodia*

The number of intertidal purple sea urchins consumed by *Pycnopodia* in South Cove was estimated by modifying a rate of prey removal equation presented by Birkeland (1974) and utilized by Duggins (1983) for *Pycnpodia* predation. The rate of sea urchins consumed *Pycnopodia*$^{-1}$ day^{-1} was calculated as:

$$\frac{\left(\frac{U}{I}\right)W}{Y} \tag{1}$$

where I is the number of *Pycnopodia* eating or digesting U sea urchins, W is the rate of successful attacks, and Y is the digestion time (in days) of one sea urchin. This equation was multiplied by 365 to yield the number of consumed sea urchins *Pycnopodia*$^{-1}$ year^{-1}. Multiplying this value by the intertidal population of *Pycnopodia* (P) in South Cove gave the estimate of annual predation for the population:

$$\frac{365\left(\frac{U}{I}\right)WP}{Y} \quad . \tag{2}$$

P was calculated by counting *Pycnopodia* at South Cove several times from February through August 2006. In February on the West Side, tidepools H–K were thoroughly searched for *Pycnopodia*; in April and May, tidepools I–K were searched. In August, I examined the entire mid and lower intertidal of the West Side, counting all *Pycnopodia* at a tidal height of 0.2 m below MLLW and higher. On the East Side at the same tidal heights, I counted all the *Pycnopodia* I could find in May, July, and August 2006.

Over the course of a spring tidal series in August, *Pycnopodia* were inspected to determine how many were eating purple sea urchins. Once a *Pycnopodia* has ingested its food, it is difficult to remove it without injuring the animal. The test of a sea urchin, however, creates a telltale bulge so that *Pycnopodia* can be checked for urchin predation without harming them. If possible, individuals were flipped over to check for prey items that had not yet been ingested. I recorded the total *Pycnopodia* inspected (I) and the total sea urchins being eaten or digested (U).

Oystercatcher foraging

Estimating total predation

On the East Side, a spotting scope was used to observe oystercatchers while they foraged on purple sea urchins 28 times from April–August 2006. Their feeding activity seemed relegated to that side of South Cove, with the exception of my first foraging observation in February, which was on the West Side. The impact of oystercatchers on the population of sea urchins on the East Side was calculated with the formula:

$$(T)(H)(O)(R) \tag{3}$$

where T is the proportion of time spent actively foraging on sea urchins, H is the annual number of hours that foraging can potentially occur, O is the average number of oystercatchers foraging at low tide, and R is the feeding rate expressed as urchins hour^{-1}.

T was calculated as total time oystercatchers spent foraging divided by the total time oystercatchers were on the East Side while foraging was possible. When more than one oystercatcher were present, data were recorded for each individual.

To calculate H, I used tidal graphs from Harbormaster (Zihua Software 1999) and the image-processing program ImageJ (Rasband 2006) to measure the hours of daylight at which the tidal height was at least 0.2 m below MLLW, corresponding with the maximum tidal height at which oystercatchers could effectively forage on sea urchins.

O was calculated as total oystercatchers observed foraging divided by the number of days that observations were recorded. Data were not included from dates when the tide was too high to allow foraging in the low intertidal.

To calculate *R*, I counted the number of sea urchins eaten by an oystercatcher during one foraging bout on multiple dates. When more than one oystercatcher was present, one or two randomly selected birds were observed.

Oystercatcher foraging behavior

A stopwatch was used to measure the amount of time taken by eight randomly-selected oystercatchers to search for, flip, and consume purple sea urchins. Handling is defined as time pursuing, capturing, and consuming one prey item (Stephens & Krebs 1986), so flipping and eating times were summed to yield total handling time. Data were collected for an oystercatcher as long as it remained in sight and continued foraging.

On eleven occasions, I measured the test diameters of sea urchins consumed by oystercatchers. I sampled as many discarded tests as I could, but this was made difficult because of deep surge channels and the need to avoid disturbing the foraging oystercatchers. I could come to within 15–20 m of an oystercatcher before it flew further away, so I maintained at least a 25 m buffer.

Raccoon predation

Though raccoons were only observed a handful of times, their predation effects were documented by counting sea urchin tests on the same low tide during which they were eaten. Raccoon predation was distinguished from that of oystercatchers by looking for broken tests, as oystercatchers did not break tests when they fed on sea urchins. If a moribund urchin still contained coelomic fluid or gut contents, it had been freshly eaten. Sea urchins were counted and measured to the nearest 0.1 cm on eighteen dates, and regression analysis was used to explore whether the amount of predation correlated with other parameters (tidal height, foraging time, low tide time of day). The sea urchin death assemblages due to predation by oystercatchers and raccoons were compared to the live size frequency distribution using a Kolmogorov-Smirnov (K-S) test, and mean test diameters were compared with a student's t-test.

Energy intake rates

The caloric content of sea urchin gonad was calculated using an equation from Snellen (2006). She used bomb calorimetry on the internal contents of 39 purple sea urchins with test diameters 1.5–8 cm and found a significant relationship ($R^2 = 0.96$, $P < 0.001$) between test diameter (D, in mm) and caloric content (K, in kcal).

$$\log_{10} K = -4.204 + 3.082(\log_{10} D) \tag{4}$$

Data for sea urchin population structure was placed into 2 mm bins. The mid-point of each bin (i.e., the odd integer) was inserted into the equation to yield average caloric content for that size class. This value was multiplied by the frequency of each size class to achieve an average caloric content curve for the population of purple sea urchins on the East Side. The sea urchin death assemblages for oystercatchers and raccoons were converted to caloric content curves in the same way.

RESULTS

Field observations and predation estimates

Purple sea urchins occur in large numbers at Cape Arago and are the most abundant benthic macroinvertebrate in portions of South Cove. On the West Side, in an area encompassing approximately 2200 m^2, I measured 72 urchins m^{-2}, for a local population exceeding 150,000 sea urchins. On the opposite side of South Cove, the East Side intertidal area of 3000 m^2 contained an average density of 60 urchins m^{-2} for a population of 180,000 purple sea urchins.

In January 2006, while collecting data from the West Side for another study, I observed massive urchin stampedes adjacent to the tidepools H, I, J, and K. As in Dayton’s (1973, 1975) descriptions, sea urchins had evacuated the tidepools and were piled up on rocks and other sea urchins around the edge of the pools. Inside the tidepools, predator densities often approached or exceeded 1 *Pycnopodia* m^{-2}. In February, the circumstances were unchanged, and I observed oystercatchers consuming sea urchins adjacent to tidepools containing the predatory sea stars. March did not include any daytime tides below MLLW, but in April I found that oystercatchers, raccoons, and *Pycnopodia* all preyed upon sea urchins in the same location on the East Side seen in Fig 1D. Observations and data collected from February–August 2006 revealed that all three predators had sizeable impacts on the population of purple sea urchins. Furthermore, oystercatchers and raccoons appeared to exhibit optimal foraging behavior, selecting larger prey than would be expected based on random foraging.

Pycnopodia

At low tide, most *Pycnopodia* were inactive in the deepest portion of tidepools. If exposed to air at low tide, they tended to nestle underneath boulders or seaweed that presumably kept them moist until the tide rose. Once the tide turned and waves began to enter the tidepools, *Pycnopodia* became active. They began moving toward the periphery of the large tidepools where sea urchins were clustered just beyond the water's edge. As the tidewaters rose to cover the sea urchins, *Pycnopodia* followed, and the inevitable attacks were hidden by the waves.

The censuses for *Pycnopodia* at South Cove are presented in Table 1. In February, after urchin stampeding was first observed at South Cove, I found 54 *Pycnopodia* in tidepools H–K on the West Side, for approximate densities of 1.3 m^{-2}. Tidepool H contained 13 *Pycnopodia* for a density of 2.6 m^{-2}. In April, only eight *Pycnopodia* were found in tidepools I–K, and this number dropped to five in May. In August, of 33 *Pycnopodia* counted on the West Side, only seven were found in tidepools H–K. On the east side, there were 29 *Pycnopodia* in May, 36 in July, and 40 in August. Though *Pycnopodia* were found in all sections of the study area, they were especially abundant in protected surge channels and underneath boulders in the sandy area and the boulder field. For the purposes of estimating total predation, total *Pycnopodia* (*P*) was set to 73, the number counted in August when all of South Cove was searched for sea stars.

Table 1. *Pycnopodia helianthoides*. Censuses of *Pycnopodia* conducted between February and August 2006; blank spaces indicate no search was made that month; [a]no exhaustive search for *Pycnopodia* was made in February, so the total given for West Side is simply the summed counts from tidepools H–K

Month	East Side	West Side	Individual Tidepools			
			SCH	SCI	SCJ	SCK
February		54[a]	13	19	8	14
April				3	3	2
May	29			2	1	2
July	36					
August	40	33	1	2	2	2

In August, the diet of *Pycnopodia* was composed almost entirely of purple sea urchins, though the sea star *Pisaster ochraceus* was being digested by one *Pycnopodia,* and a pile of shells from the black turban snail *Tegula funebralis* was discovered underneath another. Of 123 *Pycnopodia* inspected, 63 were found eating or digesting a

Table 2. *Pycnopodia helianthoides* and *Strongylocentrotus purpuratus*. Sea urchins found being consumed by *Pycnopodia* on four days during one tidal series; not all *Pycnopodia* were accessible, so the average is per Inspected sea star (U/I)

Date	*Pycnopodia*			Sea urchins Consumed	$\left(\frac{U}{I}\right)$
	Inspected	Uninspected	Total		
7 Aug	4	3	7	5	1.25
9 Aug	26	5	31	11	0.42
10 Aug	67	6	73	33	0.49
11 Aug	26	3	29	17	0.65
Total	123	17	140	66	0.5

sea urchin. Three *Pycnopodia* ingested two sea urchins at once, so $\left(\frac{U}{I}\right)=\frac{66}{123}=0.54$.

The value for $\left(\frac{U}{I}\right)$ ranged from 0.42 – 0.65 on three consecutive days (Table 2).The variable for proportion of successful attacks (W) was assumed 1, because when a *Pycnopodia* begins to attack a sea urchin, it always succeeds (Duggins 1983, pers. obs.). I did not calculate Y, but Duggins (1983) measured digestion in the laboratory to be approximately 1.2 days. Inserting each of the values into the equation, total annual predation of sea urchins by *Pycnopodia* in South Cove is:

$$\frac{365\left(\frac{U}{I}\right)WP}{Y}=\frac{365(0.54)(1)(73)}{1.2}$$

$$= 11{,}990 \text{ sea urchins}$$

$$= 164 \text{ sea urchins } \textit{Pycnopodia}^{-1}$$

Since 40 *Pycnopodia* were counted at the East Side and 33 at the West Side, the respective totals of annual sea urchin predation would be 6570 and 5420 for the study sites.

Oystercatchers

A flock of five oystercatchers was first observed foraging on sea urchins on the West Side of South Cove next to tidepools H–K. On another occasion in June, one oystercatcher was observed eating limpets from the mid-intertidal on the West Side when the low tide was only 1 m above MLLW. The rest of the observations took place on the East Side during morning low tides of 0–0.6 m below MLLW, though dead sea urchins on the West Side provided evidence that oystercatchers occasionally foraged there. I usually arrived at the study site when the tidal height was above MLLW and falling, and the oystercatchers often appeared when the tide reached MLLW or shortly thereafter. Active foraging began once the tidal level dropped to 0.2 m below MLLW and continued until most or all of the foraging areas were inundated with the rising tide. Data were collected from 24 February – 11 August, after which the absence of adequate daylight low tides prevented oystercatchers the opportunity to forage on sea urchins (Fig. 2A). Since nocturnal foraging has not been described in black oystercatchers, H (annual number of hours foraging can occur) was set to 127.4, the annual number of daylight hours that the tidal height was 0.2 m below MLLW (Andres & Falxa 1995).

The mean (± SD) number of oystercatchers foraging at low tide was 3.2 ± 1.6 (*N* = 28), which was substituted for *O* in Eq. (3). The maximum number of oystercatchers observed was five until a sixth was spotted on 28 July. The monthly means are presented in Fig. 2B. The observed birds may have included one breeding pair, as two oystercatchers usually foraged together and displayed territorial and mating behavior. The remaining birds exhibited minimal courtship behavior in May and June, but were believed to be non-breeding.

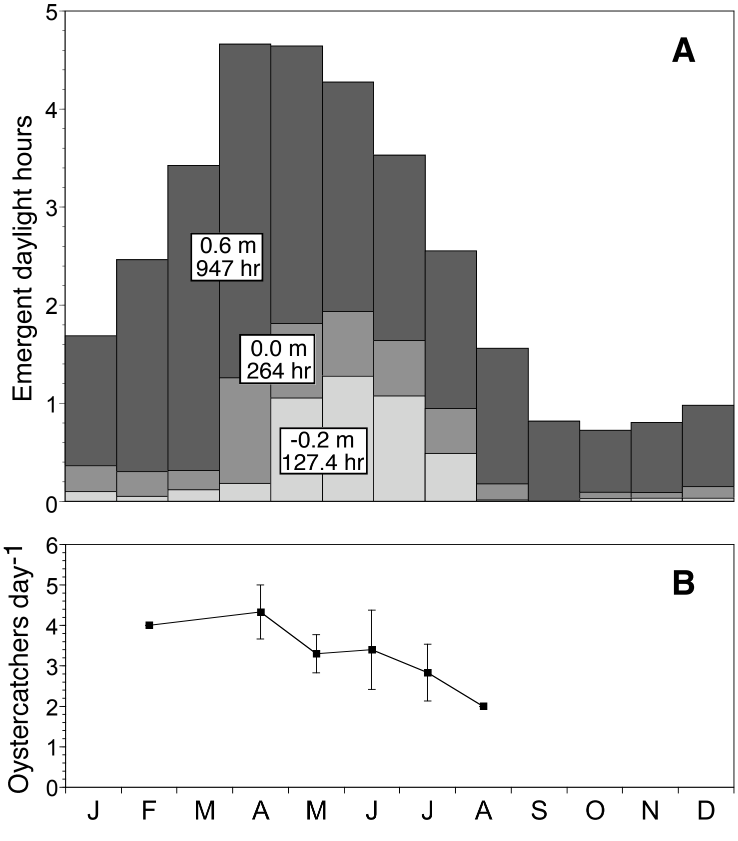


Fig. 2. *Haematopus bachmani*. (A) Hours of daylight the tidal level is below 0.6 m, 0.0 m, and –0.2 m (relative to MLLW); data are pooled per four weeks; (B) the mean (±SE) number of oystercatchers per day observed foraging on *Strongylocentrotus purpuratus* between February and August; most accessible *S. purpuratus* were below -0.2 m

Although sea urchins were present at high densities, oystercatchers continued walking while foraging, passing by many more sea urchins than they attempted to eat. An oystercatcher took several steps, touched a sea urchin with its bill, and continued walking. Multiple sea urchins were tested in this way before the oystercatcher selected one to eat. When a sea urchin was selected, the oystercatcher braced its legs, wedged its bill underneath the urchin, and used its bill as a lever to flip the urchin upside-down. After quickly puncturing the peristomial membrane and usually removing the Aristotle's lantern, the oystercatcher inserted its long bill into the urchin and consumed the gonads without ever breaking the test. The time required to complete each of these activities is displayed for eight oystercatchers in Fig. 3. The data were collected on five days, but since no more than six oystercatchers were ever seen at the East Side, a bird may be represented by more than one trial. The mean (± SD) times required to search for, flip over, and consume a sea urchin were 54.0 ± 17.3 s, 17.9 ± 12.1 s, and 56.7 ± 14.3 s respectively. The mean handling time (flipping and consumption) was 74.5 ± 18.7 s. Summing the three measurements gives 129 seconds (2.15 minutes) for an oystercatcher to find and eat one sea urchin. This is equivalent to 0.465 urchins min^{-1} or 28.0 urchins hour^{-1} (*R*).

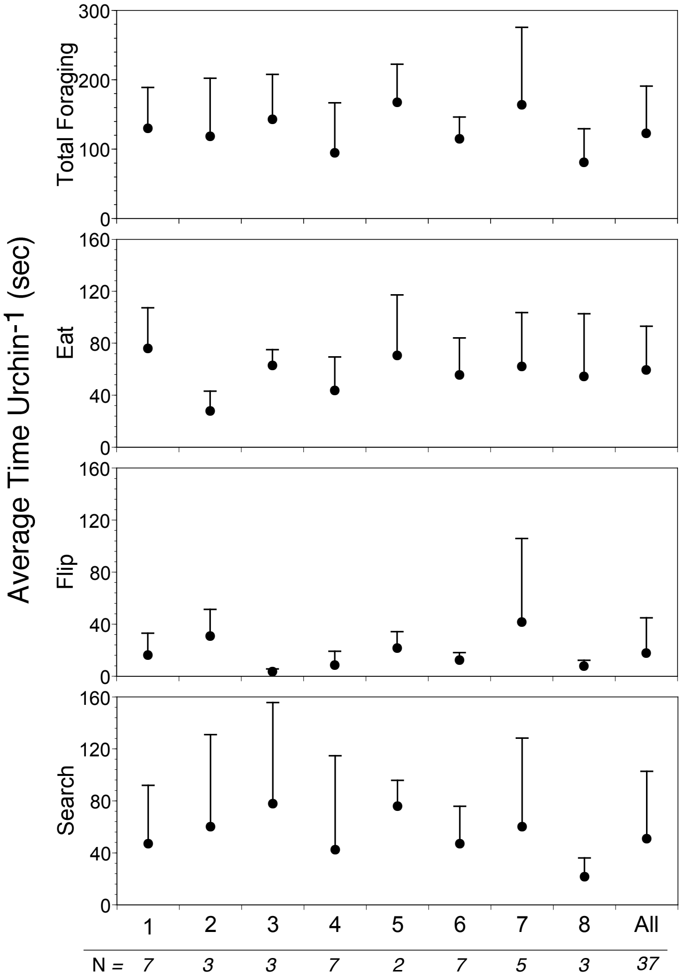


Fig. 3. *Haematopus Bachmani* and *Strongylocentrotus purpuratus*. Mean (±SD) times for oystercatchers (1-8) to search, flip, and eat sea urchins; average total time was 128.6 seconds urchin^{-1}, yielding 28.0 sea urchins hour^{-1} active foraging; *N* is the number of sea urchins eaten while each oystercatchers was observed

This value compares favorably to the calculation for *R* acquired using the foraging data in Table 3. The total time oystercatchers foraged was divided by the number of sea urchins consumed for an average foraging rate of 2.55 minutes urchin^{-1} (or 153 seconds). This value is equal to 0.391 urchins min^{-1} or 23.5 urchins hour^{-1}. The two methods were averaged, so R = 25.7 urchins hour^{-1}.

Table 3. *Haematopus bachmani*. Time spent foraging and sea urchins consumed by oystercatchers (BLOY) between February and August 2006; each Continuous Observation is for one oystercatcher, but Time Spent Foraging is averaged for all oystercatchers present that particular day; all times are in minutes; on three dates, courtship behavior allowed sex determination, so bold numbers indicate **males** and underlined numbers indicate females

		Continuous Observations			Time Spent Foraging (min)	
Date	Total BLOY Foraging	Time	Urchins consumed	Min Urchin^{-1}	Time present BLOY^{-1}day^{-1}	Time foraging BLOY^{-1}day^{-1}
24 Feb	4	11	7	1.57	49	42
19 Apr	5					
29 Apr	5	9	5	1.8	80	49
30 Apr	3	38	18	2.11	125	125
		24	16	1.5		
1 May	5	96	52	1.85	130	88
		96	**21**	**4.57**		
12 May	3	8	2	4	26	3
13 May	4					
14 May	3	10	4	2.5	60	47
		10	9	1.11		
15 May	5	25	11	2.27	57	46
		25	8	3.13		
16 May	3	**63**	**15**	**4.2**	165	165
		63	31	2.03		
17 May	5	10	4	2.5	136	136
		10	4	2.5		
26 May	1					
27 May	1	131	34	3.85	137	131
28 May	3					
12 Jun	1	8	4	2	18	17
14 Jun	5	**7**	**3**	**2.33**	62	60
		11	7	1.57		
		9	**3**	**3**		
15 Jun	1	22	10	2.67	90	49
16 Jun	5	14	5	2.8	71	41
		4	3	1.33		
28 Jun	5				47	47
12 Jul	2	29	14	2.33	86	57
		18	4	4.5		
13 Jul	2					
14 Jul	1					
24 Jul	3	10	4	2.5	93	76
		9	3	3		
26 Jul	3					
28 Jul	6				57	57
7 Aug	2				37	20
10 Aug	2	11	5	2.2	70	53
		11	4	2.75		
11 Aug	2				10	10
Total	90	792	310		1606	1320
Mean	3.2	28.3	11.1	2.55	Foraging time – 82%	
Male	4	175	42	4.17		
Female	3	170	90	1.89		

Of the time oystercatchers were observed, the proportion of time oystercatchers spent actively foraging (T) was 0.822. Often, upon completing a bout of foraging, oystercatchers flew to a high rock and preened or loafed. Time spent outside the foraging area was not included in the calculation for T, unless oystercatchers resumed foraging after a rest break. Finally, inserting all the parameters into Eq. (3) gives:

$$(T)(H)(O)(R) = (0.822)(127.4)(3.2)(25.7)$$

$$= 8612 \text{ sea urchins consumed by oystercatchers}$$

Raccoons

Raccoons were rarely observed eating sea urchins and were extremely wary, so once they detected humans they quickly left the intertidal for the remainder of that low tide. The maximum number of raccoons spotted was two, even when they were observed foraging undisturbed. Most sea urchins preyed upon by raccoons were discovered in the boulder field, though as the summer progressed, the raccoons seemed to forage with increasing frequency in the sandy area (see Fig. 1D). The foraging behavior of raccoons was observed on several occasions. A raccoon selected a sea urchin and grabbed it with its front paws, sometimes carrying it to a large boulder. The mode of feeding was dependent on the size of the sea urchin. A relatively small sea urchin (<5.5 cm) was attacked by biting through the side of the test. A raccoon accessed the insides of a larger sea urchin by biting chunks of test from the oral side until it could fit its wrist inside the cavity. The raccoon used its hand to scoop out the gonads and guts, shoveling them immediately into its mouth. Raccoons were able to forage sea urchins in the boulder field once the tidal height descended to MLLW. The predation of several kelp crabs (*Pugettia producta*), rock crabs (*Cancer productus*), and one red sea urchin (*Strongylocentrotus franciscanus*) were also attributed to raccoons, as they were found surrounded by raccoon-eaten purple sea urchins.

On eighteen collection dates, 515 sea urchins were found that had been consumed by raccoons, and as many as 68 tests were recovered during one low tide. The amount of raccoon predation on sea urchins appears to have been related to foraging time, which is defined as the time the tide is below MLLW before the first human disturbance at the site (by myself or others). A regression between consumed sea urchins and foraging time is displayed in Fig. 4. One data point was excluded because there was reason to believe that the raccoons were disturbed well before low tide. Where F is foraging time, and C is collected sea urchins ($R^2 = 0.54$, $P < 0.01$),

$$C = 24.07(F) + 6.35. \tag{5}$$

Inserting for F the number of annual daytime hours tidal height is below MLLW (264.7), the value of C is 6371 sea urchins year^{-1}. Raccoons, however are nocturnal mammals; if nighttime low tides are included in the calculation, $F = 465$ hours and $C = 11{,}193$ sea urchins year^{-1}.

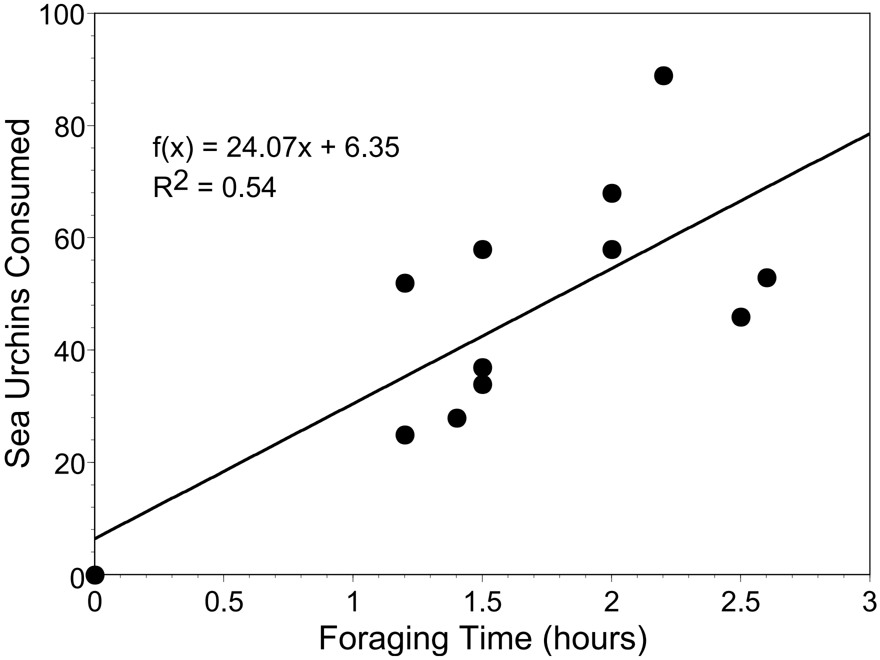


Fig. 4. *Strongylocentrotus purpuratus* and *Procyon lotor*. Relationship between sea urchins consumed by raccoons and daily amount of time foraging was possible; potential foraging time began when the falling tide reached MLLW and ended when the foraging habitat was disturbed either by the researcher or other humans

Annual predation

Direct effects for three species can be combined to estimate total sea urchin mortality due to predation at South Cove (Table 4). Calculations for *Pycnopodia* (11,990), oystercatchers (8612), and raccoons (11,193) add up to 31,795 consumed sea urchins in a population of 330,000 and a predation rate (z_{pred}) of 0.10. The predation estimates for oystercatchers and raccoons, however, come from data specific to the East Side. At that site, where all three predators foraged in the same general location, an estimated 26,375 sea urchins were eaten from a population of 180,000 ($z_{\text{pred}} = 0.15$), so the predation rate was much higher than on the West Side ($z_{\text{pred}} = 0.04$).

Sea urchin size selection by oystercatchers and raccoons

Oystercatchers and raccoons consumed significantly larger sea urchins than the average size available at the East Side (Fig. 5) (student's t-test, $P < 0.001$ for both), and the size-frequency distributions of the death assemblages are significantly different than the live population (K-S test, $P < 0.05$). The mean (± SD) test diameter of the population was 5.4 ± 1.2 cm. Sea urchins with unbroken tests, determined to have been eaten by oystercatchers, had a test diameter of 6.7 ± 0.7 cm. Sea urchins with broken tests, eaten by raccoons, had a test diameter of 7.2 ± 0.6 cm. Though abundant, sea urchins smaller than 5 cm were almost never consumed by either predator. Only 6% of live sea urchins were larger than 7 cm, but this large size class contributed 31% and 59% to the diets of oystercatchers and raccoons, respectively.

Energy intake rates

Total caloric content per size class is plotted as a frequency for live sea urchins and death assemblages in Fig. 6. Maximum gonad mass in sea urchins scales exponentially with test volume, so the most abundant size classes do not necessarily

Table 4. *Strongylocentrotus purpuratus*. Estimates of sea urchin predation by *Pycnopodia*, oystercatchers, and raccoons; predation is estimated for each side of South Cove separate and combined; *N* is the number of predators for which the estimate is applicable, and *U/N* is the annual consumption of urchins predator^{-1}; [a] foraging data were not collected on the West Side for oystercatcher and raccoon predation because it was much less common than on the East Side; [b] two raccoons were seen on three occasions, and they are presumed to account for all raccoon predation

Predator	West Side	East Side	Combined	*N*	*U/N*
Pycnopodia	5420	6570	11,990	73	164
Oystercatchers	[a]	8612	8612	3.2	2691
Raccoons	[a]	11,193	11,193	2[b]	5547
Total	5420	26,375	31,795		
Sea urchins	150,000	180,000	330,000		
Predation rate	0.04	0.15	0.10		

contain the most calories. A sea urchin with a test diameter equal to the population mean (5.4 cm) has a caloric content of 15.4 kcal. The average sea urchins consumed by oystercatchers and raccoons had caloric contents of 27.0 kcal and 33.5 kcal, respectively. The significance of this size selectivity is that oystercatchers and raccoons consumed a number of urchins disproportionate to the population. Both predators found and ate sea urchins over 1 cm larger than the average sized urchin sampled in randomly placed quadrats. The estimate of 25.7 urchins oystercatcher^{-1} hour^{-1} (Fig. 3 and Table 3) can be multiplied by 27.0 kcal urchin^{-1} to give an intake rate of 694 kcal oystercatcher^{-1} hour^{-1}. For raccoons, 1 hour is inserted into Eq. (4) as F to give C = 30.4 urchins hour^{-1}. Multiplying by an average caloric content of 33.5 kcal urchin^{-1} gives an intake rate of 1019 kcal raccoon^{-1} hour^{-1}.

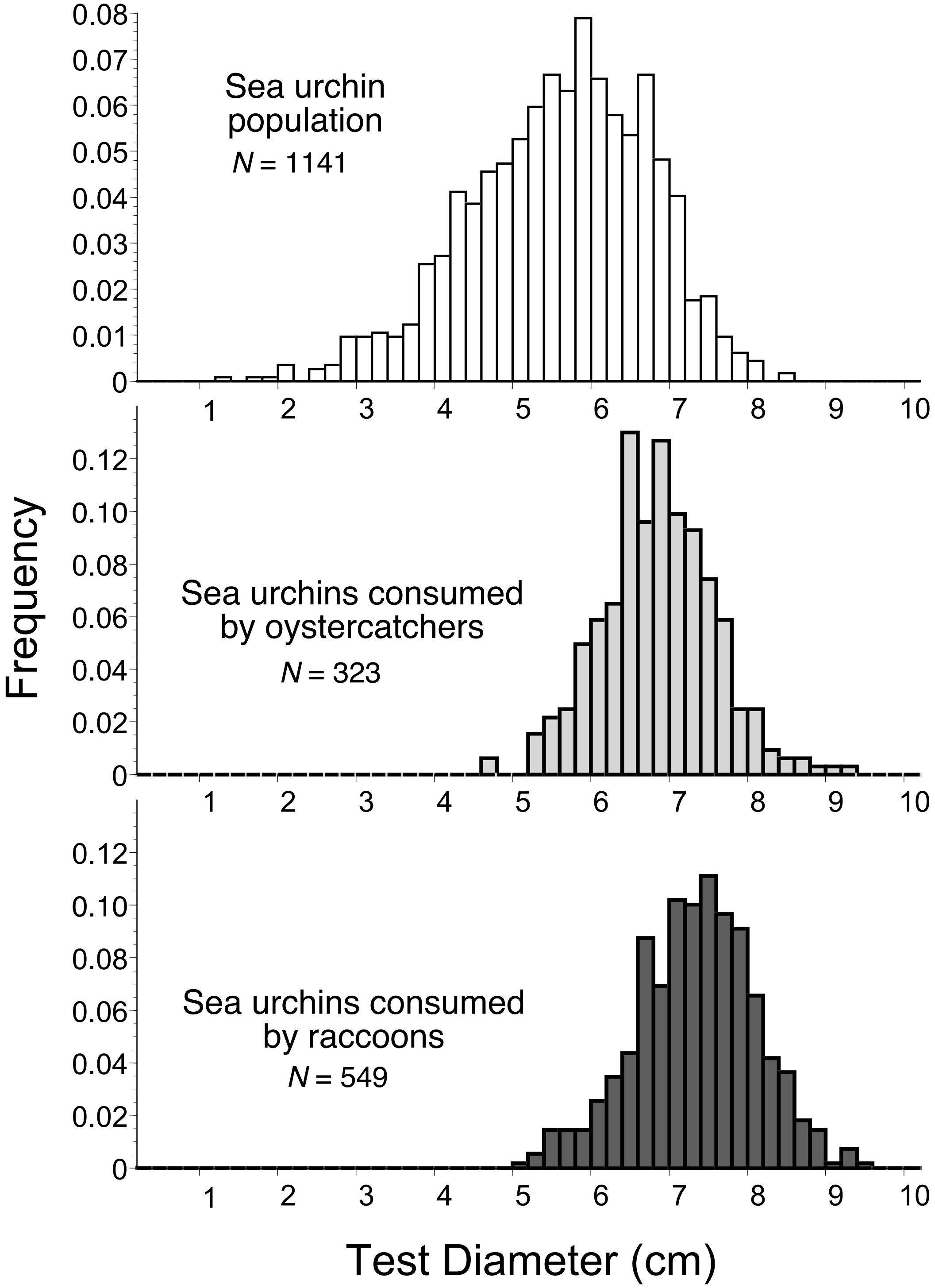


Fig. 5. *Strongylocentrotus purpuratus*. Comparison of size-frequency distributions of live sea urchins and those preyed upon by oystercatchers and raccoons; mean test diameter of sea urchins taken by predators is significantly higher than the population mean (Student's t-test, $P < 0.001$)

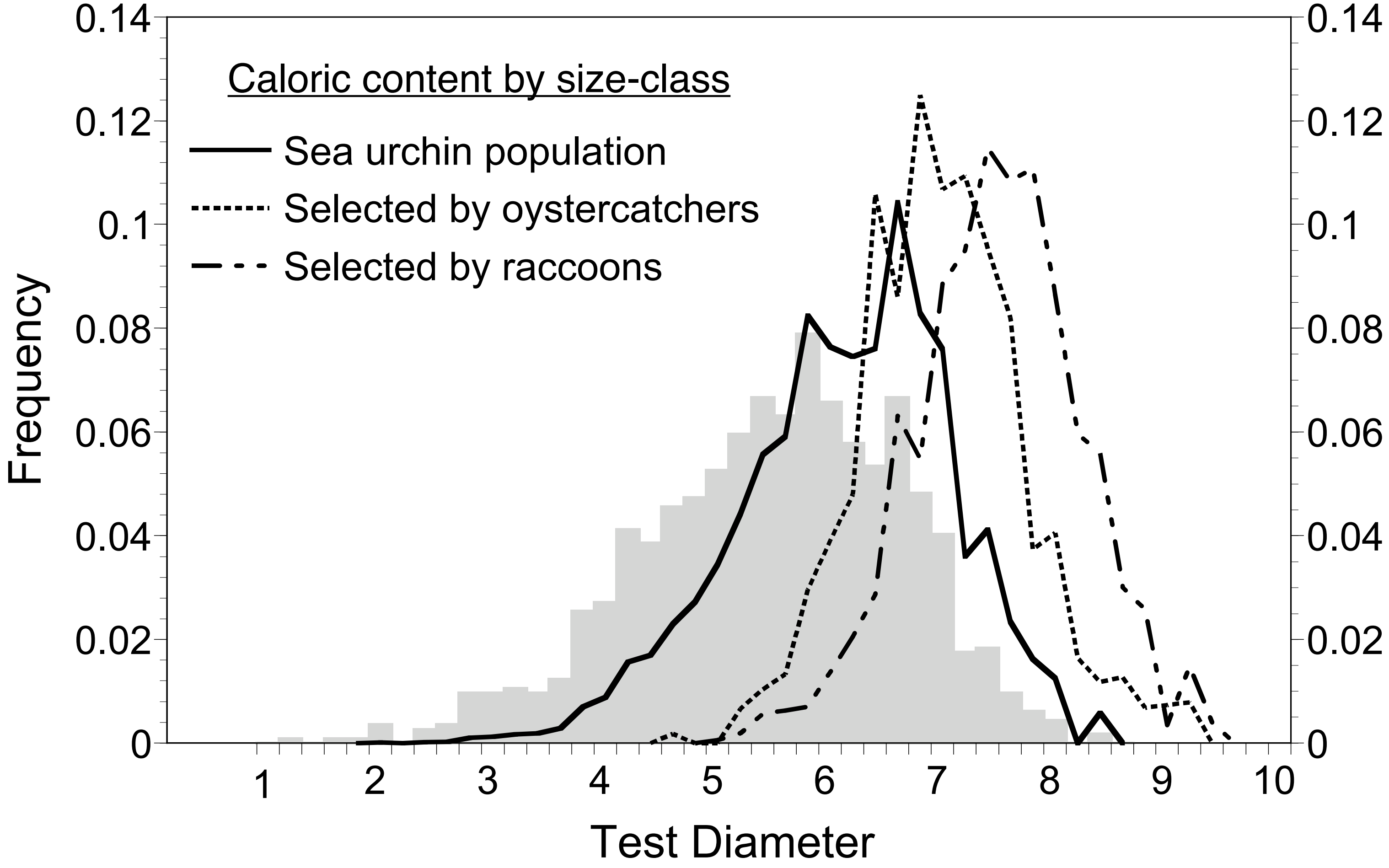


Fig. 6. *Strongylocentrotus purpuratus*. Average caloric content per size class in the sea urchin population and death assemblages; gray bars are the size-frequency distribution of test diameters; lines are the frequency caloric content in each size class of the sea urchin population (solid line), urchins eaten by oystercatchers (dotted line), and urchins eaten by raccoons (dotted and dashed line); all data are from the East Side of South Cove

DISCUSSION

Observations of abundance and foraging behavior of three predators were used to estimate the annual rate of predation 32,000 urchins out of 330,000 sea urchins in the population. On the East Side, where all three predators forage, about 26,000 of 180,000 sea urchins were predicted to be eaten, a predation rate of nearly 15%. Although South Cove's intertidal is teeming with sea urchins, if the predation rates observed in 2006 continue several years, the ramifications for the population could be significant. Considering the variable nature of sea urchin recruitment in Oregon (Ebert 1968, Ebert & Russell 1988), sea urchin abundance in South Cove could decrease by 50% in less than a decade due to predation pressure alone. I did not observe any major pulses of sea urchin recruitment in 2005 or 2006 to counteract the high mortality rate.

