FACTORS INFLUENCING JUVENILE SHELTERING IN SEA URCHINS (*STRONGYLOCENTROTUS FRANCISCANUS* AND *S. DROEBACHIENSIS*)

by

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ABSTRACT

Juvenile red sea urchins (*Strongylocentrotus franciscanus*) are often found under the spines of adults, but those of the green urchin (*S. droebachiensis*) do not shelter to the same extent. As broadcast-spawners with free-swimming larvae, two questions arise: (1) why and; (2) how does sheltering occur?

Juvenile *S. franciscanus* increased sheltering in response to increased predation risk and hydrodynamic factors, whereas juvenile *S. droebachiensis* did not. Sheltering afforded protection from a predatory starfish (i.e. *Pycnopodia helianthoides*) in *S. franciscanus* but not *S. droebachiensis*. Water velocities were reduced by 90% within 5 cm of adults where juveniles sheltered. Field surveys confirmed that juvenile abundance is positively correlated with increased water motion. However, results indicate that juveniles compete with adults for kelp, displaying lower growth rates when exposed to adults.

Juvenile *S. franciscanus* displayed consistent movement towards a secondary chemical signal released by adults exposed to *P. helianthoides,* whereas adults did not respond in the same manner. These results highlight the importance of post-settlement processes and call for the inclusion of juvenile stages in predictions of recruitment and population dynamics.

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Chapter I. Thesis Introduction.

Predicting the spatial distribution of species in coastal ecosystems is one of the most basic and long-standing goals of marine ecology. The spatial abundance of many benthic marine organisms is patchy, and the cause of such variation remains largely unknown. Early efforts focussed on processes acting upon adult populations, including Paine's seminal work, which led to a better understanding of the keystone predator and trophic cascade concepts (Paine 1966, 1971, 1974). Subsequent studies have highlighted the importance of fertilization and larval settlement in relation to the structure and distribution of benthic marine invertebrate populations (Gaines and Roughgarden., 1985, Roughgarden et al., 1988; Menge, 1991; Levitan et al., 1992; Hughes et al., 2000). There are however, few studies that have examined the importance of processes acting upon early juvenile stages (see Gosselin and Qian, 1997; Hunt and Scheibling, 1997 for review). Identifying processes during the early post-settlement period and determining their role in influencing population and community dynamics (Menge, 2000) remains an elusive goal.

Post-settlement processes may influence recruitment by altering juvenile mortality or juvenile behaviour. For example, although predation may alter the spatial abundance of a prey species (Paine, 1974), non-lethal interactions may also influence distributions by modifying behaviour. Behaviour has been called the most flexible phenotype (Hazlett, 1995), allowing organisms to react quickly to environmental stimuli. Numerous studies have indicated that many organisms display shifts in habitat (i.e. refuge habitats vs. open habitats) in response to variable levels of predation risk and food availability (Zaret and Suffern, 1976; Milinski and Heller, 1978; Sih, 1980, 1982, 1984a, 1984b ; Werner et al., 1983; Power et al., 1985). Furthermore, it has been suggested that refuge use is important in explaining the persistence of prey species (Connell, 1970; Macan, 1976). The concept of spatial refuges has received much attention, primarily in the perspective context of effects on predators, not prey (Sih et al., 1988). Although most examples of refuge use involve species hiding from predators and to a lesser degree hydrodynamic disturbance, the hydrodynamic stress of wave action may itself create a refuge from predation (Richardson and Brown, 1990; Graham, 1997). This phenomenon has been called the *harsh-benign hypothesis* (Thomson et al., 2002) and will be discussed in more detail in Chapter II.

The role of wave action in shaping the dynamics of intertidal systems may be as important as processes such as predation and competition (Paine, 1979; M^{c}Quaid and Branch, 1985) and is recognized as an important determinant of community structure in nearshore ecosystems (see Gaylord, 1999 for review). Connell (1961) reported early indirect evidence, as newly settled barnacles (*Semibalanus balanoides*) experienced higher mortality during storm events. More specifically, much work suggests that behaviour and recruitment are influenced (both positively and negatively) by wave action for many benthic marine invertebrates (Etter, 1996; Kawamata, 1998; McQuaid et al., 2000; Ford and Paterson, 2001; Naylor and

M^{c}Shane, 2001). Nevertheless, the role hydrodynamics play in the early post-settlement period for most marine invertebrates is largely unknown.

Three species of conspecific sea urchins on the west coast exhibit variation in the degree of juvenile-adult sheltering association. The adult of *S. franciscanus* create a "spine canopy" under which juvenile urchins may reside (Low, 1975; Tegner and Dayton, 1977). The large spines of *S. franciscanus* (i.e. oral spines) also create a space underneath the adult test which juveniles may occupy. This thesis explores two major questions with respect to *Strongylocentrotus franciscanus* and *S. droebachiensis*: (1) why are juvenile urchins found only under adults and; (2) how did they get there? Chapter II provides theoretical background information concerning relevant issues of life-history, recruitment, behaviour, and hydrodynamics. Chapter III addresses factors that may lead juvenile sea urchins to shelter under adults (both *S. franciscanus* and *S. droebachiensis*). Chapter IV explores a little-known mechanism, chemically-mediated juvenile behaviour, to help explain how juvenile urchins come to dwell under adults. Chapter V presents results from a field survey of juvenile urchins in relation to a suite of both physical and biological variables that support the laboratory results. In conclusion, Chapter VI provides a summary of experimental results and findings from the literature to produce a clearer explanation of juvenile sheltering in the context of recruitment ecology, behavioural ecology, and hydrodynamics.

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Chapter II. A review of marine invertebrate recruitment, behaviour, and fluid dynamics.

Abstract

Research on sea urchins has provided important insights in the fields of development, biochemistry, pharmacology, ecology, and evolution. A common subject of lab study, much is known about the anatomy, physiology, and phylogeny of sea urchins though less is known about their behaviour and ecology. This chapter will provide relevant background information pertaining to issues of natural history, recruitment, behaviour, and fluid dynamics with a focus on sea urchins. Red and green sea urchins (*Strongylocentrotus franciscanus* and *S. droebachiensis*), are long-lived benthic herbivores that reproduce via external fertilization and a free-swimming larval stage. Recruitment is spatially and temporally variable and the source of this variation remains largely unresolved. The potential role of juvenile sheltering in juvenile recruitment is discussed with respect to behaviour and hydrodynamics. Taken together, this review will provide a basis for the study of mechanisms of juvenile-adult sheltering associations such as predation, hydrodynamics, and nutrition.

Strongylocentrotus | recruitment | behaviour | fluid dynamics | juvenile

2.1. Natural history

Classification of Echinoderms

The three congeneric species of sea urchin in British Columbia are the giant red urchin, *Strongylocentrotus franciscanus* (A. Agassiz, 1863), the green urchin *Strongylocentrotus droebachiensis* (O.F. Müller, 1776), and the purple urchin *Strongylocentrotus purpuratus* (Stimpson, 1857). All three species belong to the Phylum Echinodermata, Class Echinoidea, Order Camarodonta Jackson, 1912, Family Echinometridae Gray, and Subfamily Strongylocentrotidae Gregory, 1900 (Brusca and Brusca, 1990, Littlewood and Smith, 1995). Combined morphological and molecular evidence indicate that the Camarodonts (a monophyletic group) appear to have diverged from their closest stirodont sister group (which includes the species *Arbacia lixula* (Linnaeus, 1758)) by 160 million years BP (Littlewood and Smith, 1995). However, more complete fossil evidence is needed to make more reliable inferences concerning the phylogenetic placement of the Camarodonts.

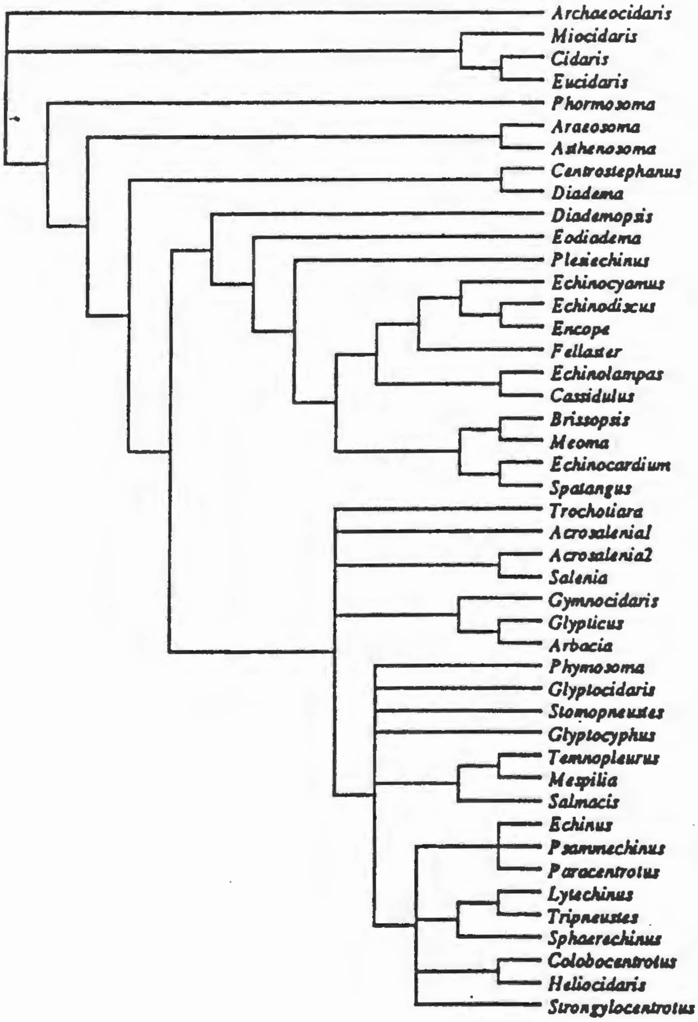

Figure 1. Phylogenetic relationships of higher taxa Echinoids. Total-evidence semistrict consensus tree with 1000 bootstrap replicates (Littlewood and Smith, 1995).

Figure 2 shows the diversity of echinoderms over geologic time. Class diversity peaked during the Ordovician (20 classes) and genus-level diversity in the Carboniferous and Cenozoic periods (300 + genera; Willmer, 1990). Many of these ancestral echinoderms displayed a bilateral although asymmetrical body form. Today there are traditionally five accepted classes of echinoderms representing about 7 000 extant species (Figure 2): Crinoids (sea lilies and feather stars), Holothurians (sea cucumbers), Echinoids, (sea urchins and sand dollars), Asteroids (starfish), and Ophiuroids (brittle stars and basket stars) in addition to a recently discovered sixth class Concentricycloidea (Baker et al., 1986). Members of this new class are found on sunken logs 1000 to 1200 metres deep off New Zealand. They lack both a mouth and gut. It is suspected that these newly discovered echinoderms absorb nutrients from the environment. Further analysis of the geological history of echinoderms by Smith and Jeffery (1998) showed that sea urchins suffered an extinction event (e.g., 36% loss) at the genus level during the late Cretaceous period. The authors state that selection during this period centered on feeding strategies related to the adult benthic form as opposed to the larval stages. Genera with feeding and non-feeding larvae suffered statistically similar rates of extinction while the feeding strategy of the adult correlated highly with survival as omnivores survived at higher rates than more specialized herbivores or grazers.

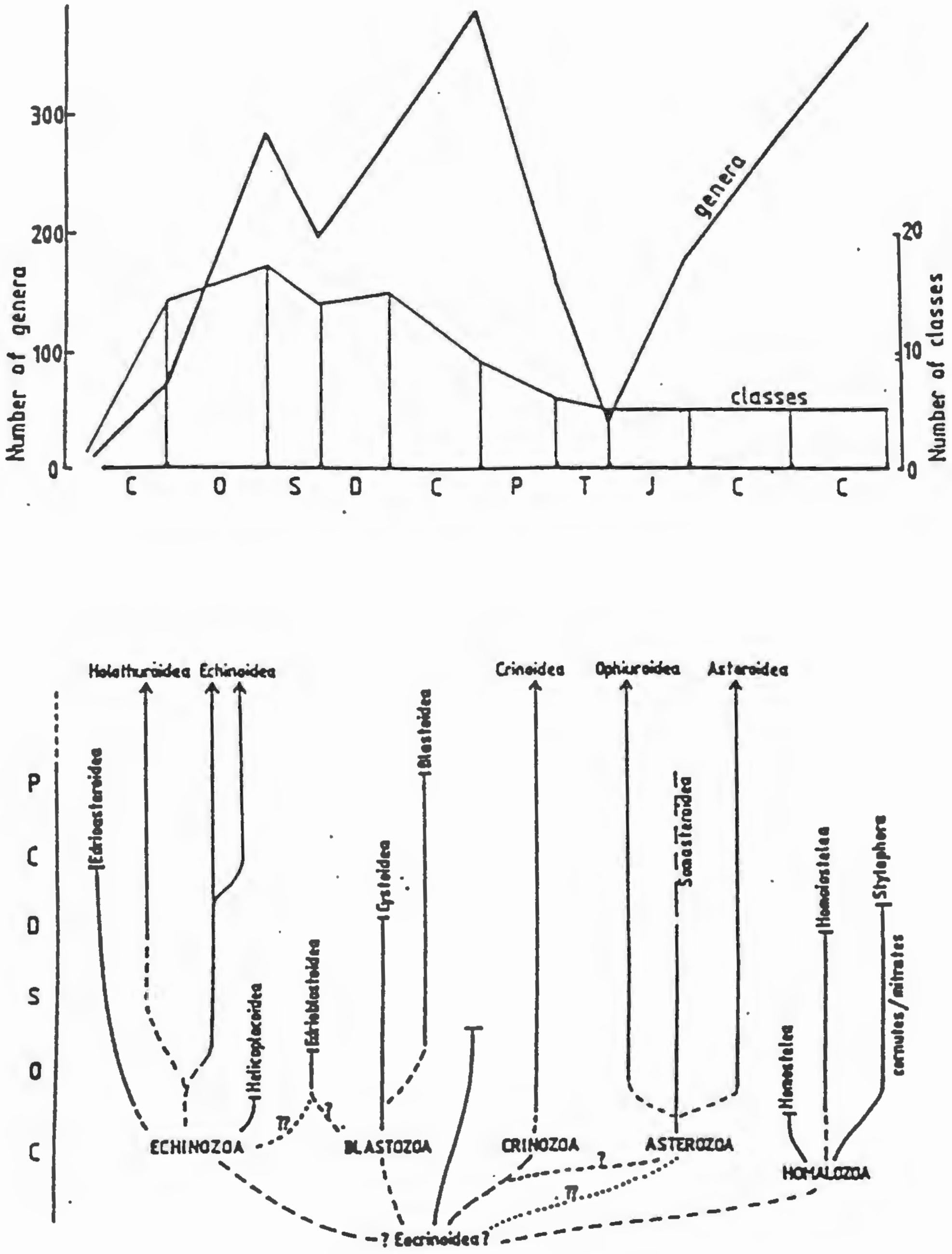

Figure 2. Echinoderm diversity over geologic time (Willmer, 1990), where the order of geologic periods are as follows: C = Cambrian, P = Permian, O = Ordovician, T = Triassic, S = Silvrian, J = Jurassic, D = Devonian, C = Cretaceous, C = Carboniferous, and C = Cenozoic.

Basic Biology and Ecology of Echinoderms

The adult form of Echinoids is characterized by pentaradial symmetry although it is derived from a bilateral larval form (Hotchkiss, 1998). The pentaradial form has developed secondarily and has been imposed on a bilateral body. Although superficial structures are clearly radial, the arrangement of internal organs such as the gut reflect their bilateral origins.

There is no cephalization or segmentation of the body, which is usually referred to as having an oral and aboral surface (Figure 3). Recent evidence indicates that Homeobox (*Hox*) genes pattern position along the length of the major body axis in various animal groups as diverse as mammals, insects, and sea urchins. How and why this gene is so conserved amongst such a wide variety of body plans however, remains unclear (Wray, 2001). The unique body form of echinoderms (i.e. secondarily derived radial symmetry) make this group an ideal candidate to study how body form has evolved and towards that end, a whole genome project has been initiated for *S. purpuratus* (Cameron et al., 2000).

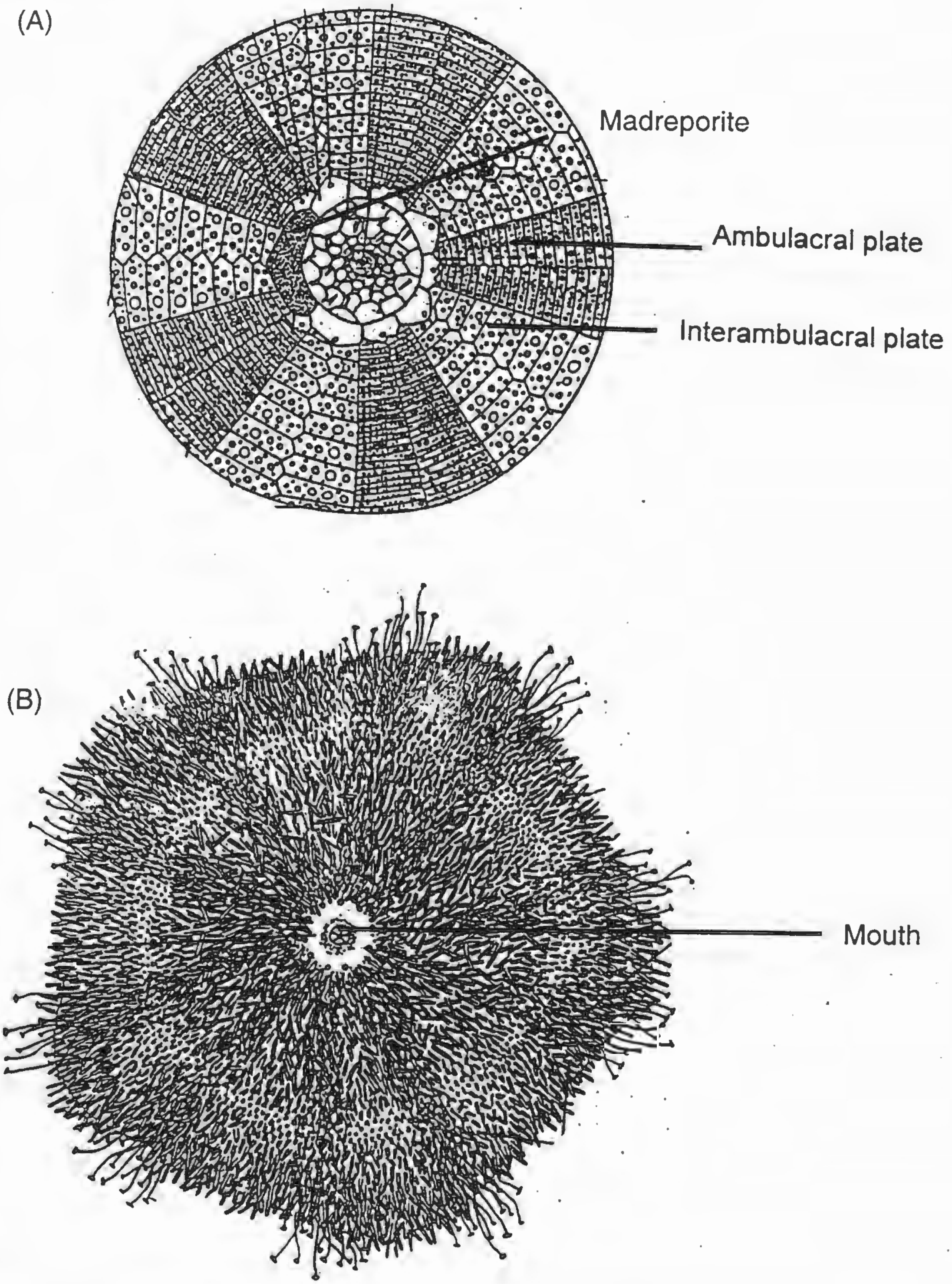

Figure 3. External anatomy of typical Echinoid, *Tripneustes ventricosus*. (A) Aboral view of test, (B) Oral view of test (Hyman, 1955).

There are two types of echinoid with differing shape. Regular echinoids live on the ocean floor and exhibit pentaradial symmetry. For example, the three species of *Strongylocentrotus* in British Columbia are all regular echinoids. Irregular echinoids exhibit weak bilateral symmetry in the antero-posterior plane and generally burrow into soft sediments (e.g., heart urchins and sand dollars).

Echinoderms have no central nervous system, but have three neuronal networks linked together by a nerve net (Brusca and Brusca, 1990). A circumoral nerve ring surrounds the esophagus and gives rise to five radial nerves. These structures are not analogous to a central nervous system, but rather are a condensation of the peripheral nervous system.