Pycnopodia **density and predation**

Pycnopodia are generalist predators that have been observed to specialize on purple sea urchins in Alaska (Duggins 1983), Washington (Mauzey et al. 1968, Dayton 1975), and California (Tegner & Dayton 1981), but they are not an obligate diet item (Mauzey et al. 1968, Herrlinger 1983). *Pycnopodia* are abundant at South Cove, often occurring in tidepools and underneath boulders or seaweed. However, the densities observed in tidepools in February 2006 (0.9–2.6 *Pycnopodia* m^{-2}) were uncommonly high. Dayton (1973), who was the first to describe urchin stampeding, said that such densities were an order of magnitude higher than what he has observed (personal communication). No published densities that I am aware of approach the 2.6 sea stars m^{-2} recorded in one tidepool. Densities reported in subtidal surveys in California, Washington, and Alaska range from 0.01 to 0.1 *Pycnopodia* $m-^{2}$ (Wobber 1975, Duggins 1981, Watanabe 1984, Kvitek et al. 1992), and Wootton (1997) reported 0.09 *Pycnopodia* m^{-1} shoreline in Washington. In South Cove, 73 *Pycnopodia* were counted along approximately a 300 m shoreline (0.24 *Pycnopodia* m^{-1} total shoreline, 0.34 *Pycnopodia* m^{-1} East Side shoreline).

Unfortunately, little can be said about the temporal change in *Pycnopodia* density because of the lack of data, which were collected sporadically during eight months in 2006. I did not visit South Cove after August 2005 until January 2006, when the observations described in this paper began, so I can only speculate as to the events preceding the urchin stampedes. It seems that for some reason, *Pycnopodia* were driven to aggregate in large tidepools during the fall of 2005 or early winter of 2006. It is possible, but highly unlikely, that the *Pycnopodia* were in the tidepools in the summer of 2005 and escaped notice. For one, the bright colors and large size (ca. 0.4–0.6 m diameter) of *Pycnopodia* made them easily visible. Second, the urchin stampedes appeared to have occurred recently because no organisms had colonized their former scars, circular patches of bare rock surrounded by coralline algae.

What might have caused dozens of large, highly mobile predators to invade the tidepools? Perhaps changes in the physical environment or in subtidal prey populations led to high intertidal predator densities. In Oregon, water temperature can alter the foraging behavior of the sea star *Pisaster ochraceus* (Sanford 2002b). During summer periods of upwelling, when water temperature dropped from 12° to 8°C, intertidal sea star density decreased as individuals moved into surge channels and the shallow subtidal. Warmer ocean temperatures in the winter could explain increased foraging activity by *Pycnopodia*, but sea surface temperatures were not particularly warm in January 2006. *Pycnopodia* has been shown to prefer the bivalve *Saxidomus giganteus* (Mauzey et al. 1968) to *Strongylocentrotus purpuratus*, and subtidal seastar populations often feed primarily on mollusks, even when sea urchins are present (Mauzey et al. 1968, Herrlinger 1983, Shivji et al. 1983). A die-off of a subtidal prey species such as *S. giganteus* might have prompted *Pycnopodia* to utilize intertidal sea urchins as a secondary food source.

Regardless of the reason that high intertidal densities of *Pycnopodia* occurred in early 2006, once there, the effects on purple sea urchins were considerable. The per capita consumption estimate of 164 urchins year^{-1} is much higher than that for a subtidal population in Torch Bay, Alaska, where individual *Pycnopodia* were estimated to eat 44 urchins year^{-1} (Duggins 1983). The frequency of *Pycnopodia* consuming sea urchins was 19% in Alaska but over 50% in South Cove, suggesting higher intake rates are partially responsible for larger estimates of predation. In this study, *Pycnopodia* also displayed greater preference for sea urchins than in Alaska, where one-third of feeding sea starts were consuming prey items other than sea urchins (Duggins 1983).

My determination of predation by Pycnopodia should be treated as tentative. First, it is problematic that predation events were enumerated only in August, because temporal variability in predation rates or prey selection would affect the estimated direct effects calculated for a whole year. Second, temperature has been shown to affect feeding in asteroids, and warmer temperatures are usually associated with higher metabolic and foraging activity (Sloan 1980, Sanford 2002a). Since average seawater temperature is higher in Oregon than Alaska, *Pycnopodia* could have higher metabolic rates and consume more sea urchins. Duggins' (1983) calculated digestion time, 1.2 days, maybe longer than the digestion time for *Pycnopodia* in Oregon, suggesting that 164 urchins year^{-1} could be an underestimate.

Indirect effects due to *Pycnopodia*

Pycnopodia's direct effects on sea urchins appeared to be substantial, but its indirect effects were even more pronounced. Dayton (1975) found that the emigration rate of sea urchins in stampedes was eight to twelve times higher than one sea star's consumption rate. I observed similarly large numbers of sea urchins stampeding from tidepools, but the risk of wave dislodgement was less than for Dayton's exposed populations, so green sea anemones were not privy to easy meals. Instead, at South Cove, trait-mediated behavior in sea urchins benefited oystercatchers and raccoons. Oystercatchers easily flipped sea urchins that had moved to tenuous locations on the tops of rocks and other urchins. The presence of *Pycnopodia* also caused many sea urchins to abandon the relative safety of their pits or the tidepool. I never observed an oystercatcher pry a sea urchin out of its pit, though one occasionally would test a pit urchin with its bill before moving on to easier targets. Even a sea urchin outside of a pit cannot be eaten by an oystercatcher if it is underwater; it was rare for an oystercatcher to put its face into the water to prey on an urchin. By chasing sea urchins out of tidepools, *Pycnopodia* caused them to be more accessible and exposed for a longer time at low tide, increasing the foraging capabilities of oystercatchers.

Urchin stampedes were most prevalent next to the boulder field where raccoons tended to forage. During the summer, there were consistently 15–25 *Pycnopodia* in the shallow surge channel adjacent to the boulder field. Like oystercatchers, raccoons indirectly benefited from the *Pycnopodia* chasing sea urchins out of the water. Many of the sea urchins in the boulder field stampeded out of subtidal surge channels that would have been more difficult for raccoons to access.

The ability to detect waterborne chemical cues allows sea urchins to flee a marine predator, but does nothing to help them avoid terrestrial predators. Annual estimated predation on the East Side is over 26,000 sea urchins, of which *Pycnopodia* only consumed 6500. The other 19,500 sea urchins were eaten by terrestrial predators that forage at low tide when sea urchins are unable to move or use chemosensory capabilities. The irony here is that by reacting to the presence of *Pycnopodia*, purple sea urchins were more likely to suffer mortality than if they had remained sedentary. *Pycnopodia*'s indirect effects led to more predation events than actual consumption.

Oystercatchers and raccoons benefited from *Pycnopodia*'s indirect effects on sea urchins, and they had their own positive indirect effects on other species. An interaction web displays this suite of interactions between sea urchins, predators, and scavengers at South Cove (Fig. 7). American crows (*Corvus brachyrhynchos*) were often seen scavenging moribund sea urchins after raccoons or oystercatchers moved away. *Larus occidentalis*, the western gull, was often present at South Cove and sometimes approached foraging oystercatchers. Kleptoparasitism was observed on several occasions, and usually consisted of a gull swallowing the discarded Aristotle's lantern. Neither gulls nor crows were observed to prey on live sea urchins at South Cove, though I often saw them near the West Side urchin stampedes. Gulls and crows have been observed to prey on sea urchins and they certainly had the opportunity to do so at South Cove (Irons et al. 1986, Wootton 1995, 1997, Snellen 2006). Another positive indirect effect of oystercatchers and raccoons exists for green sea anemones, many of which were discovered digesting sea urchins that were preyed upon by raccoons. Since South Cove is a protected site, these sit-and-wait predators did not benefit from *Pycnopodia* chasing sea urchins into positions where waves would dislodge them. Instead, during low tides, the activity of terrestrial predators created a stock of dead sea urchins that were washed around when the tide rose.

Trait-mediated indirect effects have been demonstrated in many ecosystems, and they are often stronger than direct effects (reviewed in Preisser et al. 2005). This seems to be the case at South Cove, and the species interactions described do not even consider the indirect effects of removing thousands of invertebrate grazers and space-holders from the intertidal. This complex web of community interactions was set into motion because of a change in density of one species, *Pycnopodia*. Multi-trophic studies that do not consider indirect effects could severely misestimate community dynamics, just as I would have underestimated *Pycnopodia*'s effects if I had ignored its indirect effects.

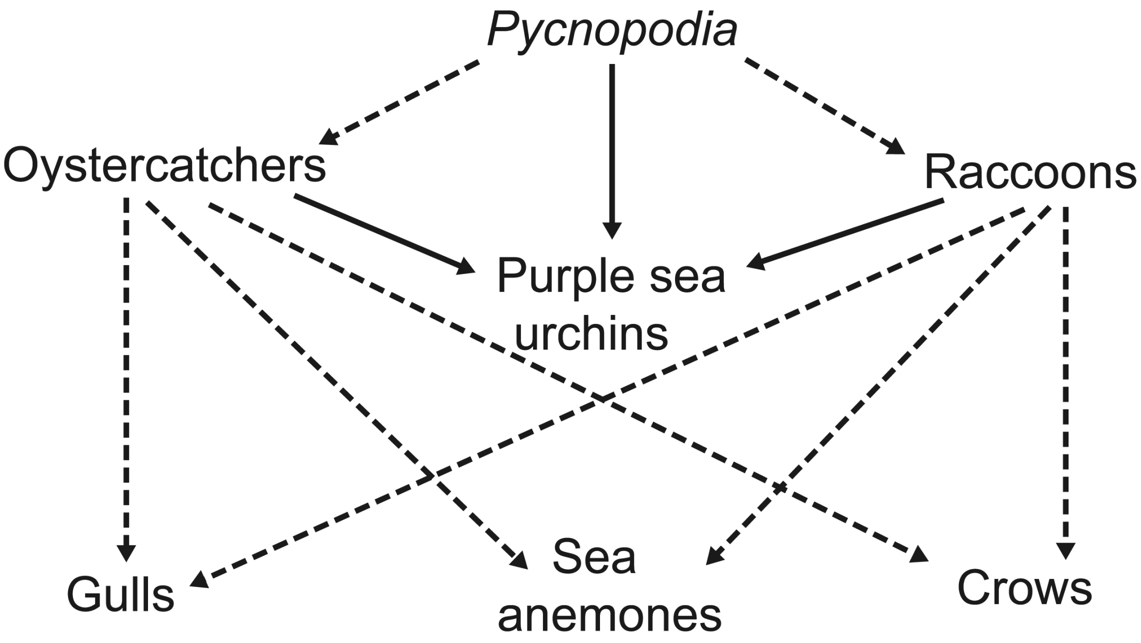


Figure 7. Interaction web for selected predators of sea urchins at South Cove; solid arrows are direct effects (predation) and dashed arrows are indirect effects where an interaction between one predator and sea urchins positively affects a third species

A new behavior at South Cove?

Before the influx of *Pycnopodia* into the intertidal zone, sea urchins were very abundant. The significant change brought on by the sea stars was to drive urchins out of the tidepools making them more susceptible to terrestrial predation. Could the many urchin stampedes caused by *Pycnopodia* have increased the number of accessible urchins to such a degree that raccoons and oystercatchers began exploiting a new food source? Raccoons are common intertidal predators (reviewed by Carlton and Hodder) and are known to prey on sea urchins at a number of intertidal sites in southern Oregon (J.

Hodder, personal communication). Broken tests were observed at South Cove in August 2005, indicating that raccoons were foraging on sea urchins before *Pycnopodia* increased in density.

Oystercatchers, too, have previously been observed to eat sea urchins (Falxa 1992, Wootton 1997), but it is unknown whether they have exhibited this behavior at South Cove. A clue that they have is the expediency they showed in taking advantage of the food source. Sea urchins are exposed for few daylight hours in the winter, and by February, oystercatchers were already foraging during those narrow windows of opportunity. Deft bill work is required to flip a sea urchin and eat its gonads, technical enough that these oystercatchers probably had prior experience eating sea urchins (Falxa 1992).

Alternatively, the death assemblage data suggest oystercatchers and raccoons may be in the initial stages of profiting from a glut of food. Kvitek et al. (1992) present sea urchin size frequency data from areas inhabited by sea otters. Sea otters prey heavily on sea urchins and within a short time can eliminate the largest size classes in an area. Despite the selection of large urchins by oystercatchers and raccoons, the population structure at South Cove still contains many large individuals, thought the mean test diameter of sea urchins outside pits did decrease by about 0.5 cm between 2005 and 2006 (see Chapter II). The hypothesis that oystercatchers and raccoons have only recently been focusing their foraging efforts on sea urchins, would be supported if sea urchin size continues to show annual decreases.

Optimal foraging behavior

Oystercatchers are known for specialization in prey type and foraging behavior. Most of the research on this topic has focused on *Haematopus ostralegus*, the European oystercatcher, while the black oystercatcher of the North American Pacific coast is better described as a generalist that is capable of exploiting a variety of food sources including limpets, mussels, worms, and sea urchins (Hartwick 1978, Frank 1982, Falxa 1992, Wootton 1997).

In several studies, Oystercatchers have been observed to exhibit optimal foraging behavior (Hartwick 1976, Zwarts & Wanink 1984, Meire & Ervynck 1986, Cayford & Goss-Custard 1990)}. Again, most literature focuses on the European oystercatcher, and my observations provide evidence that black oystercatchers are also optimal foragers. The central premise of the theory of optimality is that an organism forages on the prey type that provides the most energy per searching and handling time (Krebs & Davies 1993). My lack of size-specific searching and handling times prevents the application of an optimality model. However, by selecting sizes of sea urchins larger than what is commonly available on the East Side, both oystercatchers and raccoons seem to be choosing the most optimal prey.

Gonad production in purple sea urchins is cyclic (Boolootian 1966). Gonad index [(gonad mass) (body mass^{-1})] increases during the growing season when food is plentiful until it peaks at 15–25% in December or January when spawning occurs. Coincidentally, gonad index is smallest in March and April, soon after oystercatchers began feeding on sea urchins. (Due to this temporal variability associated with gonad indices, following calculations should be considered nothing more than rough estimates.) At South Cove, the gonad index in May 2006 was only 3.5%, down from 7.4% in February and 11.0% in August 2005 (unpublished data). Based on these measurements and Boolootian's (1966) ten-year dataset of monthly gonad indices, 7.5% is a reasonable estimation for gonad index between April and August, when most oystercatchers were observed foraging. My calculations of caloric content were based on data collected sometime between September and March (Snellen 2006), when the gonad index was probably about twice this value (Boolootian 1966, Gonor 1972). So therefore, if I decrease my caloric content calculations by half, oystercatchers are estimated to consume 13.5 instead of 27 kcal urchin^{-1} and 347 instead of 693 kcal hour^{-1}. Black oystercatchers are approximately the same size as their European counterparts (Swennen 1984, Andres & Falxa 1995), so they presumably have similar basal metabolic rates (BMR). BMR is 251 kJ day^{-1}, or 60 kcal day^{-1}, for a European oystercatcher (Kersten & Piersma 1987). Food intake rates are about 3.2 times the BMR, so 187 kcal must be ingested daily to maintain weight (Goss-Custard 1996). Given an average caloric content of 13.5 kcal urchin^{-1}, an adult oystercatcher would need to consume fourteen sea urchins to fulfill its daily energy requirement. In April and May, when gonad indices may be less than 4%, an oystercatcher might require 28 sea urchins to meet its energy needs, but much less foraging would be necessary in the fall or winter when gonad index is higher. These calculations suggest that at South Cove, black oystercatchers can consume enough sea urchins during one low tide to meet their daily energy requirement, assuming the water level is at least 0.2 m below MLLW.

Based on field observations of oystercatchers, I calculated a foraging rate of 25.7 urchins hour^{-1}, which seems excessive considering their estimated energetic needs. The possibility exists that European and black oystercatchers actually vary in their BMR, and I erred in assuming them equal. A second explanation for the high foraging rates is a bias toward field observations early in the summer (mid-April to mid-June) compared to late (mid-June to mid-August). Females lay their eggs in late May (Andres & Falxa 1995), and the additional energy required for this task could in much higher foraging rates than males (Ricklefs 1974 in Ross 1979). I was only able to distinguish between male and female birds on three days, but the data clearly showed much higher foraging rates in female oystercatchers (Table 3). My seemingly high estimates of energy intake are likely be the result of foraging by females preparing to lay eggs.

Since black oystercatchers, unlike European oystercatchers, do not forage at night (Andres & Falxa 1995), they cannot take utilize intertidal sea urchins as a food source in the winter when gonad indices peak. Raccoons, however, are nocturnal foragers and may be able to exploit the sea urchin population at South Cove year round. Winter foraging would be even more rewarding for raccoons than oystercatchers since they tend to prey on larger sea urchins (Fig. 6). The foraging behaviors of these terrestrial predators, facilitated by a marine predator, place a disproportionate pressure on the largest size classes of purple sea urchins. This complex web of indirect effects demonstrates the potential for energy flow between habitats and has implications for trophic dynamics in other coastal ecosystems.

CHAPTER VI

CONCLUDING SUMMARY

The chapters contained in this thesis stand alone, but they are also puzzle pieces that can be fit together to address a larger question: what are the effects of differential microhabitat use in *Strongylocentrotus purpuratus*? Chapter II highlights the differences between sea urchins living inside and outside pits. Morphologically speaking, pit microhabitats result in sea urchins with shorter spines, larger jaws, and different test shapes relative to those in nonpit microhabitats. Additionally, the size structure of sea urchins is affected by microhabitat, as nonpit urchins are consistently larger than pit urchins. The remaining thesis chapters relate to three hypotheses addressing this difference in size: differential growth (Chapter III), movement out of pits (Chapter IV), and differential mortality (Chapter V).

Chapter III focuses on microhabitat-specific growth rates, which were higher in sea urchins living outside pits than inside pits. Faster growth and smaller relative jaw size (Chapter II) are clues that nonpit urchins receive more food than pit urchins. However, despite faster growth, age-frequency distributions created from the growth curves indicate that the nonpit urchins were older, and thus, had been growing longer, than the pit urchins. If pit and nonpit urchins were permanently sedentary, there would be a smaller gap in size difference than what was observed. An alternative explanation for the large difference in mean diameters is that pit urchins move out of their pits once they grow to a certain size.

In Chapter IV, I investigated movement in purple sea urchins primarily by monitoring marked plots in tidepools at South Cove. Over the course of one year, I found that movement was quite rare in this intertidal population of sea urchins. In fact, at the end of the monitoring period, 94% of the sea urchins remaining had been sedentary as long as I had been observing them. Movement in *Strongylocentrotus purpuratus* seems to be very infrequent; this result was not unexpected, considering observations by other scientists and the morphological differences between pit and nonpit urchins. The movement detected, though rare, probably contributes to the larger size of nonpit urchins along with differential growth rates.

If pit urchins are smaller than nonpit urchins, it could also simply be a result of higher mortality. However, as I describe in Chapter V, the major source of mortality, predation, acted selectively on nonpit urchins. At South Cove, in the winter of 2005 – 2006, the intertidal population of the sea star *Pycnopodia helianthoides* exploded, and I observed densities that were orders of magnitude higher than normal. Since purple sea urchins are a common prey item of *Pycnopodia*, they stampeded from dozens of tidepools creating huge piles of sea urchins. It was not long before terrestrial predators began exploiting this food resource, and I observed a handful of oystercatchers and raccoons feeding on thousands of sea urchins throughout the spring and summer of 2006. These results are presented in light of trait-mediated indirect effects and optimal foraging behavior, but they also address the overall question of the effects of microhabitat on sea urchins. Predation of pit urchins was never observed, and it is possible that pits reduce rather than enhance mortality.

These chapters combine to tell a story of trade-offs between microhabitats. A sea urchin may have higher survivorship as long as it remains inside a pit. The negative trade-off of this sedentary lifestyle could be food limitation, constrained outward growth, or both, which result in smaller size than nonpit urchins. A slightly higher growth rate over several decades yields a significant difference in volume, and therefore, maximum reproductive output, which might be two-to-three times greater in a nonpit urchin than a pit urchin of the same age. So, is it preferable to risk death and grow to a large size quickly to release more gametes, or would an urchin be "wise" to remain in its pit and make a smaller contribution to (presumably) more reproductive events. The lack of movement evident at South Cove indicates that different sea urchins probably utilize both strategies; one can certainly find areas in which sea urchins occupy only one of these two microhabitats because there is no choice to be had.

The value of this research increases when one thinks outside of the world of sea urchins and considers the other invertebrates to which these findings might apply. All habitats contain various microhabitats, the most desirable of which are often selected by mobile organisms. It might be more important to consider the microhabitat of sessile and sedentary invertebrates that cannot easily escape their present physical environment. As exampled by sea urchins, these organisms could experience a high degree of microhabitat-based effects influencing growth, reproduction, and other biological and ecological factors.

APPENDIX A

SIZE STRUCTURE DATA

The size structure data in Appendix A were collected in two ways. In 2005, live sea urchins were removed from tidepools and measured. In 2006, following a growth study, the measurements of spineless tests were added to the size structure data set. Test diameters and heights were recorded to the nearest 0.01 cm, though repeated measurements of the same urchin sometimes differed by as much as 0.1 cm. Further details, including tidal heights and tidepool areas are contained in Chapter II.

Column headings are Diameter (D) and Height (H) and are in cm.

[b] test was broken upon removal from substratum
[d] sea urchin resided inside a depression that was too shallow to constitute a pit
[u] pit urchin was unremoveable, and height could not be accurately measured

Cape Blanco 2006

Tidepool A: 4 March 2006

Pit Urchins

D	H	D	H	D	H	D	H
4.85	2.82	3.03	1.49	4.33	2.25	4.16	2.04
5.06	2.74	4.59	2.34	4.09	2.23	4.20	2.17
4.70	2.74	3.05	1.68	4.27	2.09	4.42	2.00
3.94	1.87	5.84	3.17	3.58	1.89		

Nonpit Urchins

D	H	D	H	D	H	D	H
0.91	0.48	5.24	2.65	3.57	1.54	3.64	2.05
1.56	0.73	4.64	2.52	3.36	1.66	4.28	2.02
5.75	2.84	4.11	1.77	3.99	1.69	3.97	2.22

D	H	D	H	D	H	D	H
5.02	2.28	4.88	2.30	4.90	2.50	5.36	2.81
4.59	2.46	5.33	2.73	5.22	2.69	4.90	2.22
4.19	2.14	4.03	1.66	5.04	2.54		
5.60	2.86	4.52	2.35	4.83	1.98		
3.73	1.80	4.62	2.38	4.80	2.31		

Tidepool B: 4 March 2006

Pit Urchins

D	H	D	H	D	H	D	H
3.96	2.35	3.51	1.82	4.03	1.93	2.69	1.20
3.79	2.09	3.48	2.18	3.10	1.63	4.72	2.36
3.13		3.75	2.03	3.83	1.95	5.72	3.05
3.94		4.27	2.35	4.18	2.25	5.17	3.12
3.90		4.33	2.12	3.88	2.16	4.64	2.53
3.34		3.90	2.39	2.35	1.03	5.99	3.62
1.44	0.70	3.33	1.79	2.24	1.25		
3.97	2.26	3.74	1.80	3.33	1.75		

Nonpit Urchins

D	H	D	H	D	H	D	H
0.50	0.22	6.78	2.72	5.20	2.73	5.27	2.24
6.08	2.76	5.42	2.64	4.38	2.01	5.75	3.18
6.21	2.89	6.04	2.73	4.31	2.00	4.43	2.35
6.16	2.94	6.13	2.84	4.54	2.34	4.09	1.98
5.44	2.44	5.76	3.10	6.26	2.96	4.69	2.27
5.91	2.78	5.64	2.65	6.95	3.31	4.86	2.15
4.64	1.98	6.13	3.00	6.73	3.03	6.40	3.34
3.36	1.24	6.27	3.09	3.40	1.59	6.27	2.52
4.45	2.11	5.60	2.30	5.11	2.24	4.26	1.85
5.19	2.39	4.73	2.37	4.20	2.02	5.64	2.39
6.58	3.16	4.53	2.02	3.35	1.34	5.22	2.48
5.69	2.77	5.33	2.36	3.96	1.98	4.69	2.02
5.36	2.66	5.70	2.97	6.56	3.33	7.28	3.65
4.94	2.12	5.81	2.67	5.10	2.38	4.42	2.44
5.82	2.58	5.26	2.33	6.49	3.12	5.56	2.86
6.24	2.91	4.48	1.78	5.46	2.81	6.56	3.19
4.66	2.24	5.40	2.71	5.34	2.55		
4.32	2.13	5.89	2.99	4.18	2.21		
4.83	2.01	6.10	3.08	5.61	2.62		

Tidepool C: 28 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
4.84	2.83	4.42	2.30	4.40	2.39	5.70	2.82
3.82	1.78	4.71	2.26	0.55	0.25	4.24	2.39
4.39	2.72	4.08	2.20	3.94	2.23	5.39	2.90
3.86	1.93	4.10	2.14	4.17	1.86	4.15	2.42
4.54	2.74	4.66	2.33	3.80	2.12	4.28	2.38
5.19	2.86	5.55	2.81	4.48	2.36	4.13	2.09
5.57	2.99	3.15	1.39	5.39	2.94	3.43	1.64
4.93	2.74	4.03	2.12	4.07	2.14	4.79	2.78
4.25	2.19	5.19	3.12	3.35	1.69	5.85	3.08
3.95	2.08	4.01	2.36	4.26	2.66	4.63	2.48
4.57	2.15	3.51	1.68	4.96	2.75	3.79	2.01
5.45	3.12	4.41	2.43	4.53	2.28	2.60	1.18

Nonpit Urchins

D	H	D	H	D	H	D	H
6.02	3.22	5.70	2.97	6.36	3.13	1.17	0.61
5.77	2.79	5.39	2.85	4.45	2.14	5.01	2.44
6.50	3.25	5.25	2.52	3.70	1.74	4.93	2.57
5.65	2.71	5.35	2.57	4.81	2.62	3.82	1.86
6.62	3.18	4.39	2.19	3.56	1.64	5.44	2.60
6.33	3.30	4.25	1.95	5.83	3.24	4.81	2.66
4.33	2.23	4.99	2.78	5.56	2.56	4.88	2.52

Tidepool D: 28 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
4.50	2.10	3.63	2.16	4.89	2.63	3.33	1.93
2.20	1.00	3.82	1.78	3.39	1.48	3.57	1.84
4.74	2.51	4.00	2.07	5.15	2.61	1.00	
3.77	2.04	4.20	2.17	5.48	2.87		
0.75	0.35	4.29	2.35	3.92	2.23		
3.99	2.04	4.29	2.15	4.14	2.10		

Nonpit Urchins

D	H	D	H	D	H	D	H

D	H	D	H	D	H	D	H
7.19	3.25	6.33	3.01	3.68	2.04	5.80	3.13
5.27	2.48	6.38	3.44	5.97	3.33	5.51	2.78
4.01	1.94	7.00	3.40	6.07	2.60	3.77	1.59
6.87	3.28	6.91	3.62	5.51	2.72	5.54	2.79
6.65	3.36	5.43	2.70	6.17	3.21	5.06	2.56
6.10	3.41	5.84	2.53	5.63	3.22	3.46	1.66
0.70		6.23	3.05	1.03	0.47	0.74	0.34
6.66	3.28	7.15	3.64	6.34	3.16		

Tidepool E: 28 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
4.50		4.90	2.86	4.08	2.22	4.12	1.93
4.26	2.55	4.68	2.51	3.68	2.00	3.54	1.73
5.17	2.83	5.49	2.44	5.81	3.03	4.15	2.06
4.61	2.27	4.34	2.21	3.89	2.13	4.48	2.07
4.24	2.11	5.75	2.50	4.89	2.60	4.80	2.51
5.34	3.03	4.21	2.17	1.42	0.60	4.81	2.57
5.79	3.16	5.69	2.75	4.73	2.40	3.77	2.07
6.35	2.57	3.92	2.10	1.41	0.62	4.00	2.09
4.93	2.51	3.96	2.03	4.71	2.93	5.05	2.87
4.31	2.20	4.02	2.03	6.43	3.34	0.80	
4.44	2.46	4.38	2.55	4.46	2.46	0.40	

Nonpit Urchins

D	H	D	H	D	H	D	H
2.95	1.40	6.78	3.43	4.49	2.41	5.61	2.94
6.44	3.37	6.54	3.22	5.93	3.25	5.58	3.02
6.68	3.73	5.38	2.91	5.73	3.28	5.33	2.54
5.73	2.66	4.31	2.01	5.64	3.02	5.50	2.95
3.81	1.44	4.05	1.75	6.00	3.41	5.22	3.22
6.70	3.29	5.47	2.83	6.69	3.31	5.88	3.40
5.23	2.59	5.88	2.81	4.77	2.77	6.69	3.26
4.90	2.55	6.26	3.05	5.73	3.25	0.87	0.40
5.84	2.79	5.00	2.80	4.80	2.30	1.21	0.54
6.31	3.60	5.68	3.07	4.37	2.07	2.51	1.17
6.24	3.29	3.77	1.76	6.25	3.33	2.57	1.32
5.83	2.99	5.82	3.30	6.86	3.43	3.70	2.11
5.10	2.50	5.53	2.95	5.79	2.82	3.96	1.81
6.77	3.62	5.33	2.94	3.44	1.62	4.52	2.43

D	H	D	H	D	H	D	H
4.66	2.19	4.87	2.22	5.91	3.32	0.55	0.22
5.06	2.99	5.55	2.90	6.37	3.23		
5.22	2.78	5.38	3.10	5.97	3.26		

Cape Blanco 2005

Tidepool F: 26 April 2005

Pit Urchins

D	H	D	H	D	H	D	H
1.59	0.68	3.18	1.72 [b]	3.89	1.87	4.29	2.34
2.07	1.02	3.18	2.14	3.89	2.43	4.34	2.10
2.59	1.29	3.47	1.78	3.97	2.32 [b]	4.93	2.65
2.66	1.22	3.56	1.91	4.04	2.05	5.13	2.54
2.85	1.74 [b]	3.57	2.04 [b]	4.08	2.18		
2.96	1.51	3.64	1.62	4.16	1.96 [b]		
3.10	1.68	3.72	1.75	4.24	2.22		

Nonpit Urchins

D	H	D	H	D	H	D	H
1.39	0.57	4.60	2.37	5.10	2.67 [d]	5.33	2.39
2.25	0.95	4.68	2.04	5.19	2.36	5.44	2.55
2.50	1.07	4.81	2.60	5.21	2.58 [d]	5.63	2.77
4.24	2.11	5.01	3.09 [d]	5.31	2.30	5.63	2.63
4.48	2.12 [d]	5.06	2.49	5.32	2.41	5.84	2.96
5.87	2.77	5.94	2.69	6.17	2.89		
5.88	3.06	5.97	3.27	6.34	3.18		
5.92	3.04	6.10	3.07	6.58	3.06		

Tidepool G: 29 April 2005

Pit Urchins

D	H	D	H	D	H	D	H
2.37	1.15	2.69	[u]	3.07	1.62	3.72	[u]
3.26	1.74	2.98	[u]	3.68	2.11	3.54	1.97
3.20	1.64	2.58		3.04	1.65	4.03	2.20
3.03	1.65	3.09	1.71	2.25	1.20	3.71	1.72
3.68	[u]	3.36	1.71	4.79	[u]	4.23	2.42
3.75	[u]	2.92	[u]	3.46	[u]	4.77	[u]
4.79	[u]	2.22	[u]	3.51	1.89	3.47	[u]
2.89	1.55	3.79	[u]	2.72	[u]	4.42	[u]
3.48	[u]	3.72	[u]	4.54	[u]	4.59	2.61
2.54	1.20	2.71	1.60	3.84	[u]	5.35	2.78

D	H	D	H	D	H
3.92	2.17				

Nonpit Urchins

D	H		D	H		D	H		D	H	
4.73	2.54		4.12	2.16		4.31	1.89		6.99	3.19	
3.07	1.43		4.82	2.42		2.64	1.13		7.29	3.57	
3.26	1.59	d	4.47	2.04		6.14	3.03	d	2.41	1.11	
4.17	2.10		3.96	2.12		6.69	3.28		5.39	3.09	
4.45	2.20		4.00	1.71		5.17	3.16		3.70	1.74	
3.88	1.84		4.82	0.00	u	5.28	2.47		5.12	2.48	
1.98	0.91		4.99	2.56		5.70	2.77		4.75	2.21	
3.59	1.60		2.98	1.56		5.91	3.39		6.30	3.21	
5.37	3.16		4.45	2.39		6.24	2.89		4.48	2.02	
4.07	1.92	d	4.86	2.53		5.68	2.70		6.59	3.36	
4.45	2.23		4.76	2.21		5.48	2.65		5.49	2.59	
4.21	2.04	d	5.66	3.10		6.21	3.07		3.06	1.25	
2.76	1.22	d	4.16	2.18		4.60	2.25		4.12	2.22	d
4.88	0.00	d u	3.67	1.45	d	6.88	3.30				
3.74	1.83		7.58	3.41		5.32	2.59				
3.61	1.77	d	5.71	3.05		5.44	2.79				

Tidepool H: 26 April 2005

Pit Urchins

D	H	D	H	D	H	D	H
3.38	1.42	5.03	2.62	3.62	1.74	6.11	3.60
3.56	1.96[b]	5.05	3.07	3.34	1.68	5.75	3.20
3.65	2.30	5.12	2.63	4.70	2.65	4.74	2.64
3.80	2.00	5.14	2.71	4.86	2.56	2.99	1.49
3.84	1.93	5.54	2.84	3.85	2.19	4.01	2.35
4.03	2.37	5.85	3.51	4.68	2.62	3.99	1.90
4.03	1.88	5.93	3.18	5.01	2.86	3.97	1.97
4.10	1.83	4.35	2.20	3.74	1.71	3.49	1.72
4.14	2.27	5.19	2.64	4.09	2.16	4.31	2.12
4.39	1.75	5.44	3.12	3.08	1.68	4.44	2.47
4.53	2.15	4.98	2.42	5.25	3.00	5.33	3.13
4.59	2.50	2.96	1.48	4.79	2.56	5.35	3.12
4.59	2.39	2.95	1.25	6.62	3.62	4.36	2.26
4.84	2.37	4.36	2.03	5.62	3.24	4.85	2.48
4.87	2.84	4.52	2.20	6.52	3.51	4.77	2.59
4.99	2.86	4.56	2.32	6.70	3.46	5.49	2.97

Nonpit Urchins

D	H	D	H	D	H	D	H
2.16	1.88	5.57	3.32[d]	5.31	2.55		
3.18	1.33	4.62	2.58[d]	2.74	1.19		
3.24	1.42	2.57	2.32[d]	4.42	1.91		
3.45	1.46	5.12	2.70	4.27	2.09		
3.69	1.75	5.56	2.40	6.56	3.14		
3.82	1.79[d]	6.39	3.13[d]	5.75	3.05		
3.90	1.96[d]	5.16	2.68[d]	4.42	2.10		
4.08	1.94	6.21	3.09[d]	4.60	1.99		
4.14	2.01[d]	4.24	2.04	5.53	2.79		
4.74	2.17	4.51	2.10	4.39	2.30		
5.17	2.80	1.97	0.80	5.62	2.62		
5.29	2.87[d]	5.94	3.05	2.53	1.06		
5.31	2.57	6.58	3.58	2.40	1.02		
5.62	2.67	6.45	3.08	5.27	2.45[d]		
5.75	3.33[d]	6.49	3.56	4.95	2.23[d]		
6.66	3.33[d]	4.85	2.67	4.88	2.69[d]		
3.42	1.39[d]	5.64	2.93	2.90	1.57[d]		
3.66	1.66[d]	4.35	2.18[d]	3.78	1.81		
1.56	0.68[d]	6.85	3.56	5.33	3.22		
5.16	2.84	7.00	3.58	6.55	3.00		
5.56	2.52	5.62	3.16[d]	2.33	0.91		
5.61	2.71	3.35	1.27	4.72	2.33		

Middle Cove 2006

Tidepool A: 14 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
6.90	3.60	3.94	1.71	4.11	2.05	4.08	2.46
6.39		4.97	2.58	4.53	2.09	5.07	2.51
4.36	1.92	4.27	2.09	1.80	0.80	1.45	0.53
6.25	3.43	3.81	1.73	5.46	2.73	4.33	2.10
4.65		4.77	2.44	3.89	1.93	5.92	2.87
5.27	2.41	4.54	2.11	4.73	2.66	4.52	2.03
6.13	2.96	3.79	1.95	3.92	1.94	4.74	2.27
6.03	3.10	4.83	2.21	4.64	2.48	4.20	2.60
5.25	2.85	3.35	1.69	4.75	2.47	4.75	
5.71	3.14	3.73	1.63	2.78	1.23	2.60	1.10
4.88	2.32	4.46	1.87	3.08	1.40	6.64	3.73
3.67	1.72	3.96	1.62	3.44	1.74	6.75	3.21
4.04	2.20	3.98	1.69	4.46	2.35	6.42	2.68
3.33	1.70	5.44	3.35	3.02	1.37	3.97	1.86
5.38	2.68	4.28	2.10	2.84	1.31	4.57	2.63
4.26	2.13	4.67	2.06	3.87	1.71	2.80	1.30
2.61	1.24	5.86	2.81	3.77	1.98	3.61	1.55
4.13	2.23	3.94	2.13	3.39	1.51	3.95	1.91
4.69	2.30	6.27	3.44	2.86	1.38	3.39	1.59
5.75	2.75	3.70	1.76	4.80	2.10		
5.49	2.39	3.60	1.68	3.58	1.75		
4.05	1.75	4.16	2.08	4.81	2.40		

Nonpit Urchins

D	H	D	H	D	H	D	H
5.51	2.55	3.24	1.55	3.72	1.71	4.15	1.85
4.79	2.19	4.80	2.79	5.54	2.45	3.42	1.55
4.11	1.80	3.85	1.80	4.92	2.71	5.78	3.18
3.88	1.77	4.75	2.06	2.94	1.32	6.76	3.89
4.74	2.20	6.36	2.96	4.56	2.07	4.23	1.91
5.69	2.72	4.05	1.82	4.82	2.39	3.90	1.84
8.45	4.55	5.18	2.69	5.16	2.41	6.41	2.96
6.31	3.38	5.60		7.14	3.67	3.31	1.51
4.96	2.14	3.30	1.46	3.30	1.50	4.28	2.06
3.50	1.54	4.89	2.30	3.64	1.60	3.90	1.86
5.51	2.70	3.58	1.75	6.25	3.28	2.08	0.89

D	H	D	H	D	H	D	H
3.38	1.60	2.64	1.09	2.14	0.98	6.97	3.72
3.33	1.55	1.86	0.80	2.77	1.26	6.96	3.45
3.31	1.47	6.20		2.87	1.13	6.48	3.60
3.95	1.85	2.04	0.92	7.56	4.34		
4.48	2.05	3.99	1.66	7.49	3.67		
3.03	1.47	2.33	1.00	7.07	3.29		

Tidepool B: 14 & 17 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
5.44	2.80	4.40	2.14	5.49	2.70	4.13	1.97
5.58	3.43	2.86	1.35	7.91	4.17	4.96	2.90
5.65	2.91	2.80	1.45	6.80	3.03	7.10	
6.28	3.28	6.05	3.18	6.26	3.01	4.20	1.92
5.63	2.98	4.73	2.20	6.64	3.20	4.45	2.04
4.45	2.27	4.15	2.13	6.44	3.58	6.32	3.38
5.55	2.66	6.16	3.36	6.44	3.66	5.26	2.57
5.47	2.67	5.06	2.22	1.65	0.82	3.95	1.74
5.03	3.02	4.61	2.76	6.50	2.80	6.17	3.43
3.32		6.33	3.67	7.11	4.40	6.47	3.17
6.25	2.85	4.35	2.44	5.30		5.49	2.65
5.65	2.77	4.66	2.53	2.66	1.37	4.82	2.41
5.19	2.25	4.44	2.24	7.24		5.53	2.87
4.78	2.45	6.01	3.03	6.10	3.43	3.39	1.60
5.34	2.87	5.74	3.37	5.97	3.11	2.62	1.09
4.52	2.37	3.46	1.69	4.47	2.09	6.25	3.24
4.96	2.70	5.59	2.65	6.86	3.54	3.88	2.14
6.80	3.60	4.27	1.86	3.01	1.54	0.96	0.40
5.64	2.95	5.99	3.16	4.00	2.00	6.89	3.69
6.11	2.81	4.12	1.93	4.49	2.38	6.72	4.17
7.49	4.27	3.50	1.70	6.03	2.96	7.26	3.57
6.51	3.20	1.80	0.70	5.76	3.31	6.97	3.71
3.86	1.93	5.49	2.72	5.67	2.53	6.93	3.92
4.79	2.67	5.02	2.65	6.27	3.41	6.98	3.43
4.40		3.91	1.75	6.69	3.67	6.49	3.37

Nonpit Urchins

D	H	D	H	D	H	D	H
6.51	3.56	5.70	3.09	4.80	2.20	6.04	2.87
6.25	3.14	5.22	2.82	3.80	1.53	6.41	3.05

D	H	D	H	D	H	D	H
5.15	2.32	7.02	3.12	6.89	3.76	5.49	2.60
6.30	3.13	6.85	3.78	4.31	1.94	5.64	3.10
5.96	3.10	6.26	3.16	6.74	3.73	5.69	2.74
6.32	2.95	7.08	4.08	6.36	2.89	5.87	2.93
6.01	2.91	6.72	3.82	1.46	0.69	6.17	3.28
6.03	3.24	6.77	4.13	6.13	2.68	6.35	3.70
5.93	3.06	5.79	2.61	5.81	2.87	6.71	3.52
5.12	2.25	2.99	1.29	6.51	3.38	6.52	3.40
2.97	1.21	6.36	3.31	6.75	3.32	6.98	3.38
2.31	0.99	6.60	3.34	6.79	4.11	6.93	3.18
6.02	3.19	6.28	3.21	4.94	2.06	7.07	3.51
6.71	3.30	6.53	3.39	5.76	2.81	7.01	3.76
7.29	3.45	6.77	3.33	3.71	1.52	6.94	3.63
6.46	2.53	6.31	3.35	6.69	3.39	7.35	3.70
6.95	3.81	5.24	2.45	5.58	2.68	8.11	4.57
7.21	3.41	6.34	3.75	6.78	3.32	7.31	3.86
6.22	3.43	6.68	3.47	5.99	3.10	7.27	3.63
6.59	3.09	6.39	3.53	6.81	3.17	7.17	3.83
8.24	4.05	6.58	3.96	7.17	3.76	7.33	3.77
7.29	4.44	7.19	3.46	6.12	3.18	7.45	4.09
7.22	3.89	5.46	2.53	3.38	1.64	7.09	3.98
7.25	3.94	6.38	3.23	1.45	0.61		
7.13	3.52	7.12	3.12	0.52	0.18		

Tidepool C: 17 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
4.79	2.14	5.67	2.96	4.94	2.30	4.71	2.17
3.90	2.01	6.06	2.80	3.90		5.33	2.38
5.61	2.71	5.86	3.06	6.51	3.11	4.80	2.13
6.82	3.90	5.28	2.50	7.38	3.60	5.30	2.52
6.20	3.21	4.61	2.22	7.14	3.33	5.64	3.27
6.57	3.30	4.85	2.05	5.53	2.91	5.56	2.74
6.07	2.81	5.36	2.84	6.54	3.37	6.34	3.40
2.71	1.23	3.57	1.85	5.25	2.36	5.39	2.46
5.44	2.66	4.75	2.32	5.83	3.10	4.21	2.15
4.57	2.17	5.28	2.38	5.41	2.59	4.25	1.74
7.22	4.26	5.57	2.97	4.98	2.38	5.49	3.14
6.74	3.54	6.20	3.01	7.06	3.86	5.07	2.73

D	H	D	H	D	H	D	H
5.82	2.82	3.27	1.50	5.06	2.39	7.34	4.03
4.77	2.19	5.50	2.58	3.85	1.75	7.37	3.93
4.68	2.16	6.87	3.76	3.89	1.86	7.94	3.88
3.50	1.52	4.93	2.33	2.44	1.15	7.43	3.82
6.43	3.37	1.25	0.54	4.04	1.82	7.32	4.37
5.11	2.24	4.54	2.28	5.97	2.80	7.52	3.73
2.33	1.04	4.78	2.36	5.71	2.89	7.44	3.19
5.88	2.47	4.09	1.81	5.65	2.57	7.45	3.71
5.44	2.61	4.45	2.11	5.11	2.21	7.71	3.91
4.55	2.12	6.88	3.46	3.53	1.59	3.33	1.41
6.69	3.37	1.52	0.63	5.26	2.51	3.58	1.58
4.40	2.29	4.80	2.28	4.67	2.14	4.89	1.94
6.48	3.24	5.61	3.03	3.80	1.64		
5.67	2.73	4.63	2.07	6.66	3.43		

Nonpit Urchins

D	H	D	H	D	H	D	H
7.38	3.22	4.03	1.72	7.10	3.80	7.58	3.54
2.02	0.94	7.38	3.62	7.10	3.98	3.87	1.56
1.84	0.86	7.35	3.52	6.75	3.49	3.53	1.60
1.21	0.55	5.42	2.54	6.69	3.26	6.06	3.00
1.27	0.58	6.55	3.32	7.02	3.35	3.07	1.34
1.33	0.64	5.64	2.81	6.52	2.87	5.03	2.55
1.24	0.53	7.50	3.92	7.21	3.98	6.56	3.40
1.45	0.66	3.89	1.78	7.65	3.43	5.45	2.38
7.14	3.14	5.27	2.52	7.56	3.67	7.34	3.40
6.95	3.42	6.96	3.49	7.09	3.49	5.78	2.88
6.89	3.52	4.88	2.34	7.07	3.46	1.11	0.54
6.71	3.02	4.80	2.03	7.30	3.77	6.32	3.00
5.00	2.48	4.72	2.17	5.40	2.55	5.08	2.28
5.29	2.32	5.92	3.03	7.05	3.32	6.32	2.87
5.24	2.56	7.36	3.92	6.29	3.02	3.44	1.42
6.96	3.48	5.45	2.42	6.39	3.20	4.91	2.26
5.27	2.75	6.67	3.34	7.17	3.63	6.88	4.03
5.94	2.98	3.38	1.43	7.00	3.72	6.69	3.77
6.63	3.91	4.90	2.13	6.06	3.01	4.54	2.06
6.29	3.19	3.69	1.43	7.59	3.97	4.21	1.89
7.00	3.68	5.29	2.37	4.91	2.17	7.01	3.14
7.02	3.28	3.41	1.46	4.27	1.87	5.86	3.11
6.59	3.19	4.60	2.26	5.53	2.76	4.08	1.89
4.55	2.28	4.89	2.25	2.66	1.07	5.58	2.71

D	H	D	H	D	H	D	H
4.80	2.27	8.29	3.40	7.63	3.60	7.69	3.84
6.91	3.75	7.71	3.95	6.71	3.58	7.67	3.88
7.03	3.29	7.61	4.42	8.07	4.14	8.26	4.29
7.08	3.69	7.57	3.69	7.63	4.17	8.17	4.17
6.76	3.21	6.54	3.78	7.83	3.81	7.67	4.03
6.02	3.02	8.54	4.38	7.64	4.29	7.63	4.01
6.25	3.22	8.11	4.12	7.77	4.33	8.10	4.08
6.64	3.59	7.63	4.23	7.71	3.92	7.63	4.11
8.67	4.50	8.10	4.07	7.17	3.76	7.63	3.73
8.30	4.86	7.76	4.09	7.51	3.46	7.70	3.58

Middle Cove 2005

Tidepool D: 20 February 2005

Pit Urchins

D	H	D	H	D	H	D	H
6.51	3.43	7.68	3.92	1.30	b	6.67	3.62
5.83	3.31	6.25	2.98	5.85	3.25	6.77	3.19
4.65	2.39	7.17	3.85	2.67	1.29	5.56	2.62
3.52	1.95	3.29	1.63	3.33	1.56	6.52	3.22
5.62	3.28	5.95	3.34	5.55	2.79		

Nonpit Urchins

D	H	D	H	D	H	D	H
1.24	0.51	8.36	4.19	7.78	4.57	8.65	4.52
6.80	3.71	6.55	3.33	5.84	3.24	7.49	3.87
6.16	2.78	7.43	3.09	7.48	3.71	3.89	1.88
3.98	1.56	7.16	3.16	5.69	2.80	6.22	2.66
2.94	1.28	5.79	2.66	6.75	3.59	7.24	3.67
3.79	1.69	7.40	0.00	7.77	3.03		

Tidepool E: Unknown 2005

Pit Urchins

D	H	D	H	D	H	D	H
5.42	2.92	3.91	1.74	3.45	1.38	3.01	1.30
5.50	2.73	3.10	1.41	3.81	1.65	4.96	2.64
1.70	0.70	0.86	0.37	5.23	2.58	4.38	2.09
5.57	2.99	6.89	3.86	5.62	2.43	1.56	0.54
6.47	3.96	5.84	3.03	5.53	2.74	5.03	2.42
6.12	3.33	7.58	3.71	6.07	3.02	6.03	3.08

D	H	D	H	D	H	D	H
6.15	3.37	7.41	3.76	6.35	3.26	5.46	2.58
3.62	1.58	5.69	2.57	3.08	1.31	4.86	2.23
5.43	2.60	5.56	2.55	7.36	3.95	5.15	2.52
7.12	3.65	6.43	3.17	6.64			

Nonpit Urchins

D	H	D	H	D	H	D	H
3.26	1.23	7.87	3.66	6.93	3.26	6.90	3.56
6.91	3.21	7.72	3.87	4.38	1.93	6.24	2.82
3.24	1.36	6.52	2.95	7.05	3.31	6.83	3.54
3.42	1.41	4.64	2.09	6.25	3.44	4.12	1.85
6.63	3.47	6.63	3.32	6.90	3.28	7.48	3.73
7.51	3.95	7.64	3.83	6.13	3.29	7.49	3.73
7.09	3.91	6.58	3.28	8.36	4.41	5.95	2.89
8.09	3.87	7.81	3.90	6.34	3.01	3.58	1.51
7.41	4.07	5.07		6.49	2.73	7.12	3.45
2.02	1.03	7.87		8.80	4.15	6.03	2.63
6.85	3.49	7.59	3.53	8.68	3.88	6.16	3.14
7.63	3.42	7.50	3.80	7.63	3.13	6.13	2.79
1.74	0.80	1.57	0.65	3.98	1.68	4.35	1.66
3.85	1.55	6.58	3.19	6.32	2.78	5.35	2.01
7.61	3.68	7.82	3.15	5.04	1.97	3.79	1.82
8.27	4.53	7.31	3.72	3.29	1.11	1.23	0.48
4.43	2.03	8.79	3.99	3.22	1.19	5.45	2.32
3.96	1.72	7.48	3.82	6.60	2.79	7.84	4.43
3.50	1.26	8.24	3.85	7.35	3.64	4.23	1.68
8.68	4.38	7.63	3.94	7.26	3.44	7.67	3.88
4.59	1.91	6.63	3.17	1.78	0.62	1.81	0.59
4.12	2.04	5.66	2.58	3.25	1.25		
7.71	3.58	7.90	4.21	6.79	3.03		

Tidepool F: 10 May 2005

Pit **Urchins**

D	H	D	H	D	H	D	H
6.32	3.37	4.26	1.96	5.85	2.84	4.36	1.94
6.34	3.19	6.82	3.66	6.54	3.23	4.34	2.09
6.05	3.30	5.21	2.40	3.79	1.83	3.68	1.66
6.02	3.20	5.57	2.78	1.54	0.59	3.21	1.23
7.15	3.86	5.31	2.92	5.89	2.89	5.01	2.71
5.41	2.96	7.09	3.46	5.11	2.58	4.37	1.98
5.52	2.71	5.73	2.83	3.50	2.14	4.59	2.06
5.46	2.47	6.42	3.19	5.22	2.46	4.16	2.09
6.85	3.57	5.29	2.78	5.20	2.58	3.72	1.56
5.83	2.76	5.79	2.63	4.53	2.21	4.96	2.26
2.92	u	6.11	3.04	5.05	2.57	4.75	2.31

D	H	D	H	D	H	D	H
4.42	2.04	4.60	2.33	5.29	2.64	4.64	2.09
4.41	2.05	4.50	2.57	4.73	2.11	4.63	2.26
3.35	1.58	1.80	0.74	2.99	1.26	4.85	2.18
4.81	2.37	5.38	2.95	6.04	2.74	2.78	1.33
3.78	1.86	3.93	1.68	1.88	0.79	4.85	2.34
4.05	1.94	5.15	2.40	4.52	2.29	0.67	0.29
2.90	1.20	5.23	2.72	4.20	1.88	4.88	2.43
4.35	1.95	2.87	1.10	5.62	2.97	4.02	2.05
4.30	2.01	4.53	2.25	5.32	2.55	4.70	2.41
3.98	1.69	5.50	3.01	4.96	2.78	1.45	0.57
4.07	1.59	4.58	2.00	4.78	2.52	4.60	2.44
4.87	2.56	5.22	2.51	4.62	2.21	3.49	1.77
4.92	2.30	4.98	2.01	5.55	2.78	1.45	0.59
4.48	2.10	2.77	1.11	4.20	1.85	4.46	2.03
3.27	2.18	5.27	2.62	4.64	1.85		

Nonpit Urchins

D	H		D	H		D	H	D	H
2.89	1.32		1.25	0.49		5.32	2.51	5.76	2.90
7.60	3.83	d	7.18	4.20		6.52	3.40	4.63	2.32
6.99	3.45	d	5.68	2.73		6.82	3.21	5.63	2.54
6.21	3.11	d	6.99	3.51		5.96	2.79	0.88	0.36
6.54	3.18	d	6.26	2.88		5.28	2.84	1.02	0.44
6.31	3.14		4.32	1.66		3.19	1.80	2.88	1.22
6.58	3.59		6.03	2.74		8.04	4.24	1.93	0.71
7.26	3.78		7.66	3.98		6.97	3.28	3.57	1.44
5.95	2.90		7.75	4.58		6.26	3.22	3.26	1.48
6.52	3.70	d	5.51	2.86		6.46	3.14	6.37	2.96
3.48	1.50	d	6.97	3.55		6.96	2.81	5.63	2.72
7.08	3.38	d	5.37	2.46		2.88	1.15	6.68	3.28
6.01	3.26		6.54	3.25		2.65	1.11	5.18	2.73
5.88	3.01	d	6.68	3.69		4.72	2.33	5.55	2.44
6.09	2.87	d	6.01	2.88		4.85	2.05	5.90	2.86
4.96	2.71		4.92	2.08		2.98	1.18	6.59	2.98
5.70	2.78		5.50	2.47		2.48	1.01	6.59	2.97
5.55	2.79	d	6.78	3.54		5.28	2.44	5.16	2.67
6.06	3.32		6.80	3.44		3.60	1.52	5.71	2.70
7.58	3.81		5.36	2.61		2.48	1.03	5.62	2.63
6.23	2.96		5.46	2.45		6.79	3.02	5.26	2.44
6.40	3.28		3.92	1.78		2.56	1.00	2.87	1.33
6.40	2.61	d	5.56	2.52		5.65	2.86	1.47	0.55
2.87	1.08		6.48	3.11	d	3.56	1.64	1.12	0.43
4.50	1.74		6.26	3.00		6.55	3.31	4.81	2.26
3.86	1.62		7.40	3.46		6.74	3.59	2.99	1.16
6.71	3.24		6.90	3.15		5.10	2.48	5.94	2.97
5.76	2.86		5.81	3.01		6.35	3.10	3.63	1.50
6.47	3.49		6.87	3.20		6.45	3.17	5.10	2.28
6.60	3.41		7.50	3.44		5.60	2.85	5.12	2.46

D	H	D	H	D	H	D	H
5.17	2.53	2.57	1.05	2.96	1.12	5.75	2.99
6.09	2.96	3.87	1.73	2.90	1.12	5.27	2.34
6.32	3.23	3.17	1.38	2.39	0.99	2.94	1.55
5.92	3.24	2.99	1.26	5.98	3.10		

Tidepool G: 20 February 2006

Pit Urchins

D	H	D	H	D	H	D	H
5.42	2.69	3.46	1.58	4.65	2.33	7.84	4.36
6.15	3.64	7.11	3.61	7.15	3.68	3.65	1.72
4.54	2.18	6.57	3.41	4.58	2.44	8.17	4.17
6.23	3.45	3.34	1.70	3.79	1.92	5.12	2.81
6.54	3.65	4.04	1.62	0.94	0.41		
6.62	3.27	5.97	3.03	5.22	2.98		
3.84	2.09	4.42	2.24	5.08	2.34		

Nonpit Urchins

D	H	D	H	D	H	D	H
4.83	2.25	1.65	0.66	7.45	4.36		
1.37	0.58	6.97	3.83	2.58	1.04		
3.44	1.61	6.62	3.53	0.94	0.41		

Tidepool H: 9 May 2005

Pit Urchins

D	H	D	H	D	H	D	H
2.47	1.19	4.66	2.48	5.39	2.78	6.10	3.24
2.48	1.08	4.69	2.39	5.49	3.17 u	6.14	3.75
3.07	1.60	4.77	2.53	5.53	2.64	6.17	2.82
3.36	1.46	4.77	2.51	5.54	2.90	6.17	3.14
3.42	1.46	4.82	2.47	5.57	2.79	6.22	2.96
3.77	1.57	4.82	2.46	5.64	3.30	6.25	3.18
3.81	1.86	4.98	2.83	5.65	2.66	6.26	3.51
3.95	1.95	4.99	2.36	5.65	2.94	6.34	3.64
3.96	1.98	5.18	2.61	5.69	3.63	6.36	3.52
3.99	1.99	5.19	2.59	5.69	u	6.53	3.00
4.03	1.91	5.25	2.48	5.70	3.11	6.56	2.94
4.20	1.83	5.29	2.98	5.81	2.78	6.57	3.14
4.28	2.30	5.31	2.63	5.83	3.11	6.60	3.10
4.33	2.10	5.31	2.45	5.83	3.21	6.62	3.42
4.37	1.83	5.32	2.73	5.96	2.90	6.72	3.31
4.41	2.20	5.36	2.56	6.01	2.89	6.73	2.97
4.57	2.20	5.38	2.72	6.06	3.15	6.74	3.11

D	H	D	H	D	H
6.74	3.59	6.88	3.65	7.35	4.08
6.81	3.37	6.96	3.29		

Nonpit Urchins

D	H	D	H	D	H	D	H
0.69	0.25	5.58	2.77[d]	6.26	3.37	6.76	3.35
1.04	0.39	5.64	2.91[d]	6.34	3.04	6.76	3.84
2.79	1.21	5.67	2.73	6.50	3.13	6.77	3.36
2.86	1.22[d]	5.69	2.90	6.54	3.28	6.82	3.70
3.32	1.41[d]	5.90	2.90	6.58	3.38	6.91	3.32[d]
3.65	1.53	5.98	3.03	6.59	3.29	7.02	3.47
3.86	1.70	6.01	3.32	6.64	2.98	7.38	3.47
4.30	2.37[d]	6.04	2.98	6.70	3.35		
4.78	2.41	6.06	3.20	6.72	3.60		
5.53	3.10	6.23	3.42	6.74	3.39		

South Cove 2006

Tidepool A: 1 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
6.25	3.32	5.75	2.95	5.87	2.96	6.35	3.35
5.84	3.17	2.92	1.31	5.91	3.11	6.07	3.17
5.02	2.59	1.82	0.76	5.49	3.18	4.93	2.62
4.26	2.07	4.21	1.86	4.69	2.22	3.54	1.68
5.43	2.98	6.05	3.10	5.56	2.95	5.45	3.09
4.91	2.69	6.21	3.50	4.95	2.57	1.83	0.82
6.10	3.53	4.97	2.71	5.07	2.57	5.06	2.80
5.91	3.22	5.60	2.97	5.10	2.46	3.50	1.59
4.30	2.02	6.14	3.15	4.89	2.60	4.82	2.51
5.30	3.22	4.90	2.41	4.61	2.21	5.92	2.90
6.32	3.59	4.79	2.77	5.47	3.28	3.70	1.80
4.67	2.15	5.82	3.08	5.71	3.33	5.46	3.33
4.71	2.88	5.82	3.26	3.30	1.70	5.89	3.05
6.00	3.40	5.64	2.97	5.86	3.43	5.25	2.65
4.35	2.11	5.52	3.14	4.53	2.39	3.13	1.64

Nonpit Urchins

D	H	D	H	D	H	D	H
6.49	3.33	5.96	3.19	1.12	0.59	6.56	3.58
6.31	3.17	5.86	3.17	5.53	2.92	5.94	2.85
5.64	2.64	5.56	2.91	6.52	3.20	6.17	3.54
6.10	3.31	5.57	3.17	5.85	3.02	6.34	2.80
6.76	3.52	7.08	3.99	4.27	1.94	5.65	3.03
5.63	3.07	6.49	3.40	6.97	3.29	5.60	2.70
3.77	1.82	6.91	3.35	6.90	3.29	5.05	2.94
5.79	2.94	5.71	3.23	5.71	3.35	6.20	3.59
6.42	3.61	4.76	2.57	5.12	2.48	2.31	1.00
7.23	3.81	5.68	2.73	5.37	2.68	0.93	0.43
5.98	3.69	6.42	3.26	7.38	3.93	6.02	3.01
5.21	2.59	5.71	3.09	6.11	2.93	6.25	3.26

Tidepool B: 1 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
6.30	3.33	5.79	3.03	5.08	2.68	5.26	2.88
6.85	3.67	5.40	2.37	5.61	3.35	3.89	1.87
5.42	2.96	6.71	3.51	4.85	2.78	5.71	2.66
6.58	3.82	5.87	3.41	4.63	2.57	6.46	3.48
4.83	2.55	4.90	2.46	6.10	3.24	6.48	3.05
5.40		5.88	3.24	3.40	1.60	4.26	2.17
5.60	2.84	5.95	3.08	4.66	2.77	5.04	2.75
6.11	3.00	5.02	2.43	4.62	2.37	5.38	2.76
4.70	2.42	5.71	3.46	3.58	1.69	2.97	1.15
4.65	2.20	6.27	3.00	6.81	3.60	3.84	
5.85	2.74	3.11	1.38	6.29	3.33	4.17	2.10
5.38	2.90	3.61	2.38	5.00	2.39	5.78	3.28
5.45	2.81	5.80		6.16	3.44		
6.13	3.48	4.37	2.30	5.89	3.29		

Nonpit Urchins

D	H	D	H	D	H	D	H
6.63	3.76	4.99	2.26	4.66	2.20	4.50	2.30
6.28	3.84	3.60	1.90	3.82	2.08	6.83	3.17
4.85	2.40	6.27	3.28	7.22	4.18	3.68	1.61
7.81	3.95	6.05	3.20	7.72	3.82	5.66	3.52
6.45	3.43	5.99	3.31	0.82	0.33	2.88	1.51
6.77	3.63	3.63	1.51	6.33	2.99	7.13	3.52

D	H	D	H	D	H	D	H
6.13	3.20	6.03	3.13	2.71	1.20		
6.51	3.51	6.29	3.26	1.69	0.70		
4.17		6.79	3.73	1.45	0.66		

Tidepool C: 1 April 2006

Pit Urchins

D	H	D	H	D	H	D	H
6.12	3.45	5.08	3.00	6.28	3.39	4.28	1.85
5.79	2.93	6.89	3.20	5.01	2.53	4.30	2.04
6.15	3.23	5.03	2.70	4.26	2.38	5.35	3.05
4.96	2.62	5.86	3.32	5.31	2.59	4.30	2.02
4.81		5.34	3.08	5.64	3.31	2.85	1.31
5.05	2.85	5.94	3.43	4.56	2.18	4.42	2.30
3.90	2.33	6.60	3.90	3.52	1.90	4.29	2.09
0.54	0.24	4.59	2.52	4.14	1.97	3.75	2.21
1.15	0.49	6.17	3.68	5.03	2.90	3.94	1.88
0.94	0.43	4.60	2.93	5.93	3.17	3.93	1.96
2.95	1.48	5.31	2.77	5.98	3.35	5.66	2.95
3.33	1.54	6.97	4.25	4.74	2.20	4.59	2.28
4.42		6.11	3.24	5.30	3.12	4.07	1.94
4.42		5.51	2.80	3.93	2.05	4.01	1.93
4.82	2.42	6.03	3.38	6.13	3.37	4.22	2.09
5.28	2.99	6.41	3.62	4.94	2.78	5.18	2.88
6.54	4.29	5.98	3.38	3.89	2.08	5.44	2.93
5.33	2.81	5.89	2.99	6.17	3.47	4.32	2.26
5.79	3.61	4.56	2.16	5.05	2.84	5.68	3.63
6.07	3.78	5.91	3.41	5.67	3.16	3.27	1.46
5.96	3.12	5.87	3.36	4.72	2.63		
4.30	1.92	3.90	2.05	3.84	2.21		
4.72	2.58	5.59	3.59	4.61	2.44		