Sea urchins possess an array of sensory responses associated with spines, podia, and pedicellariae, which are all connected to the nervous system and react to external stimulus. For instance, sea urchins display a geotactic righting behaviour when overturned. It is assumed that small structures in the ambulacral areas called sphaeridia are responsible for maintaining equlibria (Hyman, 1955). Moreover, closely related sand dollars are able to orient themselves in relation to water current (Nakamura, 1994). As benthic dwellers, urchins also display a photonegative response, seeking shelter from intense light. Other echinoderms (starfish and brittlestars) can even be "trained" to modify their behaviour. Although these behaviours are retained only for short periods, they are notable given the lack of a central brain (Meglitsch and Schram, 1991).

Whereas echinoderms are found in all climates (tropics to Antarctica) and at a variety of depths, they are strictly marine. The inability of echinoderms to adjust water balance adequately has been cited as a major factor in limiting their distribution (Meglitsch and Schram, 1991; Tunnicliffe, 1999) and arises from the water vascular system, a defining characteristic of sea urchins and echinoderms in general. This system is used for respiration, movement, and sensory reception (Meglitsch and Schram, 1991). The water vascular system is open to the environment via an opening called the madreporite (Figure 3A) located on the aboral surface. This leads to the ring canal that gives rise to five radial canals, which in turn lead to the podia. In sea urchins (*S. droebachiensis*), it is known that the madreporite provides an influx of seawater into the body (though less than in Asteroids), which is necessary for fluid homeostasis (Ferguson, 1996). Still, there are many unanswered questions regarding the nature and functioning of the water vascular system (Brusca and Brusca, 1990). For instance, the origin of the water vascular system fluid and the exact function of the madreporite are still not well understood.

Sea urchins are important grazers of the kelp forest. They feed on kelp using a structure called the Aristotle's lantern located on the oral surface. It is made up of five protractible plates (pyramids) that converge within the mouth (Figure 3B). The entire lantern can be manipulated to move at angles towards food (Brusca and Brusca, 1990). Agar-dissolving bacteria have been found in the intestine of *S. purpuratus* (Meglitsch and Schram, 1991). A lack of digestive glands in the gut wall seems to indicate that these microbes may be the source of digestive enzymes for sea urchins.

The calcite endoskeleton of a sea urchin is called a test and can reach 16 cm in diameter for *S. franciscanus* (Sloan, 1991). An epidermal layer covers a layer of skeletal elements called ossicles. In sea urchins, these ossicles are fused to form the test. As a consequence of the test, the body wall musculature has been greatly reduced except in those muscles associated with spines, pedicellariae, podia, and gills (Meglitsch and Schram, 1991).

The test is divided into five ambulacral areas and five interambulacral areas. The ambulacral areas are depicted in Figure 3A as the narrow dark regions while the interambulacral areas are represented by the wider light regions. The ambulacral areas have pores through which the podia pass. The anus is located in the centre of the periproct, shown above as the dark region in the middle of the test. Around the periproct are five genital plates each with a gonopore. The gonopores in turn lead to five separate gonads. One of the genital plates serves as the madreporite, which helps to maintain pressure in the water vascular system.

Sharp spines that serve as protection and aid in locomotion cover the test. Spines can be classified as primary, secondary, or tertiary based on size. For species of *Strongylocentrotus,* the distinction between primary and secondary is not discrete (Hyman, 1955). The spines are rigid and made of calcium carbonate (same as the test). There are two types of musculature associated with spines, one to set the spine in place and another to manipulate the spine. This allows the spine to be kept either rigid, or mobile depending on need. The spines of *S. franciscanus* (< 7 cm) are longer than those of *S. droebachiensis* or *S. purpuratus* (< 2.5 cm). These longer spines can be used as an effective deterrent against potential predators such as starfish, where for example, the spines can pinch the soft arms of a starfish preventing them from attacking (Moitoza and Phillips, 1979; personal observation). Indeed, when both *S. franciscanus* and *S. purpuratus* are placed in a tank with *Pycnopodia helianthoides*, the short-spined *S. purpuratus* are eaten first (Moitoza and Phillips, 1979).

For echinoids, podia help serve locomotion, feeding, chemoreception, attachment, and gas exchange functions (Hyman, 1955; Brusca and Brusca, 1990; Leddy and Johnson, 2000). There are three types of podia in echinoids, which are (1) buccal or oral, (2) locomotory, and (3) papillate or sensory (Hyman, 1955; Megalitsch and Schram, 1991). Podia on the oral surface aid in adhesion and locomotion, and are characterized by a flattened section of epithelium called the terminal disc (Meglitsch and Schram, 1991). The stalk of the podia, while extremely flexible, is supported by imbedded calcareous speckles. Whereas podia on the aboral surface may help secure drifting kelp, many of the aboral podia lack terminal discs and serve in a sensory role (Hyman, 1955). Aboral podia also function as the major respiratory surface (Leddy and Johnson, 2000).

Spines aid in locomotion though movement is also achieved with the use of podia that are controlled through hydraulic pressure (Brusca and Brusca, 1990). Adult *S. franciscanus* (~ 160 cm test diameter) were observed in the field to move at rates > 50 cm / day (Mattison et al., 1977). To extend podia, fluid is forced into the podium. Once the terminal disc (sucker) contacts a surface (e.g. substratum), the epidermis secretes adhesive (i.e. proteinaceous film) to help the podium hold onto the substratum. Longitudinal muscles in the stalk then contract forcing fluid out of the podium, causing the tube foot to shorten. The podium releases by relaxing the longitudinal muscles, which allows fluid back into the tube foot. Differential contraction of these longitudinal muscles also allows the tube foot to bend.

Sea urchins have another external feature called pedicellariae. These are thin, flexible stalks upon which a three-jawed organ sits. The four types of pedicellariae are called (1) tridentate, (2) triphyllous, (3) ophiocephalous, and (4) floriferous. Figure 4 shows the shape of a globiferous pedicellariae for a species of *Strongylocentrotus*. The specific function of each of the different types of pedicellariae remains unclear. They may serve as defense to remove debris from the spines of the urchin. Another possibility is that the pedicellariae may absorb dissolved nutrients or even trap small organisms for digestion and absorption (Brusca and Brusca, 1990).

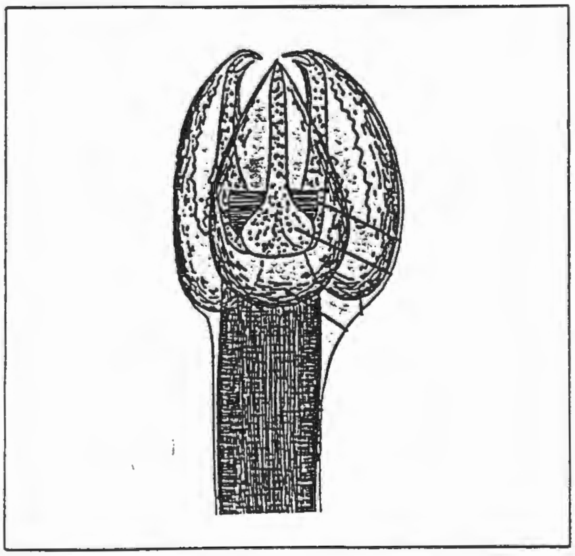

Figure 4. Globiferous pedicellariae for species of *Strongylocentrotus* (Hyman, 1955).

Life History

Estimates of longevity for urchins are difficult to make (Smith et al., 1998). While studying *S. purpuratus*, Ebert and Russell (1988) found that small individuals produced more than one growth ring per year (on interambulacral plates) and large individuals might not produce a ring due to slow growth. Moreover, Ebert (1967) also found that *S. purpuratus* monitored over a year could decrease in size. Urchin morphology is influenced by resource abundance and temperature (Rogers-Bennett et al., 1994; Russell et al., 1998; Miller and Emlet, 1999). Recent evidence indicates that urchins are slow-growing and long-lived. Ebert and Russell (1992) forwarded the notion that urchins experience rapid growth early in life and may continue growing slowly for their entire life. Estimates of life span have been calculated for both *S. franciscanus* and S. *droebachiensis* via fluorescent tags of the demi-pyramids, or "jaws". Both species may exceed one hundred years of age (Ebert, 1998; Russell et al., 1998). In British Columbia, *S. franciscanus* reproduce at 50 mm test diameter whereas evidence from Alaska and Nova Scotia indicate that *S. droebachiensis* first reproduce at 46-50 mm test diameter and 25-35 mm test diameter respectively (Campbell and Harbo, 1991).

Sea urchins are dioeceous, broadcast spawners with fertilization occurring in the water column. On the west coast of North America, spawning occurs from March to September after which a free-swimming larva disperses before settling. Larvae are planktotrophic and remain in the water column for 62 – 131 days (Strathmann, 1978), although increased food concentration can shorten this period to 23 days in the lab (Rogers-Bennett, 1994). A more detailed explanation of fertilization ecology is provided below.

Juvenile *S. franciscanus* are often observed sheltering under the spines of adults. The main body (test) of the adult sits upon short spines that create a small space for the juveniles to reside within (Tegner and Dayton, 1977). Sheltering of juveniles by adults has been observed for *S. franciscanus* (Low, 1975; Tegner and Dayton, 1977; Breen et al., 1985), *S. purpuratus* (Ebert, 1968), and *S. droebachiensis* (Rogers-Bennett, 1989). Sloan et al., (1987) showed that juvenile *S. franciscanus* were commonly found with adult congregations as opposed to solitary adults. The authors also showed that the smallest juveniles were found nearest to the adult, (under test) while larger juveniles were found near the outer regions of the spine canopy. In British Columbia, this adult sheltering has been proposed as a factor in reducing juvenile mortality for *S. franciscanus* (Sloan et al., 1987; Campbell and Harbo, 1991; Nishizaki and Ackerman, 2001). Conversely, adult sheltering did not improve survivorship for a species of sea urchin in New Zealand, *Evechinus chloroticus* (Andrew and Choat, 1985). Although the idea of increased survivorship has been proposed for *S. franciscanus* and *S. droebachiensis*, it is not known if juveniles under the spine canopy show increased survivorship. The notion that the presence of an adult spine canopy increases juvenile survival is based on differences in observed size-frequency distributions between habitats with and without adults (Tegner and Dayton, 1977; Sloan et al., 1987). This thesis seeks to examine several hypotheses that may help to explain the observed distributions in the aforementioned studies. A more detailed explanation of juvenile sheltering will be provided in section 2.2.

As mentioned previously, there are three congeneric species of sea urchin in British Columbia (Kozloff, 1996). The red urchin, *S. franciscanus* reaches 160 mm test diameter and is found subtidally from Baja California to Alaska and extending to Japan (Kato and Schroeter, 1985). The green urchin *S. droebachiensis* is smaller (test diameter < 100 mm) and is found subtidally from Washington to Alaska (Campbell and Harbo, 1991). A third species, *S.* purpuratus is similar in size to *S. droebachiensis* (test diameter < 100 mm) but is found in more wave-exposed habitats throughout the intertidal (Campbell and Harbo, 1991). The habitat of all three species overlap to some degree and all develop indirectly through a free-swimming, planktotrophic larval stage.

S. franciscanus and *S. droebachiensis* are generally found between the low intertidal and subtidal zones. Purple urchins can be found in the middle to low intertidal zone where breaking waves predominate. All three species occur on rocky substratum. On the west coast of North America, some *S. purpuratus* reside in pockets created in the rocky substratum using their feeding apparatus. These burrows protect the urchin from high wave action (Brusca and Brusca, 1990). Figure 5 shows these rock "bowls" on the west coast of Vancouver Island during low tide.

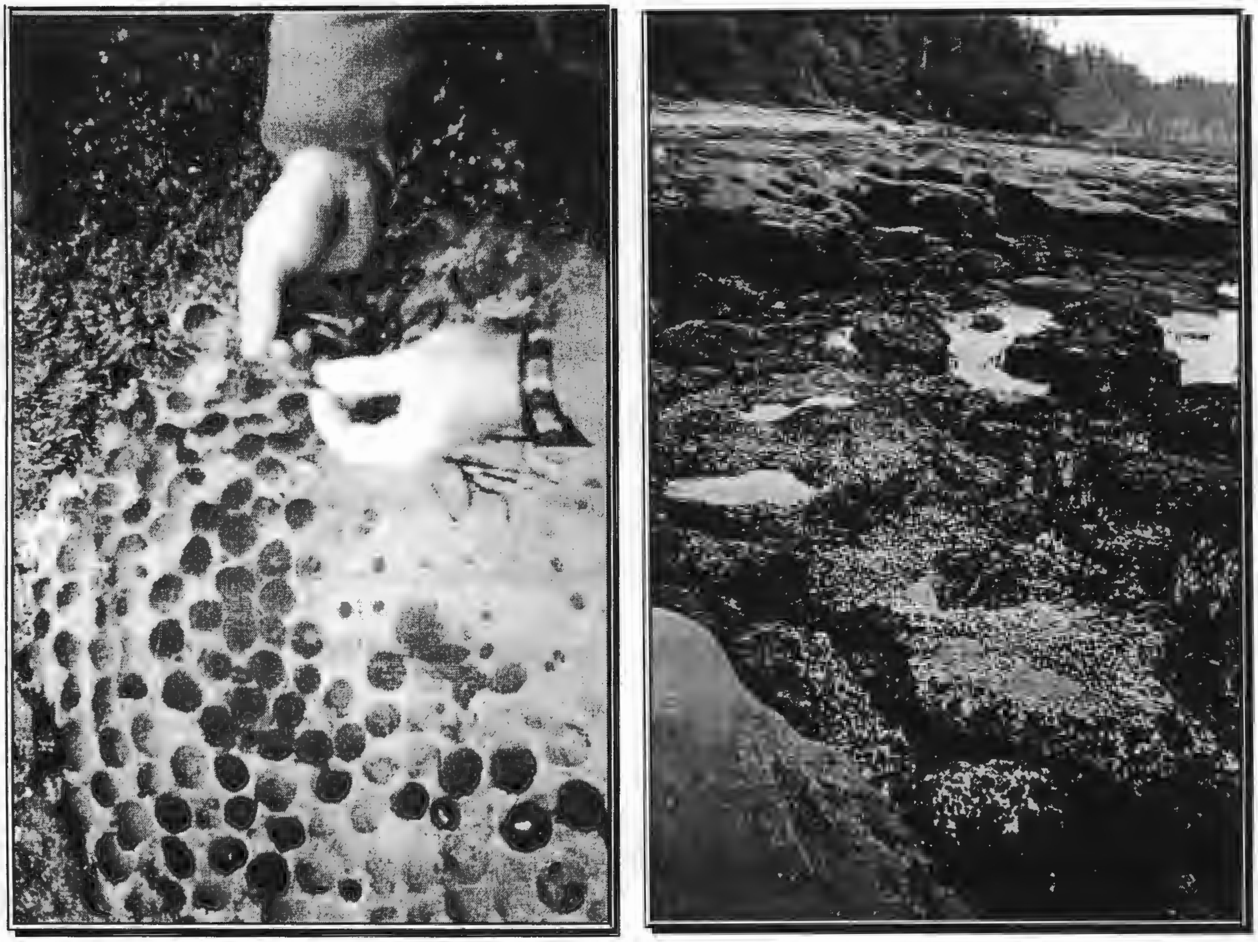

Figure 5. Rock scoured bowls.

S. franciscanus residing in shallow habitats were found to be morphologically distinct from those found in deeper waters (Rogers-Bennett et al., 1995). In shallow waters, adults sometimes congregate around food-rich habitats and were found to be more sedentary than adults from deeper habitats. This aggregation may also increase reproductive success as adult densities of greater than 4 individuals/m^2 are required to ensure fertilization successes of 82% (Levitan et al., 1992). In these areas, adults were twelve times more likely to be found sheltering young than adults found in deeper waters (Rogers-Bennett et al., 1994). Whether this difference in sheltering rates is a shaped by environmental conditions or simply by differences in juvenile abundance between the two habitats remains unknown.

Urchins are omnivorous, preferring kelp (mainly *Nereocystis leutkeana, Macrocystis spp.*), but will also feed on other species of kelp and even animal matter (Brusca and Brusca, 1990). Sea urchins are important grazers of the kelp forest in subtidal communities. In sufficient densities, sea urchins can remove macroalgae leaving exposed areas called barren grounds (North and Pearse, 1970; Keats et al., 1982). Urchins begin feeding at the attached end (holdfast) of kelps, causing them to break free. The importance of drift kelp (i.e. detached kelp that is deposited on the sea floor) to sea urchins has not been measured. However, it is assumed that *S. purpuratus* trapped in rock-scoured bowls from which they cannot escape must rely on drift kelp brought to them by the water current (Brusca and Brusca, 1990; Rogers-Bennett et al., 1995). This is a plausible explanation as to how confined individuals survive in the intertidal. It should be noted that sea cucumbers (*Parastichopus californicus* and *Eupentacta quinquesemita*) feed only during part of the year, the remainder of which their guts are empty or absent (Byrne, 1985; Cameron and Fankboner, 1986). Importantly, for sea urchins in British Columbia, the reproductive season coincides with an increase in drift kelp brought in after the winter storm season.

Sea otters (*Enhydra lutris*) are significant predators of sea urchins. Estes and Duggins (1995) showed that when sea otters were either constantly absent or present, *S. franciscanus* populations were stable. However, in areas where otters were reintroduced, *S. franciscanus* populations declined significantly (i.e. 50% to nearly 100%). In addition, it was discovered that sea otters feed preferentially on larger *S. franciscanus.* In British Columbia, other potential predators include starfish (*P. helianthoides* and *Dermasterias imbricata*) and crabs (*Cancer productus, Lopholithodes spp.* and *Acantholithoides hispidus*) (Breen et al., 1985). Furthermore, work by Wootton (1995) demonstrated a trophic cascade as *S. purpuratus,* when freed from predation by birds, reduced the abundance of algae in the intertidal.

2.2. Marine Invertebrate Recruitment Processes

Marine Benthic Invertebrates

Recruitment is the addition of a juvenile to a population whereas dispersal involves the movement of individuals (usually larvae and juveniles) away from their home range. It has been suggested that recruitment plays an important role in marine invertebrate population dynamics (Underwood and Denley, 1984; Roughgarden et al., 1985; Roughgarden et al., 1988; Sutherland, 1990). Recruitment is comprised of three stages (Cameron and Schroeter, 1980): (1) larval supply; (2) settlement; and (3) post-settlement survival. Larval supply refers to the density of competent larvae ready to settle in a given area. Settlement processes meanwhile, affect the transition from the larvae in the water column to metamorphosis on the substrate. Finally, post-settlement processes include factors that influence survival of benthic juveniles after metamorphosis (Harrold et al., 1991).

There have been a number of hypotheses proposed to explain the spatial and temporal variation in the recruitment of marine benthic invertebrates. Levitan et al., (1992) indicated that the distribution of adults may impose limitations on successful fertilization thus limiting larval supply. Factors such as aggregation, group size, and position within group all affected fertilization success rates. It is thus predicted that at low adult densities, the per capita fertilization rate also remains low. Gaines and Bertness (1992) forwarded the trans*port hypothesis*, which states that differences in the transport of larvae (i.e., availability) may account for variation in recruitment patterns. Therefore, it would be expected that the distribution of a population should correlate with hydrographic events and geographic features. Over a nine year period, settlement rates of *Semibalanus balanoides* in California correlated positively with longer flushing times (an indication of larval retention within the site; Gaines and Bertness, 1992). In 1974, Crisp (see Cameron and Schroeter, 1980) found that *preferential settlement* occurred in response to an environmental cue such as food, resident adults, or predators. The '*desperate larvae hypothesis'*. (Knight-Jones, 1951, 1953; Wilson, 1953; Pechenik, 1990) has been advanced to explain how gregarious species disperse to previously uncolonized areas. Larvae that are unable to locate appropriate habitats to settle upon become increasingly less discriminating in their choice of substratum on which they will settle. This theory postulates that larvae that are unable to locate conspecifics cannot continue their planktonic existence and are forced to settle into uninhabited areas. In the same study, Toonen and Pawlick (1994, 2001a, 2001b) present an alternate hypothesis to explain the same phenomenon. They present evidence that there are two *distinct behavioural types of larvae* produced by the same species. This polymorphism in settlement preference results in one larval type colonizing uninhabited areas whereas a second colonizes in response to conspecifics. In their study, polychaete larvae showed consistent patterns of settlement regardless of previous exposure to suitable habitat. Young and Gotelli (1988) demonstrated that *predation of larvae* could influence recruitment for marine invertebrates. Barnacle predation on larvae had nonexistent or indetectable effects on settlement for many species (description below). It was predicted that recruitment could be reduced in habitats with predators, though this effect was easily confounded by other factors. Highsmith (1982) hypothesized that variable recruitment was a result of *reduced post-settlement mortality* rather than settlement processes. From this, it was expected that recruitment would be higher in areas where mortality was reduced (i.e. refuges). Finally, migration is a possible mechanism that could explain observed patterns of distribution. Crowe and Underwood (1998) show how migration of intertidal gastropods (*Bembicium auratum*) to more favorable habitats, as opposed to recruitment or mortality can maintain population distributions. Table 1 lists the theories presented to explain recruitment variation. Research from this study will focus mainly on the theories of reduced post-settlement mortality and juvenile migration.

Table 1. Current theories regarding marine benthic recruitment

Theory	Cited Author(s)	Model	Prediction
Fertilization Limitation	Pennington, 1985 Levitan et al., 1992	In broadcast spawners, increased dilution of gametes limits fertilization success	Allee effect for small populations
Transport Hypothesis	Gaines and Bertness, 1992	Variations in the transport of larvae determine if competent larvae are distributed to favourable habitats	Distributions will correlate to hydrographic events and geographic features
Differential Settlement	Crisp, 1984; Cameron and Schroeter, 1980	Preferential settlement of larvae in response to some environmental cue	Recruitment affected by resident adults, food sources, predators
Desperate Larvae Hypothesis	Toonen and Pawlick, 1994	Larvae unable to find conspecifics are unable to prolong their planktonic lives and settle in uninhabited areas	Predicts gregarious populations founded by "desperate larvae" leading others to settle in these new areas
Differential Larval Behaviour	Toonen and Pawlick, 1994	Fundamental difference in larval behaviour within a species	Predicts gregarious populations founded by one type of larvae leading a second type to settle in new areas
Larval Predation Hypothesis	Young and Gotelli, 1988	Consumption of larvae by predators	Recruitment diminished in areas with resident predators
Reduced Post-Settlement mortality	Highsmith, 1982	Variation in survival of post-settlement juveniles	Recruitment will be enhanced in areas of refuge where mortality is reduced
Juvenile Migration	Crowe and Underwood, 1998	Behaviour rather than recruitment or mortality maintains distribution pattern	Distribution will concentrate near favourable habitats

Regardless of the specific mechanisms (Table 1), there are many factors that affect recruitment in marine benthic invertebrates. These factors fall into three main life history categories including: (1) pre-settlement; (2) settlement; and (3) metamorphosis and survival in the benthic environment (i.e. early life-history; Harrold et al., 1991). Table 2 provides a summary of the various processes that affect recruitment for benthic marine organisms.

Table 2. Summary of pre-settlement, settlement and post-settlement processes and factors affecting benthic marine organisms. The duration ranges are given in parentheses (based on Todd, 1998).

PRE-SETTLEMENT PROCESSES and FACTORS [Seconds-Months]

1. Predation on larvae (in the water column)
2. Oceanographic and local hydrographic influences (e.g. tidal currents, upwelling, Ekman transport)
3. Larval 'quality' (are all larvae equal?)
4. Larval behaviour (e.g. vertical migration, responses to salinity)
5. Substratum electivity (making the 'correct' choice)
6. Benthic predation (e.g. inhibitory effects of adult suspension feeders)

SETTLEMENT and RECRUITMENT PROCESSES and FACTORS [Minutes-Hours]

1. Successful encounter of, or attachment to, the substratum
2. Responses to substratum cues (e.g. flow regime, particle size, bacteria, surface biofilms, chemical cues, substratum texture and orientation)
3. Detection of conspecifics or founders (gregarious species)
4. Detection/avoidance of competitors and predators
5. Responses to allelochemical agents
6. Successful completion of metamorphosis

POST-SETTLEMENT PROCESSES [Seconds-Decades]

1. Intra/Inter-specific competition
2. Predation [including numerical responses], grazing
3. Parasitism and disease
4. Physical disturbance (including displacement due to hydrodynamic factors)
5. Reproductive performance and success
6. Sublethal and lethal abiotic stresses
7. Density-related immigration/emigration of juveniles and adults

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While in the water column, larvae are exposed to pelagic predators such as planktivorous fish, medusa, ctenophores and other larvae (Thorson, 1950; Barnes, 1959; Huntley and Hobson, 1978; Morgan, 1995). Possible defensive mechanisms in larvae include nematocysts, spicules, spines, shells, mucous, transparency, chemical defense, and migration (Morgan, 1995).

For successful recruitment, there must be an adequate pool of larvae available to settle (larval supply). There are many oceanographic factors such as currents, upwellings, and tides that influence larval supply. Ekman transport results from wind blowing over the surface of the ocean. This occurs due to the Coriolis force, which causes water to deflect 15 - 20° to the right of the direction of the wind in the northern hemisphere (Shanks, 1995). With increased depth, the current caused by surface winds dissipates creating an Ekman spiral that results in a net movement of water that is slightly to the right of wind direction (Ekman transport). When on the continental shelf, Ekman transport causes upwellings or downwellings depending on the direction of the wind (Shanks, 1995). Roughgarden et al. (1988) found that recruitment of barnacles correlated with the strength of upwelling along the coast.

Local hydrographic conditions may also influence larval dispersal. For coral larvae, it has been shown that near-field circulation can also influence recruitment (Sammarco and Andrew, 1988). For some annelids (*Prionospio japonica* and *Doliodrilus tener*) recruitment is influenced by tidal action (Hsieh and Hsu, 1999).

Recent modelling techniques (Gaylord et al., 2002) confirm that although most kelp propagules disperse only meters, some spores may disperse several kilometres. One major limitation to such models however, is a knowledge gap concerning bottom topography and hydrodynamic conditions on a local scale (< 10 m). This interaction between flow and bottom topography may be reciprocal, with bottom roughness elements altering patterns of flow (Nowell and Jumars, 1984) and in turn flow changing bottom topography (i.e. bedload transport). Moreover, biological structures such as kelp canopies, urchin spines and seagrass blades also alter local patterns of flow (Eckman et al., 1989; Ackerman and Okubo, 1993).

Recruitment can also be affected by differences between individual larvae. As indicted above, Toonen and Pawlick (1994) showed that there was a distinct subpopulation of "founder" larvae that will settle in new areas without conspecifics. The remaining population of larvae only settled in the presence of conspecifics. Another study by Gibson (1995) found intra-clutch variation in time to competence for larvae of the opisthobranch, *Haminaea callidegenita*. This larval variation affects recruitment by allowing for both short-distance and long-distance dispersal.

Positioning behaviour by larvae in the water column may affect dispersal. Chia et al., (1984) reviewed many aspects of larval locomotion supporting the notion that vertical rather than horizontal migration was more likely for slow swimming larvae. This vertical change in depth allows larvae to affect dispersal by placing themselves within baroclinic currents (change with depth) running over the continental shelf. This type of phenomena was found in larvae of rocky intertidal fish, which were able to resist offshore transport by swimming (Marliave, 1986). There is also evidence that echinoid larvae orientation may be associated with pycnoclines (density), haloclines (salinity), turbidity fronts, and tidal bores (Metataxas and Young, 1998).

Benthic predators may also play a role in removing larvae from the water column (Highsmith, 1982). According to Thorson (1950), an average-sized *Mytilus edulis* can remove about 100 000 lamellibranch larvae from the water column in 24 hours. The effects of barnacle predation on larval recruitment were found to be variable and easily confounded by other factors for bryozoans (*Schizoporella errata*), colonial ascidians (*Didemnum* sp., *Diplosoma glandulosum*, *Distaplia bermudensis*), barnacles (*Balanus* spp.), serpulid polychaetes (*Pomatoceros americanus*), and solitary ascidians (*Styela plicata*) (Young and Gotelli, 1988).

A second important stage in recruitment is settlement of larvae onto the substratum. Substratum cues are an important part of larval settlement and metamorphosis for many species. For a wide variety of larvae, factors such as chemical cues, water velocity, biofilms, and substratum roughness have been demonstrated to influence recruitment (Highsmith, 1982; Rittschoff et al., 1984; Pawlick, 1986; Pawlick et al., 1991; Tamburri et al., 1992; Unabia and Hadfield, 1999).

Whereas some larvae have been found to settle near conspecifics (Highsmith, 1982) others like the acorn barnacle (*Balanus glandula, B. crenatus*) have been found to avoid settling near competitors (Grosberg, 1982). Keough (1998) found only 12 of the ~100 settler-resident combinations examined had significant effects on larval settlement (both positive and negative), which were much weaker relative to the effects of biofilms on larvae settlement.

Once larvae have settled, there remain many processes that affect distribution. After choosing a site, some larvae can re-enter the water column and undergo secondary settlement (Pawlick et al., 1991). In some marine bivalves, secondary settlement can occur via thread drifting, bubble formation, or rafting on macroalgae (review in Ackerman et al., 1994). Mussels such as *Mytilus edulis* settle first on filamentous algae, hydroids, or byssal threads of adults and after metamorphosis, cut their byssal threads freeing them to re-enter the water column. Similar post-metamorphic movements are found in other taxa. Analogous phenomena are found in corals, which have larvae that re-enter the water column by reversible metamorphosis (Richmond, 1985).

Although recruitment may be an important predictor of adult distribution, its influence can be modified by post-settlement processes (Pfister, 1996; Menge, 2000). Bhaud (1998) demonstrated that the area available to settling larvae did not necessarily predict adult distributions and post-settlement constraints were assumed to play an important role in limiting recruitment. Caley et al., (1996) called for greater attention towards post-settlement processes that can reduce recruitment and/or lead to post-settlement migration (Iribarne et al., 1994). Subsequent work has focussed on the recruitment related to predation (Navarrettes, 1996), parasitism (Boglio and Lucas, 1997), disease (Scheibling and Hennigar, 1997), and intra-specific and inter-specific competition (Caroll, 1996; Hunt and Scheibling, 1998). Interestingly, inter-cohort predation by juveniles on post larvae (i.e. megalopae) for blue crabs (*Callinectes sapidus*) was found to significantly reduce recruitment (Mokesnes et al., 1997). Côté and Jelnikar (1999) discovered that blue mussels (*Mytilus edulis*) showed increased aggregating behaviour in the presence of a predator (European lobster, *Homarus gammarus*). Other species such as the mytilid, *Choromytilus chorus* are limited in dispersal to areas under macroalgae (*Gymnogongrus furcellatus),* which serve as refuges from predators like *Nucella crassilabrum* (Moreno, 1995).

Currently, interactions between flow and ecological processes such as predation, herbivory or competition remain unclear. The *harsh-benign hypothesis* (Thomson et al., 2002 for review) predicts that the hydrodynamic stresses of wave action create refuges for organisms from predation and/or herbivory. Recent evidence, however, indicates that organisms at wave-exposed sites may actually experience the highest levels of predation (Robles et al., 2001). Clearly, field research examining how wave forces affect interactions such as predation, herbivory or competition is warranted.

Predation can also have sub-lethal effects that can indirectly modify recruitment patterns. Rawlings (1994) found that when *Nucella emarginata* were held downstream of a predator, they stopped spawning and lost weight over three months. It was hypothesized that this weight loss was a result of an increased metabolic rate (i.e. stress) resulting from exposure to the predator. Thus predation may have more subtle impacts that affect distribution.

Physical disturbance may also play a role in limiting recruitment. A study of barnacle (*Semibalanus balanoides)* recruitment showed that the sweeping of algal fronds (*Fucus spiralis*) inhibited successful recruitment (Jenkins et al., 1999). Moreover, Leonard (1999) found that the negative effect on recruitment of barnacles by mechanical abrasion resulting from the algae *Ascophyllum nodosum* was twice as large as the positive effect of reducing predation under the algae.

A depensatory density dependent effect (Allee effect) whereby sea urchin fertilization rates increase as adult densities increase has been demonstrated by a number of researchers (Pennington, 1985; Denny and Shibata, 1989; Levitan, 1991; and Levitan et al., 1992). It is possible that distribution patterns could be related to reproductive success. However, it should be noted that there is a trade-off between fertilization success and intra-specific competition related to population density.

There are many examples of refuge use by juveniles in marine systems. Juvenile invertebrates such as Iceland scallops and Dungeness crabs hide under shells and rocks (Arsenault and Himmelman, 1996; M^{c}Donald et al., 2001). Juvenile barnacles are often found to occupy physical refuges such as crevices or empty tests (Miller and Carefoot, 1990; Schubart et al., 1995). Kelp holdfasts can provide refuge habitat for juvenile kelps (Anderson et al., 1997). For some species of ophiuroid, juveniles recruit onto the surface of sponges. For other ophiuroid species, juveniles cling to conspecific adults and in some cases this behaviour is interspecific (Hendler et al., 1999).

Sea Urchins

Recruitment of juveniles into sea urchin populations is variable although the cause of this variability is as yet, unknown (Raymond and Scheibling, 1987; Rowley, 1989; Campbell and Harbo, 1991). Like many benthic marine invertebrates, urchin populations are comprised of many separate subpopulations (e.g., metapopulations) linked by dispersing larvae (Quinn et al., 1993). Local habitats that produce large numbers of juveniles are called "hot spots" and can be identified in a wide variety of terrestrial and aquatic species (Rogers-Bennett et al., 1995).

For red urchins in California, it was shown that recruitment was higher in shallow habitats characterized by the bowls described above.

The issue of larval supply has been shown to be an important factor in sea urchin recruitment. It has been demonstrated that low recruitment of *S. purpuratus* correlates with areas of predictable upwellings (Ebert and Russell, 1988; Wing et al., 1995; Morgan et al., 2000). In addition, areas characterized by offshore advection displayed lower settlement of *S. franciscanus* and *S. purpuratus* than in areas with greater water retention (Ebert et al., 1994). These results were confirmed by Miller and Emlet (1997) who linked settlement events of *S. franciscanus* and *S. purpuratus* to onshore advection. Whereas Harris and Chester (1996) showed a positive correlation between water motion and larval supply, they found no correlation of either parameter to recruitment in *S. droebachiensis.* However, a subsequent study by Lambert and Harris (2000) suggested that onshore wind currents influenced recruitment.

Variation in recruitment appears on the local scale as well. It has been found that juvenile urchins are found under the spine canopy provided by adult aggregations in all three species native to British Columbia (Ebert, 1968; Low, 1975; Tegner and Dayton, 1977; Cameron and Schroeter, 1980; Breen et al., 1985; Sloan et al., 1987; Rogers-Bennett, 1989; Rogers-Bennett et al., 1995). Adults are often found in aggregations, forming a spine canopy, which provides cover for juvenile urchins. The juveniles of *S. franciscanus,* in particular appear to be limited to adult-associated habitats. Tegner and Dayton (1977) found that over ninety percent of juvenile *S. franciscanus* were found under the spines of either adult *S. franciscanus* or *S. purpuratus.* Recent genetic analysis (allozyme electrophoresis) has revealed significant differences in allelic frequencies between juvenile *S. franciscanus* and the adults under whom they shelter (Moberg and Burton, 2000).

If sea urchins are broadcast spawners with a larval period of several months, then the questions that arise are: (1) why are juvenile urchins typically found under adults and; (2) how did they get there? To date, there are no definitive answers to these questions.

Cameron and Schroeter (1980) identify three possible mechanisms that could explain the phenomenon of adult sheltering. The mechanisms were: (1) differential settlement by larvae; (2) migration of juveniles to adult dominated habitats; and (3) reduced post-settlement mortality.

It has been shown that urchin larvae are largely unselective when settling on substrates (Cameron and Schroeter, 1980; Pearce and Scheibling, 1991; Schroeter et al., 1996). The only settlement cue that has been identified for sea urchins is coralline red algae (Cameron and Schroeter, 1980; Lambert and Harris, 2000). Interestingly, it has recently been shown that metamorphosis in some species of sea urchin is triggered by floridoside, which occurs only in members of the red algae (Williamson et al., 2000). Further studies have also shown that urchin metamorphosis can be induced by glutamine, which is associated with the corraline algae *Melobesia* (Yazaki and Harashima, 1994; Yazaki, 1995; Naidenko 1996).

The role of migration at the early juvenile stage remains unclear. For example, *S. intermedius*, juveniles rarely moved in the first year post-settlement (Anonymous, 1985). Russell et al., (1998) did record migration of juvenile *S. droebachiensis*, although the authors state that they did not monitor juveniles < 15 mm test diameter, and it was possible that there is no migration at this stage as was reported by Himmelman (1986). A plausible explanation for finding juveniles in the presence of adults is reduced post-settlement mortality. Rogers-Bennett et al., (1994) indicated that only 5.3% of juveniles survived from competent larvae to one year of age in the lab. If reduced post-settlement mortality accounts for spatial recruitment variation, one must explain how mortality is reduced within the spine canopy.

A common explanation for reduced mortality is that the spine canopy affords juveniles protection from predation. Early work predicted that reduction of predation pressure by lobsters resulted in increased populations of *S. droebachiensis* (Mann and Breen, 1972; Breen and Mann,1976). However, other work suggests that predation is not the most important factor in regulating sea urchin populations (Miller, 1985). Vadas et al. (1986) showed that adult aggregation was not a defensive response for *S. droebachiensis.* In the presence of predators (and injured con-specifics) urchins did not aggregate, and simply moved to avoid predators. This behaviour was subordinate only to the presence of food, which did induce the aggregating behaviour. Rogers-Bennett (1994) showed that of eight predatory sea star species examined in California, only two, the sun star *P. helianthoides* and the leather star *Dermasterias imbricata* ate juvenile *S. franciscanus.* The sea stars ate juveniles at a rate of 1.66 and 0.6 juveniles per day respectively. Mann (1985) concluded that predation is most likely not controlling populations of *S. droebachiensis* on the east coast of North America.

A second possible advantage of the spine canopy may be related to nutrition. Tegner and Dayton (1977) noted that juvenile urchins appeared to be sharing food with the adults under which they sheltered. Urchins have been shown to aggregate as a response to algal resources (Vadas et al., 1986) making these aggregations a possible source of dissolved nutrients for juveniles as adult feeding liberates much organic matter. Adult sheltering may reduce fluctuations in water velocity and hence the dispersion of water-borne nutrients from under the spine canopy. At this stage, absorption of organic material (a characteristic of urchin larvae) may be the only means of juvenile feeding (Manahan, 1983). Kempf and Todd (as cited in Havenhand, 1995) argued that the retention of larval feeding ability might enhance survival in the early post-settlement period.

Work by Rogers-Bennett et al., (1994) showed that juvenile *S. franciscanus* did not have functional jaws until 80 days post-settlement. This period was accompanied with high mortality until jaws emerged and feeding on kelp commenced (Rowley, 1990, Rogers-Bennett et al., 1994). The hydrodynamic protection afforded by the spine canopy could reduce energetic costs and thus mortality. Water movement has been shown to impose a metabolic demand that can exceed the capacity of aerobic metabolism in adults (Pace, 1975). Moreover, water movement has also been indicated as a factor influencing urchin morphology and mobility (Ebert, 1968; Lissner, 1983; Lewis and Storey, 1984; Rogers-Bennett et al., 1995). It is reasonable to suggest that these pre-feeding juveniles may require sheltering in energetic shallow habitats (e.g. periodic velocities up to 1 - 5 m/s), to ensure their survival.

The resolution of which factors govern recruitment for juvenile urchins remains elusive. Cameron and Schroeter (1980) showed settlement was not the key factor influencing urchin recruitment over thirty years ago. Since then research has had some modest success in understanding large-scale spatial variation in recruitment patterns (i.e., oceanographic factors). However, it has been over thirty years since the discovery of spatial variation on a microscale (i.e., adult canopy) by Tegner and Dayton (1977). As yet, there has been no factor or mechanism found to explain recruitment patterns observed in the field. Results from this research on the role of the spine canopy will help to answer that question.

2.3. Behaviour

Phenotypic plasticity is the ability to produce alternate forms of morphology, physiological state, and/or behaviour from one genotype (West-Eberhard, 1989) and behaviour is often considered the most plastic of these phenotypic traits (Hazlett, 1995). More specifically, behaviour can be considered as highly "labile", or prone to change (West-Eberhard, 1989) and this flexibility in defensive behaviour has been termed "risk-balancing" (Fraser and Huntingford, 1986). Although behaviour may affect all aspects of an organism's life, this discussion will be limited to the defensive aspects of behaviour.