Nonpit Urchins

D	H	D	H	D	H	D	H
5.26	2.77	1.06	0.51	4.71	2.73	5.64	2.74
4.81	2.30	0.89	0.41	5.78	2.96	6.29	3.73
5.76	3.41	0.76	0.35	6.18	3.26	6.45	3.18
4.32	2.06	1.19	0.47	3.47	1.46	5.07	2.75
6.04	3.49	4.88	2.94	4.81	2.46	6.42	3.53
1.59	0.73	6.07	3.21	5.89	3.17	4.38	2.14
0.90	0.39	6.11	3.20	5.73	3.49	4.33	2.00

D	H	D	H	D	H	D	H
6.66	3.57	4.86	2.45	5.89	2.92	2.10	0.87
6.40	2.96	6.04	3.38	6.17	3.55	7.57	4.13
6.02	3.26	5.96	3.89	7.06	3.81	6.24	3.16
5.70	2.67	6.18	3.37	5.74	3.03	4.15	2.05
5.62	3.08	6.15	2.97	6.77	3.23		

South Cove 2005

Tidepool D: 24 – 25 April 2005

Pit Urchins

D	H	D	H	D	H	D	H
2.45	1.22	5.62	3.35	6.95	4.10	4.64	2.32
3.89	2.29	5.64	3.20	5.94	2.86	5.58	2.97
4.01	2.09	5.66	2.93	5.99	3.58	5.41	2.79
4.07	2.47	5.77	2.90	5.59	2.94	5.20	2.31
4.11	2.40	5.78	3.09	5.54	2.98	4.24	2.33
4.12	2.09	5.88	3.06	6.81	3.65	4.58	2.36
4.26	2.22	5.91	3.16	5.58	2.86	5.08	2.82
4.30	2.01	6.01	2.99	6.36	2.98	5.28	2.73
4.32	2.24	6.04	3.18	6.16	3.07	5.67	3.53
4.52	2.64	6.04	2.77	1.84	0.72	3.79	1.86
4.60	2.34	6.15	3.21	5.49	3.32	6.56	3.50
4.77	2.79	6.17	3.21	3.09	1.36	3.80	2.59
4.86	2.80	6.17	3.46	5.04	2.50	4.90	2.83
4.88	2.83	6.18	3.45	5.45	3.06	5.74	2.83
4.89	2.96	6.19	3.56	5.13	2.82	4.60	2.55
4.95	2.70	6.21	3.39	3.76	2.01	6.02	3.39
5.06	2.78	6.23	3.75	5.88	3.27	5.15	3.27
5.26	3.37	6.26	3.50	4.39	2.56	4.56	2.39
5.26	3.32	6.32	4.18	5.76	3.20	6.15	3.35
5.27	3.25	6.42	3.48	7.17	3.41	5.89	3.52
5.30	3.26	6.48	3.56	6.07	3.13	5.62	3.32
5.33	2.76	6.64	3.53	5.62	3.09	5.62	3.09
5.35	2.64	6.69	3.71	5.18	2.78	6.22	3.44
5.41	3.55	6.75	4.07	3.75	1.59	4.20	2.58
5.43	3.56	6.80	3.65	6.78	3.48	6.60	3.43
5.48	3.04	6.91	3.68	7.07	3.87	5.47	3.14
5.49	3.10	6.93	3.89	2.10	0.99	5.12	3.11
5.52	3.31	7.02	3.46	5.22		3.90	2.43
5.52	3.20	7.07	3.69	5.52	3.04	5.24	2.71
5.55	2.97	7.12	3.34	5.00	u		
5.55	2.73	7.37	3.74	6.42	2.97		
5.56	3.19	7.58	3.72	6.31	3.52		
5.61	3.00	5.66	3.06	4.88	2.70		

Nonpit Urchins

D	H		D	H		D	H		D	H	
3.48	1.78	d	7.46	3.45		6.59	3.79	d	5.84	3.06	d
3.51	1.98	d	7.65	3.45	d	6.62	3.33	d	5.84	3.42	d
3.77	1.74		7.82	4.08		6.51	3.33		4.46	2.60	d
4.05	1.79		7.37	3.66		4.43	1.80	d	5.39	3.08	d
4.65	2.38		1.84	0.78		6.32	3.33	d	3.78	2.18	d
4.71	2.46		6.98	3.36		5.57	2.85	d	5.90	2.91	d
4.77	2.52	d	7.17	3.51		5.28	2.68		6.95	3.63	d
4.84	2.54	d	4.23	1.71		5.73	2.79	d	7.67	3.85	d
4.86	2.73		5.94	3.06		5.52	2.96	d	5.20	2.87	
5.45	3.47		6.39	3.34		3.98	1.79	d			
5.49	2.92		5.57	2.98		2.40	0.94				
5.74	2.78		4.41	2.06	d	5.38	2.65	d			
5.79	3.01		5.61	2.88	d	5.65	2.95	d			
5.88	3.22		5.33	3.32	d	6.00	3.04	d			
5.93	2.98		5.57	2.99	d	4.42	1.90	d			
5.94	3.29		7.98	3.99	d	5.55	2.87	d			
5.94	3.15		6.16	3.44	d	5.74	2.97	d			
5.96	3.22		3.87	1.93	d	7.00	3.61				
5.98	3.45		4.13	2.06	d	5.58	3.09	d			
5.99	2.81		4.04	1.96	d	5.62	3.03	d			
6.02	3.62		5.25	2.44	d	4.17	2.01				
6.10	3.18	d	7.47	4.08	d	6.41	3.42	d			
6.19	3.21		6.23	3.48	d	4.30	1.82				
6.23	3.27		7.09	3.58	d	5.26	2.85	d			
6.25	3.31		5.83	2.75	d	5.20	2.66				
6.27	3.46		5.84	3.13	d	4.96	2.70	d			
6.28	3.15		4.34	2.10	d	6.49	3.50	d			
6.40	3.38		6.51	3.51	d	3.93	1.97	d			
6.40	4.00		6.37	3.59	d	5.20	2.31	d			
6.40	2.54		6.80	3.71	d	5.88	3.17	d			
6.41	3.52		6.41	3.40	d	6.30	3.04	d			
6.41	4.21		8.64	4.67	d	3.53	1.70	d			
6.43	3.37		6.31	3.23		2.94	1.43	d			
6.46	3.24		6.62	3.47		5.62	3.17	d			
6.46	3.47		5.44	3.30		7.17	3.56	d			
6.49	2.97		6.47	3.88		6.55	3.84	d			
6.53	3.59		6.68	3.59		6.21	3.15	d			
6.54	3.58		5.34			3.39	1.35	d			
6.55	3.77		4.24	1.90		4.43	2.58	d			
6.59	4.05		6.11	3.03		5.40	2.66	d			
6.69	3.99	d	5.38	3.05		2.90	1.34	d			
6.70	3.49		5.68	2.94	d	5.73	3.07	d			
6.91	3.89		6.19	3.35		6.95	3.55	d			
7.12	3.70	d	5.82	3.37	d	4.95	3.31	d			
7.34	3.88		4.76	2.71		6.20	3.21	d			
7.36	4.22		5.33	2.79		3.69	1.95				
7.36	4.02		1.63	0.68		5.71	3.23	d			
7.41	4.39		6.09	3.20	d						

Tidepools E1 and E2 are actually the same pool and are combined in the analysis for Chapter II. However, when I collected the data, I made a distinction between two portions of the pool, one on the seaward (E1) and one on the landward (E2) side of a large rock.

Tidepool E1: 13 May 2005

Pit Urchins

D	H		D	H		D	H		D	H	
2.73	1.32		4.40	2.21		5.30	2.91		5.81		u
2.97	1.36		4.50	2.32		5.32		u	5.84	2.85	
3.51	2.09		4.52	2.46		5.38	2.68		5.91		u
3.61	2.17		4.56	2.24		5.40	2.69		5.94	2.57	
3.70	1.79		4.68	2.18		5.43	2.91		5.98	2.69	
3.70	1.87		4.69	2.04		5.47	3.14		6.12	3.42	
3.72	1.95		4.78	2.31		5.57	2.67		6.21	3.11	
3.83	2.58		4.96	2.77		5.59	3.25	u	6.25		u
3.86	2.18		4.97	2.60		5.62	3.06		6.47		u
3.87	1.99	u	5.01	2.49		5.66	3.10		6.92		u
4.32	2.42		5.11	2.43		5.66	2.88				
4.37	2.25		5.22		u	5.70		u			

Nonpit Urchins

D	H		D	H
			5.48	3.12
3.15	1.35	d	5.48	2.61
5.01	2.51	d	5.66	2.81
6.23	3.76		5.80	3.30
2.60	1.21	u	5.87	3.48
3.58	1.39		5.89	3.57
3.59	1.60		5.97	2.92
3.79	1.96		6.00	3.51
3.94	2.27		6.17	3.29
4.12	2.35		6.25	3.25
4.32	2.48		6.25	2.98
4.57	2.23		6.28	2.72
4.60	1.76		6.28	3.50
4.60	2.15		6.34	3.40
4.62	2.29		6.35	3.09
4.65	2.46		6.46	3.56
4.95	2.74		6.53	3.12
4.96	2.17		6.60	3.55
4.96	2.51		6.71	3.24
5.01	2.40		6.78	3.49
5.05	2.42		6.85	3.37
5.26	2.47		7.54	4.25
5.43	2.82			

Tidepool E2: 13 May 2005

Pit Urchins

D	H		D	H		D	H		D	H	
3.01	1.18		3.78	1.46		5.43	2.92		4.64	2.65	
5.27	2.68		6.36	3.20		4.02	2.08		6.01	3.17	
3.30	1.68		2.35	0.98		4.91	2.45		6.03	3.46	
5.79	3.16		6.68	3.19		5.02		u	5.36	2.55	
5.28	3.39		4.77	2.43		4.45	2.20		4.80	2.64	
2.62	1.12		5.58		u	3.02	1.17		5.24	2.58	
5.89		u	5.10	2.52		3.69	1.51		2.65	0.97	
4.83	2.42		5.10	2.52		4.60	2.11		3.75	1.84	
5.41	2.72		4.10	1.74		3.73	1.89		3.55	1.76	
6.40	3.05		2.59	1.16		5.20	2.85		5.54	2.73	
5.48	2.51		4.88		u	4.85	2.35		5.47	2.82	
5.66	3.12		5.31	2.65		5.38	3.18		6.51	3.23	
5.66	3.28		5.92	3.15		6.54	2.94		4.93	2.47	
5.74	3.31		5.50	2.77		5.59	3.09		4.33	2.31	
5.03	3.26		4.70	2.39		5.03	2.33		4.82	2.24	
5.92	2.80		4.04	1.94		5.17	2.87		6.63	3.59	
4.94	2.79	b	5.26	2.75		4.21	2.13		5.90	2.86	
4.08	1.90		4.58	2.46		5.65	3.02		3.50	1.39	
5.00	2.59		3.78	1.90		5.49	2.46		4.42	2.39	
4.21	1.88		4.65	2.38		5.95	2.71		5.65	2.95	
3.80	1.65		3.82	1.74		4.63	2.48		5.78	2.83	
5.82	2.75		5.29	3.72		3.62	1.85				

Nonpit Urchins

D	H		D	H		D	H		D	H	
5.68	3.01		4.71	2.22		5.49	2.41		5.15	2.99	
6.02	3.10		6.28	3.11		6.29	3.29		5.98	2.77	d
6.64	3.26		7.41	3.49		7.00	4.66		5.14	2.64	d
5.67	2.79		5.92	3.32		6.21	3.81		4.83	2.30	d
5.00	2.71		6.92	3.71		6.62	3.51		7.02	3.82	
6.77	3.98		6.14	3.19		7.36	4.55		6.31	3.26	
7.10	3.50		7.46	3.60		6.28	3.04		5.53	2.67	
5.53			7.84	4.08		6.41	3.10		7.03	3.53	
7.89	4.07		6.19	3.07		6.50	3.08		6.66	3.14	
4.87	2.31	d	6.56	3.26		5.28	3.42		7.34	3.86	
5.01	2.48	d	5.90	3.14		5.39	2.40	d	6.06	3.15	
7.46	3.49		5.14	2.82	d	3.09	1.21		5.81	2.60	
5.96	3.28		6.86	3.50		5.71	2.93		5.83	3.22	
7.68	3.96		5.70	3.15		5.51	2.78	d	5.28	2.88	
5.26	2.24	d	7.02	3.84		6.58	3.71		5.25	2.52	
1.73	0.56		3.22	1.30		7.60	4.19				
5.83	3.18		7.12	3.52		6.03	2.91				
6.04	3.11	d	6.68	3.01		6.92	3.67				
6.52	3.42	d	6.72	3.53		6.53	3.34				
5.09	2.95	d	6.22	2.98		3.36	1.23	d			

Tidepool F: 2 May 2005

Pit Urchins

D	H	D	H	D	H	D	H
2.52	0.94	4.07	1.82	4.63	2.15	5.51	2.60
3.24	1.55	4.13	1.93	4.66	2.24	5.56	2.66
3.30	1.40	4.21	1.84	4.82	2.03	5.62	2.90
3.48	1.40	4.25	2.11	5.00	2.54	5.70	3.07
3.49	1.27	4.34	2.63	5.03	2.10	5.72	3.27
3.52	1.33	4.45	2.25	5.08	2.55	5.86	2.91
3.87	1.76	4.47	1.97	5.11	2.37	5.90	2.76
3.87	1.81	4.52	1.80	5.17	2.61	6.00	3.76
3.89	1.91	4.56	1.94	5.26	2.65	6.07	2.65
3.95	1.87	4.57	2.64	5.35	2.68	6.08	3.21
3.95	1.73	4.60	2.19	5.39	2.60	6.19	3.26
3.98	1.88	4.60	2.40	5.51	2.49		

Nonpit Urchins

D	H		D	H		D	H		D	H	
1.36	0.47		4.75	2.22	d	5.78	2.77	d	6.70	3.44	d
1.36	0.50		4.75	2.30		5.81	2.76		6.75	3.67	
2.54	0.96		4.76	2.19	d	5.85	3.13	d	6.78	3.55	d
3.03	1.55		4.82	2.76		5.88	2.75		6.84	3.23	
3.28	1.46		4.95	2.32		5.90	3.18		6.94	3.70	
3.30	1.49		4.97	2.46		5.91	3.08	d	6.95	3.56	
3.31	1.48		5.09	2.11		5.95	2.79	d	6.97	3.68	
3.59	1.77		5.09	2.38		5.95	2.57		6.98	3.45	d
3.60	1.67	d	5.10	2.28	d	5.97	2.98		6.98	3.28	
3.62	2.40	d	5.16	2.25	d	5.99	2.88		7.02	3.72	
3.66	1.48	d	5.16	2.08	d	6.03	3.2	d	7.19	3.36	
3.67	1.77	d	5.22	2.41		6.07	3.19		7.22	3.74	
3.68	1.88	d	5.23	2.40	d	6.08	3.09		7.23	3.85	
3.74	1.65	d	5.26	2.60	d	6.09	3.07		7.24	3.95	d
3.82	2.15	d	5.28	2.68	d	6.09	3.03		7.24	3.94	d
3.95	2.25	d	5.28	2.45		6.11	2.8		7.25	3.51	
3.95	1.80		5.35	2.85		6.18	3.01		7.32	3.5	
3.98	1.64		5.36	2.39	d	6.22	2.68	d	7.37	3.58	
4.13	2.11	d	5.37	2.64	d	6.22	3.07	d	7.38	3.97	
4.16	1.77		5.45	2.70	d	6.30	3.29		7.39	3.52	
4.17	1.89	d	5.45	2.95		6.31	3.12	d	7.44	4.08	
4.31	1.83	d	5.52	2.86		6.36	3.19	d	7.47	3.77	
4.32	2.02		5.53	2.75		6.39	3.61		7.47	3.62	
4.40	1.87	d	5.54	2.75	d	6.43	3.25	d	7.52	4.13	
4.41	2.10		5.55	2.59	d	6.43	3.57		7.52	4.3	
4.45	1.97		5.55	2.97		6.5	3.18		7.68	3.75	
4.50	2.04	d	5.55	3.05		6.53	3.38	d	7.71	3.83	
4.53	2.22	d	5.64	2.74	d	6.62	3.08		7.78	3.94	
4.53	2.26	d	5.68	2.97		6.63	3.1		7.84	3.88	
4.56	2.08		5.70	2.84		6.64	3.28		8.13	4.23	
4.61	1.80	d	5.70	2.70		6.67	3.12	d	8.87	3.79	
4.69	2.30	d	5.76	2.70		6.68	3.41				

APPENDIX B

MORPHOLOGY DATA

These are the raw data from 180 *Strongylocentrotus purpuratus* collected haphazardly in August 2005 from the three research sites. Chapter II describes data collection in detail. Spine length was the average of three primary spines removed from the ambitus, so the lengths of all three spines are given in this appendix.

Column Codes: Si – Site Ti – Tidepool Mi - Microhabitat
Di – Test diameter He – Test height Pd – Peristomial diameter
S1 – 1st Spine S2 – 2nd Spine S3 – 3rd Spine
Sp – Average spine length Ma – Mass Cs – Compression strength
Go – Gonad mass Gu – Gut mass La – Lantern mass
Ja – Jaw Length Sk – Skeletal mass Te – Test thickness

Site Codes: CB – Cape Blanco (collected 20 August 2005)
MC – Middle Cove (collected 6 August 2005)
SC – South Cove (collected 4 August 2005)

Tidepools were numbered 1 – 5 at each site and were selected haphazardly.

Microhabitat Codes: P – Pit
NP - Nonpit

Mass is total wet mass prior to dissection. Gut mass includes gut contents that were not spilled. Skeletal mass is the entire test and all spines.

Units:

All lengths are reported in cm, except test thickness, which is reported in mm. All masses are reported in g, except compression strength, which is reported in lbs (converted to kg in Chapter II Table 2).

Values in **bold** are questionable.

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
CB	1	P	5.690	2.952	1.936	0.752	0.824	0.826	0.801	84.25	140	4.76	8.23	2.36	1.382	43.52	1.06
CB	1	P	5.502	2.922	1.884	0.788	0.868	0.834	0.830	83.17	145	5.15	8.20	2.39	1.298	39.09	1.12
CB	1	P	5.224	2.848	1.700	0.686	0.726	0.712	0.708	71.46	90	7.94	8.14	1.81	1.236	38.92	1.00
CB	1	P	4.678	2.392	1.630	0.796	0.642	0.818	0.752	51.51	60	6.42	3.06	1.5	1.134	30.68	0.88
CB	1	P	4.580	2.354	1.614	0.792	0.800	0.886	0.826	46.19	65	2.84	6.62	1.22	1.092	23.84	0.86
CB	1	P	4.446	1.974	1.536	0.982	1.006	0.822	0.937	38.45	42.5	1.04	5.19	1.08	0.898	20.04	0.80
CB	1	NP	6.584	3.944	2.068	1.076	1.032	0.950	1.019	141.08	151.8	18.07	9.74	2.72	1.528	67.83	1.28
CB	1	NP	5.314	3.162	1.822	0.736	0.804	0.844	0.795	80.42	80	5.06	9.13	2.14	1.468	42.66	1.08
CB	1	NP	5.660	2.744	1.784	0.884	0.732	0.848	0.821	78.42	110	8.39	7.92	2.17	1.346	42.40	1.26
CB	1	NP	5.700	2.632	1.778	1.086	0.922	0.900	0.969	79.09	70	11.58	10.91	1.77	1.200	42.39	1.06
CB	1	NP	5.506	2.448	1.758	0.758	0.732	0.654	0.715	65.09	92.5	3.30	8.01	1.9	1.216	33.37	1.00
CB	1	NP	4.412	2.142	1.594	0.884	0.922	0.912	0.906	42.04	**50**	2.77	4.88	1.44	1.152	23.57	0.94
CB	2	P	5.660	3.202	1.826	0.934	0.658	0.794	0.795	93.08	87.5	8.04	8.67	2.67	1.498	48.30	1.14
CB	2	P	5.432	3.042	1.828	0.910	0.744	0.860	0.838	81.05	92.5	9.12	7.54	2.41	1.406	38.64	1.28
CB	2	P	5.334	2.916	1.890	0.766	0.758	0.710	0.745	80.09	90	11.18	6.81	2.07	1.384	39.20	1.08
CB	2	P	5.272	2.878	1.942	0.762	0.730	0.712	0.735	77.63	67.5	3.79	8.46	2.81	1.500	37.04	1.06
CB	2	P	5.056	2.530	1.822	0.802	0.764	0.756	0.774	60.09	52.5	3.49	6.81	1.88	1.284	32.29	1.02
CB	2	P	4.492	2.466	1.784	0.674	0.714	0.638	0.675	50.19	72.5	3.90	6.47	1.89	1.254	25.56	1.00
CB	2	NP	6.400	2.970	1.962	1.000	1.070	1.006	1.025	93.55	92.5	6.50	6.70	2.14	1.282	46.73	1.14
CB	2	NP	5.744	2.982	1.952	0.958	1.108	1.108	1.058	88.30	100	11.95	9.60	2.19	1.278	48.57	0.90
CB	2	NP	5.804	2.694	1.884	0.966	0.990	0.972	0.976	90.15	127.5	12.81	7.46	2.12	1.344	48.31	1.22
CB	2	NP	4.700	2.300	1.650	0.714	0.878	0.890	0.827	52.56	95	4.95	3.01	1.56	1.202	30.88	0.92
CB	2	NP	4.700	2.192	1.678	0.578	0.800	0.734	0.704	49.93	60	3.54	5.14	1.45	1.100	29.35	0.88
CB	2	NP	4.502	2.184	1.530	0.858	0.902	0.818	0.859	42.58	77.5	4.03	3.59	1.11	1.016	25.43	0.76
CB	3	P	6.174	3.144	2.050	1.054	0.948	0.966	0.989	111.44	110	11.65	9.34	3.18	1.548	56.05	1.02
CB	3	P	5.774	3.108	1.978	0.838	0.824	0.844	0.835	94.13	92.5	6.84	11.07	3.07	1.518	45.42	1.14
CB	3	P	5.962	2.816	1.906	0.872	0.806	0.808	0.829	90.74	92.5	4.15	8.00	2.44	1.318	50.69	1.10
CB	3	P	5.514	2.984	1.852	0.724	0.698	0.644	0.689	80.37	90	5.53	10.40	2.46	1.452	42.92	0.94
CB	3	P	5.174	3.236	1.788	0.810	0.844	0.830	0.828	75.57	85	7.93	10.95	2.27	1.346	38.76	1.16
CB	3	P	5.276	2.638	1.684	0.978	0.848	0.974	0.933	68.90	80	6.71	8.64	1.88	1.258	38.29	1.04

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
CB	3	NP	6.638	3.518	2.074	0.954	0.906	0.938	0.933	124.36	157.5	7.41	8.89	2.64	1.386	64.46	1.40
CB	3	NP	5.956	3.174	1.972	0.802	0.828	0.796	0.809	96.38	145	4.46	6.90	2.27	1.364	48.00	1.14
CB	3	NP	6.038	3.046	1.996	0.782	0.834	0.726	0.781	87.67	107.5	12.41	4.30	2.02	1.252	44.23	1.06
CB	3	NP	5.578	2.846	1.842	0.966	1.074	0.922	0.987	81.14	92.5	11.64	3.84	1.83	1.304	42.04	1.12
CB	3	NP	5.178	2.332	1.722	0.738	0.806	0.798	0.781	58.91	82.5	4.94	3.77	1.56	1.168	32.74	0.98
CB	3	NP	5.068	2.512	1.762	0.828	0.894	0.932	0.885	56.46	62.5	5.59	3.13	1.83	1.188	32.97	0.92
CB	4	P	6.564	3.844	2.062	1.200	1.018	0.892	1.037	145.57	70	18.58	6.11	2.76	1.532	70.87	1.24
CB	4	P	5.692	3.698	2.098	0.946	0.852	0.946	0.915	112.35	135	14.50	8.22	3.13	1.624	55.51	1.08
CB	4	P	5.794	3.476	1.842	0.628	0.648	0.884	0.720	108.54	70	8.65	6.55	2.96	1.610	50.93	1.14
CB	4	P	5.900	3.290	2.038	1.072	0.874	0.968	0.971	100.64	95	10.28	5.74	2.77	1.436	51.07	1.20
CB	4	P	5.704	3.258	1.946	1.038	0.928	1.116	1.027	93.17	100	13.49	6.41	2.84	1.360	47.59	1.18
CB	4	P	5.456	3.302	1.858	0.826	0.788	0.712	0.775	87.12	65	9.15	5.24	2.96	1.466	41.43	1.12
CB	4	NP	6.104	3.182	1.982	1.272	1.256	1.276	1.268	119.70	80	10.13	5.44	3.12	1.564	61.00	1.22
CB	4	NP	5.912	2.792	1.926	1.138	1.148	1.004	1.097	95.97	60	12.01	4.89	2.19	1.362	46.99	1.16
CB	4	NP	5.736	3.102	1.860	0.676	0.756	0.654	0.695	85.87	90	5.71	5.07	1.69	1.308	43.60	1.18
CB	4	NP	5.290	2.736	1.874	1.212	0.990	1.212	1.138	71.01	45	5.78	6.17	1.78	1.228	36.69	0.84
CB	4	NP	5.466	2.558	1.886	1.038	1.204	1.030	1.091	75.44	77.5	10.19	5.75	1.86	1.280	39.47	0.98
CB	4	NP	5.386	2.638	1.694	0.880	0.924	0.698	0.834	70.26	47.5	5.52	7.71	1.59	1.236	34.25	1.00
CB	5	P	5.022	2.406	1.582	0.740	0.784	0.720	0.748	56.62	77.5	5.16	3.87	2.05	1.302	32.87	1.10
CB	5	P	5.032	2.794	1.658	0.966	0.944	0.728	0.879	62.15	65	5.44	5.24	2	1.268	34.19	1.04
CB	5	P	4.674	3.206	1.688	0.658	0.634	0.560	0.617	61.28	87.5	11.85	3.15	2.12	1.334	30.11	1.02
CB	5	P	4.756	3.056	1.696	0.578	0.660	0.638	0.625	55.54	15	6.16	3.18	2.56	1.374	28.64	0.98
CB	5	P	4.932	2.558	1.706	0.722	0.594	0.598	0.638	52.82	85	6.43	3.29	1.96	1.292	28.26	1.06
CB	5	P	4.446	2.228	1.632	0.784	0.686	0.664	0.711	41.93	60	5.43	3.93	1.4	1.174	23.19	0.98
CB	5	NP	5.118	2.548	1.656	0.884	0.996	1.060	0.980	60.94	77.5	4.64	3.02	1.45	1.056	34.46	1.06
CB	5	NP	5.144	2.536	1.694	0.892	0.870	0.900	0.887	64.05	85	5.15	3.86	1.57	1.210	36.21	1.22
CB	5	NP	4.846	2.336	1.638	0.856	0.636	0.808	0.767	53.02	75	5.44	2.79	1.42	1.090	30.03	1.12
CB	5	NP	4.964	2.462	1.598	0.792	0.884	0.774	0.817	53.46	70	5.56	4.41	1.29	1.146	34.91	1.04
CB	5	NP	4.600	2.208	1.588	0.816	0.618	0.720	0.718	42.68	72.5	3.88	2.87	1.29	1.084	23.84	1.10
CB	5	NP	4.640	2.102	1.598	0.774	0.946	0.828	0.849	44.89	67.5	6.54	3.32	1.11	1.080	26.77	1.18

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
MC	1	P	6.172	3.276	2.038	1.334	1.168	1.414	1.305	106.48	100	7.32	12.37	3.30	1.416	53.43	1.30
MC	1	P	6.262	2.948	2.054	0.978	0.886	1.070	0.978	104.40	105	6.82	8.87	3.56	1.472	53.32	1.08
MC	1	P	5.658	2.950	1.960	0.912	0.824	1.074	0.937	83.05	75	10.18	8.49	2.81	1.394	42.33	1.08
MC	1	P	5.796	3.332	1.912	0.984	1.138	0.824	0.982	91.84	130	0.99	12.73	3.44	1.400	42.14	1.22
MC	1	P	5.692	2.796	1.896	1.170	1.204	1.118	1.164	81.85	110	4.90	10.43	2.51	1.346	43.99	1.08
MC	1	P	4.610	2.536	1.704	1.114	0.906	0.954	0.991	47.17	127.5	2.05	4.95	1.72	1.246	26.37	0.98
MC	1	NP	6.472	3.256	2.070	1.796	1.494	1.692	1.661	128.78	95	8.36	11.73	2.96	1.432	65.43	1.28
MC	1	NP	6.078	2.996	2.008	1.170	1.206	1.284	1.220	100.20	70	5.81	11.63	3.14	1.364	55.89	1.28
MC	1	NP	6.018	2.936	1.984	1.412	1.454	1.628	1.498	99.95	147.5	7.96	15.58	3.20	1.316	53.57	1.26
MC	1	NP	6.222	3.056	2.068	1.548	1.290	1.480	1.439	104.29	102.5	6.70	15.88	3.15	1.324	56.37	1.28
MC	1	NP	4.634	2.298	1.624	1.276	1.352	1.308	1.312	45.36	65	0.48	5.87	1.80	1.006	24.44	0.92
MC	1	NP	4.242	1.722	1.514	1.062	1.006	1.058	1.042	35.04	50	1.62	5.92	1.43	1.052	21.25	1.04
MC	2	P	6.524	4.134	2.148	0.976	1.090	1.188	1.085	148.04	122.5	9.73	9.89	3.48	1.560	64.58	1.16
MC	2	P	6.910	3.622	2.348	1.126	1.088	1.098	1.104	142.15	85	10.65	10.46	3.45	1.558	64.93	1.22
MC	2	P	6.600	3.206	2.246	1.098	1.166	0.998	1.087	122.66	137.5	9.51	7.62	3.72	1.552	57.66	1.32
MC	2	P	5.884	3.086	1.740	1.434	1.240	1.432	1.369	99.84	80	6.89	17.06	2.06	1.334	48.95	0.96
MC	2	P	5.842	2.644	1.888	1.242	1.238	1.176	1.219	84.61	77.5	10.70	11.79	2.56	1.306	45.75	1.30
MC	2	P	5.066	2.638	1.880	1.390	1.142	1.020	1.184	63.12	80	7.14	8.79	2.52	1.382	32.84	1.16
MC	2	NP	7.270	4.116	2.362	1.574	1.518	1.658	1.583	174.04	150	17.75	11.32	4.00	1.534	92.93	1.30
MC	2	NP	6.512	3.614	1.924	1.562	1.684	1.422	1.556	133.55	107.5	8.60	10.35	2.28	1.526	63.77	1.26
MC	2	NP	6.884	3.694	2.168	1.064	1.198	1.246	1.169	144.48	120	11.57	9.23	3.09	1.670	67.10	1.36
MC	2	NP	6.228	3.184	2.092	1.294	1.892	1.882	1.689	115.05	102.5	9.45	17.38	2.17	1.350	67.89	1.38
MC	2	NP	6.032	3.202	1.958	1.452	1.524	1.472	1.483	99.12	122.5	6.73	12.62	1.96	1.372	50.14	1.38
MC	2	NP	5.618	2.912	1.860	1.602	1.478	1.492	1.524	83.27	67.5	5.37	11.28	1.88	1.198	40.57	1.10
MC	3	P	6.672	3.040	2.188	0.912	0.864	0.830	0.869	123.07	87.5	8.08	11.03	2.91	1.528	64.89	1.12
MC	3	P	6.190	3.342	2.088	0.872	0.826	0.708	0.802	108.93	162.5	11.77	7.85	2.95	1.596	51.71	1.60
MC	3	P	5.932	3.382	2.060	0.866	0.790	1.040	0.899	99.46	167	10.94	7.34	3.50	1.504	49.16	1.08
MC	3	P	5.020	2.444	1.732	1.190	0.982	0.998	1.057	61.22	122.5	5.78	6.10	1.78	1.236	34.38	0.92
MC	3	P	5.212	2.294	1.814	1.008	0.856	0.754	0.873	65.60	70	4.95	7.37	2.04	1.274	33.14	1.36
MC	3	P	5.008	2.314	1.644	1.208	1.028	1.030	1.089	59.68	92.5	5.93	6.28	1.72	1.266	32.95	1.00