Defensive strategies may be either constitutive (i.e. fixed) or inducible (i.e. phenotypically plastic traits; Leonard et al., 1999). Whereas constitutive defenses should be favored when danger is permanently present (Pettersson and Brönmark, 1997), inducible defenses should be favored when threats (i.e. predation, hydrodynamic disturbance) are strong and unpredictable and when the costs of defense are high (Karban, 1993, Leonard et al., 1999; Relyea, 2002). A set of definitions for the classification of induced responses by Karban and Myers (1989) is presented in Table 3. The difference between induced resistance and an induced defense is that a defense increases the fitness of the prey organism (Karban and Myers (1989). There is growing evidence in marine systems that inducible defenses are characteristic across many phyla as such defenses have been reported for bivalves (Leonard et al., 1999), gastropods (Appleton and Palmer, 1988), barnacles (Lively et al., 2000), echinoderms (Snyder and Snyder, 1970), bryozoans (Ratchford and Eggleston, 2000), and algae (Van Alstyne, 1988). These defense strategies can be triggered by either direct or remote stimulus. Mechanical contact can elicit morphological changes (i.e. spine growth) in a marine bryozoan (Ratchford and Eggleston, 2000). Likewise, direct grazing by herbivores induces the production of chemical defenses in a marine alga (Van Alstyne, 1988). Finally, direct contact has been shown to induce chemical signaling for both gastropods and algae (Montgomery, 1966; Toth and Pavia, 2000).

Table 3. Classification of induced responses (based on Karban and Myers 1989).

Number	Characteristic
	Does stress or injury change organism integrity?
1	NO: No response
1'	YES: INDUCED RESPONSE (Go to 2)
	Does the induced response decrease predator/herbivore preference or performance?
2	NO: No effect or induced susceptibility
2'	YES: INDUCED RESISTANCE (Go to 3)
	Does reduced preference/performance increase organisms fitness?
3	NO: The organism is not defended by the response
3'	YES: INDUCED DEFENSE

Aggregating behaviour may confer several advantages including collective detection of predators, decreased vigilance, group defense, and a dilution effect (Allee, 1931; see Mauck and Harkless, 2001 for review). However, the cost of such close associations is often an increase in competition for resources (Allee, 1931; Werner and Gilliam, 1984; Dill, 1987; Lima and Dill, 1990; Werner and Anholt, 1993; Grand and Dill, 1999).

The influence of fluid dynamics on behaviour such as predation, herbivory and/or competition remains unclear. Connell (1970), indicated that predators were more susceptible to environmental factors, classified under a broad category called "weather", than prey. Moreover, wave shock is a source of mortality for predators such as *Thais lapillus* (dogwhelk) and may limit foraging to crevice habitats. The *harsh-benign hypothesis* (Thomson et al., 2000) predicts that the hydrodynamic stress of wave action creates refuge for organisms from predation and/or herbivory. Recent evidence, however, indicates that organisms at wave-exposed sites may actually experience the highest levels of predation (Robles et al., 2001). Using two predator species (slow-moving whelks, *Busycon carica* and fast-moving blue crabs, *Callinectes sapidus*) and two prey species (mobile bay scallops, *Argopecten irradians* and sedentary hard clams, *Mercenaria mercenaria*), it has been shown that predator-prey interactions may or may not be influenced by fluctuations in water motion depending the relative ability of each species to detect chemical signals (which is affected by mobility). Whether predation success is enhanced or hindered is also dependent on the degree to which predator and prey species are able to detect chemical signals. Clearly, research examining how water motion affects behaviour in marine benthic systems is warranted. Such questions however, can only be addressed by understanding the nature of water motion, a field called *fluid dynamics.*

2.4. Fluid Dynamics

In marine ecosystems the motion of water can affect the distribution, behaviour, and morphology of the constituent organisms. More specifically, water motion has been found to be a significant factor affecting the ecology of sea urchins. For example, Kawamata (1998) examined the effect of water movement on feeding and movement of the sea urchin *Strongylocentrotus nudus.* Feeding was reduced at velocities of 0.3 m/s and virtually ceased at 0.4 m/s. Movement was reduced by half at speeds of 0.3 to 0.4 m/s and nearly ceased at velocities above 0.7 m/s. In the field, it was predicted that peak velocities < 0.4 m/s would occur 70% of the time. Comparable water velocities around urchin populations were measured near Bamfield, BC by Levitan (1998). Average daily water velocities (U) ranged from 0.02 to 0.23 m/s while instantaneous velocities ranged from 0 to 0.85 m/s. An examination of fluid dynamics related to the post-settlement success of sea urchins, would therefore, be warranted.

A simple and powerful measurement in fluid dynamics is the Reynolds number. This variable is a ratio of inertial to viscous forces (Equation 1) and can be used to characterize the fluid environment in which a sea urchin lives. It is calculated as:

$$Re = \frac{\rho l U}{\mu} \qquad \text{(Equation 1)}$$

where ρ is the density (kg/m^3), l is the characteristic length (m), U is the fluid velocity (m/s), and μ is the dynamic viscosity (Pas). As the Reynolds number increases far beyond one, inertial forces dominate, so viscous forces can be ignored. Conversely, as the Reynolds number decreases below one, viscous forces dominate, making the influence of fluid momentum less impotent. By calculating the Reynolds number, one can describe flow as either laminar or turbulent with the transition occurring at the critical Reynolds number characteristic of the system (e.g., transition at Re ~ 2000 for pipe flow). In 1914, Prandtl discovered that flow in a boundary layer could be either laminar or turbulent and the transition between flow regimes proved to be essential in solving problems associated with flow separation (Schlichting, 1979). Reynolds number is invaluable in experimental approaches that investigate flow patterns using scaling (either scaling up small structures, or scaling down large structures). Other approaches include the use of Reynolds number to assess the relative contributions of skin friction and pressure drag, though the shape of an object must still be accounted for.

Early work concerning fluid dynamics was based on the assumption of a frictionless, non-viscous fluid (Vogel, 1994). Pioneers such as Bernoulli and later Euler laid the foundations for the field of theoretical hydrodynamics. One of the major problems, however, was the discrepancy between theoretical and experimental results (i.e. pressure loss in pipes). Every fluid is viscous to some extent, and as such the assumption of an absence of friction was, and remains, impractical.

A second branch of fluid dynamics developed in response to the practical problems associated with the classical theory of hydrodynamics. Based mainly on empirical results, the field of hydraulics arose as a second approach to fluid dynamics (White, 1994).

The unification of these two branches of fluid dynamics was initiated in 1904 with Prandtls' presentation of the boundary layer. The theory postulated that flow over any surface was composed of two layers: a layer near the surface where friction is of great importance and a second layer above that which is generally free from the forces of friction (Vogel, 1994). Most importantly, Prandtls' boundary layer theory was supported with empirical results that demonstrated its importance and universal applicability.

Boundary layer theory is based on a simple, fundamental assumption. A fluid moving over a solid surface exhibits the "no-slip condition" (Vogel, 1994), which, simply stated, means that water immediately adjacent to the surface of any stationary object has a velocity of zero. The viscosity of the water dictates that in moving away from the surface, a gradient of velocity is formed. Shear between the near-bed fluid (which has a velocity of zero) and the fluid far from the surface (which is moving at free-stream velocities) creates a region of retarded velocities adjacent to the boundary. This region of fluid whose velocities are influenced by the friction at the fluid-solid interface is known as the boundary layer (Figure 6), and represents the change in water velocity normal to the stationary surface (dU / dz) where z is the distance from boundary.

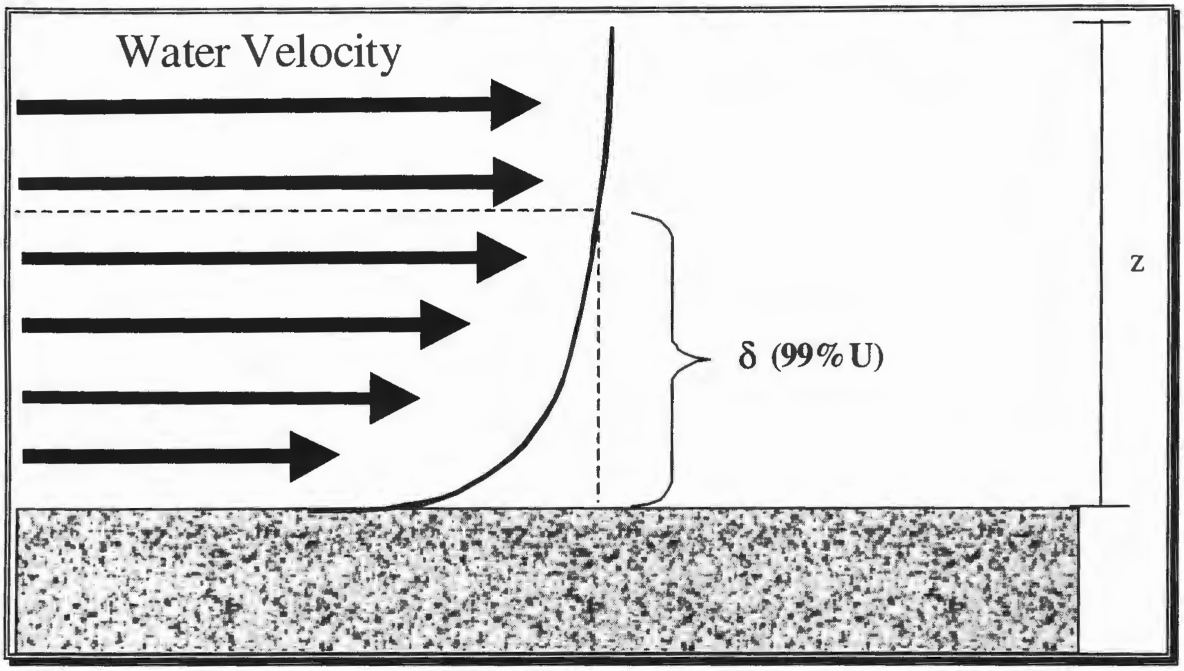

Figure 6. Boundary layer in developing, steady flow, based on Nowell and Jumars, 1984.

Boundary layer thickness depends on (1) the velocity, (2) the viscosity, and (3) position from leading edge where the water first contacts the boundary (x). The local Reynolds number (Re_x) provides an indication of whether the boundary layer is laminar or turbulent with a critical Re_x of $3 - 5 \times 10^5$ for flat plates. Laminar boundary layer thickness (δ_L) can be calculated using the following equation:

$$\delta \approx 5\sqrt{\frac{x\mu}{\rho U}} \qquad \text{(Equation 2)}$$

where x is the distance downstream from the leading edge (m), μ is the dynamic viscosity (Pa), ρ is water density (kg / m^3), and U is the free-stream water velocity (m/s). Free-stream velocities are measured at a distance sufficiently far from a surface that the influence of the boundary layer is minimized. Turbulent boundary layer thickness (δ_T) is generally defined as the distance from the boundary at which velocities attain 99% of the free stream velocity (see Figure 6).

$$\delta_T \approx 0.37x\left\{\frac{\bar{U}x}{\nu}\right\}^{-0.2} \qquad \text{(Equation 3)}$$

For organisms in the benthic environment, the influence of boundary layers can be significant. Boundary layers can play a major role in determining the rate of transport for gases, heat, and dissolved nutrients (Vogel, 1994). Beyond these influences, however, the presence of boundary layers has additional impacts on the biology of organisms living in moving water. Boundary layers also have an effect on the drag an object (or organism) must face when attached to the substrate.

The drag experienced by an object can be roughly divided into two categories based on size scales and flow conditions. At low Reynolds numbers (i.e., laminar flows) viscous drag (or skin friction) is of importance. Viscous drag is a function of the amount of shear stress in relation to the surface area affected by the boundary layer.

$$D = \frac{1}{2}C_d\rho U^2 A \qquad \text{(Equation 4)}$$

where C_d is the drag coefficient and A is the surface area of the object (m^2).

The per unit area drag, or shearing force at the boundary caused by the no-slip condition is given by the shear stress τ. Measurements of boundary layer characteristics (dU/dz) facilitate the calculation of τ, using boundary layer theory (law of the wall).

$$\tau = \rho u_*^2 \qquad \text{(Equation 5)}$$

where u_* is shear velocity.

The second type of drag is known as pressure or form drag, and is the primary source of drag at high Reynolds numbers (i.e., turbulent conditions). Although viscous drag is still present, its relative contribution is negligible. Under certain conditions (generally under high velocities for non-streamlined, bluff objects), there may be a separation of the boundary layer from the surface as water moves by an object. This boundary layer separation changes the pattern of flow near the surface and water motion is locally reversed. This flow reversal leads to the formation of either stable or unstable vortices on the lee side of objects in moving fluids. For spherical shapes, low velocities and relatively low Reynolds numbers ($10 < Re < 40$), the vortex is reasonably stable, and remains 'attached' to the object (Vogel, 1994). As Reynolds numbers increase ($40 < Re < 200\,000$), vortices thus formed separate from the object and are convected downstream (Schlichting, 1979). Vortex creation and shedding alter the distribution of pressure around an object effectively pulling the object backwards (see Figure 7) and are the basis for pressure drag.

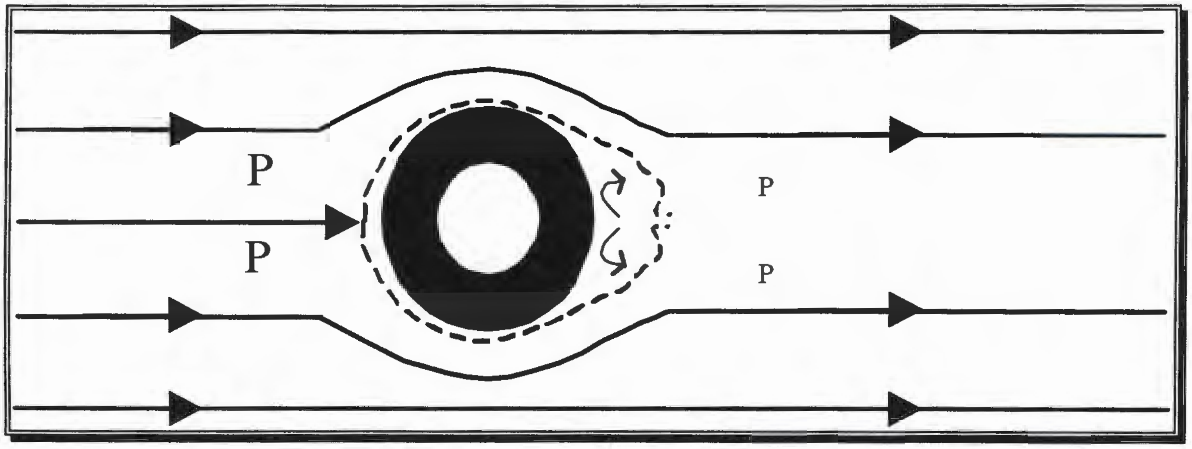

Figure 7. Boundary layer separation and vortex shedding related to drag, based on Denny, 1988.

Although viscous drag is more important than pressure drag at low Reynolds numbers, at higher Reynolds numbers, the opposite is true for bluff bodies. Thus, the shape of an object becomes more important in these high Reynolds number conditions (Vogel, 1994).

Whereas water flow imposes drag forces pulling an object backwards, lift is a force that pulls an organism up off the substratum. Figure 8 illustrates the source of lift forces acting on a benthic organism. As water rushes past the organism, a constriction of flow occurs over the top of the organism increasing velocity, and decreasing pressure is a consequence of Bernoulli's principle. The region above the organism experience lower pressure than ambient, and this pressure imbalance causes the organism to lift.

$$L = \frac{1}{2} C_L \rho U^2 A \qquad \text{(Equation 6)}$$

where C_L is the coefficient of lift.

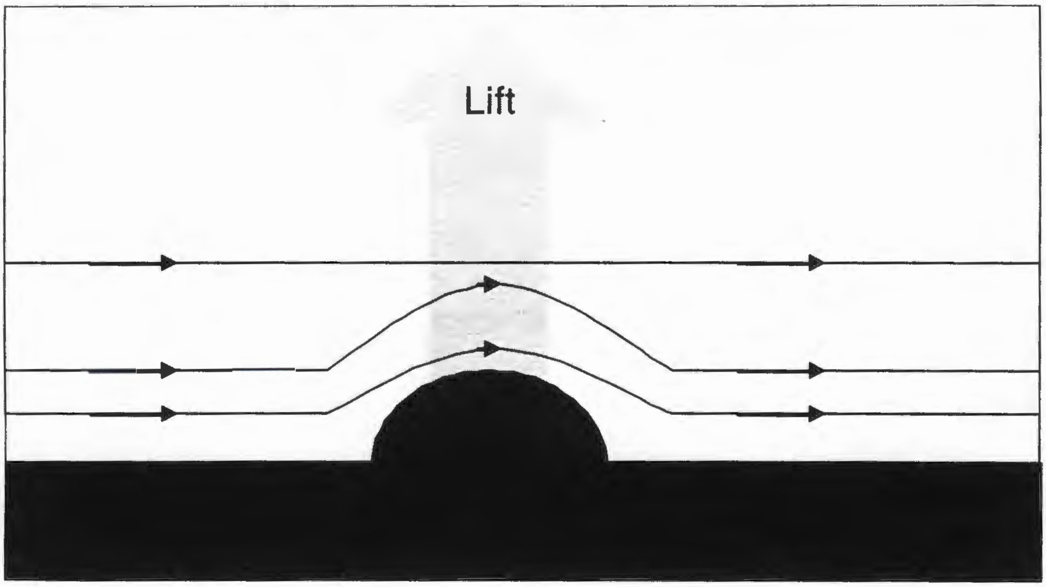

Figure 8. Pressure differences experienced by a benthic organism causing lift, based on Denny, 1988.

Many parameters that describe the physical conditions in moving fluids are based on measurements that assume that the fluid is moving at a relatively constant velocity (Figure 9). However, the moving water of marine intertidal and near-shore environments is, by nature, characterized by velocities that are highly variable at a wide range of temporal and spatial scales (Denny, 1988). Flows that are typified by high frequency fluctuations in both flow direction and velocity are classified as turbulent. "Turbulent fluid motion is an irregular condition of flow in which the various quantities show a random variation with time and space coordinates, so that statistically distinct average values can be discerned" (Hinze, 1959).

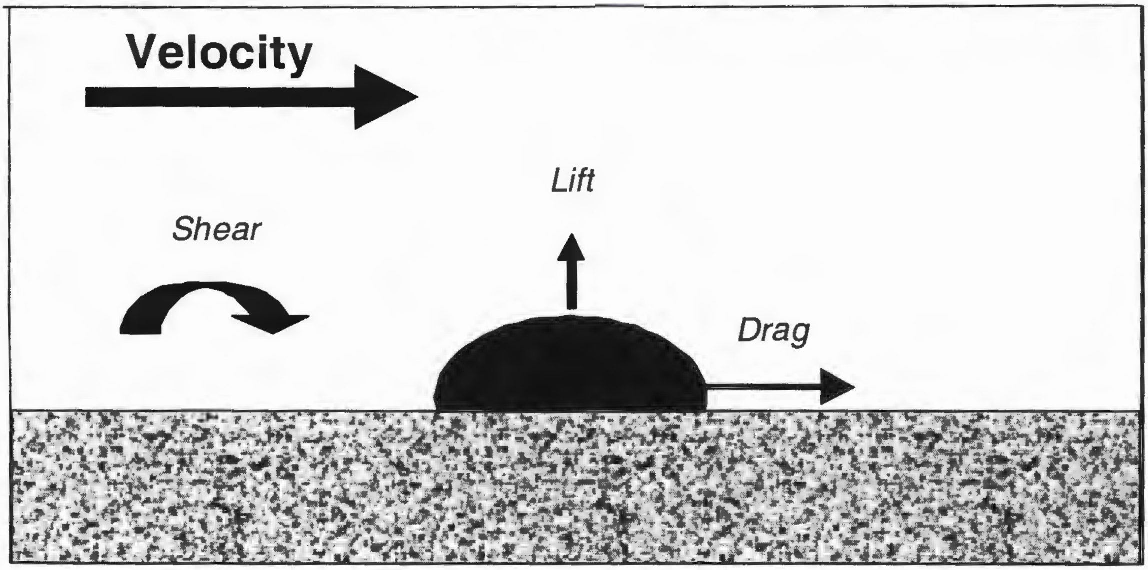

Figure 9. Fluid forces acting on a benthic marine invertebrate.

Due to the fluctuations associated with turbulent flows, measurements such as velocity and shear stress are usually described as mean values. While $\bar{U}$ represents the time-averaged velocity, U signifies an instantaneous observation of velocity (or momentary velocity). The absolute value of the fluctuation (u') can be calculated from the following equation:

$$U = \bar{U} - u' \qquad \text{(Equation 7)}$$

Further, the average value of u can then be used to calculate levels of turbulence where TI is turbulence intensity:

$$TI = \frac{\left(\sqrt{u^2}\right)}{\bar{U}} \qquad \text{(Equation 8)}$$

In benthic marine systems, turbulence intensity is most significant near the top of roughness elements (Denny, 1988).

Characterization of the patterns of flow-substrate interaction is also of importance when describing the environment of benthic marine organisms. Flow over a bed with irregular geometry can be classified as belonging to one of three categories: skimming, interactive, and independent flow (Vogel, 1994). If the objects are widely spaced, two stable vortices (front and back) form preventing interaction between objects (independent flow). If the objects are placed closer together, the vortices at the front and rear combine to reduce the stability of flow (intermediate flow). If the objects are even closer, the flow begins to skim above the objects (skimming flow). Denny (1988) states that most intertidal and shallow subtidal areas populated with plants and animals are likely characterized by skimming flow. Roughness features in these zones can provide refuge from high water velocities for a variety of marine organisms. For example, the body size of littorine snails was found to be limited to the size of the roughness features of the substratum (Emson and Faller-Fritsch, 1976). Figure 10 shows three types of flow interactions for multiple objects.

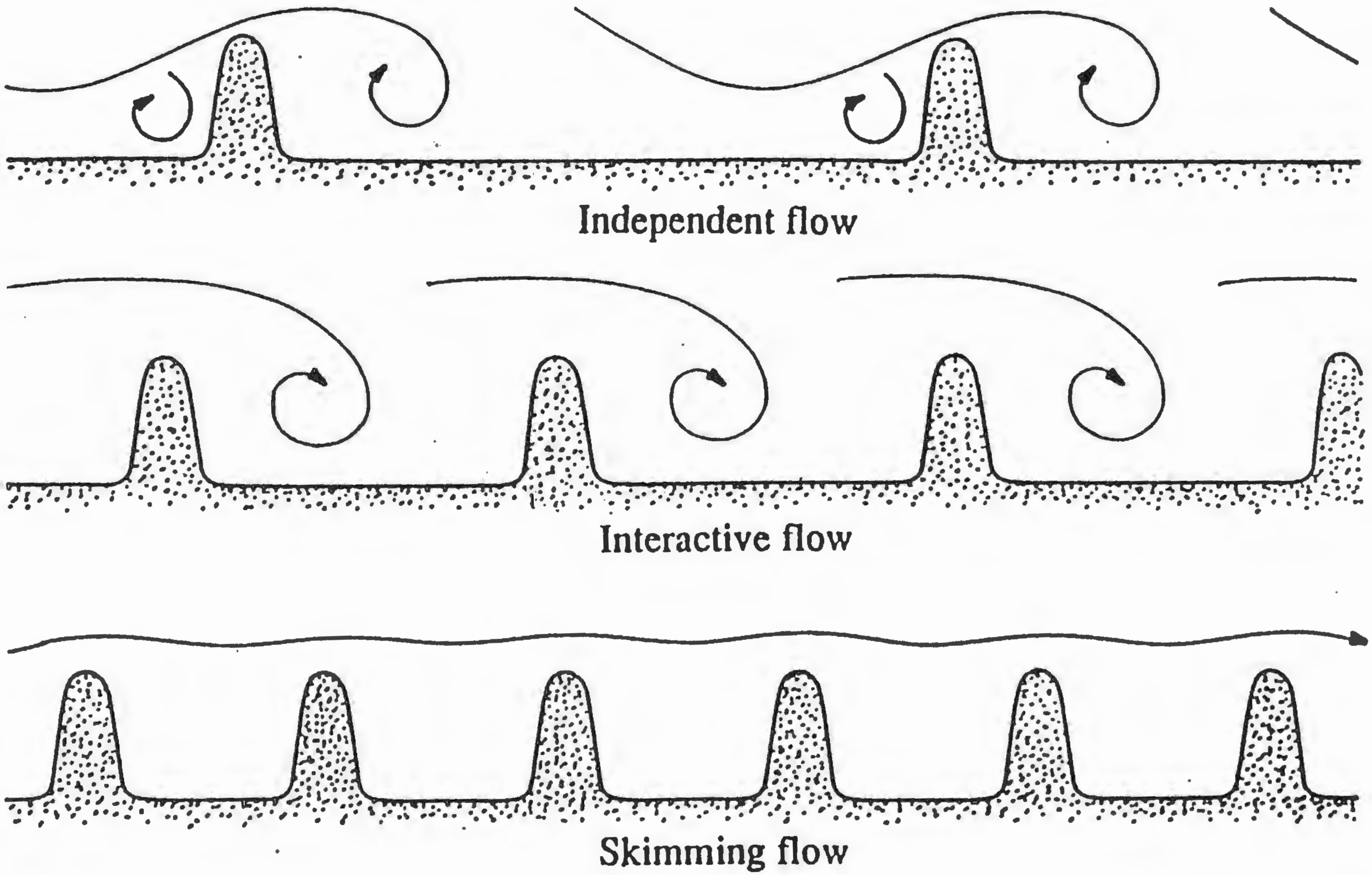

Figure 10. Independent, interactive, and skimming flow (Vogel, 1994).

Roughness Reynold's number can be calculated as:

$$\mathrm{Re}_* = \frac{Z_0 * u_*}{\upsilon} \qquad \text{(Equation 9)}$$

where Z_0 is the roughness length (m), U_* is the friction velocity, and υ is the kinematic viscosity (m^2/s).

In many instances, a description of the hydrodynamic forces created by steady flow (i.e. drag, lift) is inadequate to describe the total forces experienced by an object in naturally occurring marine environments. The acceleration of the water column by breaking or near-breaking waves creates additional forces that are unaccounted for by steady flow models (Denny, 1988). Gaylord et al., (1994) found that optimal size predictions for the algae *Iridaea flaccida* were accurate only when both drag and acceleration were accounted for. Water acceleration imposes unique forces separate from those associated with steady flow (i.e. drag and lift). As water rushes by a stationary object, a force must be applied to resist oncoming flow:

$$F = ma \qquad \text{(Equation 10)}$$

where m is the mass of the object (kg) and a is the acceleration of the water (m^2 / s). As the water accelerates, a volume of water acts as though it is "tied" to the stationary object. This means that extra force is needed to keep this water, called *added mass* from "pulling" the object away. Added mass can be calculated using Equation 11 below.

$$F_{am} = C_a \rho V a \qquad \text{(Equation 11)}$$

where C_a is the added mass coefficient and V is the volume of the object. The added mass coefficient is closely related to the shape of the object in question. Figure 11 lists added mass coefficients for various shapes.

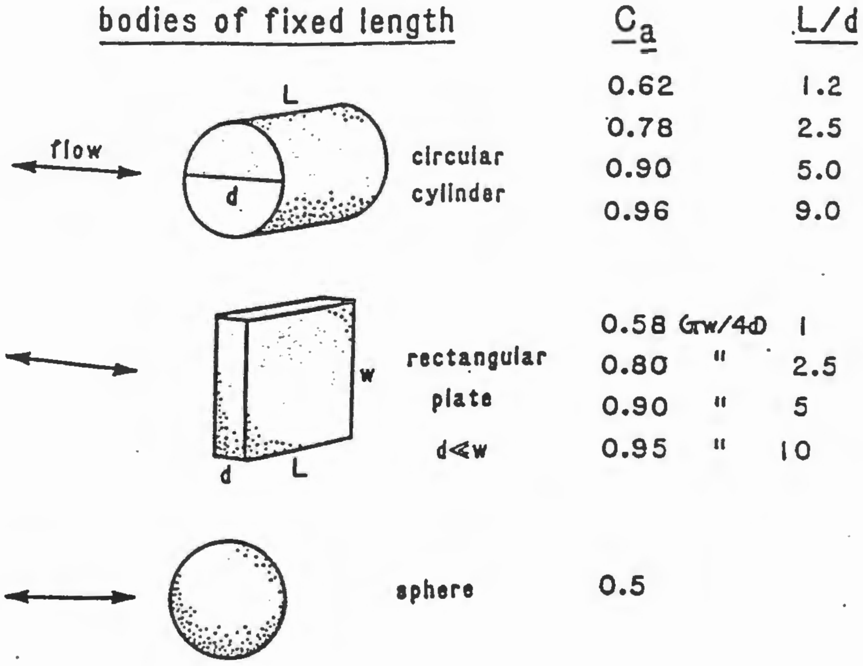

Figure 11. Added mass coefficients (Denny, 1988).

In addition to the added mass force, there is a second force called the virtual buoyancy. The object requires a force to simply remain stationary. This force must be large enough to move a parcel of water of equal volume in the opposite direction as the accelerating flow. This force is analogous to the force a stationary bubble would require to resist gravitational acceleration. This force (F_b) is:

$$F_b = \rho V a \qquad \text{(Equation 12)}$$

Together, the added mass and virtual buoyancy forces are combined into a single measure called the acceleration reaction (Equation 13) below.

$$F_a = (1 + C_a)\rho Va \qquad \text{(Equation 13)}$$

Figures 12 and 13 show the direction of the acceleration reaction in both accelerating and decelerating flows. Note that acceleration always opposes the direction of velocity change. Drag will always act in the direction of flow regardless of whether the flow is accelerating or decelerating. Acceleration reaction, however will act in the same direction as drag in accelerating flow and opposite of drag in decelerating flow.

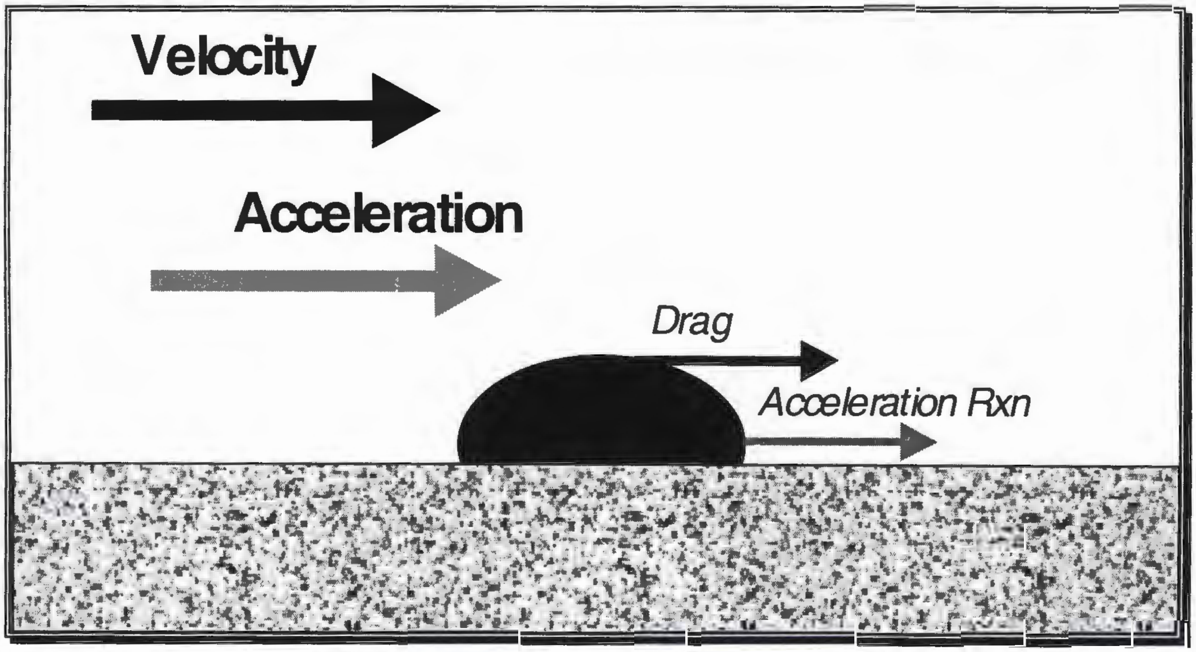

Figure 12. Hydrodynamic forces in accelerating flow.

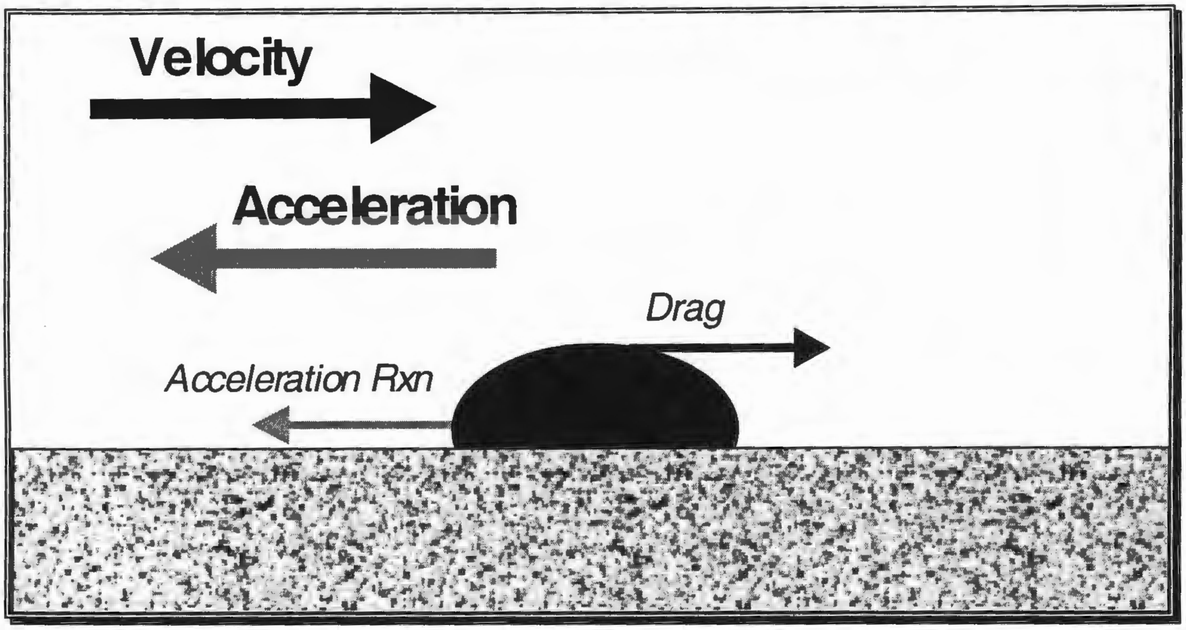

Figure 13. Hydrodynamic forces in decelerating flow.

Acceleration reaction is a measure of the rate of change of hydraulic forces acting upon an organism on the substrate (a dynamic measure). The more rapid the rate of increase or decrease, or the greater the change in momentum, the greater the stress acting upon the organism, in much the same way the rapid deceleration during a automobile accident causes greater stress than the same stress statically applied. Drag, however, represent the static forces acting to pull an organism on the substrate backwards.

Denny and Gaylord (1996) compared the force imposed by water acceleration in three species of sea urchin. The first urchin, *Colobocentrotus atratus* is found on fully exposed shores and exhibited a reduction in added mass force (related to acceleration). A second co-occurring urchin, *Echinometra mathaei* found in more protected environments showed a higher added mass coefficient. For comparison, *S. purpuratus* was used due to its inhabitance of moderate to fully exposed shores.

Even though *C. atratus* and *E. mathaei* were more closely related phylogenetically, the added mass coefficients of the urchins in wave exposed environments (*C. atratus* and *S. purpuratus)* were more similar. This served as an indication that water acceleration could be a determining factor shaping the morphology of wave-exposed urchins.

2.5. Conclusion

There is much to be gained from combining the study of recruitment, behaviour, and fluid dynamics. Recruitment is a complex, multi-stage process, and only recently has attention focussed on the importance of early juvenile stages. During these vulnerable stages, defensive behavioural strategies may be of importance. Current interest in this field centres on whether defenses are constitutive or induced and the costs associated with each. Behaviour may be influenced by variations in water motion (fluid dynamics) based in part on changes in an organism's ability to detect chemical signals. Finally, though there is much to learn in the field of fluid dynamics, a series of tools exist to quantify the nature of water motion on the scale of a sea urchin.

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Chapter III. Adult-juvenile associations in sea urchins (*Strongylocentrotus franciscanus* and *S. droebachiensis*): influence of predation, hydrodynamics, and competition with adults.

Abstract. Juvenile red sea urchins (*Strongylocentrotus franciscanus)* have long been observed under the spines of adults. Yet a congeneric species, the green urchin (*S. droebachiensis*) resides in the same habitat and does not appear to shelter to the same degree. Currently, explanations for these differences in early life-history strategy remain unknown. In this study, three possible advantages of juvenile sheltering are examined: (a) Increased protection from predators; (b) Increased protection from water motion; and (c) Increased access to food (i.e. macroalgae). Results from laboratory behaviour experiments indicate that the occurrence of juvenile sheltering in *S. franciscanus* was significantly increased by both risk of predation ($F_{(1, 56)} = 9.35$, $p = 0.003$) and water motion ($F_{(1, 56)} = 19.08$, $p < 0.001$). In contrast, juvenile *S. droebachiensis* subjected to high water flows sheltered under adults at a much lower frequency (3 ± 2 %) compared to *S. franciscanus* (52 ± 7 %). Interspecific sheltering was low between combinations of juvenile *S. franciscanus* and adult *S. droebachiensis* (16 ± 5 %) but higher than the rate for juvenile *S. droebachiensis* and adult *S. franciscanus* (5 ± 2 %).

The sunflower star *Pycnopodia helianthoides* showed a preference for juvenile *S. franciscanus* over *S. droebachiensis* (binomial test; $n = 9$, $p <0.01$) in predation experiments run in the laboratory. However, adult associations resulted in higher juvenile survival rates in *S. franciscanus* (100% survival) relative to *S. droebachiensis* (40 % survival).

Comparisons from a related laboratory growth experiment showed that small juveniles survived and grew best on diets of whole kelp blades versus ground kelp or exudate from adult feeding. Juveniles cultured in the presence of adults, however, had lower growth rates than juveniles grown alone. Manipulations of food availability indicated that this difference in relative growth rates appears to be a result of competitive interactions between adults and juveniles for kelp. It is proposed that juvenile sheltering is an adaptive behaviour that lowers exposure to both predation and water motion even though it increases competition for food with adults.

Strongylocentrotus | sea urchin | induced defense | recruitment | behaviour

3.1. Introduction

Marine benthic invertebrates with planktonic larvae experience high mortality during dispersal, settlement, and the early juvenile stage (Gosselin and Qian, 1997; Pechenik, 1999). Sea urchins are no exception given that juvenile mortality has been reported at 70-80 % during the first 24 days (Rowley, 1990). Yet juvenile red urchins (*Strongylocentrotus franciscanus*) have been found under the spine canopy created by aggregations of adults, often at remarkably high frequencies (e.g. 90 %) (Low, 1975; Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987). This would appear to be an unlikely association for an organism with pelagic larvae and, therefore, it would be appropriate to examine the potential benefits of this association for recruitment into adult populations.

One question that arises is how juvenile sea urchins come to dwell under adults. Cameron and Schroeter (1980) proposed three mechanisms that could influence juvenile recruitment: (a) Larval supply; (b) Larval settlement; and (c) Juvenile mortality. Harris and Chester (1996), reported that sea urchin recruitment was not associated with larval supply. Furthermore, Cameron and Schroeter (1980) indicated that urchin larvae did not settle preferentially in response to adult-associated cues. The lack of evidence for the larval supply or larval settlement models suggests that urchin recruitment may be a consequence of early juvenile mortality and/or behaviour.

In contrast to *S. franciscanus*, juvenile green urchins (*Strongylocentrotus droebachiensis*) have been observed as "solitary" and well dispersed (Low 1975; Scheibling and Hamm, 1991) even though adults appear to aggregate (Hagen and Mann, 1994). Likewise, juvenile purple urchins (*S. purpuratus*) appear to recruit independent of the adult presence (Low 1975; Tegner and Dayton 1977). It has been suggested that differences in the distribution of these closely related species might be a consequence of juvenile behavior (Breen et al., 1985; Hagen and Mann, 1994).

A number of studies have reported juvenile urchins residing under the adult spine canopy (Low, 1975; Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987), but few have concentrated on the mechanisms underlying this association. It has long been suggested that juvenile sheltering is a strategy to avoid predators such as the sunflower star *Pycnopodia helianthoides* (Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987) since *P. helianthoides* rarely feeds on large adult urchins (Duggins, 1983). There may also be a hydrodynamic advantage afforded by the spine canopy with respect to reduced flow, as water motion is known to influence the morphology and mobility of adult urchins (Lissner, 1983; Rogers-Bennett et al., 1995; Kawamata, 1998). Moreover, Pace (1975) reported that water motion could impose a metabolic demand exceeding the capacity of aerobic metabolism in adult urchins, which could also be of importance to juvenile sea urchins. A third possible reason for juvenile sheltering is that juveniles under the spine canopy may gain a nutritional advantage compared to juveniles found elsewhere. Tegner and Dayton (1977) noted that juvenile urchins appeared to be "sharing" food with the adults under which they resided. In addition, the spine canopy may reduce water velocities and hence the dispersion of water-borne nutrients liberated by adult feeding activities. This would be especially important if juveniles retain the ability to absorb dissolved organic material from the larval stage (Kempf and Todd, 1989). A contrasting opinion however, is that some urchin populations are regulated by competition for food between adults and juveniles for food (Low, 1975).