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
MC	3	NP	7.752	3.854	2.452	1.452	1.652	1.750	1.618	176.70	166	12.57	7.12	3.74	1.668	81.77	1.18
MC	3	NP	7.050	3.446	2.466	1.314	0.782	1.414	1.170	140.70	105	14.58	8.36	3.46	1.542	68.00	1.36
MC	3	NP	6.172	2.964	2.164	1.404	1.302	1.040	1.249	99.98	102.5	7.47	9.85	2.68	1.314	54.31	1.44
MC	3	NP	5.590	2.648	1.876	1.118	1.170	1.044	1.111	73.42	65	5.95	8.37	2.24	1.390	40.48	1.22
MC	3	NP	5.314	2.408	1.846	1.364	1.292	1.128	1.261	68.88	55	4.06	7.97	1.79	1.162	38.88	0.98
MC	3	NP	4.546	1.910	1.564	0.978	1.138	1.000	1.039	39.86	92.5	2.94	5.50	1.30	1.040	23.65	0.96
MC	4	P	6.822	4.098	2.300	1.198	1.092	1.036	1.109	152.36	117.5	15.03	16.77	3.04	1.598	69.00	1.28
MC	4	P	6.688	3.424	2.472	1.236	1.118	1.246	1.200	135.29	112.5	11.52	9.88	3.37	1.668	66.05	1.06
MC	4	P	7.372	3.582	2.434	0.914	0.936	0.894	0.915	159.29	100	20.61	10.07	3.29	1.636	71.99	1.34
MC	4	P	5.908	3.118	2.038	1.226	1.296	1.052	1.191	97.56	107.5	9.69	8.37	2.90	1.376	52.02	1.12
MC	4	P	5.608	2.918	2.030	1.324	0.942	0.980	1.082	83.89	102.5	8.88	6.10	2.93	1.394	44.94	1.16
MC	4	P	4.738	2.024	1.790	1.548	1.604	1.444	1.532	44.36	47.5	3.63	3.10	1.65	1.190	24.81	0.82
MC	4	NP	8.028	3.938	2.506	1.086	1.274	1.282	1.214	204.55	150	20.99	10.65	3.61	1.636	91.38	1.36
MC	4	NP	6.538	3.458	2.190	1.558	1.534	1.484	1.525	135.38	100	9.68	10.29	3.62	1.610	64.75	1.16
MC	4	NP	6.822	3.386	2.410	1.174	1.182	0.978	1.111	129.95	135	10.99	12.88	3.56	1.562	64.93	1.08
MC	4	NP	6.526	3.424	2.108	1.606	1.474	1.588	1.556	126.53	127.5	9.48	7.77	3.23	1.498	61.44	1.16
MC	4	NP	5.370	2.714	1.836	1.350	1.334	1.052	1.245	73.16	75	5.67	8.52	2.05	1.270	38.12	1.14
MC	4	NP	5.252	2.628	1.800	1.216	1.014	1.040	1.090	65.57	85	5.54	5.97	1.75	1.229	31.12	0.94
MC	5	P	7.026	3.620	2.200	1.472	1.556	1.034	1.354	143.58	125	7.31	15.62	3.78	1.570	68.97	1.22
MC	5	P	6.732	3.292	2.212	1.488	1.422	1.490	1.467	129.02	125	9.57	15.82	2.78	1.428	66.63	1.20
MC	5	P	6.434	3.372	2.106	1.328	1.196	1.568	1.364	115.45	75	4.50	18.95	2.51	1.334	58.29	1.16
MC	5	P	6.460	3.554	2.002	1.300	1.204	1.232	1.245	121.20	65	5.51	17.98	3.41	1.710	58.30	1.28
MC	5	P	5.644	3.126	1.964	1.144	1.120	0.994	1.086	87.32	75	6.57	12.98	2.33	1.334	41.24	1.04
MC	5	P	5.414	2.888	1.928	0.776	1.030	0.968	0.925	77.25	55	5.90	12.33	2.32	1.332	36.15	1.24
MC	5	NP	6.878	3.508	2.226	1.494	1.236	1.538	1.423	142.50	90	9.93	12.54	3.08	1.362	69.45	1.18
MC	5	NP	6.684	3.456	2.082	1.596	1.544	1.570	1.570	130.11	100	10.20	11.21	3.10	1.476	70.48	1.16
MC	5	NP	6.338	3.264	1.938	1.564	1.302	1.288	1.385	108.39	117.5	8.83	8.84	2.60	1.546	54.44	1.02
MC	5	NP	6.314	3.326	2.156	1.516	1.354	1.134	1.335	108.33	132	6.99	13.19	2.65	1.432	55.62	1.18
MC	5	NP	5.596	2.446	1.832	1.444	1.364	1.582	1.463	73.88	75	8.38	10.66	2.10	1.322	41.10	1.16
MC	5	NP	5.224	2.512	1.798	1.266	1.250	1.272	1.263	59.98	72.5	6.41	10.87	1.84	1.236	32.77	1.00

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
SC	1	P	7.048	3.982	2.294	1.274	0.958	0.988	1.073	159.46	132	11.07	19.29	3.37	1.576	73.77	**1.68**
SC	1	P	6.168	3.592	2.156	0.768	0.672	0.682	0.707	121.81	115	13.12	10.1	3.3	1.690	56.89	1.24
SC	1	P	5.854	3.450	1.944	1.006	0.828	1.102	0.979	107.99	115	16.54	8.09	2.63	1.368	50.7	1.24
SC	1	P	5.946	3.422	2.098	0.660	0.710	0.698	0.689	105.91	115	7.12	14.88	2.87	1.460	49.41	1.34
SC	1	P	4.978	3.264	1.800	0.778	1.042	0.944	0.921	75.21	82.5	8.12	4.28	2.46	1.348	35.33	0.96
SC	1	P	5.166	2.488	1.746	1.164	0.984	0.762	0.970	63.15	62.5	8.13	5.61	2.12	1.272	31.81	1.14
SC	1	NP	6.836	4.198	2.226	1.042	0.996	1.118	1.052	163.00	120	19.39	6.41	3.67	1.426	81.70	1.50
SC	1	NP	6.220	3.198	2.066	0.780	0.732	0.664	0.725	110.66	112.5	8.25	13.92	2.99	1.478	57.09	1.48
SC	1	NP	6.794	3.766	2.094	0.756	0.688	0.726	0.723	144.72	65	10.70	7.36	3.47	1.364	69.14	1.32
SC	1	NP	4.472	2.256	1.594	0.650	0.766	0.732	0.716	43.66	52.5	2.19	6.30	1.78	1.120	26.30	1.42
SC	1	NP	6.200	3.226	2.158	0.814	0.864	0.908	0.862	110.16	97.5	10.51	15.32	2.78	1.592	65.68	1.20
SC	1	NP	5.242	2.576	1.688	0.820	0.824	0.804	0.816	60.08	52.5	8.98	6.16	2.10	1.128	34.47	1.46
SC	2	P	5.646	2.890	2.020	0.844	0.860	0.638	0.781	77.21	54	8.41	6.35	2.74	1.310	43.18	1.22
SC	2	P	4.938	2.582	1.628	0.728	0.770	0.626	0.708	55.76	64	3.72	5.15	1.24	1.194	30.03	1.08
SC	2	P	5.898	3.282	1.984	1.016	0.912	0.952	0.960	101.29	116	11.52	6.79	2.31	1.356	48.85	1.40
SC	2	P	5.596	3.190	1.910	0.852	1.072	1.000	0.975	94.87	108	7.72	4.92	2.49	1.502	46.17	1.20
SC	2	P	5.764	3.080	1.908	0.834	0.896	0.900	0.877	92.30	70	5.74	9.50	2.57	1.512	47.40	**1.60**
SC	2	P	6.138	3.226	1.860	0.844	0.872	0.666	0.794	113.19	86	9.02	11.82	2.58	1.492	57.44	1.32
SC	2	NP	6.000	2.910	2.052	0.670	0.862	0.736	0.756	93.97	123	7.89	8.36	2.63	1.278	52.05	1.14
SC	2	NP	7.266	3.796	2.276	0.990	1.024	1.028	1.014	167.86	109	17.53	7.84	3.08	1.606	80.07	1.28
SC	2	NP	6.668	3.392	2.050	1.128	0.976	1.090	1.065	128.30	103	15.47	8.44	3.00	1.592	70.53	1.53
SC	2	NP	6.148	3.370	1.942	0.884	0.990	1.018	0.964	107.66	130	9.81	12.47	2.45	1.466	51.53	1.2
SC	2	NP	5.616	2.858	1.884	0.848	0.876	0.828	0.851	88.66	85	18.39	8.53	2.29	1.338	45.34	1.18
SC	2	NP	5.418	2.802	1.748	0.828	0.856	0.826	0.837	75.32	114	13.11	4.92	2.75	1.388	42.84	1.06
SC	3	P	5.892	2.904	1.876	0.792	0.746	0.690	0.743	88.26	145.5	8.46	8.34	2.44	1.338	48.08	1.52
SC	3	P	6.210	3.362	2.032	0.796	0.938	0.826	0.853	111.87	122.5	20.52	8.35	2.42	1.472	52.02	1.16
SC	3	P	5.658	3.050	1.846	0.884	1.022	0.878	0.928	88.83	100	8.43	6.97	1.82	1.330	42.19	1.10
SC	3	P	6.172	3.302	1.986	0.712	0.764	0.788	0.755	102.33	95	10.27	6.84	2.22	1.314	47.05	1.24
SC	3	P	5.906	3.746	2.010	0.718	0.740	0.788	0.749	105.55	52.5	18.28	13.42	2.36	1.444	52.54	1.28
SC	3	P	4.664	2.190	1.562	0.766	0.800	0.850	0.805	47.30	30	5.36	3.44	1.21	1.140	28.37	1.12

Si	Ti	Mi	Di	He	Pd	S1	S2	S3	Sp	Ma	Cs	Go	Gu	La	Ja	Sk	Te
SC	3	NP	7.094	4.210	2.394	0.900	0.998	0.908	0.935	178.60	150	24.76	10.27	4.19	1.340	90.83	**1.96**
SC	3	NP	7.210	3.672	2.302	1.224	1.214	1.104	1.181	160.62	135	25.56	11.53	3.64	1.620	83.62	**1.56**
SC	3	NP	6.262	3.916	2.076	0.760	0.844	0.746	0.783	129.53	67.5	12.93	12.82	4.14	1.648	59.94	1.40
SC	3	NP	5.576	3.024	1.804	0.690	0.854	0.784	0.776	86.07	120	8.71	7.85	2.85	1.362	45.12	1.20
SC	3	NP	5.540	3.148	1.892	0.646	0.780	0.758	0.728	90.11	80	15.33	9.29	3.10	1.238	43.04	1.46
SC	3	NP	5.268	2.628	1.686	0.712	0.680	0.618	0.670	60.69	77.5	4.81	6.98	2.67	1.304	32.32	1.06
SC	4	P	5.900	3.421	2.090	0.828	0.942	0.790	0.853	105.98	110	8.34	11.51	3.73	1.590	59.05	1.24
SC	4	P	5.962	3.648	2.060	0.780	0.916	0.890	0.862	109.73	105	10.82	9.00	3.46	1.490	54.69	1.34
SC	4	P	6.206	3.152	2.190	0.982	0.960	1.074	1.005	114.75	70	13.06	6.65	2.78	1.426	55.88	1.34
SC	4	P	6.328	3.110	2.042	0.962	0.896	1.000	0.953	104.45	75	7.54	9.12	2.37	1.432	49.67	1.38
SC	4	P	5.234	2.632	1.796	0.776	0.686	0.668	0.710	67.00	65	8.41	6.37	2.04	1.286	35.09	1.18
SC	4	P	5.664	2.944	2.102	0.796	0.748	0.762	0.769	86.14	70	7.69	5.44	1.90	1.296	41.46	0.94
SC	4	NP	6.020	3.272	2.096	0.786	1.016	0.932	0.911	106.99	98	9.79	7.39	3.66	1.444	55.25	1.52
SC	4	NP	6.844	3.530	2.146	1.028	0.934	0.898	0.953	142.26	77.5	19.67	7.54	2.71	1.598	78.09	1.64
SC	4	NP	5.874	3.694	1.860	0.882	0.830	0.808	0.840	114.89	106	9.69	8.15	2.35	1.666	58.64	1.38
SC	4	NP	5.576	3.354	1.792	1.044	1.000	1.046	1.030	88.38	60	6.86	6.60	2.07	1.298	43.64	1.08
SC	4	NP	5.022	2.562	1.710	0.780	0.802	0.822	0.801	60.16	62.5	6.73	6.19	1.80	1.128	36.05	0.92
SC	4	NP	5.094	2.576	1.720	1.086	0.958	1.052	1.032	61.66	70	8.55	5.25	1.63	1.222	34.17	1.24
SC	5	P	5.568	2.834	1.968	0.824	0.910	0.778	0.837	83.38	60	10.72	8.73	2.61	1.212	53.72	1.26
SC	5	P	6.690	3.760	2.224	0.840	0.882	0.982	0.901	146.13	135	16.91	11.48	2.53	1.528	63.98	1.18
SC	5	P	5.910	3.336	2.002	0.774	0.898	0.786	0.819	102.18	145	12.06	6.53	2.51	1.372	48.64	0.92
SC	5	P	5.306	2.938	1.802	0.894	0.806	0.862	0.854	77.60	78	10.92	7.76	2.96	1.356	40.42	1.12
SC	5	P	4.844	2.770	1.790	0.836	0.796	0.726	0.786	64.23	135	10.07	7.12	1.55	1.296	34.58	1.18
SC	5	P	4.648	2.168	1.656	0.864	0.944	0.994	0.934	47.18	110	7.31	4.21	1.56	1.092	25.57	0.90
SC	5	NP	6.786	3.936	2.322	1.178	1.250	1.148	1.192	160.18	90	16.70	7.46	3.46	1.548	79.68	1.24
SC	5	NP	6.384	3.214	2.206	1.198	1.188	1.066	1.151	119.83	110	11.45	6.91	2.61	1.346	61.22	1.24
SC	5	NP	6.122	2.962	2.140	1.086	0.926	1.000	1.004	100.28	132.5	9.21	6.77	2.90	1.530	55.57	1.38
SC	5	NP	5.922	3.190	2.014	0.958	0.718	0.772	0.816	107.01	80	8.05	4.60	2.25	1.394	58.12	1.18
SC	5	NP	5.250	2.912	1.838	0.638	0.746	0.788	0.724	75.46	102.5	7.22	4.19	1.87	1.344	39.68	1.20
SC	5	NP	4.928	2.562	1.782	0.824	1.002	1.112	0.979	57.99	95	5.75	5.37	1.52	1.158	31.37	0.86

APPENDIX C

GROWTH DATA

These data provided the basis for Chapter III, and the methods of collection are provided in great detail.

Column codes:
Si – Site
Ti – Tidepool
Mi – Microhabitat (P or NP)
– ID Number
Di – Diameter
He – Height
Jaw1 – Jaw size at collection
Jaw0 – Jaw size at tagging
TotGr – Total growth
EsGr – Esophageal Growth
LaGr – Labial growth
Ye – Years of growth
Sex – M(ale) or F(emale)

When sea urchins were sacrificed, they were inspected for ripe gonads without a microscope. Sex was recorded if it could be determined. Sea urchins that do not have any growth information did not have visible fluorescent markings on their jaw.