Not surprisingly, a number of hypotheses have been forwarded to explain why juvenile urchins reside under adults. These can be categorized in three main hypotheses: (a) The predation hypothesis – that risk of predation is lower under adult urchins; (b) The hydrodynamic hypothesis – that average flow and fluctuations in water velocity are lower under adults; and (c) The food availability hypothesis – that food such as macroalgae is more accessible to juveniles under adults.

Undoubtedly these three hypotheses are not mutually exclusive and may each contribute to explaining the juvenile sheltering phenomenon.

Whitman (1985) states that spatial refuges protecting organisms from disturbance and predation can have a disproportionately large influence on the distribution and abundance of a species. Given the potential importance of adult sheltering in the early life history of sea urchins, the potential mechanism responsible for juvenile sheltering warrants investigation. The purpose of this study is to identify the reasons for juvenile sheltering through a comparison of behavior in two closely related species *S. franciscanus* and *S. droebachiensis*, which are known to shelter at different rates.

3.2. Materials and Methods

Unfiltered seawater (temperature = 8.80 to 13.20 °C, salinity = 25.93 to 34.66 ppt, pH 7.50 to 8.30, Dissolved oxygen = 43.20 to 100.00 % saturation) used in all experiments was supplied by the Bamfield Marine Sciences Centre (BMSC), which is drawn from Bamfield Inlet at a depth of 25 m. Adults of the giant red urchin, *S. franciscanus* (A. Agassiz, 1863) (80 to 161 mm test diameter) and the green urchin, *S. droebachiensis* (O.F. Müller, 1776) (48 to 64 mm test diameter) were obtained by SCUBA divers, kept in tanks with flowing seawater, and fed macroalgae (*Macrocystis integrifolia*) over the course of the study. Juvenile urchins (0.59 to 10.06 mm test diameter) were obtained from an experimental hatchery, (Island Scallops, Qualicum Beach, British Columbia, Canada) and maintained in aquaria with flowing seawater and fed benthic diatoms. The sunflower star, *P. helianthoides* (Brandt, 1835) was obtained by SCUBA divers and used as a predator in all experiments. All statistical analysis was conducted using SPSS 10.0.5 for Windows© software (SPSS Inc., Chicago, IL).

Question # 1 – Does sheltering provide hydrodynamic protection?

(i). Characterization of flow fields around adult sea urchins.

The fluid environment around adult urchins was examined to determine whether sheltering provides a hydrodynamic refuge to juveniles. Specifically, do adult urchins affect water motion in the vicinity of juveniles? All fluid dynamic testing was conducted in a flow chamber connected to the BMSC's seawater system (see Figure 14). The chamber was 162 cm long, 20.5 cm wide, and the water depth was 18 cm. Water flow at constant head was provided from a 180 L header tank through a 7.6 cm diameter pipe into the chamber via gravity and controlled by a ball-and-socket valve on the inlet the pipe. The test section extended from 120 to 150 cm downstream from the collimators of the chamber.

The chamber was adjusted to an average velocity of 9.14 ± 0.03 cm/s measured 130 cm downstream and 1.80 cm from the bottom using a three dimensional Acoustic Doppler Velocimeter (sampling rate = 25 Hz; ADV; Sontek, San Diego, CA). The Reynolds number (Re) of the flow chamber was calculated as 18 000 using the hydraulic diameter.

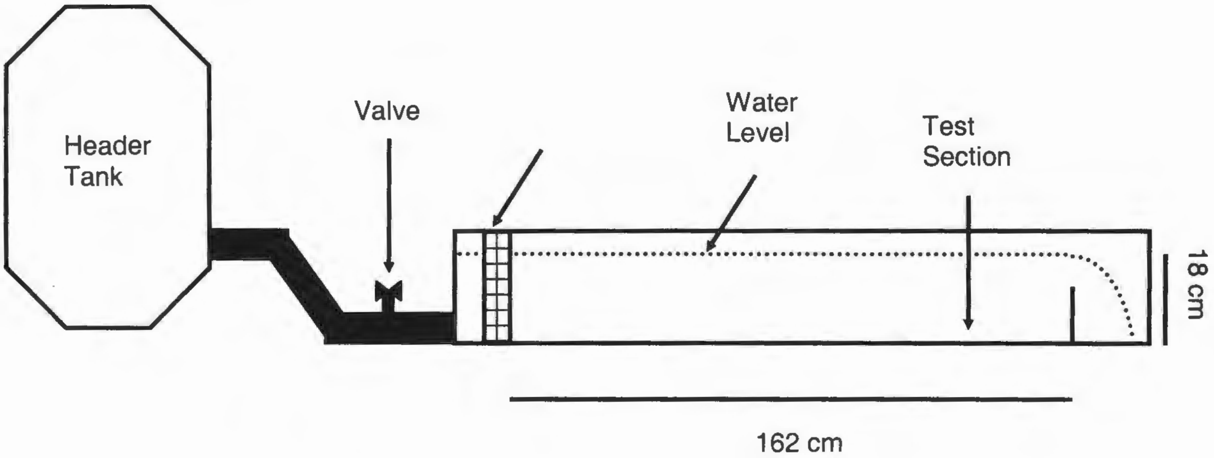


Figure 14. Schematic of flow chamber.

A vertical profile of velocity was measured in the center of the chamber at 130 downstream. Three measures of velocity (i.e. in the X, Y, and Z planes) were recorded simultaneously for each point in the profile. Within the bottom 3.00 cm of the chamber, points were spaced vertically by 0.04 to 0.20 cm and at 0.00 to 1.16 cm intervals in the upper portion of the profile. Each point was an average of 4500 samples (180 seconds at 25 Hz). Figure 15 presents the results of the vertical velocity profile in three planes. The bottom shear, or friction velocity, associated with this profile was 0.36 cm/s based on a linear regression of the velocity data plotted against the natural logarithm of the distance from the bottom of the flow chamber (N = 20, $r^2 = 0.49$, p = 0.001; Nowell and Jumars, 1984).

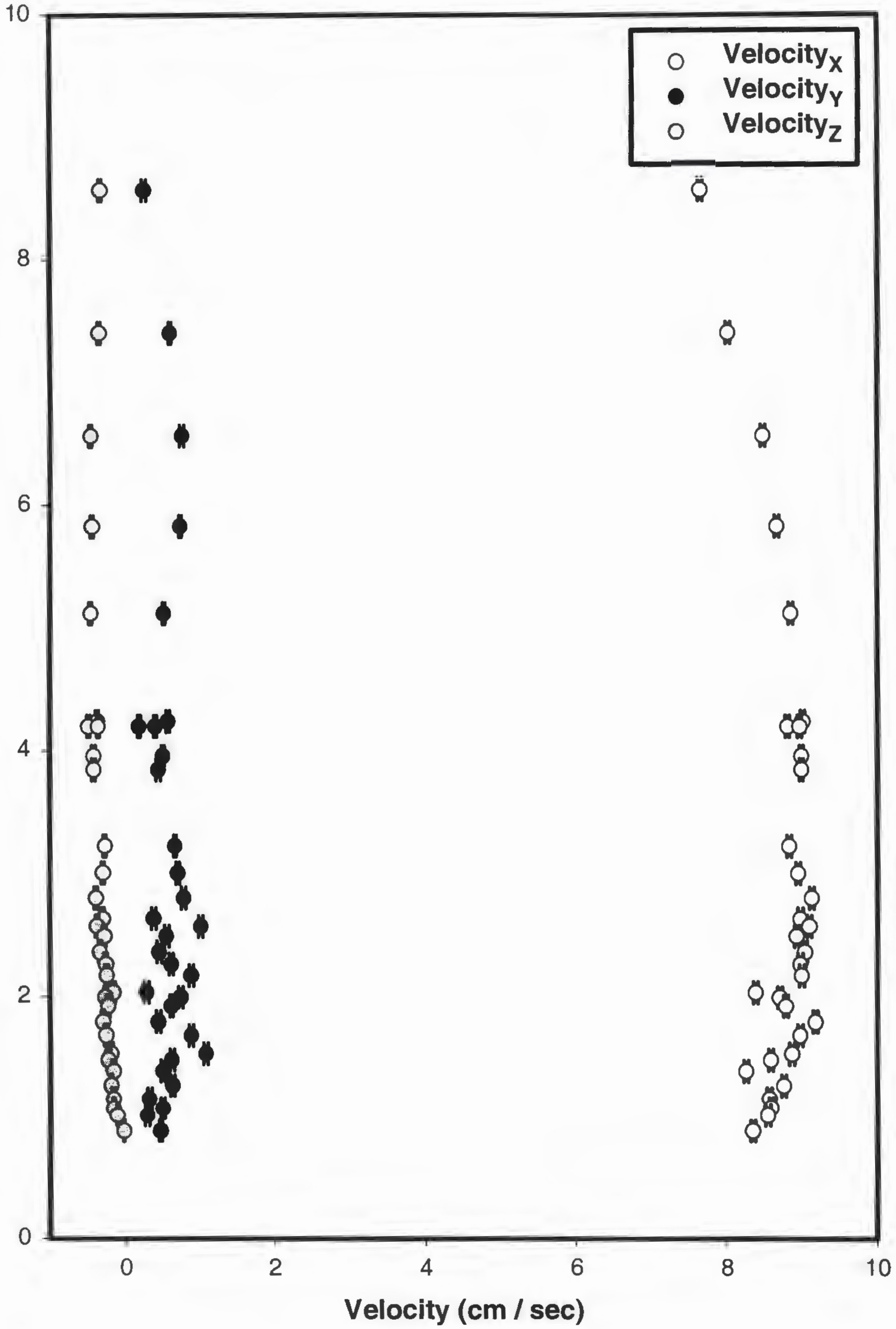


Figure 15. Velocity profile measured at 130 cm downstream of the leading edge of the flow chamber. Points for profiles in the X (open points), Y (black points), and, Z (grey points) directions were recorded simultaneously. Data are mean ± 1 SE representing 4500 data points averaged over 180 seconds.

An adult *S. franciscanus* (test diameter 6 cm) was relaxed in menthol for ~ 30 minutes so that tube feet and spines on the bottom side were immobile whereas the spines on the sides and top of the body remained erect. This allowed for a naturally positioned urchin to be held stationary in the flow chamber for over an hour so that measurements could be made in the region where sheltering juvenile sea urchins would be located. This characterization would provide an indication as to hydrodynamic forces that juvenile sea urchins would experience under the spine canopy of adults. Velocities were measured on a grid of points 1.8 cm above the bottom surface of the flow chamber. The horizontal resolution of the grid was 2 cm by 2 cm and each measurement was made over 180 seconds at a sampling frequency of 25 Hz (i.e. 4500 observations per grid point).

The turbulence intensity (TI) was determined from the quotient of the root mean square velocity and the average velocity:

$$TI = \frac{\sqrt{(U'_x)^2}}{\overline{U}} \qquad \text{(Equation 1)}$$

where U'_x represents fluctuations from the mean downstream velocity and $\overline{U}$ is the time-averaged velocity.

(i). The sheltering response of juvenile sea urchins under different flows.

Laboratory experiments were undertaken to examine the effects of hydrodynamic conditions on juvenile behaviour (i.e. sheltering under adult spines). It would be expected that juveniles would be more likely to shelter under adults at high water motion if the spine canopy provides hydrodynamic protection.

All experiments were conducted in a glass aquarium (Figure 16) of dimensions 60 cm × 30 cm × 30 cm. Water flow (10 – 12 °C) was supplied via nozzles, above the left and right sides of the aquarium (see Figure 16B). Two levels of water motion (low and high) were used during the experiment corresponding to the range of velocities observed 10-50 cm above urchin beds near Bamfield (i.e. average velocities between 0.2 and 23 cm/s, maximum velocities of 85 cm/s; Levitan et al., 1992; Levitan, 1998). Under low water motion, each nozzle provided water at a rate of 1.5 L/min, whereas at high flow water was provided at 15 L/min per nozzle. In both cases, excess water passed over the top of the aquarium. Water velocities were measured 1 cm above the bottom of the aquarium using the ADV and are represented in Table 4.

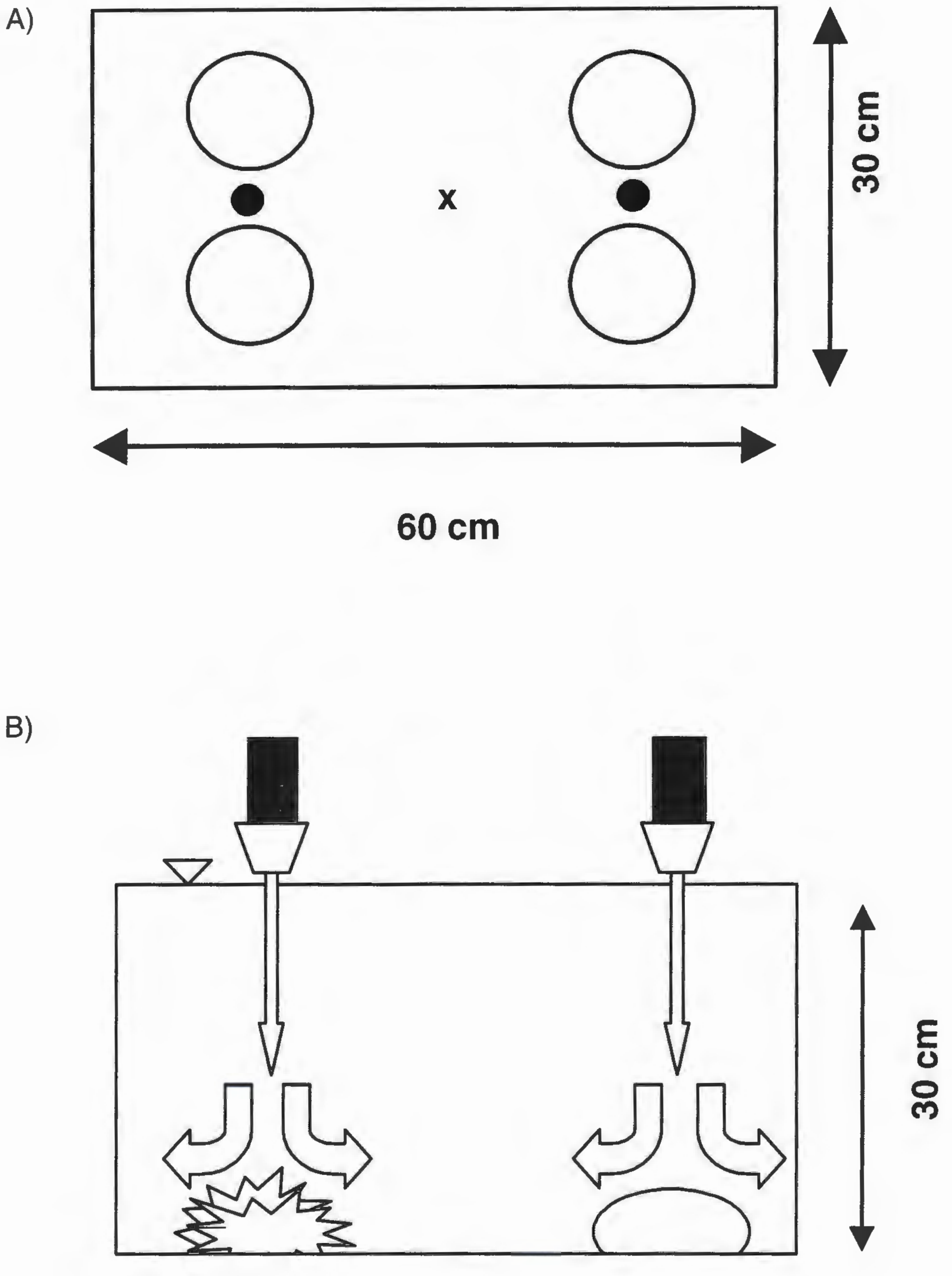


Figure 16. Experimental design for juvenile association experiment. (A) Top-view of the aquarium with four cages indicated by large circles, release point for juveniles represented by the x, and the location of the two inlet nozzles indicated by the dark circles, (B) Side-view of the aquarium with adult urchin (left) and rock (right). Open arrows indicate principle direction of flow. Total volume of tank is 54 L.

Cages were constructed using eight pieces of wood (13 cm x 0.5 cm x 0.1 cm) protruding from the floor of the aquarium to prevent adult urchin movement. One cage was placed in each of the four quadrants of the aquarium (large circles in Figure 16A). For each trial, two cages contained adult *S. franciscanus* (test diameters [TD] of 80 mm) that had been starved for three to four days. Available area underneath adult urchins accounted for 3 % of the total surface area within the aquarium. The remaining two cages contained rocks of similar size to the adult urchins. The placement of adults and rocks was changed among trials so that all possible configurations were examined. At the beginning of each trial (fifteen trials per treatment) five juvenile urchins (6.50 ± 0.11 mm TD) were placed in the centre of the aquarium floor ("x" in Figure 16A). The position of each juvenile was noted after 12 hours (i.e. under adult spines, under/on rock, on bottom of aquarium, on glass walls of aquarium, or on wood cages). The proportion of juveniles sheltering under adults after twelve hours for each treatment was recorded and used with results from the predation experiment described below in a two-way ANOVA.

Table 4. Water velocities under low and high flow conditions measured in the aquarium (see Figure 16). Velocities were measured in the x, y, and, z directions (U_x, U_y, U_z; ± standard error) at a frequency of 25 Hz for 180 seconds, N = 4.

Velocity	*Source*	*Residence Time (sec)*	*U_x (cm/s)*	*U_y (cm/s)*	*U_z (cm/s)*
Average	Low Flow	108	1.7 ± 0.5	0.6 ± 0.6	1.0 ± 0.2
	High Flow	54	-3.2 ± 1.0	1.4 ± 0.6	0.5 ± 0.2

Question # 2 – Does sheltering provide protection from predation

(i). The sheltering response of juvenile sea urchins to predators

The potential effect of predation risk on juvenile behaviour (i.e. sheltering under adult spines) was examined using the same protocol described above. However, in this case, water was allowed to pass over a predator (*P. helianthoides*), which had been starved for one week, before entering the aquaria. A two-way analysis of variance was employed to determine the effect of water motion and predation risk on the proportion of juveniles sheltering.

(ii). The effect of predation on juvenile urchins.

Two juvenile predation experiments were conducted to examine whether adult sheltering reduced predation risk for juveniles. Both experiments were run in tanks measuring 170 cm long x 72 cm wide x 12 cm deep. Pair-wise feeding experiments were employed to determine predator preference between the two species of juvenile urchins. In each trial a predator, *P. helianthoides* was presented with one juvenile *S. franciscanus* and one juvenile *S. droebachiensis* of similar test diameters (11.07 ± 1.23 mm; difference in test diameter size between paired juveniles < 3.7 %). Predators were starved between one and two weeks and all trials were run until one of the juveniles was eaten (up to 24 hours). Preference by *P. helianthoides* for either juvenile species was tested using a two-tailed binomial test with the null hypothesis being that each species has an equal chance of being eaten.

In the second experiment, both adult and juvenile urchins were placed alone or together in a tank with two *P. helianthoides* (starved for two weeks) to determine if adult sheltering decreased juvenile mortality. Using the same tank design described above, five juvenile *S. franciscanus* (TD = 14.35 ± 1.94 mm) were presented to a predator either (a) alone or (b) with four adults (TD = 145.58 ± 11.14 mm). Similarly, five juvenile *S. droebachiensis* (TD = 14.48 ± 2.00 mm) were presented to *P. helianthoides* either (a) alone or (b) with 14 adults (TD = 62.50 ± 1.19 mm). The greater number of adult *S. droebachiensis* was used to provide an equal amount of adult-sheltered habitat in the two treatments (based on area covered by adults). One trial for each treatment was run for fifteen days and no statistics were performed as there was only one replicate of each treatment.

Question # 3 – Does shelter provide a nutritional benefit?

(i). What form of kelp is utilized by juvenile sea urchins?

Experiments were undertaken to determine what form of kelp (*Macrocystis integrifolia*) is utilized by juvenile urchins. This is an important question as it is not known when juveniles develop functional jaws and are able to feed on kelp, nor is it known whether juveniles could absorb dissolved organic material, which would be produced from the scraping and ripping of kelp as adult urchins feed. Juvenile *S. franciscanus* 41-186 days after larval settlement were maintained in flowing water (11°C) over the course of two months (Sept. 26 to Nov. 19, 1999). Juvenile *S. droebachiensis* were maintained over the course of one month (Nov. 8 to Dec. 13, 2000), In each case, juveniles were grown under the following treatments: (1) whole kelp blades - blades of *M. integrifolia* (~ 40 grams each); (2) ground kelp - *M. integrifolia* (~ 40 grams plus 250 ml of seawater) ground in a blender; (3) adult exudates – exudates (~ 40 grams of material produced by adult red urchins fed *M.*

integrifolia plus 250 ml seawater collected from under the feeding adult); and (4) no food (starved) - 1 mm filtered seawater only;. Each treatment was replicated in 3 separate 500 ml containers (16 cm tall x 8 cm diameter; 12 containers total) and 15 juveniles were placed in each container resulting in 45 juveniles per treatment (total of 180 juveniles for entire experiment).

Juveniles were inspected for the presence of jaws at the beginning of the experiment and test diameters (TD) were also measured at that time. Initially, juvenile *S. franciscanus* averaged 1.42 ± 0.02 mm TD and there were no statistical differences in initial TD among treatments ($F_{(3,\ 176)} = 0.03$, $p = 0.995$). The corresponding size of juvenile *S. droebachiensis* was 2.57 ± 0.07 mm and there were no differences among treatments ($F_{(2,\ 132)} = 0.14$, $p = 0.867$). Survivorship and test diameters were recorded throughout the experiment. A Model I one-way analysis of variance was used to compare the change in test diameter between treatments using the results from each container as a replicate.

(ii). Does sheltering increase access to kelp for juvenile sea urchins?

The hypothesis tested in this experiment was whether the growth rate of juvenile urchins is affected by the presence of adults. It was expected that the presence of adult urchins would facilitate faster growth rates for juveniles compared to juveniles raised alone. Further, it was expected that three factors (water motion, algal form, and urchin species) should influence the adult-juvenile association. Specifically, it was predicted that juvenile sheltering would be favored: (a) for *S. franciscanus* compared to *S. droebachiensisi* as the longer spines of adult *S. franciscanus* were expected to enable more efficient capture of kelp; (b) under high water motion over low water motion and; (c) when kelp was presented in whole form over a ground form.

Juvenile urchins were cultured in controlled laboratory conditions to determine if juveniles experience nutritional gains when associating with adults. The experiment consisted of 24 plastic tanks (77 cm high x 46 cm diameter) with a plastic “floor” inserted restricting the test section to the top 25 cm of the tank. Water temperatures varied from 8.8 to 13.2 °C (9.61 ± 0.03 °C); pH from 7.7 to 8.1 (7.851 ± 0.003); and salinity from 26.02 to 30.70 ppt (27.91 ± 0.04 ppt) throughout the experiment.

Water was supplied by an overhanging nozzle and the flow rates for the high and low water motion treatments were 8.34 ± 0.02 L/min and 1.87 ± 0.01 L/min respectively. Macroalgae (*Macrocystis integrifolia*) was collected from the field and was maintained in flowing seawater. Kelp was presented to juvenile urchins either as 50 g of “whole” material, which included the blade, stipe and bulb, or as “ground”, where the above material was ground in a blender. Kelp was added three times per week and tanks were cleaned of faeces and any algal film before each feeding.

Treatments for *S. franciscanus* juveniles contained either (a) two adult *S. franciscanus* (HSW_{red} = high water motion, sheltered by adults, whole pieces of kelp; and LSW_{red} = low water motion, sheltered by adults, whole pieces of kelp; TD = 146 ± 3 mm) or (b) no adults (HUW_{red} = high water motion, unsheltered, whole pieces of kelp; and LUW_{red} = low water motion, unsheltered, whole pieces of kelp), whereas *S. droebachiensis* juvenile treatments contained either (c) four adult urchins (HSW_{green} = High water motion, sheltered by adults, whole pieces of kelp)

(TD = 50 ± 1 mm) or (d) no adults (HUW_{green} = High water motion, unsheltered, whole pieces of kelp). The density of adults used in this experiment (1.6 individuals per m^2 determined from the ratio of area covered by adult tests and the surface area of the aquaria) approximated natural densities observed in the field (Adkins et al., 1981; Sloan et al., 1987; Campbell 1998; Jamieson et al., 1998a; Jamieson et al., 1998b; Jamieson et al., 1998c; Jamieson and Schwartz, 1998). Ground kelp treatments (HSG_{red} = high water motion, sheltered by adults, ground kelp; and HUG_{red} = high water motion, unsheltered, ground kelp) were considered as controls for the whole kelp treatment. Kelp in these treatments would be available to all juveniles regardless of the presence of adults. The eight treatments shown in Table 5 were replicated three times (a total of twenty-four tanks).

Table 5. Experimental design for the growth experiment.

Abbreviation	Urchin Species	Water Flow	Adult Urchins	Kelp Form	Comparison
HSW_{red}	Red	High	Present	Whole	1,2,3
HUW_{red}	Red	High	Absent	Whole	1,2,3
LSW_{red}	Red	Low	Present	Whole	1
LUW_{red}	Red	Low	Absent	Whole	1
HSG_{red}	Red	High	Present	Ground	2
HUG_{red}	Red	High	Absent	Ground	2
HSW_{green}	Green	High	Present	Whole	3
HUW_{green}	Green	High	Absent	Whole	3

Five juveniles were measured (test diameter = 7.73 ± 0.09 mm, wet weight = 0.21 ± 0.01 g) and placed in each tank on October 27, 2000 and measured each week until March 9, 2001. There were no significant differences in the initial size of juvenile urchins at the beginning of the experiment ($F_{(23,\ 95)} = 0.22$, $p > 0.999$). Before measuring each week, the position of each juvenile was recorded as (a) sheltering under an adult, (b) in the open, or (c) on kelp.

In order to examine whether the ground kelp treatments conferred a nutritional benefit to juveniles , the growth period was divided into Period A and Period B, with the former including the first 8 weeks and the latter period constituting the final 11 weeks of the experiment. In Period B, all treatments were continued as in Period A except the two ground kelp treatments (HSG_{red} and HUG_{red}), which received no further kelp (renamed HSN_{red} and HUN_{red}).

Treatment effects (presence of adults, water motion, algal form, and urchin species) were analyzed with three separate two-way Analysis of Variance (ANOVA). The dependent variable, growth rate was measured both as changes in test diameter and body mass (per month). Data were tested for heteroscedasticity using a homogeneity-of-variance test (Levene's test).

Adult test diameters were also measured three times during the experiment (beginning, near the end of Period A, and near the end of Period B) and analyzed using one-way ANOVA comparing mean test size between dates for *S. droebachiensis*. A t-test was used for as test diameters were only measured at the beginning and end of the experiment.

To determine whether interactions between adults and juveniles occurred, juvenile behavior was measured via two methods: (1) monitoring the location of juveniles in different habitats once per week throughout the duration of the growth experiment; and (2) intensive monitoring of juvenile movement rates over a three hour period during the growth experiment. For the first experiment a Kruskal-Wallis test was performed to determine whether treatment and/or time (Period A vs. Period B) affected the occurrence of juvenile sheltering. In the second experiment, Kruskal-Wallis tests were used to determine whether adult presence (i.e. with or without), or the presence of kelp affected juvenile movement. Movement rates were normalized by test diameter as juveniles in the various treatments ranged from 6.25 to 20.52 mm. In the second experiment, a model analysis was also undertaken to assess the potential influence of juveniles that were obscured from view (i.e. sheltered underneath adults) on movement rates. Average movement rates were recalculated using a range of model movement rates for all sheltered juveniles. Since adult urchins averaged ~ 15 cm in test diameter, juvenile movement rates between 0 and 15 body lengths/hour were used in this model (i.e. sensitivity analysis). Data from the model were entered in two separate Kruskal-Wallis tests to compare the combined effects of: (1) water motion (i.e. high vs. low) and adult presence (i.e. with and without) and; (2) algal form (i.e. whole vs. none) and adult presence (i.e. with and without) on juvenile movement rates.

Question # 4 – Is sheltering behaviour affected by cues related to adults?

(i). Interspecific sheltering behaviour

Interspecific sheltering experiments were conducted to assess whether juvenile sheltering is affected by adult cues (i.e. is sheltering a species-specific or more general behaviour). Following the same protocols used in the juvenile sheltering experiment described above (see Question # 1(ii)), tests were conducted using juveniles and adults of both species to see if juveniles would shelter under adults of a different species. All trials were conducted under the "high flow" condition without predators. Data was analyzed with a two-way ANOVA.

(ii). The influence of juvenile-adult proximity on sheltering.

An experiment was conducted using a different initial placement of juvenile urchins to determine whether juvenile sheltering is affected by the proximity of juveniles to adults (i.e. sheltering is a consequence of the delivery of a chemical signal released by adults). In this case, trials were run at both high and low flows (without predators), but the five juveniles were placed directly underneath an adult at the beginning of the experiment rather than in the open (the x in Figure 16a). The null hypothesis tested was that juvenile proximity to an adult would have no effect on the rate of juvenile sheltering. Data were analyzed with a two-way ANOVA.

3.3. Results

Question # 1 – Does sheltering provide hydrodynamic protection?

(i). Characterization of flow field around adult sea urchins.

The velocity field surrounding the adult urchin is shown in Figure 17 where the contours of the velocity components are presented. Water velocities varied little from those measured for the velocity profile (at 1.8 cm height) except for regions within ~ 5 cm and downstream of the adult urchin. Mean velocities were reduced markedly within ~ 5 cm of the adult urchin, and downstream 20 cm where velocities were generally under 3 cm/s (Figure 17A). A small region on the centerline, directly behind the adult urchin was found to have a negative average velocity -0.4 ± 0.03 cm/s, indicating an area of re-circulation or eddy. Variance (Root Mean Squared; RMS) in water velocity was much smaller than the mean flow for all regions (Figure 17B). Generally, the RMS recorded downstream of the urchin were lower than those upstream of the urchin.

Turbulence intensities (i.e. RMS/mean velocity) were generally low in all regions of the test section with the exception of a region 5 – 20 cm downstream of the urchin (Figure 17C). In this region, alternating regions of high and low turbulence downstream indicate eddies produced by Von Karman's vortex streets being shed by the urchin body (Re = 5 700 calculated using urchin test diameter; Vogel 1992).

Mean velocities in the y (cross-stream) and z (vertical) directions were much lower (< 10 %) than the velocities in the x (downstream) direction (Figure 18), indicating that the flow was primarily two-dimensional in the chamber (see Figure 15).

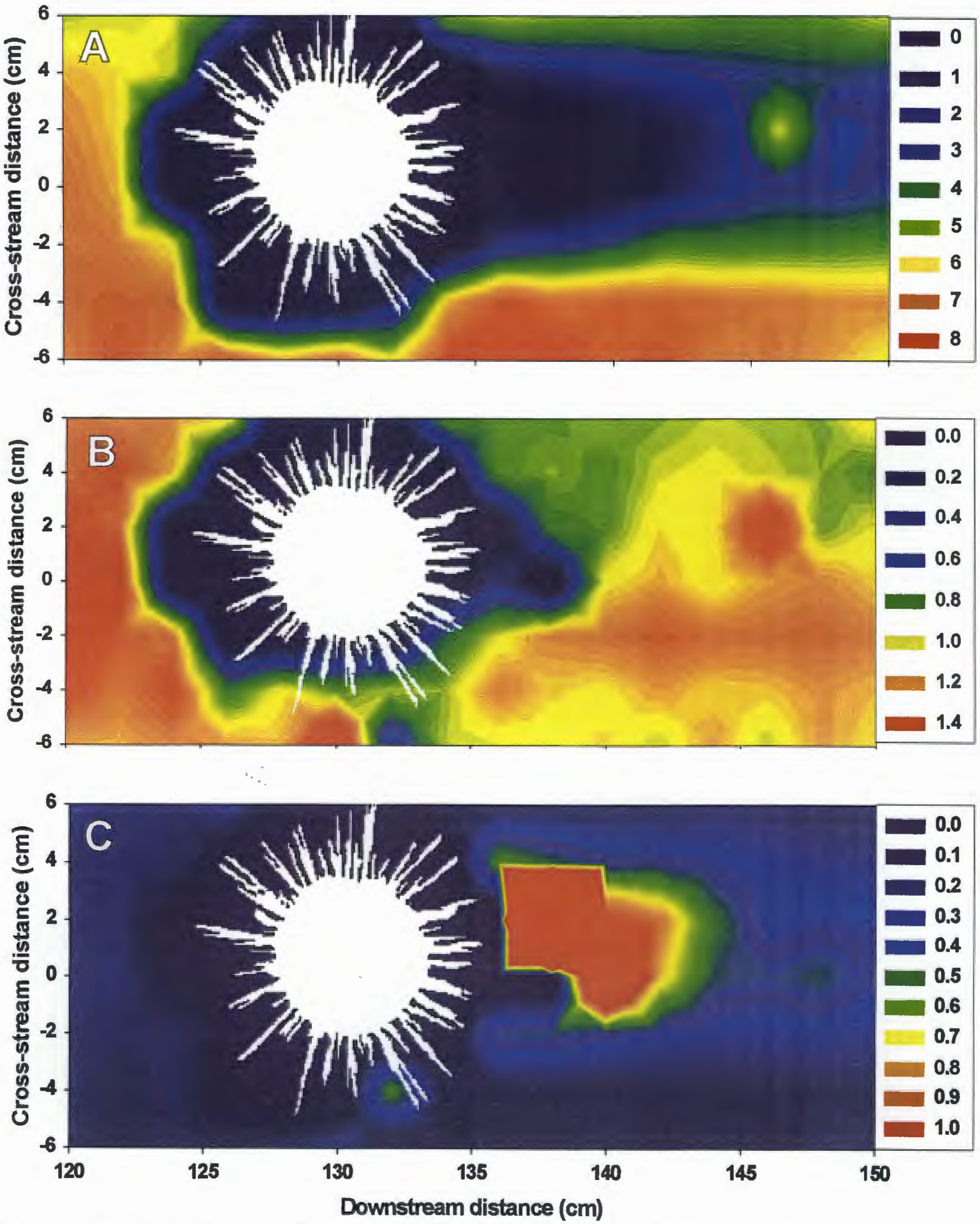


Figure 17. Plot of water flow around an adult urchin. Contours of: (A). average velocity (cm/sec); (B). RMS (cm/sec) and; (C). turbulence intensity (ranging 0 to 1) in x (downstream) direction. All measurements averaged from 4500 data points over 180 seconds at 1.8 cm above the bottom of the chamber. The resolution of the grid was 2 cm by 2 cm.

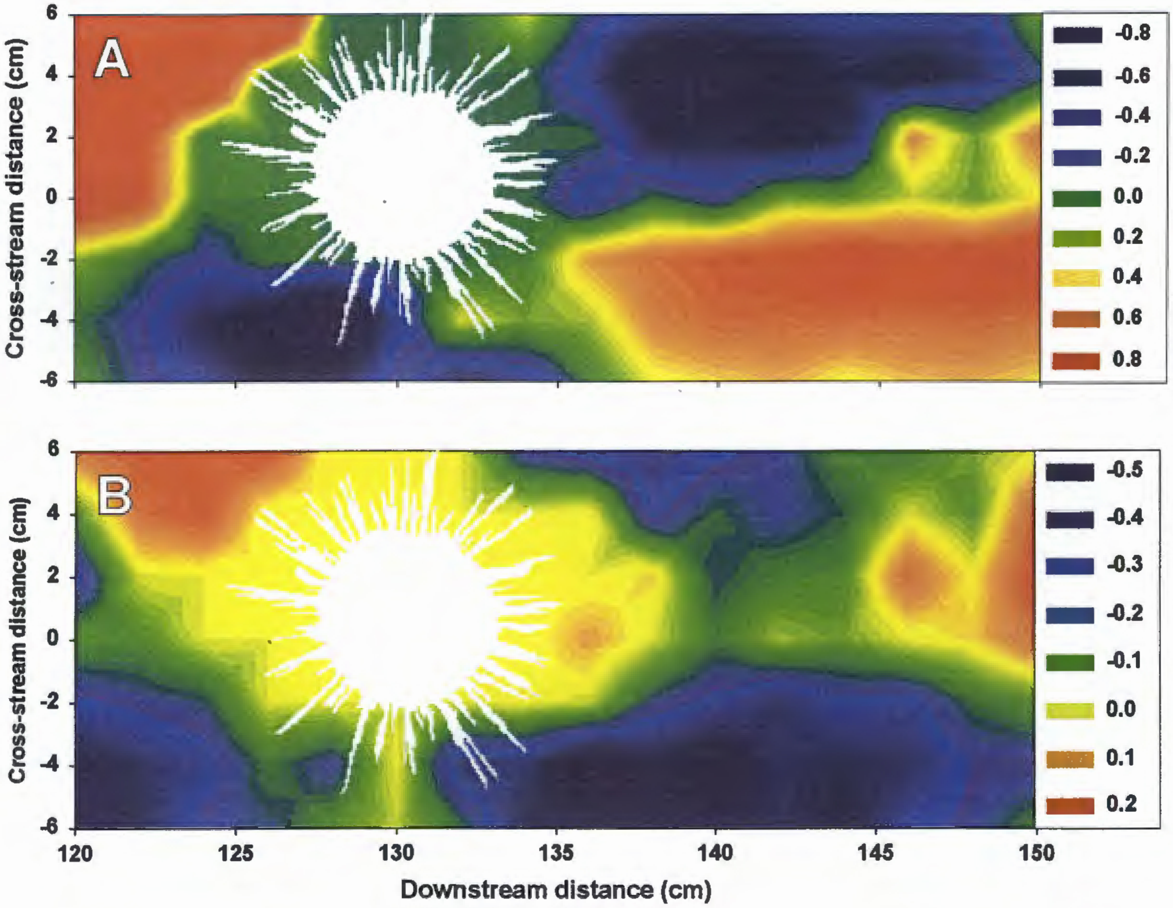


Figure 18. Plot of water flow around an adult urchin. Contours of average velocity (cm/sec) in the: (A). y (cross-stream) and; (B). z (vertical) directions. All measurements averaged from 4500 data points over 180 seconds at 1.8 cm above the bottom of the chamber. The resolution of the grid was 2 cm by 2 cm. The resolution of the grid was 2 cm by 2 cm. The legend at left is provided in units of cm/s.

(ii). The sheltering response of juvenile sea urchins under different flows. and

Question # 2 (i). Does sheltering provide protection from predation?

At the beginning of each trial, juveniles moved about in a seemingly haphazard manner using their tube feet. Juveniles were often found attached in a variety of locations (i.e. in the open, on glass walls, on wood cages, under rocks, or under adult urchins) within the first six hours of the experiment. After 12 hours however, many juveniles were found sheltering under adults and these associations, once formed, persisted over long periods (up to 72 hours). Under low water motion and without predators, only 13 ± 4 % of the juvenile urchins were found sheltering under adults (Figure 22). Under high water motion, however, the proportion of sheltering juveniles increased to 52 ± 7 %. Interestingly, when water was passed over a predator before entering the tank, the percentage of juveniles remaining was relatively high for both low (44 ± 6 %) and high flow conditions (59 ± 7 %). The difference in the proportion of juveniles sheltering under adults at different levels of water motion was significant ($F_{(1, 56)} = 19.08$, $p < 0.001$) as was the difference in the proportion sheltering in the presence or absence of a chemical signal from a predator ($F_{(1, 56)} = 9.35$, $p = 0.003$). The interaction between the two factors was not found to be significant ($F_{(1, 56)} = 3.86$, $p = 0.054$).