Si	Ti	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Years	Sex
CB	A	P	1	4.85	2.822	1.231	1.2271	0.004	0.0039	0.0000	0.989	M
CB	A	P	2	5.055	2.735	1.099	1.0886	0.0104	0.0078	0.0026	0.989	
CB	A	P	3	4.704	2.744	1.174	1.1649	0.009	0.0091	0.0000	0.989	M
CB	A	P	4	3.936	1.871	0.85	0.746	0.104	0.0884	0.0156	0.989	F
CB	A	P	5	3.033	1.494	0.827	0.7178	0.1092	0.091	0.0182	0.989	
CB	A	P	6	4.593	2.34	1.062	1.0503	0.0117	0.0117	0.0000	0.989	M
CB	A	P	7	3.045	1.681	0.842					0.989	M
CB	A	P	8	5.843	3.169	1.303					0.989	F
CB	A	P	9	4.331	2.251	1.041	1.0345	0.007	0.0065	0.0000	0.989	F
CB	A	P	10	4.093	2.232	1.018	1.0102	0.008	0.0078	0.0000	0.989	F
CB	A	P	11	4.267	2.086	1.027	0.9984	0.0286	0.0273	0.0013	0.989	F
CB	A	P	12	3.583	1.888	0.845	0.8333	0.0117	0.0117	0.0000	0.989	F
CB	A	P	13	4.161	2.04	0.973	0.9665	0.007	0.0065	0.0000	0.989	
CB	A	P	14	4.204	2.171	0.948	0.87	0.078	0.0598	0.0182	0.989	M
CB	A	P	15	4.419	2.002	0.916	0.903	0.013	0.013	0.0000	0.989	M
CB	A	NP	16	0.912	0.475	0.258					0.989	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	A	NP	17			0.526					0.989	F
CB	A	NP	18	1.56	0.734	0.418					0.989	
CB	A	NP	19	5.754	2.837	1.123					0.989	F
CB	A	NP	20	5.242	2.649	1.1	1.087	0.013	0.013	0.0000	0.989	M
CB	A	NP	21	4.642	2.521	1.008					0.989	M
CB	A	NP	22	4.106	1.767	0.906					0.989	M
CB	A	NP	23	3.569	1.543	0.778	0.7104	0.0676	0.0572	0.0104	0.989	
CB	A	NP	24	3.356	1.664	0.767					0.989	M
CB	A	NP	25	3.993	1.691	0.831	0.7504	0.0806	0.065	0.0156	0.989	M
CB	A	NP	26	3.642	2.052	0.863	0.8435	0.0195	0.0182	0.0013	0.989	M
CB	A	NP	27	4.275	2.022	1.082					0.989	
CB	A	NP	28	3.973	2.219	0.989	0.9695	0.0195	0.013	0.0065	0.989	M
CB	A	NP	29	5.024	2.284	1.044	1.0219	0.0221	0.0143	0.0078	0.989	M
CB	A	NP	30	4.587	2.464	1.086	1.0769	0.0091	0.0078	0.0013	0.989	
CB	A	NP	31	4.192	2.143	0.904	0.8676	0.0364	0.0286	0.0078	0.989	
CB	A	NP	32	5.601	2.856	1.263	1.25	0.013	0.0078	0.0052	0.989	
CB	A	NP	33	3.728	1.795	0.82					0.989	M
CB	A	NP	34	4.881	2.304	1.064	1.0536	0.010	0.0104	0.0000	0.989	M
CB	A	NP	35	5.328	2.726	0.989	0.9591	0.0299	0.0247	0.0052	0.989	F
CB	A	NP	36	4.033	1.661	0.833					0.989	F
CB	A	NP	37	4.517	2.348	1.087	1.0727	0.0143	0.0143	0.0000	0.989	M
CB	A	NP	38	4.62	2.378	1.063	1.05	0.013	0.013	0.0000	0.989	F
CB	A	NP	39	4.895	2.496	1.121	1.0924	0.0286	0.0182	0.0104	0.989	F
CB	A	NP	40	5.22	2.692	1.116	1.1121	0.004	0.0039	0.0000	0.989	F
CB	A	NP	41	5.042	2.544	1.153	1.1244	0.0286	0.026	0.0026	0.989	M
CB	A	NP	42	4.83	1.981	0.994					0.989	
CB	A	NP	43	4.798	2.312	1.116					0.989	F
CB	A	NP	44	5.364	2.811	1.191					0.989	M
CB	A	NP	45	4.898	2.216	1.065	1.0468	0.0182	0.013	0.0052	0.989	F
CB	B	P	47			0.764	0.6886	0.0754	0.065	0.0104	0.989	F
CB	B	P	48			0.799					0.989	F
CB	B	P	49	3.962	2.345	1.114					0.989	M
CB	B	P	50			0.913					0.989	
CB	B	P	51	3.794	2.091	0.885					0.989	M
CB	B	P	52			0.893					0.989	F
CB	B	P	53			1.154					0.989	
CB	B	P	54	3.129		0.834					0.989	F
CB	B	P	55	3.936		0.922					0.989	F
CB	B	P	56			0.967					0.989	
CB	B	P	57	3.903		1.001					0.989	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	B	P	58	3.342		0.892	0.84	0.052	0.052	0.0000	0.989	
CB	B	P	59	1.44	0.7	0.39					0.989	
CB	B	P	60	3.966	2.262	1.022					0.989	F
CB	B	P	61	3.508	1.822	0.851					0.989	M
CB	B	P	62	3.478	2.182	1.002					0.989	M
CB	B	P	63	3.751	2.034	0.88					0.989	M
CB	B	P	64	4.266	2.349	1.053	1.0309	0.0221	0.0143	0.0078	0.989	F
CB	B	P	65	4.326	2.117	0.946	0.7218	0.2242	0.18	0.0442	0.989	F
CB	B	P	66	3.899	2.389	0.977					0.989	M
CB	B	P	67	3.325	1.794	0.905					0.989	M
CB	B	P	68	3.743	1.8	0.938	0.9276	0.0104	0.0078	0.0026	0.989	M
CB	B	P	69	4.026	1.93	0.918	0.9141	0.0039	0.0026	0.0013	0.989	M
CB	B	P	70	3.104	1.63	0.768					0.989	M
CB	B	P	71	3.826	1.949	0.942					0.989	
CB	B	P	72	4.181	2.252	1.046	1.0252	0.0208	0.0156	0.0052	0.989	F
CB	B	P	73	3.882	2.157	0.98	0.896	0.084	0.076	0.0080	0.989	M
CB	B	P	74	2.353	1.031	0.552	0.3192	0.2328	0.186	0.0468	0.989	
CB	B	P	75	2.237	1.246	0.629	0.3064	0.3226	0.255	0.0676	0.989	
CB	B	P	76	3.325	1.749	0.812					0.989	F
CB	B	P	77	2.685	1.197	0.651					0.989	
CB	B	P	78	4.723	2.363	1.004	0.9741	0.0299	0.026	0.0039	0.989	F
CB	B	P	79	5.724	3.049	1.18					0.989	M
CB	B	P	80	5.172	3.119	1.083					0.989	M
CB	B	P	81	4.636	2.532	1.136					0.989	M
CB	B	P	82	5.991	3.621	1.283					0.989	M
CB	B	NP	83	0.495	0.224	0.147					0.989	
CB	B	NP	84			1.274	1.2636	0.0104	0.0078	0.0026	0.989	F
CB	B	NP	85	6.08	2.76	1.126					0.989	F
CB	B	NP	86	6.208	2.886	1.281	1.2511	0.0299	0.0221	0.0078	0.989	M
CB	B	NP	87	6.164	2.937	1.234					0.989	M
CB	B	NP	88	5.436	2.441	1.157	1.1548	0.002	0.0022	0.0000	0.989	M
CB	B	NP	89	5.912	2.783	1.17					0.989	F
CB	B	NP	90	4.642	1.984	1.003					0.989	
CB	B	NP	91	3.363	1.242	0.744					0.989	
CB	B	NP	92	4.447	2.109	0.987					0.989	M
CB	B	NP	93	5.194	2.392	1.075	1.0749	0.000	0.0001	0.0000	0.989	M
CB	B	NP	94	6.578	3.161	1.279	1.2621	0.0169	0.0143	0.0026	0.989	M
CB	B	NP	95	5.692	2.773	1.14	1.0919	0.0481	0.0403	0.0078	0.989	M
CB	B	NP	96	5.358	2.662	1.127	1.0919	0.0351	0.0286	0.0065	0.989	M
CB	B	NP	97	4.938	2.119	0.987					0.989	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	B	NP	98	5.824	2.576	1.107	1.1069	0.000	0.0001	0.0000	0.989	F
CB	B	NP	99	6.244	2.911	1.023					0.989	M
CB	B	NP	100	4.655	2.237	1.236					0.989	M
CB	B	NP	101	4.316	2.126	1.003					0.989	F
CB	B	NP	102	4.833	2.014	1.001					0.989	F
CB	B	NP	103	6.775	2.723	1.159	1.107	0.052	0.052		0.989	F
CB	B	NP	104	5.42	2.638	1.173	1.1483	0.0247	0.0195	0.0052	0.989	M
CB	B	NP	105	6.043	2.726	1.124					0.989	M
CB	B	NP	106	6.125	2.842	1.221					0.989	M
CB	B	NP	107	5.763	3.101	1.263					0.989	F
CB	B	NP	108	5.639	2.652	1.111					0.989	F
CB	B	NP	109	6.132	3.002	1.164					0.989	F
CB	B	NP	110	6.272	3.091	1.123	1.0967	0.0263	0.0263	0.0000	0.989	F
CB	B	NP	111	5.603	2.297	1.045	1.0131	0.0319	0.0254	0.0065	0.989	M
CB	B	NP	112	4.731	2.37	1.076	1.0604	0.0156	0.0143	0.0013	0.989	F
CB	B	NP	113	4.527	2.017	0.963					0.989	M
CB	B	NP	114	5.326	2.355	1	0.9272	0.0728	0.0624	0.0104	0.989	F
CB	B	NP	115	5.699	2.97	1.154	1.1337	0.0203	0.0164	0.0039	0.989	M
CB	B	NP	116	5.808	2.672	1.117	1.0936	0.0234	0.0221	0.0013	0.989	M
CB	B	NP	117	5.263	2.331	1.035					0.989	F
CB	B	NP	118	4.478	1.783	0.907					0.989	F
CB	B	NP	119	5.396	2.708	1.216					0.989	M
CB	B	NP	120	5.894	2.991	1.104					0.989	F
CB	B	NP	121	6.1	3.08	1.153	1.1213	0.0317	0.0265	0.0052	0.989	M
CB	B	NP	122	5.199	2.734	1.104	1.0819	0.0221	0.0221	0.0000	0.989	M
CB	B	NP	123	4.376	2.005	0.913	0.891	0.022	0.0176	0.0044	0.989	M
CB	B	NP	124	4.31	2.004	1.005	0.9731	0.0319	0.0254	0.0065	0.989	M
CB	B	NP	125	4.539	2.338	1.069					0.989	F
CB	B	NP	126	6.261	2.961	1.243	1.23	0.013	0.013	0.0000	0.989	M
CB	B	NP	127	6.953	3.306	1.335	1.3103	0.0247	0.0182	0.0065	0.989	F
CB	B	NP	128	6.731	3.025	1.204					0.989	F
CB	B	NP	129	3.401	1.585	0.75	0.5669	0.1831	0.148	0.0351	0.989	F
CB	B	NP	130	5.113	2.239	1.156	1.1482	0.008	0.0078	0.0000	0.989	M
CB	B	NP	131	4.201	2.022	0.955	0.9342	0.0208	0.0208	0.0000	0.989	F
CB	B	NP	132	3.345	1.337	0.756					0.989	
CB	B	NP	133	3.961	1.977	0.836					0.989	M
CB	B	NP	134	6.555	3.326	1.234					0.989	M
CB	B	NP	135	5.099	2.384	1.205	1.203	0.002	0.002	0.0000	0.989	F
CB	B	NP	136	6.488	3.116	1.182	1.1338	0.0482	0.041	0.0072	0.989	M
CB	B	NP	137	5.462	2.814	1.124					0.989	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	B	NP	138	5.341	2.548	1.057					0.989	M
CB	B	NP	139	4.182	2.208	1.006	0.9787	0.0273	0.0247	0.0026	0.989	M
CB	B	NP	140	5.609	2.62	1.08	1.0464	0.0336	0.0286	0.0050	0.989	M
CB	B	NP	141	5.27	2.242	1.079					0.989	F
CB	B	NP	142	5.748	3.183	1.065	1.0494	0.0156	0.0143	0.0013	0.989	M
CB	B	NP	143	4.434	2.345	1.049	1.0427	0.006	0.0063	0.0000	0.989	M
CB	B	NP	144	4.087	1.984	0.943					0.989	
CB	B	NP	145	4.69	2.273	1.11					0.989	M
CB	B	NP	146	4.864	2.152	1.024					0.989	F
CB	B	NP	147	6.397	3.342	1.284	1.2773	0.007	0.0067	0.0000	0.989	M
CB	B	NP	148	6.269	2.521	1.239	1.2356	0.003	0.0034	0.0000	0.989	M
CB	B	NP	149	4.259	1.849	0.932					0.989	M
CB	B	NP	150	5.637	2.39	1.009					0.989	F
CB	B	NP	151	5.224	2.483	1.108	1.0472	0.0608	0.0574	0.0034	0.989	M
CB	B	NP	152	4.691	2.022	1.051					0.989	M
CB	B	NP	153	7.275	3.651	1.422	1.4051	0.0169	0.0169	0.0000	0.989	M
CB	B	NP	154	4.421	2.442	1.044					0.989	
CB	B	NP	155	5.562	2.861	1.234	1.2158	0.0182	0.0182	0.0000	0.989	
CB	B	NP	156	6.557	3.193	1.298					0.989	
CB	C	P	900			0.882					1.066	
CB	C	P	901	4.841	2.826	1.149					1.066	
CB	C	P	902	3.817	1.782	0.865	0.6412	0.2238	0.177	0.0468	1.066	
CB	C	P	903	4.386	2.716	1.143					1.066	M
CB	C	P	904	3.86	1.927	0.879					1.066	
CB	C	P	905	4.538	2.741	1.1	1.0948	0.005	0.0052	0.0000	1.066	M
CB	C	P	906	5.192	2.862	1.199	1.1834	0.0156	0.0104	0.0052	1.066	F
CB	C	P	907	5.567	2.988	1.089	1.076	0.013	0.0091	0.0039	1.066	F
CB	C	P	908	4.928	2.737	1.134	1.1275	0.007	0.0065	0.0000	1.066	
CB	C	P	909	4.25	2.191	1.012	0.9912	0.0208	0.0156	0.0052	1.066	
CB	C	P	910	3.948	2.077	0.916	0.8653	0.0507	0.0416	0.0091	1.066	
CB	C	P	911	4.565	2.154	0.982	0.9716	0.010	0.0104	0.0000	1.066	
CB	C	P	912	5.447	3.116	1.218	1.2102	0.008	0.0078	0.0000	1.066	
CB	C	P	913	4.424	2.299	1.021	0.9612	0.0598	0.052	0.0078	1.066	M
CB	C	P	914	4.713	2.262	0.992					1.066	M
CB	C	P	915	4.076	2.196	0.963					1.066	
CB	C	P	916	4.096	2.144	0.881					1.066	
CB	C	P	917	4.655	2.332	0.957	0.9037	0.0533	0.0429	0.0104	1.066	
CB	C	P	918	5.548	2.806	1.066	1.0283	0.0377	0.0325	0.0052	1.066	F
CB	C	P	919	3.145	1.39	0.719					1.066	
CB	C	P	920	4.03	2.119	0.964					1.066	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	C	P	921	5.191	3.121	1.131					1.066	
CB	C	P	922	4.008	2.362	0.962	0.9009	0.0611	0.0546	0.0065	1.066	
CB	C	P	923	3.506	1.677	0.767					1.066	
CB	C	P	924	4.412	2.427	1.091	1.0624	0.0286	0.0208	0.0078	1.066	
CB	C	P	925	4.4	2.389	1.09					1.066	
CB	C	P	926	0.551	0.247	0.18					1.066	
CB	C	P	927	3.941	2.225	0.934					1.066	
CB	C	P	928	4.171	1.862	0.923	0.713	0.21	0.198	0.0120	1.066	
CB	C	P	929	3.795	2.122	0.904	0.8897	0.0143	0.0117	0.0026	1.066	
CB	C	P	930	4.484	2.36	0.965	0.9221	0.0429	0.0377	0.0052	1.066	M
CB	C	P	931	5.386	2.936	1.212	1.1964	0.0156	0.0156	0.0000	1.066	
CB	C	P	932	4.069	2.141	0.895	0.8781	0.0169	0.013	0.0039	1.066	
CB	C	P	933	3.346	1.694	0.771	0.6475	0.1235	0.1014	0.0221	1.066	
CB	C	P	934	4.258	2.656	0.997	0.9723	0.0247	0.0195	0.0052	1.066	
CB	C	P	935	4.961	2.75	1.035	1.0272	0.008	0.0078	0.0000	1.066	
CB	C	P	936	4.531	2.276	0.928	0.8994	0.0286	0.0208	0.0078	1.066	
CB	C	P	937	5.698	2.82	1.244	1.2362	0.0078	0.0065	0.0013	1.066	
CB	C	P	938	4.241	2.391	1.004	0.9871	0.0169	0.0143	0.0026	1.066	
CB	C	P	939	5.386	2.901	1.124	1.1097	0.0143	0.0104	0.0039	1.066	M
CB	C	P	940	4.15	2.42	1.017					1.066	
CB	C	P	941	4.277	2.376	0.952					1.066	
CB	C	P	942	4.126	2.094	0.896	0.8817	0.0143	0.0117	0.0026	1.066	
CB	C	P	943	3.433	1.635	0.757					1.066	
CB	C	P	944	4.793	2.778	1.096	1.0752	0.0208	0.013	0.0078	1.066	
CB	C	P	945	5.851	3.076	1.119					1.066	F
CB	C	P	946	4.629	2.483	1.045	1.0255	0.0195	0.0156	0.0039	1.066	F
CB	C	P	947	3.785	2.007	0.867	0.8137	0.0533	0.0429	0.0104	1.066	
CB	C	P	948	2.599	1.175	0.656					1.066	
CB	C	NP	950	6.023	3.221	1.163	1.1552	0.008	0.0078	0.0000	1.066	
CB	C	NP	951	5.771	2.786	1.216	1.2108	0.005	0.0052	0.0000	1.066	
CB	C	NP	952	6.504	3.246	1.237	1.2266	0.0104	0.0078	0.0026	1.066	
CB	C	NP	953	5.651	2.713	1.137					1.066	
CB	C	NP	954	6.619	3.18	1.298	1.2668	0.0312	0.0312	0.0000	1.066	
CB	C	NP	955	6.328	3.301	1.226	1.2221	0.004	0.0039	0.0000	1.066	M
CB	C	NP	956	4.328	2.231	1.014					1.066	F
CB	C	NP	957	5.702	2.966	1.167	1.1527	0.0143	0.0091	0.0052	1.066	M
CB	C	NP	958	5.389	2.846	1.252	1.2104	0.0416	0.0312	0.0104	1.066	M
CB	C	NP	959	5.248	2.518	1.036	0.9307	0.1053	0.0754	0.0299	1.066	
CB	C	NP	960	5.346	2.567	1.14					1.066	
CB	C	NP	961	4.391	2.188	0.971					1.066	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	C	NP	962	4.25	1.953	0.926					1.066	
CB	C	NP	963	4.987	2.779	1.109	1.096	0.013	0.013	0.0000	1.066	
CB	C	NP	964	6.361	3.129	1.256	1.2482	0.008	0.0078	0.0000	1.066	
CB	C	NP	965	4.447	2.136	1.023	0.9099	0.1131	0.0845	0.0286	1.066	
CB	C	NP	966	3.699	1.735	0.915	0.692	0.223	0.184	0.0390	1.066	
CB	C	NP	967	4.809	2.615	1.103	1.0926	0.010	0.0104	0.0000	1.066	
CB	C	NP	968	3.556	1.641	0.908	0.6512	0.2568	0.21	0.0468	1.066	
CB	C	NP	969	5.831	3.241	1.144	1.1271	0.0169	0.0156	0.0013	1.066	
CB	C	NP	970	5.558	2.558	1.135					1.066	
CB	C	NP	971	1.168	0.609	0.345					1.066	
CB	C	NP	972	5.006	2.44	1.036					1.066	
CB	C	NP	973	4.929	2.568	1.06	1.0236	0.0364	0.0364	0.0000	1.066	M
CB	C	NP	974	3.816	1.855	0.869	0.6527	0.2163	0.176	0.0403	1.066	
CB	C	NP	975	5.441	2.599	1.132	1.1216	0.0104	0.0078	0.0026	1.066	
CB	C	NP	976	4.806	2.66	1.09	1.0419	0.0481	0.0429	0.0052	1.066	
CB	C	NP	977	4.875	2.52	1.045	0.993	0.052	0.0455	0.0065	1.066	M
CB	D	P	978	4.5	2.1	0.965	0.6841	0.2809	0.225	0.0559	1.063	F
CB	D	P	979	2.2	1	0.485					1.063	
CB	D	P	980	4.739	2.511	1.07	1.0414	0.0286	0.0208	0.0078	1.063	
CB	D	P	981	3.771	2.039	0.968					1.063	
CB	D	P	982	0.746	0.352	0.21					1.063	
CB	D	P	983	3.992	2.044	0.914					1.063	
CB	D	P	984	3.632	2.156	0.882					1.063	
CB	D	P	985	3.818	1.778	0.874	0.5596	0.3144	0.252	0.0624	1.063	
CB	D	P	986	3.996	2.07	0.991					1.063	
CB	D	P	987	4.2	2.174	0.967					1.063	
CB	D	P	988	4.29	2.347	0.973	0.9444	0.0286	0.0234	0.0052	1.063	M
CB	D	P	989	4.291	2.147	0.988	0.9568	0.0312	0.0312	0.0000	1.063	
CB	D	P	990	4.886	2.626	1.03					1.063	
CB	D	P	991	3.385	1.482	0.8	0.499	0.301	0.249	0.0520	1.063	
CB	D	P	992	5.146	2.606	1.106	1.067	0.039	0.0299	0.0091	1.063	
CB	D	P	993	5.475	2.872	1.139	1.1286	0.0104	0.0078	0.0026	1.063	
CB	D	P	994	3.916	2.225	0.929					1.063	
CB	D	P	995	4.143	2.101	0.937	0.6201	0.3169	0.261	0.0559	1.063	
CB	D	P	996	3.329	1.928	0.916	0.9082	0.008	0.0078	0.0000	1.063	
CB	D	P	997	3.574	1.841	0.807	0.6246	0.1824	0.146	0.0364	1.063	
CB	D	P	998	1							1.063	
CB	D	NP	999	7.189	3.251	1.38	1.3644	0.0156	0.0156	0.0000	1.063	
CB	D	NP	1000	5.271	2.475	1.068	1.0017	0.0663	0.0585	0.0078	1.063	M
CB	D	NP	1001	4.012	1.938	0.814	0.5418	0.2722	0.228	0.0442	1.063	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	D	NP	1002	6.867	3.281	1.396					1.063	M
CB	D	NP	1003	6.65	3.36	1.318					1.063	M
CB	D	NP	1004	6.1	3.411	1.27	1.2479	0.0221	0.0182	0.0039	1.063	M
CB	D	NP	1005	0.7							1.063	
CB	D	NP	1006	6.662	3.282	1.332	1.3138	0.0182	0.0182	0.0000	1.063	
CB	D	NP	1007	6.33	3.01	1.293	1.2878	0.005	0.0052	0.0000	1.063	
CB	D	NP	1008	6.384	3.443	1.261	1.2506	0.0104	0.0091	0.0013	1.063	
CB	D	NP	1009	7.002	3.396	1.19	1.1601	0.0299	0.0234	0.0065	1.063	
CB	D	NP	1010	6.912	3.624	1.42					1.063	F
CB	D	NP	1011	5.427	2.704	1.07	1.0349	0.0351	0.0299	0.0052	1.063	
CB	D	NP	1012	5.843	2.534	1.131	1.0621	0.0689	0.052	0.0169	1.063	
CB	D	NP	1013	6.227	3.054	1.234	1.1469	0.0871	0.078	0.0091	1.063	
CB	D	NP	1014	7.146	3.639	1.36	1.3314	0.0286	0.0208	0.0078	1.063	F
CB	D	NP	1015	3.678	2.036	0.897	0.8385	0.0585	0.0468	0.0117	1.063	
CB	D	NP	1016	5.972	3.329	1.228	1.1903	0.0377	0.0312	0.0065	1.063	M
CB	D	NP	1017	6.065	2.595	1.158					1.063	
CB	D	NP	1018	5.506	2.723	1.087	1.074	0.013	0.013	0.0000	1.063	
CB	D	NP	1019	6.174	3.206	1.137	1.111	0.026	0.026	0.0000	1.063	F
CB	D	NP	1020	5.633	3.224	1.158	1.1255	0.0325	0.0273	0.0052	1.063	M
CB	D	NP	1021	1.029	0.465	0.272					1.063	
CB	D	NP	1022	6.336	3.163	1.151	1.1198	0.0312	0.0312	0.0000	1.063	
CB	D	NP	1023	5.8	3.126	1.17					1.063	M
CB	D	NP	1024	5.512	2.78	1.102	1.0617	0.0403	0.0325	0.0078	1.063	F
CB	D	NP	1025	3.765	1.591	0.868					1.063	
CB	D	NP	1026	5.538	2.792	1.116	1.0952	0.0208	0.0182	0.0026	1.063	
CB	D	NP	1027	5.06	2.559	0.998	0.9681	0.0299	0.026	0.0039	1.063	F
CB	D	NP	1028	3.461	1.655	0.787	0.5972	0.1898	0.156	0.0338	1.063	
CB	D	NP	1029	0.743	0.339	0.214					1.063	
CB	E	P	1030			0.961					1.063	
CB	E	P	1031	4.5		1.038	1.0276	0.0104	0.0078	0.0026	1.063	F
CB	E	P	1032	4.262	2.545	1.009					1.063	
CB	E	P	1033	5.171	2.83	1.173					1.063	F
CB	E	P	1034	4.609	2.272	0.989					1.063	
CB	E	P	1035	4.241	2.112	0.876					1.063	
CB	E	P	1036	5.344	3.027	1.012					1.063	
CB	E	P	1037	5.794	3.164	1.325					1.063	
CB	E	P	1038	6.346	2.568	1.183	1.1557	0.0273	0.0208	0.0065	1.063	M
CB	E	P	1039	4.933	2.512	1.039	0.8659	0.1731	0.138	0.0351	1.063	
CB	E	P	1040	4.31	2.2	0.891					1.063	
CB	E	P	1041	4.439	2.462	1.145					1.063	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	E	P	1042	4.898	2.856	1.125	1.1249	0.000	0.0001	0.0000	1.063	F
CB	E	P	1043	4.676	2.509	1.141					1.063	F
CB	E	P	1044	5.492	2.44	1.16	1.0833	0.0767	0.0624	0.0143	1.063	
CB	E	P	1045	4.344	2.209	1.041	1.028	0.013	0.013	0.0000	1.063	
CB	E	P	1046	5.745	2.497	1.251	1.238	0.013	0.0117	0.0013	1.063	
CB	E	P	1047	4.213	2.172	0.935					1.063	
CB	E	P	1048	5.694	2.749	1.315					1.063	
CB	E	P	1049	3.92	2.104	0.94	0.8971	0.0429	0.0377	0.0052	1.063	
CB	E	P	1050	3.958	2.029	0.895	0.8794	0.0156	0.0117	0.0039	1.063	
CB	E	P	1051	4.016	2.026	0.873	0.86	0.013	0.0091	0.0039	1.063	
CB	E	P	1052	4.375	2.546	1.017					1.063	
CB	E	P	1053			1.033					1.063	
CB	E	P	1054	4.08	2.22	0.965					1.063	
CB	E	P	1055	3.679	2.001	0.979					1.063	
CB	E	P	1056	5.812	3.032	1.266					1.063	
CB	E	P	1057	3.891	2.129	0.926	0.9	0.026	0.0208	0.0052	1.063	
CB	E	P	1058	4.89	2.603	1.063	1.0422	0.0208	0.0156	0.0052	1.063	
CB	E	P	1059	1.424	0.596	0.398					1.063	
CB	E	P	1060	4.734	2.396	1.103					1.063	
CB	E	P	1061	1.408	0.619	0.353					1.063	
CB	E	P	1062	4.706	2.934	1.115	1.0981	0.0169	0.0117	0.0052	1.063	
CB	E	P	1063	6.427	3.344	1.305	1.2985	0.007	0.0065	0.0000	1.063	
CB	E	P	1064	4.459	2.459	1.113					1.063	
CB	E	P	1065	4.121	1.926	0.925	0.91	0.015	0.015	0.0000	1.063	
CB	E	P	1066	3.542	1.727	0.83					1.063	
CB	E	P	1067	4.153	2.063	0.921					1.063	
CB	E	P	1068	4.475	2.067	0.959					1.063	
CB	E	P	1069	4.804	2.513	1.058					1.063	
CB	E	P	1070	4.811	2.571	1.059					1.063	
CB	E	P	1071	3.769	2.07	0.939					1.063	
CB	E	P	1072	4.004	2.092	0.914					1.063	
CB	E	P	1073	5.046	2.869	1.162					1.063	
CB	E	P	1074	0.8							1.063	
CB	E	P	1075	0.4		0.127					1.063	
CB	E	NP	1076	2.951	1.397	0.683					1.063	
CB	E	NP	1077	6.442	3.372	1.241	1.2163	0.0247	0.0221	0.0026	1.063	
CB	E	NP	1078	6.682	3.727	1.398	1.3915	0.0065	0.0052	0.0013	1.063	
CB	E	NP	1079	5.728	2.655	1.125	1.1172	0.0078	0.0052	0.0026	1.063	
CB	E	NP	1080	3.814	1.437	0.812	0.7145	0.0975	0.0858	0.0117	1.063	
CB	E	NP	1081	6.695	3.294	1.44	1.4231	0.0169	0.0143	0.0026	1.063	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	E	NP	1082	5.23	2.591	1.109					1.063	
CB	E	NP	1083	4.899	2.551	1.093	1.0592	0.0338	0.0338	0.0000	1.063	
CB	E	NP	1084	5.838	2.786	1.152	1.1286	0.0234	0.0208	0.0026	1.063	M
CB	E	NP	1085	6.309	3.603	1.258	1.2437	0.0143	0.013	0.0013	1.063	
CB	E	NP	1086	6.235	3.29	1.207	1.1537	0.0533	0.0429	0.0104	1.063	
CB	E	NP	1087	5.831	2.992	1.049	0.9931	0.0559	0.0416	0.0143	1.063	M
CB	E	NP	1088	5.099	2.496	1.034	0.9586	0.0754	0.0624	0.0130	1.063	M
CB	E	NP	1089	6.767	3.617	1.289					1.063	M
CB	E	NP	1090	6.784	3.432	1.241					1.063	M
CB	E	NP	1091	6.541	3.219	1.342	1.316	0.026	0.0208	0.0052	1.063	
CB	E	NP	1092	5.382	2.907	1.236	1.2152	0.0208	0.0182	0.0026	1.063	M
CB	E	NP	1093	4.305	2.006	0.889	0.842	0.047	0.0379	0.0091	1.063	
CB	E	NP	1094	4.045	1.748	0.885					1.063	
CB	E	NP	1095	5.465	2.826	1.165					1.063	
CB	E	NP	1096	5.882	2.812	1.23	1.2027	0.0273	0.0234	0.0039	1.063	
CB	E	NP	1097	6.257	3.048	1.209	1.1882	0.0208	0.0182	0.0026	1.063	F
CB	E	NP	1098	4.998	2.801	1.126	1.1078	0.0182	0.0169	0.0013	1.063	
CB	E	NP	1099	5.679	3.071	1.156	1.0897	0.0663	0.0585	0.0078	1.063	
CB	E	NP	1100	3.771	1.762	0.844					1.063	
CB	E	NP	1101	5.824	3.295	1.184	1.1645	0.0195	0.0195	0.0000	1.063	F
CB	E	NP	1102	5.532	2.951	1.129	1.1069	0.0221	0.0208	0.0013	1.063	
CB	E	NP	1103	5.33	2.938	1.241					1.063	
CB	E	NP	1104	4.485	2.406	0.958	0.9151	0.0429	0.0403	0.0026	1.063	
CB	E	NP	1105	5.928	3.246	1.16	1.1405	0.0195	0.0156	0.0039	1.063	
CB	E	NP	1106	5.726	3.278	1.23					1.063	
CB	E	NP	1107	5.641	3.021	1.168	1.1472	0.0208	0.0182	0.0026	1.063	
CB	E	NP	1108	6.003	3.408	1.179	1.1686	0.010	0.0104	0.0000	1.063	
CB	E	NP	1109	6.689	3.312	1.272	1.246	0.026	0.0247	0.0013	1.063	M
CB	E	NP	1110	4.772	2.767	1.099					1.063	
CB	E	NP	1111	5.727	3.254	1.163	1.1006	0.0624	0.0494	0.0130	1.063	
CB	E	NP	1112	4.798	2.304	1.068	1.0316	0.0364	0.0312	0.0052	1.063	
CB	E	NP	1113	4.373	2.071	0.901					1.063	
CB	E	NP	1114	6.252	3.33	1.214	1.1919	0.0221	0.0221	0.0000	1.063	M
CB	E	NP	1115	6.856	3.431	1.355					1.063	M
CB	E	NP	1116	5.792	2.819	1.214	1.1997	0.0143	0.0117	0.0026	1.063	
CB	E	NP	1117	3.435	1.619	0.767					1.063	
CB	E	NP	1118	5.607	2.94	1.19	1.1718	0.0182	0.013	0.0052	1.063	
CB	E	NP	1119	5.577	3.017	1.253	1.188	0.065	0.0507	0.0143	1.063	
CB	E	NP	1120	5.327	2.535	1.181	1.142	0.039	0.0312	0.0078	1.063	
CB	E	NP	1121	5.498	2.95	1.119	1.0878	0.0312	0.026	0.0052	1.063	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
CB	E	NP	1122	5.217	3.215	1.147					1.063	
CB	E	NP	1123	5.875	3.402	1.195	1.1833	0.0117	0.0091	0.0026	1.063	
CB	E	NP	1124	6.691	3.259	1.32	1.2914	0.0286	0.0234	0.0052	1.063	M
CB	E	NP	1125	0.873	0.395	0.237					1.063	
CB	E	NP	1126	1.211	0.539	0.291					1.063	
CB	E	NP	1127	2.51	1.172	0.585					1.063	
CB	E	NP	1128	2.573	1.317	0.639	0.4856	0.1534	0.1222	0.0312	1.063	
CB	E	NP	1129	3.7	2.114	0.915					1.063	
CB	E	NP	1130	3.955	1.805	0.865					1.063	
CB	E	NP	1131	4.517	2.431	1.006					1.063	
CB	E	NP	1132	4.663	2.19	0.949					1.063	
CB	E	NP	1133	5.063	2.991	1.08	1.0501	0.0299	0.0299	0.0000	1.063	M
CB	E	NP	1134	5.215	2.779	1.038	0.9964	0.0416	0.0338	0.0078	1.063	F
CB	E	NP	1135	4.873	2.222	1.042	0.9718	0.0702	0.0611	0.0091	1.063	F
CB	E	NP	1136	5.55	2.904	1.12					1.063	M
CB	E	NP	1137	5.381	3.102	1.124	1.0694	0.0546	0.0429	0.0117	1.063	F
CB	E	NP	1138	5.914	3.324	1.289	1.2786	0.0104	0.0091	0.0013	1.063	M
CB	E	NP	1139	6.372	3.226	1.218					1.063	
CB	E	NP	1140	5.967	3.263	1.191	1.178	0.013	0.0104	0.0026	1.063	
CB	E	NP	1141	0.547	0.221	0.156					1.063	
MC	A	NP	630	2.036	0.92	0.538					1.008	
MC	A	NP	631	3.985	1.663	0.9					1.008	
MC	A	NP	632	2.334	1.002	0.534					1.008	
MC	A	NP	633	2.139	0.976	0.529					1.008	
MC	A	NP	634	2.767	1.261	0.638					1.008	
MC	A	NP	635	2.873	1.133	0.658					1.008	
MC	A	NP	636	7.562	4.335	1.339					1.008	F
MC	A	NP	637	7.49	3.671	1.492					1.008	M
MC	A	NP	638	7.066	3.292	1.291					1.008	M
MC	A	NP	639	6.974	3.72	1.352					1.008	
MC	A	NP	640	6.961	3.451	1.255					1.008	M
MC	A	NP	641	6.484	3.604	1.204					1.008	M
MC	B	P	642	5.443	2.799	1.141	1.1033	0.0377	0.0299	0.0078	1.005	F
MC	B	P	643	5.575	3.433	1.341					1.005	
MC	B	P	644	5.648	2.913	1.142					1.005	M
MC	B	P	645	6.282	3.281	1.226	1.2182	0.008	0.0078	0.0000	1.005	F
MC	B	P	646	5.634	2.975	1.289	1.2708	0.0182	0.0143	0.0039	1.005	F
MC	B	P	647	4.445	2.265	1.127	1.1187	0.0083	0.0078	0.0005	1.005	
MC	B	P	648	5.547	2.655	1.148	1.1376	0.0104	0.0078	0.0026	1.005	
MC	B	P	649	5.473	2.671	1.257					1.005	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	B	P	650	5.03	3.017	1.112	1.105	0.007	0.0065	0.0005	1.005	
MC	B	P	651	3.318		0.839					1.005	M
MC	B	P	652	6.251	2.846	1.255					1.005	F
MC	B	P	653	5.646	2.766	1.169	1.1607	0.0083	0.0078	0.0005	1.005	F
MC	B	P	654	5.186	2.25	1.11	1.1022	0.0078	0.0065	0.0013	1.005	
MC	B	P	655	4.783	2.454	1.046	1.0135	0.0325	0.0221	0.0104	1.005	
MC	B	P	656	5.341	2.868	1.164	1.1531	0.0109	0.0104	0.0005	1.005	M
MC	B	P	657	4.521	2.369	1.05	1.0448	0.005	0.0052	0.0000	1.005	
MC	B	P	658	4.958	2.695	1.089	1.0786	0.010	0.0104	0.0000	1.005	F
MC	B	P	659	6.802	3.604	1.285	1.2668	0.0182	0.0156	0.0026	1.005	F
MC	B	P	660	5.638	2.946	1.246	1.207	0.039	0.0299	0.0091	1.005	F
MC	B	P	661	6.112	2.809	1.231	1.1972	0.0338	0.0338	0.0000	1.005	F
MC	B	P	662	7.491	4.268	1.442	1.4376	0.0044	0.0039	0.0005	1.005	
MC	B	P	663	6.511	3.195	1.276					1.005	
MC	B	P	664	3.859	1.925	0.944	0.9271	0.0169	0.0143	0.0026	1.005	M
MC	B	P	665			1.104					1.005	
MC	B	P	666	4.787	2.673	1.09	1.0778	0.0122	0.0117	0.0005	1.005	M
MC	B	P	667	4.4		1.058					1.005	
MC	B	P	668	4.404	2.14	1.005	0.9902	0.0148	0.0143	0.0005	1.005	F
MC	B	P	669	2.858	1.352	0.713					1.005	
MC	B	P	670	2.796	1.446	0.72	0.7031	0.0169	0.0143	0.0026	1.005	
MC	B	P	671	6.05	3.175	1.245	1.2346	0.0104	0.0078	0.0026	1.005	F
MC	B	P	672	4.731	2.199	1.119	1.1021	0.0169	0.0169	0.0000	1.005	M
MC	B	P	673	4.145	2.134	0.956	0.7542	0.2018	0.168	0.0338	1.005	
MC	B	P	674			1.123	1.1191	0.004	0.0039	0.0000	1.005	F
MC	B	P	675	6.158	3.358	1.315	1.3085	0.007	0.0065	0.0000	1.005	
MC	B	P	676	5.061	2.221	1.062					1.005	
MC	B	P	677	4.61	2.764	1.077	1.0523	0.0247	0.0247	0.0000	1.005	F
MC	B	P	678	6.325	3.667	1.353					1.005	M
MC	B	P	679	4.348	2.439	1.029	0.9627	0.0663	0.0559	0.0104	1.005	F
MC	B	P	680	4.66	2.529	1.03	1.0079	0.0221	0.0208	0.0013	1.005	
MC	B	P	681	4.441	2.244	1.034					1.005	
MC	B	P	682	6.013	3.025	1.227	1.2114	0.0156	0.0156	0.0000	1.005	
MC	B	P	683	5.74	3.373	1.227					1.005	M
MC	B	P	684	3.464	1.685	0.902	0.8279	0.0741	0.0585	0.0156	1.005	
MC	B	P	685	5.586	2.646	1.177	1.1679	0.0091	0.0078	0.0013	1.005	M
MC	B	P	686	4.272	1.862	0.947	0.7016	0.2454	0.196	0.0494	1.005	
MC	B	P	687	5.992	3.16	1.326	1.3117	0.0143	0.0117	0.0026	1.005	F
MC	B	P	688	4.122	1.927	0.977					1.005	F
MC	B	P	689	3.5	1.7	0.866	0.8192	0.0468	0.039	0.0078	1.005	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	B	P	690			1.405					1.005	
MC	B	P	691			0.864	0.7717	0.0923	0.0676	0.0247	1.005	
MC	B	P	692	1.8	0.7	0.406					1.005	
MC	B	P	693	5.491	2.721	1.19	1.1817	0.0083	0.0078	0.0005	1.005	F
MC	B	P	694	5.023	2.652	1.113	1.1091	0.004	0.0039	0.0000	1.005	F
MC	B	P	695	3.907	1.751	0.84	0.8296	0.010	0.0104	0.0000	1.005	
MC	B	P	696	5.49	2.7	1.309	1.3064	0.003	0.0026	0.0000	1.005	
MC	B	P	697	7.905	4.165	1.549					1.005	M
MC	B	P	698	6.804	3.027	1.299					1.005	M
MC	B	P	699	6.257	3.007	1.321	1.321	0.000	0.0000	0.0000	1.005	M
MC	B	P	700	6.638	3.197	1.378					1.005	M
MC	B	P	701	6.44	3.58	1.417	1.4022	0.0148	0.0143	0.0005	1.005	M
MC	B	P	702	6.443	3.655	1.16	1.1392	0.0208	0.0143	0.0065	1.005	
MC	B	P	703	1.651	0.815	0.447					1.005	
MC	B	NP	704	6.505	3.556	1.299	1.2881	0.0109	0.0104	0.0005	1.005	M
MC	B	NP	705	6.252	3.142	1.216	1.1861	0.0299	0.0247	0.0052	1.005	
MC	B	NP	706	5.696	3.088	1.258					1.005	M
MC	B	NP	707	5.216	2.821	1.086	1.0418	0.0442	0.0416	0.0026	1.005	
MC	B	NP	708	4.804	2.2	0.956					1.005	
MC	B	NP	709	3.799	1.531	0.809	0.5591	0.2499	0.207	0.0429	1.005	
MC	B	NP	710	6.036	2.874	1.257					1.005	F
MC	B	NP	711	6.411	3.054	1.348	1.3376	0.0104	0.0078	0.0026	1.005	F
MC	B	NP	712	5.151	2.315	1.033					1.005	
MC	B	NP	713	6.301	3.129	1.158					1.005	M
MC	B	NP	714	5.958	3.1	1.156	1.0676	0.0884	0.0767	0.0117	1.005	M
MC	B	NP	715	6.321	2.951	1.296					1.005	M
MC	B	NP	716	6.009	2.909	1.178					1.005	M
MC	B	NP	717	6.028	3.242	1.248					1.005	M
MC	B	NP	718	5.927	3.061	1.291					1.005	F
MC	B	NP	719	5.117	2.25	1.017					1.005	
MC	B	NP	720	2.966	1.209	0.647	0.2854	0.3616	0.294	0.0676	1.005	
MC	B	NP	721	2.31	0.994	0.595	0.2236	0.3714	0.309	0.0624	1.005	
MC	B	NP	722	6.015	3.192	1.178	1.1598	0.0182	0.013	0.0052	1.005	F
MC	B	NP	723	6.708	3.301	1.205					1.005	F
MC	B	NP	724	7.292	3.452	1.405	1.3972	0.0078	0.0065	0.0013	1.005	M
MC	B	NP	725	6.461	2.525	1.285					1.005	M
MC	B	NP	726	6.946	3.808	1.271	1.2606	0.010	0.0104	0.0000	1.005	M
MC	B	NP	727	7.211	3.411	1.397					1.005	M
MC	B	NP	728	6.215	3.434	1.246	1.2122	0.0338	0.0338	0.0000	1.005	
MC	B	NP	729	6.589	3.086	1.287					1.005	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	B	NP	730	8.24	4.049	1.546					1.005	M
MC	B	NP	731	7.286	4.437	1.366					1.005	M
MC	B	NP	732	7.22	3.888	1.333					1.005	M
MC	B	NP	733	7.245	3.939	1.288					1.005	
MC	B	NP	734	7.125	3.52	1.276	1.2677	0.0083	0.0078	0.0005	1.005	M
MC	B	NP	735	7.015	3.118	1.259					1.005	M
MC	B	NP	736	6.851	3.782	1.27	1.2622	0.0078	0.0026	0.0052	1.005	F
MC	B	NP	737	6.264	3.155	1.299					1.005	F
MC	B	NP	738			1.451					1.005	
MC	B	P	739			1.259					1.014	
MC	B	P	740	6.5	2.8	1.312	1.2964	0.0156	0.0104	0.0052	1.014	M
MC	B	P	741	7.107	4.397	1.403	1.3783	0.0247	0.0247	0.0000	1.014	F
MC	B	P	742	5.3		1.211	1.1954	0.0156	0.013	0.0026	1.014	M
MC	B	P	743	2.658	1.365	0.68	0.537	0.143	0.1209	0.0221	1.014	M
MC	B	P	744			1.186	1.1652	0.0208	0.0208	0.0000	1.014	M
MC	B	P	745			1.032	0.9774	0.0546	0.039	0.0156	1.014	F
MC	B	P	746	7.24		1.369	1.3625	0.007	0.0065	0.0000	1.014	F
MC	B	P	747	6.1	3.426	1.266	1.253	0.013	0.0117	0.0013	1.014	F
MC	B	P	748	5.972	3.109	1.298	1.2772	0.0208	0.0156	0.0052	1.014	M
MC	B	P	749	4.465	2.086	0.91					1.014	F
MC	B	P	750	6.864	3.541	1.378					1.014	
MC	B	P	751	3.014	1.539	0.799					1.014	
MC	B	P	752	4	2	0.955	0.8419	0.1131	0.0962	0.0169	1.014	M
MC	B	P	753	4.49	2.381	1.039	0.9948	0.0442	0.0377	0.0065	1.014	M
MC	B	P	754	6.031	2.964	1.295					1.014	
MC	B	P	755	5.756	3.306	1.352					1.014	F
MC	B	P	756	5.671	2.532	1.294	1.2844	0.0096	0.0091	0.0005	1.014	M
MC	B	P	757	6.268	3.414	1.268	1.2433	0.0247	0.0247	0.0000	1.014	F
MC	B	P	758	6.69	3.673	1.339					1.014	M
MC	B	P	759	4.128	1.97	0.962	0.7277	0.2343	0.194	0.0403	1.014	F
MC	B	P	760	4.959	2.901	1.168	1.1602	0.008	0.0078	0.0000	1.014	
MC	B	P	761	7.1		1.468					1.014	F
MC	B	P	762	4.204	1.923	0.943	0.6755	0.2675	0.222	0.0455	1.014	M
MC	B	P	763	4.452	2.044	0.978					1.014	M
MC	B	P	764	6.316	3.381	1.283	1.2713	0.0117	0.0104	0.0013	1.014	M
MC	B	P	765	5.262	2.569	1.146	1.1382	0.0078	0.0065	0.0013	1.014	M
MC	B	P	766	3.951	1.739	0.946	0.8095	0.1365	0.117	0.0195	1.014	M
MC	B	P	767	6.172	3.426	1.217					1.014	
MC	B	P	768	6.472	3.172	1.287					1.014	M
MC	B	P	769	5.493	2.651	1.163					1.014	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	B	P	770	4.817	2.409	1.072					1.014	M
MC	B	P	771	5.531	2.872	1.169					1.014	F
MC	B	P	772	3.393	1.601	0.846	0.7706	0.0754	0.0624	0.0130	1.014	
MC	B	P	773	2.616	1.094	0.599					1.014	
MC	B	P	774	6.251	3.244	1.241					1.014	F
MC	B	P	775	3.879	2.137	0.919	0.8943	0.0247	0.0156	0.0091	1.014	F
MC	B	P	776	0.96	0.401	0.282					1.014	
MC	B	P	777	6.893	3.69	1.276					1.014	F
MC	B	P	778	6.721	4.166	1.277					1.014	M
MC	B	P	779	7.264	3.565	1.467					1.014	F
MC	B	P	780	6.974	3.707	1.325					1.014	F
MC	B	P	781	6.927	3.916	1.4					1.014	M
MC	B	P	782	6.975	3.432	1.32					1.014	
MC	B	P	783	6.492	3.366	1.276					1.014	F
MC	B	NP	784	7.084	4.079	1.298	1.2941	0.004	0.0039	0.0000	1.014	M
MC	B	NP	785	6.724	3.818	1.312	1.2886	0.0234	0.0208	0.0026	1.014	M
MC	B	NP	786	6.772	4.129	1.317					1.014	
MC	B	NP	787	5.791	2.611	1.154					1.014	M
MC	B	NP	788	2.986	1.293	0.702					1.014	
MC	B	NP	789	6.363	3.312	1.272					1.014	M
MC	B	NP	790	6.598	3.336	1.358	1.3476	0.010	0.0104	0.0000	1.014	F
MC	B	NP	791	6.284	3.209	1.278					1.014	M
MC	B	NP	792	6.531	3.392	1.372	1.3551	0.0169	0.0156	0.0013	1.014	M
MC	B	NP	793	6.768	3.326	1.341					1.014	M
MC	B	NP	794	6.312	3.353	1.225					1.014	M
MC	B	NP	795	5.235	2.454	1.131	1.0465	0.0845	0.0715	0.0130	1.014	F
MC	B	NP	796	6.339	3.747	1.298	1.2845	0.0135	0.013	0.0005	1.014	M
MC	B	NP	797	6.675	3.469	1.278	1.2619	0.0161	0.0156	0.0005	1.014	
MC	B	NP	798	6.39	3.526	1.267					1.014	F
MC	B	NP	799	6.582	3.959	1.335					1.014	
MC	B	NP	800	7.19	3.457	1.434	1.4275	0.007	0.0065	0.0000	1.014	
MC	B	NP	801	5.462	2.53	1.189					1.014	F
MC	B	NP	802	6.375	3.225	1.367					1.014	M
MC	B	NP	803	7.121	3.123	1.315					1.014	M
MC	B	NP	804	6.891	3.764	1.381					1.014	M
MC	B	NP	805	4.306	1.94	0.872					1.014	M
MC	B	NP	806	6.742	3.728	1.345	1.3281	0.0169	0.013	0.0039	1.014	M
MC	B	NP	807	6.355	2.886	1.202	1.1916	0.0104	0.0078	0.0026	1.014	M
MC	B	NP	808	1.455	0.69	0.351					1.014	
MC	B	NP	809	6.132	2.678	1.184					1.014	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	B	NP	810	5.811	2.868	1.23					1.014	M
MC	B	NP	811	6.507	3.38	1.248					1.014	M
MC	B	NP	812	6.748	3.324	1.35					1.014	M
MC	B	NP	813	6.79	4.111	1.315					1.014	M
MC	B	NP	814	4.938	2.06	0.97					1.014	M
MC	B	NP	815	5.759	2.812	1.077					1.014	M
MC	B	NP	816	3.714	1.518	0.864	0.5738	0.2902	0.246	0.0442	1.014	
MC	B	NP	817	6.686	3.386	1.292	1.2673	0.0247	0.0247	0.0000	1.014	F
MC	B	NP	818	5.583	2.681	1.069					1.014	F
MC	B	NP	819	6.783	3.315	1.29					1.014	M
MC	B	NP	820	5.986	3.104	1.253	1.2205	0.0325	0.0234	0.0091	1.014	
MC	B	NP	821	6.807	3.167	1.28					1.014	
MC	B	NP	822	7.173	3.763	1.398	1.3915	0.0065	0.0052	0.0013	1.014	F
MC	B	NP	823	6.118	3.182	1.226	1.2104	0.0156	0.0156	0.0000	1.014	F
MC	B	NP	824	3.379	1.637	0.814					1.014	
MC	B	NP	825	1.453	0.606	0.363					1.014	
MC	B	NP	826	0.515	0.18	0.1027					1.014	
MC	B	NP	827	5.494	2.599	1.109					1.014	F
MC	B	NP	828	5.64	3.104	1.239					1.014	
MC	B	NP	829	5.688	2.738	1.178					1.014	F
MC	B	NP	830	5.871	2.926	1.182					1.014	
MC	B	NP	831	6.171	3.279	1.276	1.2396	0.0364	0.0325	0.0039	1.014	F
MC	B	NP	832	6.347	3.701	1.332					1.014	
MC	B	NP	833	6.709	3.516	1.391	1.3827	0.0083	0.0078	0.0005	1.014	
MC	B	NP	834	6.515	3.399	1.351					1.014	M
MC	B	NP	835	6.976	3.376	1.254					1.014	
MC	B	NP	836	6.928	3.182	1.317	1.2988	0.0182	0.0182	0.0000	1.014	
MC	B	NP	837	7.068	3.508	1.5					1.014	M
MC	B	NP	838	7.013	3.76	1.418					1.014	M
MC	B	NP	839	6.941	3.632	1.199					1.014	F
MC	B	NP	840	7.353	3.701	1.34	1.3218	0.0182	0.0143	0.0039	1.014	M
MC	B	NP	841	8.112	4.57	1.448					1.014	
MC	B	NP	842	7.308	3.856	1.346					1.014	M
MC	B	NP	843	7.271	3.628	1.342					1.014	M
MC	B	NP	844	7.17	3.825	1.391	1.3819	0.0091	0.0065	0.0026	1.014	M
MC	B	NP	845	7.332	3.772	1.422					1.014	F
MC	B	NP	846	7.449	4.09	1.342					1.014	M
MC	B	NP	847	7.085	3.981	1.27	1.2518	0.0182	0.0182	0.0000	1.014	M
MC	C	P	1300	4.794	2.137	0.982					1.003	M
MC	C	P	1301	3.896	2.008	0.943	0.7688	0.1742	0.1144	0.0598	1.003	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	P	1302	5.608	2.71	1.162	1.162				1.003	
MC	C	P	1303	6.82	3.9	1.402					1.003	M
MC	C	P	1304	6.2	3.212	1.256	1.1962	0.0598	0.0507	0.0091	1.003	F
MC	C	P	1305	6.573	3.299	1.244	1.2349	0.0091	0.0078	0.0013	1.003	M
MC	C	P	1306	6.07	2.807	1.246					1.003	F
MC	C	P	1307	2.707	1.233	0.664	0.6276	0.0364	0.0364	0.0000	1.003	
MC	C	P	1308	5.439	2.656	1.148	1.1129	0.0351	0.026	0.0091	1.003	F
MC	C	P	1309	4.567	2.171	1.047	0.9547	0.0923	0.0715	0.0208	1.003	F
MC	C	P	1310	7.22	4.257	1.404					1.003	M
MC	C	P	1311	6.739	3.543	1.357	1.3466	0.010	0.0104	0.0000	1.003	M
MC	C	P	1312	5.673	2.956	1.177	1.1523	0.0247	0.0182	0.0065	1.003	F
MC	C	P	1313	6.063	2.8	1.258	1.1592	0.0988	0.091	0.0078	1.003	M
MC	C	P	1314	5.858	3.063	1.2	1.1428	0.0572	0.0494	0.0078	1.003	M
MC	C	P	1315	5.279	2.501	1.117					1.003	M
MC	C	P	1316	4.613	2.219	0.956					1.003	F
MC	C	P	1317	4.854	2.046	1.084					1.003	M
MC	C	P	1318	5.362	2.839	1.144					1.003	F
MC	C	P	1319	3.567	1.847	0.86	0.7248	0.1352	0.1079	0.0273	1.003	
MC	C	P	1320	4.745	2.318	1.016	0.8886	0.1274	0.1001	0.0273	1.003	M
MC	C	P	1321	5.284	2.375	1.029	0.917	0.112	0.0925	0.0195	1.003	F
MC	C	P	1322	5.574	2.967	1.25					1.003	F
MC	C	P	1323	6.2	3.008	1.199	1.1678	0.0312	0.0221	0.0091	1.003	F
MC	C	P	1324	4.936	2.299	1.05					1.003	F
MC	C	P	1325	3.903		1.01	0.9892	0.0208	0.0169	0.0039	1.003	
MC	C	P	1326	6.507	3.112	1.376	1.3708	0.0052	0.0026	0.0026	1.003	M
MC	C	P	1327	7.384	3.603	1.319					1.003	F
MC	C	P	1328	7.144	3.328	1.33					1.003	M
MC	C	P	1329	5.53	2.906	1.105					1.003	M
MC	C	P	1330	6.536	3.37	1.339	1.3351	0.004	0.0039	0.0000	1.003	F
MC	C	P	1331	5.248	2.359	1.041	0.9734	0.0676	0.0559	0.0117	1.003	F
MC	C	P	1332	5.827	3.101	1.182					1.003	M
MC	C	P	1333	5.413	2.592	1.024					1.003	F
MC	C	P	1334	4.98	2.38	1.059	0.968	0.091	0.0754	0.0156	1.003	M
MC	C	P	1335	7.056	3.858	1.364					1.003	M
MC	C	P	1336	4.714	2.171	1.053					1.003	M
MC	C	P	1337	5.334	2.375	1.106	0.9441	0.1619	0.132	0.0299	1.003	
MC	C	P	1338	4.804	2.128	1.024	0.8579	0.1661	0.131	0.0351	1.003	M
MC	C	P	1339	5.302	2.516	1.154	1.0734	0.0806	0.0663	0.0143	1.003	M
MC	C	P	1340	5.641	3.266	1.333	1.3109	0.0221	0.0182	0.0039	1.003	M
MC	C	P	1341	5.56	2.741	1.137					1.003	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	P	1342	6.342	3.4	1.291					1.003	M
MC	C	P	1343	5.392	2.463	1.021					1.003	M
MC	C	P	1344	4.206	2.148	0.97	0.8803	0.0897	0.0806	0.0091	1.003	F
MC	C	P	1345	4.249	1.742	0.894	0.6019	0.2921	0.27	0.0221	1.003	M
MC	C	P	1346	5.492	3.14	1.373					1.003	M
MC	C	P	1347	5.072	2.727	1.126					1.003	F
MC	C	P	1348	5.819	2.816	1.296					1.003	
MC	C	P	1349	4.773	2.186	0.971					1.003	M
MC	C	P	1350	4.679	2.161	1.048					1.003	F
MC	C	P	1351	3.497	1.52	0.778					1.003	
MC	C	P	1352	6.425	3.37	1.385					1.003	F
MC	C	P	1353	5.114	2.238	1.056	0.9013	0.1547	0.1287	0.0260	1.003	F
MC	C	P	1354	2.332	1.039	0.616					1.003	
MC	C	P	1355	5.877	2.471	1.224	1.2149	0.009	0.0091	0.0000	1.003	F
MC	C	P	1356	5.436	2.607	1.196					1.003	M
MC	C	P	1357	4.554	2.117	1.017	0.9429	0.0741	0.0572	0.0169	1.003	F
MC	C	P	1358	6.686	3.371	1.365	1.3507	0.0143	0.013	0.0013	1.003	F
MC	C	P	1359	4.403	2.289	1.07	1.0063	0.0637	0.052	0.0117	1.003	F
MC	C	P	1360	6.478	3.237	1.378	1.3728	0.005	0.0052	0.0000	1.003	F
MC	C	P	1361	5.674	2.734	1.129					1.003	M
MC	C	P	1362	3.27	1.5	0.811					1.003	F
MC	C	P	1363	5.501	2.576	1.224	1.1642	0.0598	0.0494	0.0104	1.003	F
MC	C	P	1364	6.87	3.763	1.379	1.3751	0.004	0.0039	0.0000	1.003	F
MC	C	P	1365	4.926	2.331	1.01					1.003	F
MC	C	P	1366	1.249	0.535	0.33					1.003	
MC	C	P	1367	4.539	2.281	0.965	0.9247	0.0403	0.0312	0.0091	1.003	M
MC	C	P	1368			1.422					1.003	F
MC	C	P	1369	4.78	2.36	1.018	0.9855	0.0325	0.0273	0.0052	1.003	M
MC	C	P	1370	4.09	1.8091	0.932					1.003	
MC	C	P	1371	4.45	2.108	0.98					1.003	F
MC	C	P	1372	6.88	3.463	1.496	1.4947	0.001	0.0013	0.0000	1.003	M
MC	C	P	1373	1.524	0.631	0.369					1.003	
MC	C	P	1374	4.802	2.277	1.027	0.8736	0.1534	0.1209	0.0325	1.003	M
MC	C	P	1375	5.612	3.029	1.317	1.2767	0.0403	0.0325	0.0078	1.003	F
MC	C	P	1376	4.626	2.074	1.009					1.003	F
MC	C	P	1377	5.063	2.394	1.041					1.003	F
MC	C	P	1378	3.851	1.751	0.823					1.003	
MC	C	P	1379	3.892	1.861	0.949					1.003	F
MC	C	P	1380	2.436	1.147	0.578					1.003	
MC	C	P	1381	4.043	1.818	0.894					1.003	

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	P	1382	5.965	2.795	1.194	1.0796	0.1144	0.0897	0.0247	1.003	
MC	C	P	1383	5.709	2.892	1.216	1.1939	0.0221	0.0182	0.0039	1.003	F
MC	C	P	1384	5.648	2.565	1.094					1.003	F
MC	C	P	1385	5.106	2.206	1.122	1.0401	0.0819	0.0637	0.0182	1.003	F
MC	C	P	1386	3.533	1.592	0.84					1.003	
MC	C	P	1387	5.258	2.509	1.116	1.0562	0.0598	0.052	0.0078	1.003	M
MC	C	P	1388	4.666	2.142	0.962					1.003	
MC	C	P	1389	3.797	1.643	0.833					1.003	
MC	C	P	1390	6.663	3.43	1.375	1.3659	0.009	0.0091	0.0000	1.003	M
MC	C	P	1391	7.343	4.03	1.369					1.003	M
MC	C	P	1392	7.367	3.932	1.496					1.003	M
MC	C	P	1393	7.939	3.879	1.448	1.4402	0.008	0.0078	0.0000	1.003	F
MC	C	P	1394	7.426	3.817	1.355	1.3549	0.000	0.0001	0.0000	1.003	F
MC	C	P	1395	7.322	4.37	1.524					1.003	M
MC	C	P	1396	7.515	3.725	1.576	1.563	0.013	0.013	0.0000	1.003	F
MC	C	P	1397	7.437	3.191	1.415	1.4072	0.0078	0.0052	0.0026	1.003	M
MC	C	P	1398	7.446	3.711	1.474	1.4701	0.004	0.0039	0.0000	1.003	M
MC	C	P	1399	7.711	3.911	1.532					1.003	F
MC	C	P	1400	3.333	1.412	0.745					1.003	
MC	C	P	1401	3.576	1.577	0.761					1.003	
MC	C	P	1402	4.892	1.94	1.019					1.003	
MC	C	NP	1403	7.378	3.217	1.437					1.003	
MC	C	NP	1404	2.02	0.94	0.466					1.003	
MC	C	NP	1405	1.838	0.864	0.424					1.003	
MC	C	NP	1406	1.212	0.548	0.315					1.003	
MC	C	NP	1407	1.266	0.575	0.314					1.003	
MC	C	NP	1408	1.33	0.643	0.338					1.003	
MC	C	NP	1409	1.236	0.531	0.328					1.003	
MC	C	NP	1410	1.452	0.664	0.372					1.003	
MC	C	NP	1411	7.141	3.137	1.279					1.003	M
MC	C	NP	1412	6.95	3.419	1.318					1.003	F
MC	C	NP	1413	6.89	3.523	1.362					1.003	M
MC	C	NP	1414	6.714	3.02	1.346	1.3421	0.004	0.0039	0.0000	1.003	M
MC	C	NP	1415	4.996	2.482	1.05					1.003	F
MC	C	NP	1416	5.293	2.322	1.043					1.003	F
MC	C	NP	1417	5.237	2.559	1.107	1.0654	0.0416	0.0416	0.0000	1.003	M
MC	C	NP	1418	6.962	3.483	1.412					1.003	M
MC	C	NP	1419	5.265	2.746	1.222	1.2168	0.0052	0.0039	0.0013	1.003	M
MC	C	NP	1420	5.94	2.981	1.206					1.003	M
MC	C	NP	1421	6.629	3.91	1.433					1.003	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	NP	1422	6.285	3.185	1.239					1.003	M
MC	C	NP	1423	7.002	3.681	1.47					1.003	M
MC	C	NP	1424	7.022	3.276	1.368	1.2056	0.1624	0.152	0.0104	1.003	F
MC	C	NP	1425	6.585	3.185	1.236	1.0956	0.1404	0.1144	0.0260	1.003	F
MC	C	NP	1426	4.554	2.276	1.062	0.9333	0.1287	0.1001	0.0286	1.003	F
MC	C	NP	1427	4.028	1.716	0.852					1.003	
MC	C	NP	1428	7.377	3.622	1.336	1.254	0.082	0.082	0.0000	1.003	F
MC	C	NP	1429	7.349	3.522	1.306					1.003	F
MC	C	NP	1430	5.422	2.539	1.106					1.003	M
MC	C	NP	1431	6.548	3.323	1.323					1.003	F
MC	C	NP	1432	5.644	2.813	1.153	1.0984	0.0546	0.0416	0.0130	1.003	F
MC	C	NP	1433	7.497	3.921	1.402					1.003	M
MC	C	NP	1434	3.894	1.782	0.837					1.003	M
MC	C	NP	1435	5.273	2.522	1.069					1.003	M
MC	C	NP	1436	6.961	3.488	1.347					1.003	F
MC	C	NP	1437	4.883	2.342	1.124	1.0928	0.0312	0.0312	0.0000	1.003	F
MC	C	NP	1438	4.8	2.03	0.947					1.003	
MC	C	NP	1439	4.718	2.17	0.994	0.9472	0.0468	0.039	0.0078	1.003	
MC	C	NP	1440	5.917	3.034	1.088	1.0334	0.0546	0.0468	0.0078	1.003	M
MC	C	NP	1441	7.363	3.916	1.352					1.003	M
MC	C	NP	1442	5.447	2.419	1.115	0.8093	0.3057	0.294	0.0117	1.003	F
MC	C	NP	1443	6.671	3.337	1.242					1.003	M
MC	C	NP	1444	3.376	1.43	0.755					1.003	
MC	C	NP	1445	4.895	2.127	1.049	1.0126	0.0364	0.0286	0.0078	1.003	F
MC	C	NP	1446	3.691	1.43	0.763					1.003	
MC	C	NP	1447	5.293	2.371	1.091					1.003	F
MC	C	NP	1448	3.408	1.455	0.761	0.3354	0.4256	0.345	0.0806	1.003	
MC	C	NP	1449	4.599	2.261	0.95					1.003	F
MC	C	NP	1450	4.886	2.25	0.995					1.003	M
MC	C	NP	1451	7.1	3.795	1.302					1.003	M
MC	C	NP	1452	7.095	3.982	1.605	1.5972	0.008	0.0078	0.0000	1.003	M
MC	C	NP	1453	6.746	3.493	1.356	1.33	0.026	0.0234	0.0026	1.003	F
MC	C	NP	1454	6.69	3.263	1.345					1.003	M
MC	C	NP	1455	7.022	3.35	1.331					1.003	M
MC	C	NP	1456	6.524	2.867	1.231	1.1738	0.0572	0.0481	0.0091	1.003	F
MC	C	NP	1457	7.212	3.981	1.481					1.003	M
MC	C	NP	1458	7.649	3.431	1.438					1.003	F
MC	C	NP	1459	7.556	3.674	1.492	1.4712	0.0208	0.0182	0.0026	1.003	M
MC	C	NP	1460	7.09	3.489	1.319	1.3047	0.0143	0.013	0.0013	1.003	F
MC	C	NP	1461	7.068	3.459	1.429	1.3952	0.0338	0.0234	0.0104	1.003	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	NP	1462	7.297	3.77	1.257					1.003	M
MC	C	NP	1463	5.395	2.545	1.116					1.003	M
MC	C	NP	1464	7.047	3.32	1.404					1.003	M
MC	C	NP	1465	6.292	3.023	1.275					1.003	F
MC	C	NP	1466	6.387	3.2	1.284	1.2796	0.0044	0.0039	0.0005	1.003	F
MC	C	NP	1467	7.167	3.631	1.461					1.003	M
MC	C	NP	1468	6.997	3.717	1.342					1.003	F
MC	C	NP	1469	6.058	3.006	1.208					1.003	F
MC	C	NP	1470	7.593	3.967	1.566	1.5634	0.003	0.0026	0.0000	1.003	M
MC	C	NP	1471	4.912	2.166	0.976					1.003	M
MC	C	NP	1472	4.272	1.873	0.818					1.003	M
MC	C	NP	1473	5.533	2.76	1.051					1.003	M
MC	C	NP	1474	2.657	1.074	0.58	0.5449	0.0351	0.0325	0.0026	1.003	
MC	C	NP	1475	7.576	3.543	1.468					1.003	F
MC	C	NP	1476	3.868	1.556	0.811	0.4868	0.3242	0.267	0.0572	1.003	M
MC	C	NP	1477	3.534	1.601	0.775					1.003	M
MC	C	NP	1478	6.058	2.998	1.24					1.003	M
MC	C	NP	1479	3.073	1.337	0.712	0.2214	0.4906	0.41	0.0806	1.003	
MC	C	NP	1480	5.03	2.547	1.039					1.003	M
MC	C	NP	1481	6.557	3.397	1.277					1.003	M
MC	C	NP	1482	5.449	2.376	1.102	1.0669	0.0351	0.0286	0.0065	1.003	F
MC	C	NP	1483	7.341	3.401	1.388					1.003	M
MC	C	NP	1484	5.775	2.876	1.211	1.1486	0.0624	0.0507	0.0117	1.003	F
MC	C	NP	1485	1.114	0.538	0.302					1.003	
MC	C	NP	1486	6.323	2.996	1.19					1.003	M
MC	C	NP	1487	5.083	2.275	1.008					1.003	M
MC	C	NP	1488	6.318	2.87	1.157	1.0946	0.0624	0.0494	0.0130	1.003	M
MC	C	NP	1489	3.438	1.422	0.737					1.003	
MC	C	NP	1490	4.914	2.259	1.022					1.003	M
MC	C	NP	1491	6.879	4.033	1.544					1.003	M
MC	C	NP	1492	6.687	3.766	1.317	1.3014	0.0156	0.0117	0.0039	1.003	M
MC	C	NP	1493	4.544	2.055	0.975	0.7636	0.2114	0.188	0.0234	1.003	M
MC	C	NP	1494	4.212	1.89	0.87	0.727	0.143	0.1183	0.0247	1.003	M
MC	C	NP	1495	7.014	3.143	1.399					1.003	F
MC	C	NP	1496	5.861	3.107	1.181	1.1615	0.0195	0.0117	0.0078	1.003	F
MC	C	NP	1497	4.08	1.888	0.892					1.003	M
MC	C	NP	1498	5.582	2.707	1.095					1.003	M
MC	C	NP	1499	4.802	2.27	0.955					1.003	M
MC	C	NP	1500	6.905	3.75	1.46	1.4444	0.0156	0.013	0.0026	1.003	F
MC	C	NP	1501	7.031	3.294	1.435	1.4233	0.0117	0.0104	0.0013	1.003	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
MC	C	NP	1502	7.081	3.688	1.387	1.3428	0.0442	0.039	0.0052	1.003	F
MC	C	NP	1503	6.758	3.206	1.252	1.2364	0.0156	0.0156	0.0000	1.003	M
MC	C	NP	1504	6.023	3.019	1.177	1.1562	0.0208	0.0195	0.0013	1.003	M
MC	C	NP	1505	6.25	3.218	1.348	1.2882	0.0598	0.0546	0.0052	1.003	F
MC	C	NP	1506	6.641	3.591	1.289					1.003	M
MC	C	NP	1507	8.666	4.502	1.61	1.6087	0.001	0.0013	0.0000	1.003	M
MC	C	NP	1508	8.3	4.858	1.567					1.003	M
MC	C	NP	1509	8.291	3.398	1.365	1.3468	0.0182	0.0156	0.0026	1.003	F
MC	C	NP	1510	7.71	3.954	1.629					1.003	M
MC	C	NP	1511	7.612	4.423	1.543	1.5287	0.0143	0.0143	0.0000	1.003	M
MC	C	NP	1512	7.574	3.69	1.521					1.003	M
MC	C	NP	1513	6.535	3.775	1.337					1.003	M
MC	C	NP	1514	8.543	4.384	1.604					1.003	M
MC	C	NP	1515	8.106	4.116	1.467					1.003	F
MC	C	NP	1516	7.629	4.23	1.384					1.003	M
MC	C	NP	1517	8.103	4.065	1.477					1.003	M
MC	C	NP	1518	7.763	4.091	1.534	1.5314	0.003	0.0026	0.0000	1.003	M
MC	C	NP	1519	7.63	3.601	1.445	1.4359	0.009	0.0091	0.0000	1.003	F
MC	C	NP	1520	6.713	3.575	1.367	1.3618	0.005	0.0052	0.0000	1.003	M
MC	C	NP	1521	8.068	4.144	1.583					1.003	M
MC	C	NP	1522	7.626	4.174	1.541	1.5405	0.001	0.0005	0.0000	1.003	M
MC	C	NP	1523	7.831	3.806	1.407					1.003	M
MC	C	NP	1524	7.644	4.292	1.428					1.003	M
MC	C	NP	1525	7.769	4.33	1.414					1.003	F
MC	C	NP	1526	7.707	3.916	1.466	1.4374	0.0286	0.026	0.0026	1.003	M
MC	C	NP	1527	7.168	3.761	1.414					1.003	M
MC	C	NP	1528	7.507	3.46	1.54					1.003	M
MC	C	NP	1529	7.692	3.836	1.53					1.003	F
MC	C	NP	1530	7.671	3.875	1.423					1.003	M
MC	C	NP	1531	8.264	4.29	1.515					1.003	M
MC	C	NP	1532	8.17	4.171	1.539	1.5333	0.0057	0.0052	0.0005	1.003	F
MC	C	NP	1533	7.67	4.028	1.434	1.4339	0.000	0.0001	0.0000	1.003	M
MC	C	NP	1534	7.632	4.014	1.453	1.4426	0.010	0.0104	0.0000	1.003	M
MC	C	NP	1535	8.095	4.076	1.558					1.003	F
MC	C	NP	1536	7.634	4.108	1.42	1.4122	0.0078	0.0065	0.0013	1.003	M
MC	C	NP	1537	7.632	3.732	1.49					1.003	M
MC	C	NP	1538	7.703	3.577	1.485	1.4707	0.0143	0.0143	0.0000	1.003	M
SC	A	P	157	6.253	3.322	1.054					1.011	F
SC	A	P	158	5.84	3.17	1.14					1.011	F
SC	A	P	159	5.017	2.593	1.067					1.011	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	A	P	160	4.257	2.07	0.927					1.011	M
SC	A	P	161	5.425	2.979	1.075					1.011	M
SC	A	P	162			1.241					1.011	M
SC	A	P	163	4.91	2.691	1.013	0.9727	0.0403	0.0325	0.0078	1.011	F
SC	A	P	164	6.096	3.532	1.278	1.2546	0.0234	0.0208	0.0026	1.011	F
SC	A	P	165	5.913	3.22	1.099	1.0834	0.0156	0.0156	0.0000	1.011	M
SC	A	P	166	4.302	2.017	0.837					1.011	M
SC	A	P	167	5.296	3.217	1.136	1.129	0.007	0.0065	0.0005	1.011	F
SC	A	P	168	6.318	3.591	1.101					1.011	M
SC	A	P	169	4.674	2.152	0.98	0.889	0.091	0.0754	0.0156	1.011	M
SC	A	P	170	4.714	2.878	1.053					1.011	M
SC	A	P	171	6	3.4	1.27					1.011	F
SC	A	P	172	4.346	2.114	0.975					1.011	F
SC	A	P	173	5.746	2.946	1.232	1.2242	0.008	0.0078	0.0000	1.011	M
SC	A	P	174	2.921	1.31	0.676					1.011	
SC	A	P	175	1.82	0.762	0.44					1.011	
SC	A	P	176	4.206	1.856	0.946					1.011	M
SC	A	P	177	6.049	3.099	1.168	1.1524	0.0156	0.0156	0.0000	1.011	M
SC	A	P	178	6.214	3.501	1.171					1.011	M
SC	A	P	179	4.969	2.71	1.035	1.0241	0.0109	0.0104	0.0005	1.011	M
SC	A	P	180	5.596	2.967	1.076	1.0591	0.0169	0.0156	0.0013	1.011	F
SC	A	P	181	6.144	3.154	1.247					1.011	M
SC	A	P	182	4.897	2.405	1.093					1.011	F
SC	A	P	183	4.791	2.769	1.029					1.011	M
SC	A	P	184	5.815	3.082	1.334					1.011	F
SC	A	P	185	5.82	3.261	1.218					1.011	M
SC	A	P	186	5.638	2.974	1.235	1.2272	0.008	0.0078	0.0000	1.011	F
SC	A	P	187	5.523	3.144	1.205	1.1933	0.0117	0.0104	0.0013	1.011	M
SC	A	P	188	5.874	2.962	1.094	1.0407	0.0533	0.0403	0.0130	1.011	F
SC	A	P	189	5.912	3.111	1.284					1.011	M
SC	A	P	190	5.487	3.181	1.199	1.1886	0.0104	0.0078	0.0026	1.011	M
SC	A	P	191	4.692	2.22	0.982					1.011	F
SC	A	P	192	5.558	2.95	1.083	1.0726	0.0104	0.0078	0.0026	1.011	F
SC	A	P	193	4.953	2.572	1.054	1.0215	0.0325	0.0273	0.0052	1.011	F
SC	A	P	194	5.072	2.573	1.014	1.014	0.000	0.0000		1.011	
SC	A	P	195	5.101	2.457	1.055	0.9536	0.1014	0.0806	0.0208	1.011	M
SC	A	P	196	4.889	2.603	1.029	1.0173	0.0117	0.0091	0.0026	1.011	M
SC	A	P	197	4.611	2.205	0.889					1.011	F
SC	A	P	198	5.474	3.281	1.204	1.1957	0.0083	0.0078	0.0005	1.011	M
SC	A	P	199	5.708	3.327	1.22	1.2122	0.008	0.0078	0.0000	1.011	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	A	P	200	3.3	1.7	0.857					1.011	M
SC	A	P	201	5.864	3.432	1.195	1.1911	0.004	0.0039	0.0000	1.011	F
SC	A	P	202	4.534	2.39	0.996					1.011	F
SC	A	P	203	6.35	3.353	1.311	1.2759	0.0351	0.0286	0.0065	1.011	F
SC	A	P	204	6.066	3.173	1.148	1.122	0.026	0.0182	0.0078	1.011	M
SC	A	P	205	4.928	2.622	1.1					1.011	F
SC	A	P	206	3.541	1.675	0.782					1.011	
SC	A	P	207	5.446	3.087	1.1	1.0818	0.0182	0.0182	0.0000	1.011	F
SC	A	P	208	1.826	0.819	0.442					1.011	
SC	A	P	209	5.064	2.803	1.137					1.011	F
SC	A	P	210	3.502	1.59	0.787					1.011	
SC	A	P	211	4.818	2.511	1.01	0.8452	0.1648	0.144	0.0208	1.011	F
SC	A	P	212	5.9177	2.896	1.117	1.1001	0.0169	0.013	0.0039	1.011	F
SC	A	P	213	3.701	1.796	0.8	0.4848	0.3152	0.258	0.0572	1.011	M
SC	A	P	214	5.458	3.327	1.214	1.2139	0.000	0.0001	0.0000	1.011	M
SC	A	P	215	5.891	3.051	1.256	1.23	0.026	0.0182	0.0078	1.011	F
SC	A	P	216	5.246	2.647	1.076	1.0409	0.0351	0.0299	0.0052	1.011	M
SC	A	P	217	3.128	1.636	0.677					1.011	M
SC	A	NP	218	6.492	3.329	1.376					1.011	M
SC	A	NP	219	6.308	3.168	1.17					1.011	F
SC	A	NP	220	5.64	2.637	1.087	1.0168	0.0702	0.0572	0.0130	1.011	F
SC	A	NP	221	6.097	3.313	1.309					1.011	M
SC	A	NP	222	6.761	3.518	1.251					1.011	M
SC	A	NP	223	5.633	3.069	1.131					1.011	M
SC	A	NP	224	3.768	1.816	0.773					1.011	M
SC	A	NP	225	5.787	2.94	1.157					1.011	F
SC	A	NP	226	6.418	3.609	1.317					1.011	F
SC	A	NP	227	7.23	3.81	1.459					1.011	M
SC	A	NP	228	5.976	3.686	1.304	1.3035	0.001	0.0005	0.0000	1.011	M
SC	A	NP	229	5.212	2.589	1.026					1.011	M
SC	A	NP	230	5.962	3.191	1.122					1.011	M
SC	A	NP	231	5.86	3.165	1.246	1.233	0.013	0.013	0.0000	1.011	M
SC	A	NP	232	5.561	2.909	1.066					1.011	M
SC	A	NP	233	5.571	3.167	1.11					1.011	F
SC	A	NP	234	7.081	3.987	1.475					1.011	F
SC	A	NP	235	6.494	3.401	1.222	1.1986	0.0234	0.0234	0.0000	1.011	M
SC	A	NP	236	6.91	3.351	1.241					1.011	M
SC	A	NP	237	5.708	3.234	1.083					1.011	M
SC	A	NP	238	4.758	2.574	1.063	1.0599	0.0031	0.0026	0.0005	1.011	M
SC	A	NP	239	5.675	2.726	1.246					1.011	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	A	NP	240	6.419	3.259	1.134	1.1171	0.0169	0.0169	0.0000	1.011	F
SC	A	NP	241	5.707	3.09	1.216	1.2142	0.0018	0.0005	0.0013	1.011	M
SC	A	NP	242	1.118	0.59	0.276					1.011	
SC	A	NP	243	5.525	2.919	1.064					1.011	F
SC	A	NP	244	6.522	3.196	1.219					1.011	F
SC	A	NP	245	5.851	3.016	1.035	0.9635	0.0715	0.0611	0.0104	1.011	F
SC	A	NP	246	4.272	1.938	0.894					1.011	M
SC	A	NP	247	6.969	3.289	1.324	1.3123	0.0117	0.0104	0.0013	1.011	M
SC	A	NP	248	6.897	3.292	1.25	1.2292	0.0208	0.0208	0.0000	1.011	F
SC	A	NP	249	5.709	3.348	1.113					1.011	M
SC	A	NP	250	5.12	2.482	0.983					1.011	M
SC	A	NP	251	5.365	2.68	1.045					1.011	F
SC	A	NP	252	7.379	3.927	1.424	1.4123	0.0117	0.0117	0.0000	1.011	M
SC	A	NP	253	6.111	2.934	1.138	1.1016	0.0364	0.0312	0.0052	1.011	M
SC	A	NP	254	6.562	3.579	1.287					1.011	F
SC	A	NP	255	5.935	2.853	1.154					1.011	
SC	A	NP	256	6.167	3.537	1.258					1.011	
SC	A	NP	257	6.337	2.804	1.302					1.011	M
SC	A	NP	258	5.651	3.031	1.069	1.0391	0.0299	0.0286	0.0013	1.011	M
SC	A	NP	259	5.596	2.698	1.044					1.011	M
SC	A	NP	260	5.046	2.937	1.128					1.011	M
SC	A	NP	261	6.204	3.589	1.346	1.3325	0.0135	0.013	0.0005	1.011	M
SC	A	NP	262	2.313	1.003	0.526					1.011	
SC	A	NP	263	0.928	0.428	0.24					1.011	
SC	A	NP	264	6.016	3.005	1.201					1.011	F
SC	A	NP	265	6.254	3.257	1.211					1.011	F
SC	B	P	266	6.3	3.33	1.312					1.008	M
SC	B	P	267	6.851	3.669	1.391					1.008	F
SC	B	P	268	5.423	2.959	1.152					1.008	M
SC	B	P	269	6.58	3.82	1.282	1.2659	0.0161	0.0156	0.0005	1.008	M
SC	B	P	270	4.83	2.545	1.101	1.0672	0.0338	0.0286	0.0052	1.008	M
SC	B	P	271	5.4		1.196					1.008	
SC	B	P	272	5.597	2.838	1.125	1.1115	0.0135	0.013	0.0005	1.008	M
SC	B	P	273	6.109	3.001	1.255	1.2355	0.0195	0.0143	0.0052	1.008	M
SC	B	P	274	4.703	2.418	1.048	0.9921	0.0559	0.0442	0.0117	1.008	M
SC	B	P	275	4.652	2.203	0.99	0.7472	0.2428	0.196	0.0468	1.008	M
SC	B	P	276	5.845	2.738	1.125	1.1102	0.0148	0.0143	0.0005	1.008	F
SC	B	P	277	5.375	2.898	1.18					1.008	M
SC	B	P	278	5.453	2.809	1.133	1.1239	0.0091	0.0078	0.0013	1.008	M
SC	B	P	279	6.126	3.476	1.107	1.0979	0.0091	0.0078	0.0013	1.008	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	B	P	280	5.792	3.034	1.188	1.1875	0.001	0.0005	0.0000	1.008	F
SC	B	P	281	5.4	2.368	1.031	0.9335	0.0975	0.0832	0.0143	1.008	M
SC	B	P	282	6.706	3.51	1.403	1.4017	0.001	0.0013	0.0000	1.008	M
SC	B	P	283	5.872	3.408	1.201	1.1893	0.0117	0.0104	0.0013	1.008	M
SC	B	P	284	4.896	2.456	0.978	0.9221	0.0559	0.0442	0.0117	1.008	F
SC	B	P	285	5.884	3.239	1.278					1.008	M
SC	B	P	286	5.953	3.083	1.234					1.008	M
SC	B	P	287	5.021	2.427	1.074	1.0233	0.0507	0.0338	0.0169	1.008	F
SC	B	P	288	5.71	3.456	1.198					1.008	M
SC	B	P	289	6.271	2.999	1.213	1.2013	0.0117	0.0104	0.0013	1.008	F
SC	B	P	290	3.106	1.384	0.723					1.008	
SC	B	P	291	3.606	2.379	0.983					1.008	F
SC	B	P	292	5.8		1.284	1.2614	0.0226	0.0221	0.0005	1.008	M
SC	B	P	293	4.371	2.303	1.07	1.0583	0.0117	0.0104	0.0013	1.008	F
SC	B	P	294	5.083	2.68	1.078					1.008	M
SC	B	P	295	5.611	3.348	1.203	1.2024	0.001	0.0006	0.0000	1.008	M
SC	B	P	296	4.85	2.775	0.98	0.9696	0.010	0.0104	0.0000	1.008	F
SC	B	P	297		0.23	0.16					1.008	
SC	B	P	298	4.634	2.573	1.016	0.9835	0.0325	0.0312	0.0013	1.008	M
SC	B	P	299	6.1	3.235	1.203	1.1882	0.0148	0.0143	0.0005	1.008	M
SC	B	P	300	3.4	1.6	0.834	0.6233	0.2107	0.16	0.0507	1.008	M
SC	B	P	301	4.664	2.772	1.079	1.0452	0.0338	0.0299	0.0039	1.008	F
SC	B	P	302	4.619	2.372	1.002	0.9318	0.0702	0.0598	0.0104	1.008	F
SC	B	P	303	3.578	1.686	0.873	0.6819	0.1911	0.156	0.0351	1.008	F
SC	B	P	304	6.805	3.597	1.273	1.2686	0.0044	0.0039	0.0005	1.008	M
SC	B	P	305	6.285	3.33	1.27	1.2578	0.0122	0.0117	0.0005	1.008	M
SC	B	P	306	4.999	2.391	1.044	0.9205	0.1235	0.1001	0.0234	1.008	M
SC	B	P	307	6.158	3.44	1.262	1.2607	0.001	0.0013	0.0000	1.008	M
SC	B	P	308	5.893	3.289	1.24					1.008	M
SC	B	P	309	5.263	2.881	1.195					1.008	M
SC	B	P	310	3.891	1.865	0.907	0.7614	0.1456	0.1248	0.0208	1.008	F
SC	B	P	311	5.705	2.661	1.162	1.1256	0.0364	0.0312	0.0052	1.008	F
SC	B	P	312	6.46	3.476	1.3					1.008	M
SC	B	P	313	6.481	3.05	1.157	1.1453	0.0117	0.0039	0.0078	1.008	F
SC	B	P	314	4.263	2.167	0.976	0.9305	0.0455	0.039	0.0065	1.008	F
SC	B	P	315	5.036	2.746	1.12	1.1104	0.0096	0.0091	0.0005	1.008	F
SC	B	P	316	5.382	2.762	1.165	1.1455	0.0195	0.0182	0.0013	1.008	M
SC	B	P	317	2.972	1.152	0.674					1.008	
SC	B	P	318	3.84		0.934					1.008	F
SC	B	P	319	4.171	2.1	0.875					1.008	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	B	P	320	5.777	3.284	1.222					1.008	M
SC	B	NP	321	6.628	3.757	1.241					1.008	M
SC	B	NP	322	6.282	3.839	1.335	1.3272	0.008	0.0078	0.0000	1.008	F
SC	B	NP	323	4.85	2.404	1.043	0.9702	0.0728	0.0676	0.0052	1.008	F
SC	B	NP	324	7.809	3.948	1.4					1.008	M
SC	B	NP	325	6.454	3.426	1.241	1.2327	0.0083	0.0078	0.0005	1.008	F
SC	B	NP	326	6.772	3.63	1.32	1.3187	0.001	0.0013	0.0000	1.008	M
SC	B	NP	327	4.992	2.259	0.945	0.9008	0.0442	0.0364	0.0078	1.008	F
SC	B	NP	328	3.6	1.9	0.85	0.7694	0.0806	0.0676	0.0130	1.008	F
SC	B	NP	329	6.267	3.28	1.204	1.1637	0.0403	0.0351	0.0052	1.008	F
SC	B	NP	330	6.054	3.199	1.119	1.0904	0.0286	0.026	0.0026	1.008	M
SC	B	NP	331	5.985	3.311	1.17					1.008	M
SC	B	NP	332	3.63	1.511	0.766					1.008	F
SC	B	NP	333	4.66	2.197	0.955					1.008	M
SC	B	NP	334	3.82	2.079	0.877					1.008	F
SC	B	NP	335	7.224	4.179	1.308					1.008	M
SC	B	NP	336	7.718	3.823	1.528					1.008	M
SC	B	NP	337	0.82	0.333	0.216					1.008	
SC	B	NP	338	6.327	2.993	1.268					1.008	F
SC	B	NP	339	4.5	2.303	0.966					1.008	M
SC	B	NP	340	6.83	3.165	1.253					1.008	M
SC	B	NP	341	3.682	1.609	0.783					1.008	M
SC	B	NP	342	5.657	3.515	1.154					1.008	F
SC	B	NP	343	2.877	1.514	0.718	0.5329	0.1851	0.15	0.0351	1.008	F
SC	B	NP	344	7.125	3.521	1.337	1.3331	0.0039	0.0026	0.0013	1.008	M
SC	B	NP	345	6.133	3.202	1.221	1.2153	0.0057	0.0052	0.0005	1.008	F
SC	B	NP	346	6.512	3.513	1.136					1.008	M
SC	B	NP	347	4.167		0.892	0.7438	0.1482	0.1157	0.0325	1.008	F
SC	B	NP	348	6.03	3.133	1.375	1.362	0.013	0.0052	0.0078	1.008	M
SC	B	NP	349	6.289	3.26	1.216					1.008	M
SC	B	NP	350	6.792	3.73	1.304	1.2949	0.0091	0.0039	0.0052	1.008	F
SC	B	NP	351	2.714	1.198	0.574					1.008	
SC	B	NP	352	1.689	0.702	0.393					1.008	
SC	B	NP	353	1.453	0.66	0.369					1.008	
SC	C	P	354	6.12	3.45	1.264					1.000	M
SC	C	P	355	5.79	2.93	1.126	1.1195	0.0065	0.0052	0.0013	1.000	F
SC	C	P	356	6.146	3.226	1.231					1.000	F
SC	C	P	357	4.958	2.623	1.09					1.000	M
SC	C	P	358	4.81		1.033					1.000	F
SC	C	P	359	5.049	2.853	1.064					1.000	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	C	P	360	3.9	2.33	0.948					1.000	M
SC	C	P	361	0.541	0.244	0.17					1.000	
SC	C	P	362	1.145	0.485	0.299					1.000	
SC	C	P	363	0.944	0.426	0.246					1.000	
SC	C	P	364	2.946	1.48	0.716					1.000	M
SC	C	P	365	3.325	1.536	0.777					1.000	F
SC	C	P	366	4.42		0.975					1.000	M
SC	C	P	367	4.42		1.008					1.000	M
SC	C	P	368	4.821	2.42	1.002					1.000	F
SC	C	P	369	5.284	2.992	1.108	1.082	0.026	0.0208	0.0052	1.000	M
SC	C	P	370	6.544	4.291	1.414	1.4135	0.001	0.0005	0.0000	1.000	M
SC	C	P	371	5.331	2.809	1.027					1.000	M
SC	C	P	372	5.788	3.614	1.184	1.1801	0.004	0.0039	0.0000	1.000	M
SC	C	P	373	6.07	3.779	1.317					1.000	F
SC	C	P	374	5.956	3.116	1.187	1.1787	0.0083	0.0078	0.0005	1.000	M
SC	C	P	375	4.296	1.919	0.869					1.000	M
SC	C	P	376	4.72	2.581	1.067	1.0631	0.004	0.0039	0.0000	1.000	F
SC	C	P	377	5.081	2.998	1.005	0.9816	0.0234	0.0182	0.0052	1.000	M
SC	C	P	378	6.885	3.203	1.458	1.4528	0.005	0.0052	0.0000	1.000	M
SC	C	P	379	5.032	2.695	1.011					1.000	F
SC	C	P	380	5.858	3.319	1.174					1.000	M
SC	C	P	381	5.344	3.084	1.112	1.0925	0.0195	0.0195	0.0000	1.000	M
SC	C	P	382	5.938	3.433	1.376	1.3721	0.004	0.0039	0.0000	1.000	F
SC	C	P	383	6.596	3.895	1.37	1.3695	0.001	0.0005	0.0000	1.000	M
SC	C	P	384	4.586	2.516	0.967	0.9631	0.0039	0.0026	0.0013	1.000	M
SC	C	P	385	6.172	3.677	1.236	1.2355	0.001	0.0005	0.0000	1.000	M
SC	C	P	386	4.599	2.93	1.128	1.1215	0.007	0.0065	0.0000	1.000	F
SC	C	P	387	5.309	2.766	1.008					1.000	M
SC	C	P	388	6.968	4.251	1.469	1.4664	0.0026	0.0013	0.0013	1.000	M
SC	C	P	389	6.114	3.235	1.16					1.000	M
SC	C	P	390	5.51	2.8	1.14					1.000	F
SC	C	P	391	6.027	3.378	1.25					1.000	F
SC	C	P	392	6.413	3.617	1.444					1.000	F
SC	C	P	393	5.979	3.379	1.266	1.2647	0.001	0.0013	0.0000	1.000	M
SC	C	P	394	5.888	2.992	1.137					1.000	M
SC	C	P	395	4.564	2.159	0.985					1.000	F
SC	C	P	396	5.912	3.411	1.393	1.3912	0.0018	0.0005	0.0013	1.000	F
SC	C	P	397	5.87	3.359	1.157					1.000	M
SC	C	P	398	3.896	2.052	0.857					1.000	M
SC	C	P	399	5.591	3.587	1.183	1.17	0.013	0.0104	0.0026	1.000	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	C	P	400	6.277	3.391	1.173	1.1678	0.005	0.0052	0.0000	1.000	F
SC	C	P	401	5.006	2.526	0.936					1.000	F
SC	C	P	402	4.263	2.377	0.943					1.000	F
SC	C	P	403	5.311	2.592	1.149					1.000	M
SC	C	P	404	5.636	3.306	1.203					1.000	F
SC	C	P	405	4.558	2.177	0.974					1.000	F
SC	C	P	406	3.518	1.901	0.842	0.6244	0.2176	0.176	0.0416	1.000	M
SC	C	P	407	4.14	1.97	0.9					1.000	M
SC	C	P	408	5.031	2.898	1.105	1.0972	0.008	0.0078	0.0000	1.000	F
SC	C	P	409	5.928	3.17	1.287					1.000	F
SC	C	P	410	5.976	3.347	1.221	1.2145	0.0065	0.0039	0.0026	1.000	F
SC	C	P	411	4.736	2.199	1.01					1.000	F
SC	C	P	412	5.302	3.122	1.216					1.000	F
SC	C	P	413	3.931	2.049	0.869	0.7689	0.1001	0.0832	0.0169	1.000	F
SC	C	P	414	6.132	3.366	1.279					1.000	M
SC	C	P	415	4.94	2.778	1.037	0.9837	0.0533	0.0507	0.0026	1.000	F
SC	C	P	416	3.889	2.081	0.855					1.000	M
SC	C	P	417	6.165	3.47	1.306					1.000	M
SC	C	P	418	5.046	2.843	1.069					1.000	F
SC	C	P	419	5.673	3.155	1.254	1.2436	0.0104	0.0078	0.0026	1.000	F
SC	C	P	420	4.721	2.634	1.018					1.000	F
SC	C	P	421	3.835	2.206	0.987	0.9051	0.0819	0.0754	0.0065	1.000	F
SC	C	P	422	4.607	2.44	0.977					1.000	F
SC	C	P	423	4.276	1.85	0.885					1.000	M
SC	C	P	424	4.302	2.039	0.853					1.000	M
SC	C	P	425	5.351	3.052	1.121	1.1205	0.001	0.0005	0.0000	1.000	M
SC	C	P	426	4.302	2.019	0.858	0.7527	0.1053	0.0832	0.0221	1.000	F
SC	C	P	427	2.846	1.305	0.704					1.000	M
SC	C	P	428	4.423	2.302	0.997	0.9255	0.0715	0.0611	0.0104	1.000	M
SC	C	P	429	4.288	2.093	0.906					1.000	M
SC	C	P	430	3.751	2.207	0.95					1.000	
SC	C	P	431	3.935	1.882	0.894					1.000	M
SC	C	P	432	3.934	1.956	0.919	0.7385	0.1805	0.148	0.0325	1.000	F
SC	C	P	433	5.658	2.953	1.14					1.000	F
SC	C	P	434	4.585	2.278	0.975					1.000	F
SC	C	P	435	4.073	1.936	0.84	0.7997	0.0403	0.0351	0.0052	1.000	M
SC	C	P	436	4.008	1.932	0.884	0.8437	0.0403	0.0351	0.0052	1.000	M
SC	C	P	437	4.222	2.092	0.927	0.7801	0.1469	0.1222	0.0247	1.000	F
SC	C	P	438	5.18	2.878	1.061					1.000	M
SC	C	P	439	5.444	2.925	1.15	1.1318	0.0182	0.0156	0.0026	1.000	F

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	C	P	440	4.317	2.263	0.977	0.8821	0.0949	0.0767	0.0182	1.000	M
SC	C	P	441	5.684	3.631	1.158					1.000	M
SC	C	P	442	3.267	1.462	0.701					1.000	F
SC	C	NP	443	5.255	2.772	1.124	1.0941	0.0299	0.0273	0.0026	1.000	F
SC	C	NP	444	4.806	2.303	1.008					1.000	M
SC	C	NP	445	5.758	3.405	1.22					1.000	F
SC	C	NP	446	4.318	2.057	0.855	0.777	0.078	0.0585	0.0195	1.000	M
SC	C	NP	447	6.043	3.485	1.203	1.1978	0.0052	0.0039	0.0013	1.000	M
SC	C	NP	448	1.588	0.728	0.42					1.000	
SC	C	NP	449	0.895	0.394	0.252					1.000	
SC	C	NP	450	1.062	0.507	0.279					1.000	
SC	C	NP	451	0.893	0.406	0.252					1.000	
SC	C	NP	452	0.76	0.35	0.192					1.000	
SC	C	NP	453	1.19	0.467	0.36					1.000	
SC	C	NP	454	4.884	2.944	1.065	1.0567	0.0083	0.0078	0.0005	1.000	M
SC	C	NP	455	6.067	3.206	1.148	1.1397	0.0083	0.0078	0.0005	1.000	M
SC	C	NP	456	6.112	3.204	1.332	1.3224	0.0096	0.0091	0.0005	1.000	F
SC	C	NP	457	4.708	2.734	0.926					1.000	M
SC	C	NP	458	5.784	2.958	1.101					1.000	F
SC	C	NP	459	6.179	3.263	1.352	1.3489	0.0031	0.0026	0.0005	1.000	M
SC	C	NP	460	3.466	1.462	0.784					1.000	F
SC	C	NP	461	4.807	2.457	1.036					1.000	M
SC	C	NP	462	5.886	3.174	1.217	1.1975	0.0195	0.0182	0.0013	1.000	M
SC	C	NP	463	5.729	3.49	1.116					1.000	F
SC	C	NP	464	5.635	2.739	1.218					1.000	M
SC	C	NP	465	6.286	3.73	1.193	1.1904	0.003	0.0026	0.0000	1.000	M
SC	C	NP	466	6.453	3.183	1.251	1.2497	0.001	0.0013	0.0000	1.000	M
SC	C	NP	467	5.073	2.75	1.108					1.000	M
SC	C	NP	468	6.423	3.529	1.198					1.000	F
SC	C	NP	469	4.381	2.14	0.885					1.000	M
SC	C	NP	470	4.331	2.003	0.89	0.7371	0.1529	0.136	0.0169	1.000	F
SC	C	NP	471	6.663	3.573	1.313	1.3125	0.001	0.0005	0.0000	1.000	M
SC	C	NP	472	6.399	2.96	1.292					1.000	F
SC	C	NP	473	6.023	3.259	1.268					1.000	M
SC	C	NP	474	5.696	2.665	1.104					1.000	F
SC	C	NP	475	5.62	3.081	1.151	1.1432	0.008	0.0078	0.0000	1.000	F
SC	C	NP	476	4.857	2.451	1.009					1.000	
SC	C	NP	477	6.035	3.376	1.176	1.1578	0.0182	0.0156	0.0026	1.000	M
SC	C	NP	478	5.963	3.892	1.243					1.000	M
SC	C	NP	479	6.183	3.372	1.252					1.000	M

Si	Tp	Mi	#	Di	He	Jaw1	Jaw0	TotGr	EsGr	LaGr	Ye	Sex
SC	C	NP	480	6.149	2.965	1.219					1.000	F
SC	C	NP	481	5.888	2.92	1.175	1.1646	0.0104	0.0091	0.0013	1.000	F
SC	C	NP	482	6.172	3.549	1.228	0.0104	0.0117	0.0104	0.0013	1.000	F
SC	C	NP	483	7.062	3.811	1.434	0.0026	0.0031	0.0026	0.0005	1.000	M
SC	C	NP	484	5.742	3.03	1.119					1.000	M
SC	C	NP	485	6.774	3.232	1.306					1.000	F
SC	C	NP	486	2.1	0.869	0.372					1.000	
SC	C	NP	487	7.574	4.127	1.375					1.000	F
SC	C	NP	488	6.244	3.164	1.183	0.0156	0.0182	0.0156	0.0026	1.000	M
SC	C	NP	489	4.152	2.052	0.887					1.000	F

APPENDIX D

SEA URCHIN PREDATION DATA

These data collected from the East Side of South Cove, Cape Arago are summarized in Fig. 5 and Fig. 6 in Chapter V. All data are measurements of test diameter (cm) from live sea urchins, dead sea urchins eaten by black oystercatchers (BLOY), and dead sea urchins eaten by raccoons. Fig. 1 in Chapter V displays the different areas of the East Side referred to as the Boulder Field, Sandstone Benches, Low Islands, and Sandy, Protected area.

Live Sea Urchins

Boulder Field

Quadrat 1

7.0
3.8
6.7
3.7
5.1
5.5
4.0
5.7
4.8
4.9
5.6
4.3
5.8
5.8
5.3
4.6
5.2
6.6
5.4
5.8
5.9
2.8
6.7
7.9
7.0
5.6
5.7
5.2
3.6
3.7
5.5
3.9
5.3
5.4
6.6
5.7
5.6
6.2
5.4
7.3
6.6
4.4
7.6

Quadrat 2

6.6
4.8
4.3
5.4
6.1
4.2
5.3
4.6
5.6
4.2
4.0
4.7
4.0
4.3
3.4
6.2
4.8
4.8
5.5
5.9
5.3
6.6
4.3
5.7
6.8
5.9
4.4
5.3
6.2
5.7
3.8
6.1
5.0
6.4
4.3
5.4
5.5
4.4
6.4
3.0
5.3
5.2
6.0
6.0
4.1
5.8
4.9
5.2
5.6
4.7
6.7
6.7
5.2
5.5

Quadrat 3

6.1	3.6	3.1	3.8	3.2	3.2
5.4	5.8	4.4	4.1	2.9	3.2
5.2	5.5	5.2	3.9	2.4	5.2

Quadrat 4

6.6	5.5	5.2	4.9	5.6	5.5
5.1	4.6	5.2	5.0	3.9	5.1
6.6	5.5	2.7	6.5	6.0	5.4
7.0	3.7	6.4	6.0	4.5	
6.9	5.8	4.6	4.7	5.0	
6.5	6.1	6.3	4.7	4.8	
5.7	2.4	6.9	4.9	6.3	
2.7	4.1	5.7	5.3	5.7	

Low Islands: southern "island"

Quadrat 1

5.3	6.0	3.1	4.0	6.2	6.5
4.5	4.8	5.1	4.5	5.3	4.7
4.9	5.8	6.7	6.5	5.6	3.9
6.0	5.4	4.5	3.7	5.6	5.1
5.8	6.7	5.8	4.2	6.6	5.9
4.7	5.0	6.1	6.2	5.7	5.6
6.1	4.9	6.4	6.4	6.8	5.6
3.7	6.0	4.0	4.3	5.9	6.6

Quadrat 2

6.0	4.7	6.6	6.8	4.3	4.3
4.8	5.0	6.9	6.0	6.3	5.6
3.7	4.6	5.6	5.0	6.8	6.2
2.7	5.6	6.5	7.2	5.9	6.6
6.6	5.6	5.6	6.0	4.1	7.3
6.9	5.2	6.4	6.5	7.3	5.1
2.5	5.1	5.7	4.5	5.8	5.7
3.8	4.1	6.6	6.2	3.9	6.0
5.2	4.7	7.7	5.7	5.5	5.7

4.4	4.3				

Quadrat 3

7.1	5.3	6.4	5.5	4.0	5.2
5.5	6.3	1.5	5.7	3.5	3.9
6.2	4.6	6.5	5.1	3.7	4.2
6.7	4.9	4.1	5.1	4.8	5.9
7.3	5.2	4.1	6.7	5.3	5.1
5.4	6.3	5.3	5.7	4.3	
5.5	5.1	5.6	5.2	4.5	
4.6	4.8	4.2	6.7	4.1	

Quadrat 4

6.3	4.3	3.9	6.7	5.5	5.4
5.9	6.2	6.0	2.6	4.3	5.7
5.9	5.9	5.6	5.0	2.8	4.9
5.3	6.8	4.9	5.9	4.2	4.0
6.3	4.9	5.5	5.6	6.1	
5.4	5.1	6.1	6.8	6.7	
5.8	6.0	4.0	6.6	5.9	
5.8	1.9	5.3	6.1	4.9	

Low Islands: northern “island”

Quadrat 1

3.9	7.4	5.3	4.2	6.4	4.0
6.6	2.9	5.7	6.3	4.3	6.2
5.4	4.8	5.1	4.0	4.5	4.9
5.8	6.5	5.6	3.2	4.1	5.2
6.4	5.3	4.2	6.7	5.3	4.8
5.5	3.8	3.7	4.7	5.5	
4.8	4.5	4.1	5.3	5.3	
3.7	2.7	6.8	6.2	6.4	
1.8	6.0	4.3	7.0	6.8	

Quadrat 2

6.2
5.8
4.9
6.5
6.2
5.9
3.2
3.1
5.3
5.4

4.4
4.6
5.6
5.2
4.7
5.8
5.3
5.4
5.1
6.1

5.9
6.2
4.8
3.7
2.8
5.7
5.5
4.4
5.2
6.7

4.6
5.1
5.2
4.2
5.3
4.8
5.1
4.5
6.4
6.6

4.6
5.0
6.0
6.5
5.4
3.9
5.2
5.7
4.6
6.2

6.5
5.9
5.4
5.0
4.1
7.1
4.9
6.7
6.1
5.4

Quadrat 3

5.8
4.5
4.4
6.0
4.7
6.1
5.7
5.5
5.6
4.6
5.3

4.6
4.6
4.4
5.6
5.1
6.4
6.1
5.9
3.2
4.5
3.0

4.7
4.0
4.6
6.5
6.0
4.7
4.0
5.0
5.4
5.1
2.3

6.0
5.1
4.2
4.9
5.9
4.4
4.8
5.0
4.9
5.5
4.9

5.7
4.9
5.7
5.5
5.4
6.3
4.8
6.7
4.9
3.6
6.0

5.5
5.3
6.1
5.9
5.2
4.7
4.3
5.7
4.5

Quadrat 4

4.4
1.7
5.9
6.0
3.8
6.1
6.5
5.5
3.8
5.2
4.6

4.5
5.6
3.2
3.3
5.1
4.4
4.9
6.5
4.1
3.9
6.2

5.7
3.1
3.7
4.3
5.3
3.5
5.3
5.9
4.5
5.9
3.0

6.9
5.6
4.4
5.8
3.6
6.6
4.4
3.5
3.4
7.0
5.2

5.8
5.4
4.0
5.3
5.1
4.5
6.0
5.9
3.0
6.6
5.1

5.4
4.3
3.4
4.7
5.2
5.7
6.5
3.8
6.2
5.8

Quadrat 5

7.0
5.7
4.7
4.1
5.0
5.9
4.1
5.6
5.9
5.7
4.4
5.6
4.6
5.1
6.1
5.0
5.6
3.5
3.6
5.3
4.4
5.9
6.0
4.7
6.1
5.7
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6.9
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4.2
5.4
2.8
5.1
3.3
3.7
3.4
3.0
6.1
4.4
4.3
5.6
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5.8
4.5
5.9
5.5
6.5
5.0
6.6
6.2
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5.9
5.1
5.9
5.9
4.1
4.8
6.2
5.2
5.6
4.7
4.7
5.3
5.6

Sandstone Benches

Quadrat 1

6.7
6.3
6.0
7.3
6.8
5.7
6.4
3.6
6.3
5.8
5.5
6.5
4.7
5.4
6.7
6.1
6.4
6.8
7.2
3.9
5.6
5.1
5.1
5.1
3.5
7.3
6.2
6.9
5.3
6.3
6.3
6.5

Quadrat 2

5.7
5.9
5.9
5.5
5.4
4.3
6.0
6.0
6.1
7.3
7.3
7.2
5.1

Quadrat 3

5.3
4.2
3.9
3.1
4.9
2.9
4.5
3.7
4.0
2.9
3.7
3.7
3.0
4.3
4.1
4.1
4.3
4.8
4.7
4.6
1.1
4.6
4.4
3.8
3.7
3.4
3.6
3.9
3.8
4.0
3.8
5.4
4.5
3.7
4.7
4.5
3.9

Quadrat 4

5.0
4.4
6.6
4.3
5.7
4.9
4.3
4.6
5.3
5.1
5.6
5.7
5.2
5.7
6.3
5.9
5.5
6.0
5.6
6.1
5.9
5.8
6.4
6.0
3.6
3.9
6.1
5.4

Quadrat 5

4.0
5.1
3.6
4.0
4.2
5.0
5.5
5.1
4.4
4.7
5.2
3.8
2.9
4.9
4.6
4.5
4.7
3.4
4.5
2.6
6.5
5.3
5.8
5.0
4.2
5.2
4.1
5.2
3.0
4.0
4.4
4.0
6.7
5.3
6.5

Quadrat 6

7.9
6.6
5.6
4.9
7.7
5.8
6.4
5.4
7.0
6.9
5.0
6.9
4.9
5.4
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6.1
4.3
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5.1
5.9
4.8
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7.3
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6.9
5.0
6.4
6.1
5.3
6.4
7.6
5.1
6.4
7.0
6.0
6.1
6.4
4.3
6.2

Quadrat 7

7.0
6.8
4.5
7.0
5.0
7.4
7.1
6.0
6.4
7.3
6.9
6.7
4.2
6.0
6.9
3.9
5.8
6.1
7.0
2.0
4.4
6.7
6.7
4.3
6.8
4.7
6.7
4.4
7.5
6.9
4.3
7.4
7.2

Quadrat 8

6.9
6.9
6.9
7.2
7.2
7.5

6.0	7.1	6.8	7.3	5.5	6.9
6.2	5.0	6.3	8.3	8.0	8.4
7.1	5.4	6.4	5.8	7.8	7.4
7.6	7.8	4.8	7.0	7.4	7.3
7.8	6.1	5.4	7.5	7.1	6.9
6.9	6.2	5.9	5.3	7.2	5.6
7.2	6.7	7.9	4.7	7.2	6.7

Quadrat 9

6.3	5.9	6.4	7.5	5.4	6.6
6.2	6.5	4.0	5.7	5.5	6.7
2.3	6.7	5.6	5.9	5.6	6.4
4.9	6.7	7.1	5.0	6.5	2.7
6.5	6.7	6.8	5.0	6.9	5.6
6.7	6.5	5.1	5.1	4.2	7.3
7.0	6.1	6.6	5.3	6.4	5.9
6.8	6.2	6.5	7.7	6.3	6.2
6.8	7.0	6.6	5.3	6.6	6.3
5.2	7.1	5.6	5.8	6.6	6.5
7.0	6.4	6.5	6.9	5.4	4.6
7.6	6.3	6.8	6.5	5.1	5.4
3.4	6.6	6.9	5.8	7.2	6.0
1.9	6.5	6.6	7.4	6.9	6.6

Sandstone Benches: eastern side

Quadrat 1

5.9	5.5	5.2	5.4	5.4	6.7
4.9	4.2	5.5	4.2	6.5	4.2
6.4	6.7	4.9	4.3	5.7	4.1
6.3	5.8	6.5	4.4	4.5	5.7
5.4	5.6	5.1	6.4	4.6	5.7

Quadrat 2

5.6	6.2	6.3	6.7	5.4	5.9
5.5	4.9	5.8	4.7	6.6	6.5
4.9	5.4	5.9	6.5	6.0	6.2
5.8	6.2	6.2	5.8	5.9	6.1
5.7	5.7	6.2	6.4	5.4	4.1

2.6	5.5	7.0	5.3	5.7	
6.1	7.5	4.5	4.8		
6.5	6.1	4.6	2.7		

Quadrat 3

5.9	5.8	4.9	5.6	5.3	4.9
5.7	6.8	7.5	6.2	4.6	6.1
5.9	7.1	6.6	5.0	6.5	3.3
3.6	6.2	6.2	6.4	6.4	7.3
6.5	5.2	2.3	5.5	6.6	
5.8	6.5	6.2	6.6	4.5	
7.4	6.5	3.5	4.2	6.8	
6.8	5.9	5.9	6.5	4.1	
5.2	3.4	6.6	5.8	5.7	

Sea Urchins Eaten by Oystercatchers

Low Islands: southern "island"

7.3	7.5	6.0	6.6	5.8	6.4
7.7	6.3	6.3	6.8	6.2	6.5
6.2	6.4	6.4	7.2	6.3	5.4
6.3	6.9	6.5	7.5	6.4	6.9
7.2	6.1	6.5	6.6	6.4	7.1
6.3	6.0	6.8	6.4	6.8	6.8
6.4	7.2	6.3	7.3	6.9	6.1
5.7	7.2	5.9	6.4	7.1	

Low Islands: northern "island"

7.0	6.0	6.5	6.3	7.0	7.5
6.4	6.4	6.7	7.0	5.3	6.2
6.3	6.0	6.1	5.7	6.7	7.2
5.7	6.3	5.7	5.7	5.4	
6.4	6.0	7.5	6.6	6.4	
6.7	5.7	7.4	7.0	7.2	

Sandstone Benches

7.2
6.1
6.3
6.5
6.2
6.9
7.0
6.6
7.4
7.3
7.9
7.1
7.0
6.4
7.1
7.3
7.3
6.6
6.7
7.6
7.1
7.7
7.5
6.5

5.3
6.9
6.4
6.4
6.5
7.4
5.3
7.3
6.5
6.2
6.8
6.2
5.8
7.6
7.4
6.1
6.1
6.4
6.7
6.9
6.6
6.3
5.2
6.8

6.6
6.7
9.0
6.7
8.0
7.6
5.6
6.9
7.9
7.1
6.2
7.2
6.9
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5.1
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7.4
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6.0
6.5
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6.0
6.3
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6.6
6.8
7.0
7.5
6.8
5.4

6.8
6.9
7.1
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6.1
6.7
6.9
6.7
7.2
7.9
6.0
6.2
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5.3
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6.9
7.2
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6.7
6.6

7.3
5.7
6.8
6.8
6.3
5.9
6.8
7.1
7.0
6.0
6.3
5.5
7.5
8.2
5.9
6.6
7.1
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5.7

Sandstone Benches: eastern side

7.0
7.1
6.5
7.4

6.4
6.0
6.6
5.9
5.9

6.0
6.6
7.0
5.9

5.8
6.1
6.6
6.3

5.8
7.2
6.1
7.0
6.9

7.0
7.5

Sandy, Protected Area

6.9
8.0
7.8
7.4
7.1

7.8
7.5
7.7
6.3
5.1

7.7
7.6
6.4
6.7
6.5

6.6
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7.4
6.9
8.5

5.5
5.9
6.1
7.1
7.4

6.5
6.8
6.8
7.2
8.0

8.2
6.7
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7.7
8.1
8.0
7.4
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7.0
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9.1
8.6

6.1
6.8
7.1
5.1

Dead Sea Urchins Eaten by Raccoons

Boulder Field

6.9
7.5
7.4
7.6
7.5
7.0
7.3
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6.2
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9.1
7.2
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6.1
6.8
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7.5
6.4
6.6
5.8
6.6

7.6	7.5	7.0	6.4	7.6	7.2
6.4	6.9	6.7	6.3	6.3	6.6
6.8	8.0	7.2	6.2	8.1	6.0
7.4	5.1	8.2	6.6	8.9	7.2
6.8	7.7	7.5	7.3	7.8	7.0
6.6	8.1	8.3	6.0	7.8	6.6
6.7	5.3	8.1	6.2	7.7	7.2
7.7	7.2	8.2	6.8	8.2	6.0
7.1	8.2	8.0	5.1	7.2	7.7
6.8	8.4	7.5	6.0	5.6	6.9
6.8	7.2	7.2	6.0	6.2	6.0
7.1	4.9	8.2	6.7	7.3	8.3
7.6	7.6	6.5	5.3	6.8	6.6
6.6	6.8	6.8	7.2	7.4	7.7
7.0	7.2	6.9	6.6	7.7	7.2
6.4	6.7	7.4	7.4	5.8	7.1
5.9	6.5	7.5	7.2	6.0	9.1
6.5	7.0	8.8	6.5	7.2	7.2
7.0	6.9	7.2	7.7	7.4	7.8
6.1	6.7	7.4	7.4	8.2	7.4
7.1	6.6	7.5	6.9	7.7	8.0
6.7	8.2	8.4	6.9	8.0	6.7
6.6	7.4	7.4	5.5	7.5	7.7
6.6	7.9	8.2	6.9	7.1	7.8
6.6	7.9	6.2	6.6	8.3	7.9
6.5	7.0	5.8	8.2	8.6	8.0
7.8	7.4	5.4	7.2	6.7	7.6
6.1	6.6	6.0	7.6	5.3	7.1
6.1	7.5	6.3	6.0	6.2	7.9
6.2	8.3	5.6	6.4	7.2	8.6
6.4	8.6	7.3	7.2	6.9	8.3
5.1	7.0	7.2	7.6	7.4	7.6
6.6	6.5	7.2	6.7	6.8	8.7
6.6	7.6	8.2	7.4	7.2	8.1
6.6	7.5	8.2	6.3	7.1	7.6
7.3	7.4	9.1	6.3	8.3	8.0
7.3	7.2	5.6	7.7	7.2	7.2
5.3	7.2	7.2	7.3	7.7	7.3
8.0	7.6	7.5	8.3	6.0	7.2
6.1	7.9	8.6	7.8	7.5	7.0
7.7	6.7	6.4	7.9	7.5	6.0
7.7	6.4	7.9	6.1	8.2	7.0
6.9	8.2	7.5	7.6	8.4	5.3

5.9
5.8
7.1
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9.1
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CHAPTER V

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