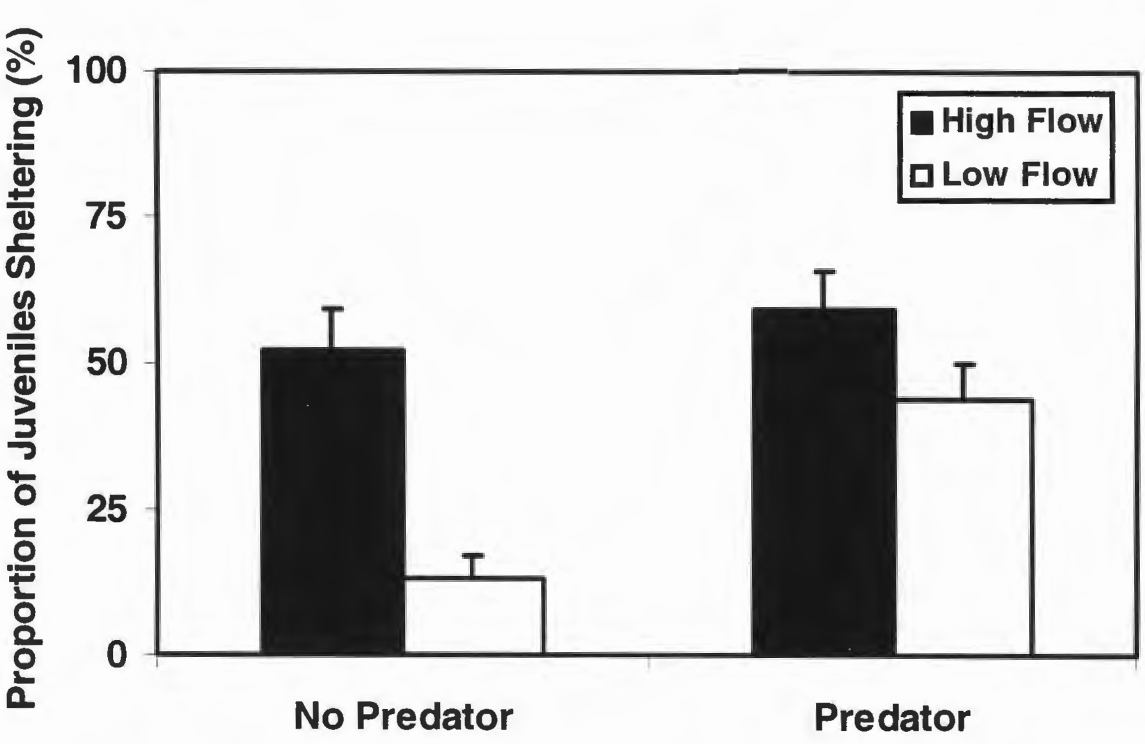


Figure 19. Mean percentage of red juveniles sheltering under adults in relation to water flow and predation risk. Black bars represent trials with high flow and the open bars represent trials with low flow. Data are means ± 1 SE for fifteen replicate trials (each trial consisted of five juveniles).

(ii). The effect of predation on juvenile urchins.

Observations indicate that *P. helianthoides* often explores the tank, sometimes coming into contact with both species (even passing mouth region over juvenile) without attacking. Even though contact was often made with both species, the *S. franciscanus* juvenile was preyed upon first by *P. helianthoides* consistently (nine out of nine trials). The results of the binomial test indicate that, assuming predation choice was independent of the species of juvenile urchin, the probability of all nine *S. franciscanus* juveniles being chosen first is < 0.01, thus the null hypothesis that predation choice is independent of juvenile species must be rejected. Predation was eventually observed on two juvenile *S. droebachiensis* (after the juvenile *S.*

franciscanus was eaten). While precise times to each predation event were not recorded, experiments ran between 10 minutes and three days.

In the second predation experiment juvenile *S. franciscanus* were observed sheltering under the spines of adults throughout the entire experiment. In contrast, juvenile *S. droebachiensis* were observed throughout the tank, with the majority of the juveniles on the sides of the tank near the air-water interface. As Figure 23 illustrates, survival was low when juveniles were presented to a predator alone (0 % for both *S. franciscanus* and *S. droebachiensis*). However, survival rates increased for juvenile *S. franciscanus* when presented together with adults (100 % survival for both juveniles and adults). In contrast, juvenile *S. droebachiensis* had relatively low survival (40 %) when presented together with adults. Adult *S. droebachiensis* also experienced lower survival (50 %) than *S. franciscanus* (100 %).

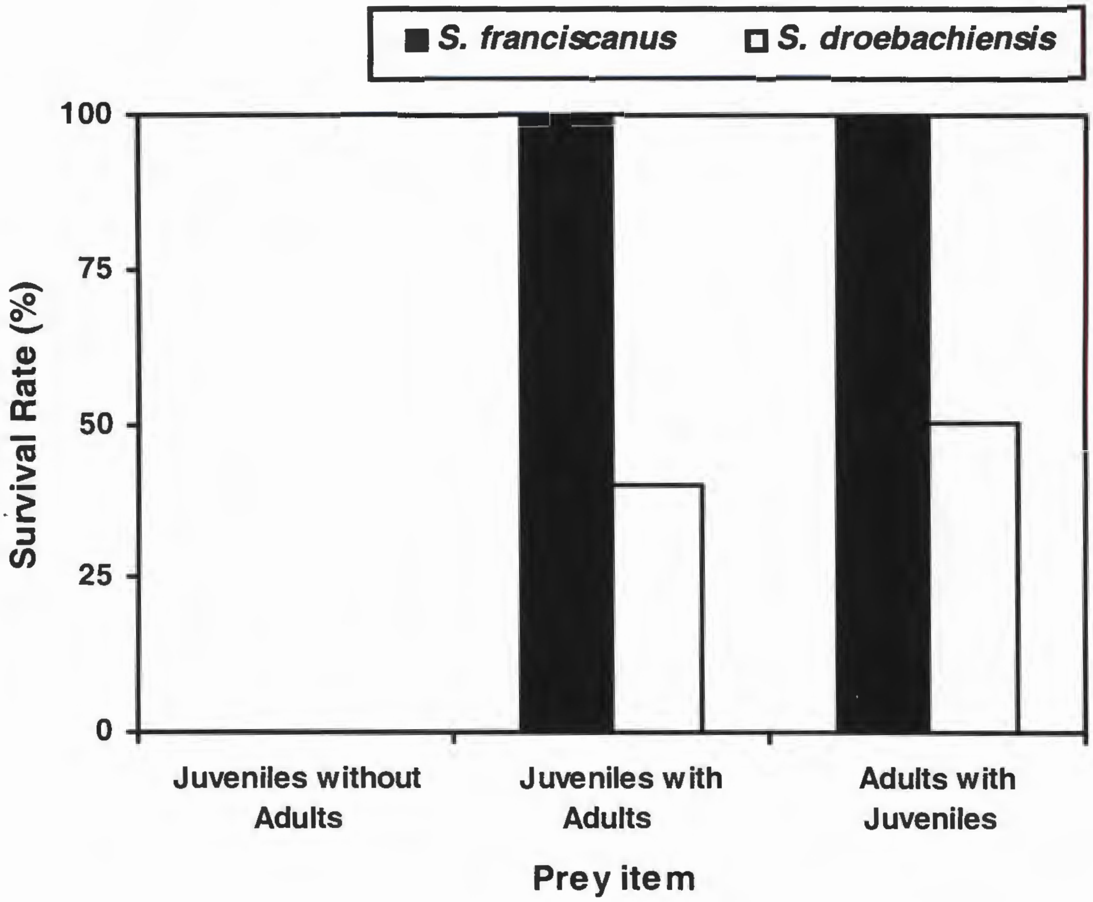


Figure 20. Survival rates (%) of juvenile and urchins in predation trials using *P. helianthoides*. Black bars represent trials using *S. franciscanus* and open bars are trials using *S. droebachiensis*. Data represent one replicate trial and are an average of five juveniles (*S. franciscanus* or *S. droebachiensis;* no measure of variance). The adult data are an average of either 4 adult *S. franciscanus* or 14 adult *S. droebachiensis*.

Question # 3 – Does shelter provide a nutritional benefit?

(i). What form of kelp is utilized by sea urchins?

On day zero of the experiment, 100% of the small juveniles (e.g. 1.42 ± 0.02 mm TD) had formed jaws. Survivorship of juveniles was variable with relatively high rates for whole and ground kelp treatments and lower rates for exudates and controls (see Figure 21A). Survival of juveniles in the 1999 and 2000 whole kelp treatments were similarly high. There were no significant differences in the proportion of juveniles surviving among treatments for both *S. franciscanus* ($F_{(3, 8)}$ = 2.142, p = 0.173) and *S. droebachiensis* ($F_{(2, 6)}$ =0.742, p = 0.515). Growth for juvenile *S. franciscanus* in the control group was not statistically different from zero (-0.04 ± 0.05 mm/month), but was higher for *S. droebachiensis* (0.22 ± 0.05 mm). In contrast, urchins that were provided whole pieces of kelp throughout the experiment experienced increased growth. Juvenile *S. franciscanus* experienced growth in 1999 (0.28 ± 0.03 mm/month), though less than in 2000 when both *S. franciscanus* and *S. droebachiensis* grew at higher rates (0.37 with no replication and 0.61 ± 0.10 mm respectively). While the urchins in the ground kelp treatment experienced little growth (0.00 ± 0.04 mm/month), whereas *S. droebachiensis* had much higher growth (0.29 ± 0.05 mm). *S. franciscanus* growing with the addition of adult-processed kelp had moderate growth rates (0.11 ± 0.08 mm/month). A significant difference ($F_{(3, 8)}$ = 6.971, p = 0.013) was found in growth between treatments (Figure 21B) and planned comparisons indicated that only the kelp blade treatment differed significantly from the control.

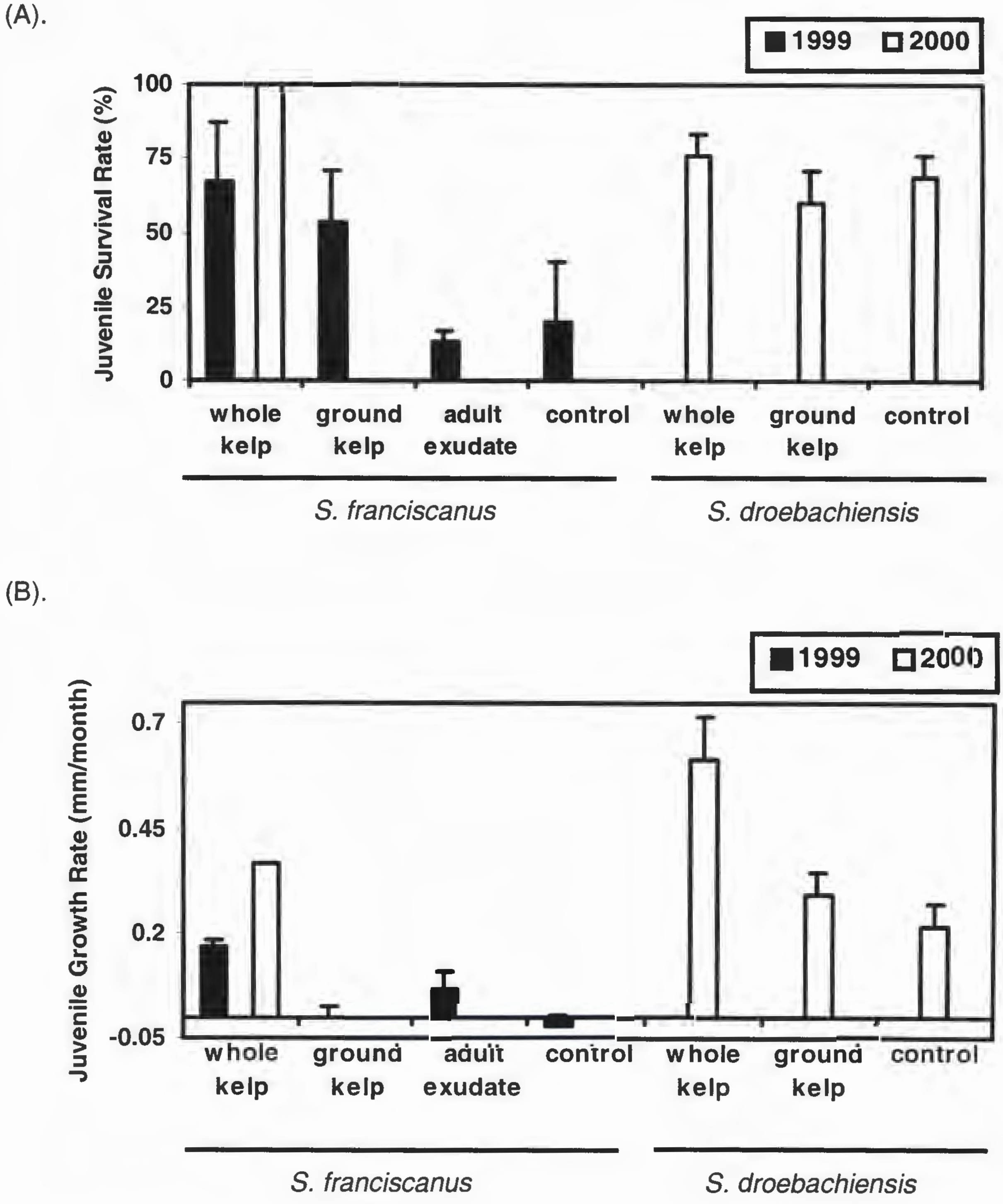


Figure 21. Black bars represent trials run in 1999 and open bars represent trials run in 2000. Data are mean ± 1 SE for three replicate aquaria, except the *S. franciscanus* 2000 treatment, which consisted of one replicate (each aquaria began with fifteen juveniles). (A). Survival rates (%) of juvenile urchins in the growth experiment. (B). Growth rate (change in test diameter) of juvenile sea urchins.

(ii). Does sheltering increase access to kelp for juvenile sea urchins?

Juvenile survival rates were generally high (≥ 73 %) for the large sized (e.g. 7.73 ± 0.09 mm TD) juvenile urchins in all treatments except in the LSW_{red} (low flow, sheltered, whole kelp, red urchin) treatment where survival rates averaged 60 ± 12 % at the end of both Period A and Period B (Figure 22). Conversely, the LUW_{red} (low flow, unsheltered, whole kelp, red urchin) treatment experienced no mortality in Period A and averaged 93 ± 7 % survival by the end of Period B. Both HSW_{red} (high flow, sheltered, whole kelp, red urchin) and HUW_{red} (high flow, unsheltered, whole kelp, red urchin) treatments displayed high rates of survival throughout the experiment (93 ± 7 % and 87 ± 7 % by the end of Period B) while HSN_{red} (high flow, sheltered, no kelp, red urchin), HUN_{red} (high flow, unsheltered, no kelp, red urchin), HSW_{green} (high flow, sheltered, whole kelp, green urchins), and HUW_{green} (high flow, unsheltered, whole kelp, green urchins) treatments all showed similar survival rates (73 ± 7 %, 87 ± 7 %, 80 ± 0 %, and 93 ± 7 %, respectively) by the end of Period B).

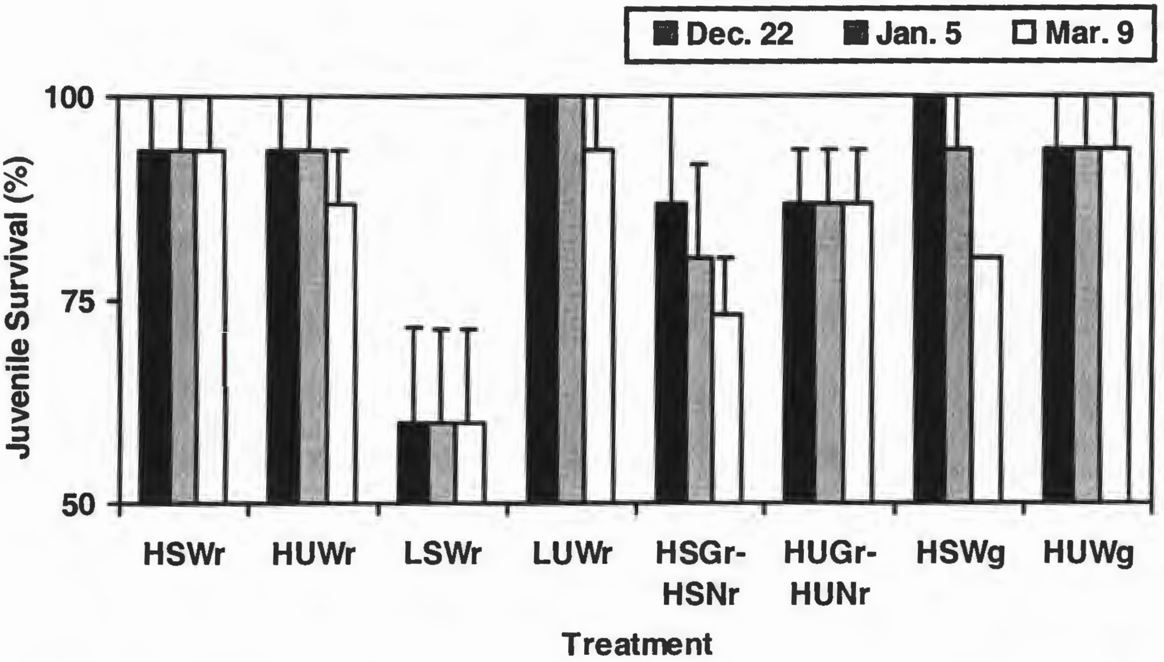


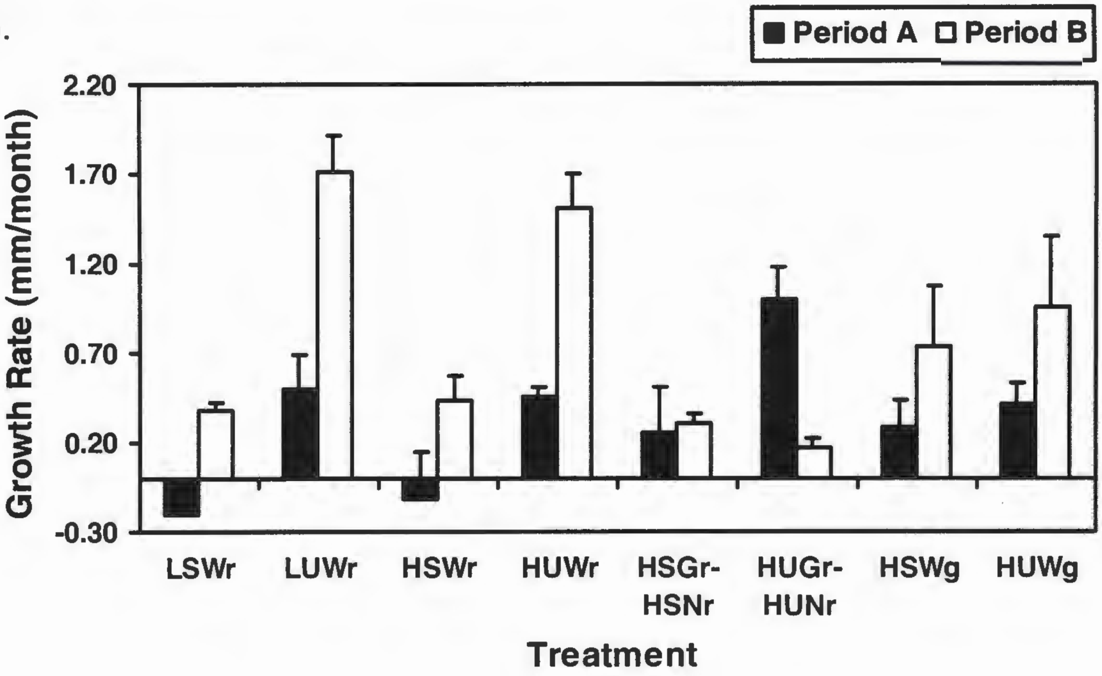
Figure 22. Survival rates (%) of juvenile urchins in the growth experiment. Black bars represent measurements taken at the end of Period A (Dec. 22), whereas grey and open bars represent measurements taken in Period B (Jan. 5 and Mar. 9 respectively. Data are mean ± 1 SE for three replicate aquaria (each aquaria began experiment with five juveniles each). For a detailed list of treatment definitions, see Table 5.

Growth was generally lower in Period A (October to December) than in Period B, (January to March) except in the two no food treatments (HSN_{red}, HUN_{red}), which did not receive kelp in Period B (Figures 23A and 23B). Mean test diameter growth for juveniles in sheltered treatments (LSW_{red}, HSW_{red}, HSG_{red}, and HSW_{green}) averaged between 0.11 ± 0.27 mm/month and 0.73 ± 0.35 mm/month whereas juveniles in the unsheltered treatments (LUW_{red}, HUW_{red}, HUG_{red}, and HUW_{green}) grew between 0.41 ± 0.12 mm/month and 1.71 ± 0.21 mm/month.

The average mass for juveniles in the LSW_{red}, HSW_{red}, HSG_{red}-HSN_{red}, and HSW_{green} treatments increased at rates of 0.03 ± 0.02 g/month, 0.01 ± 0.01

g/month, 0.05 ± 0.02 g/month, and 0.04 ± 0.02 g/month respectively in Period A and 0.17 ± 0.11 g/month, 0.12 ± 0.08 g/month, 0.04 ± 0.02 g/month, and 0.27 ± 0.04 g/month in Period B. In contrast, juveniles in the LUW_{red}, HUW_{red}, HUG_{red}-HUN_{red}, and HUW_{green} treatments grew an average of 0.06 ± 0.03 g/month, 0.06 ± 0.02 g/month, 0.12 ± 0.04 g/month, and 0.06 ± 0.01 g/month respectively in Period A and 0.27 ± 0.12 g/month, 0.21 ± 0.09 g/month, 0.12 ± 0.04 g/month, and 0.36 ± 0.07 g/month in Period B.

(A).



(B).

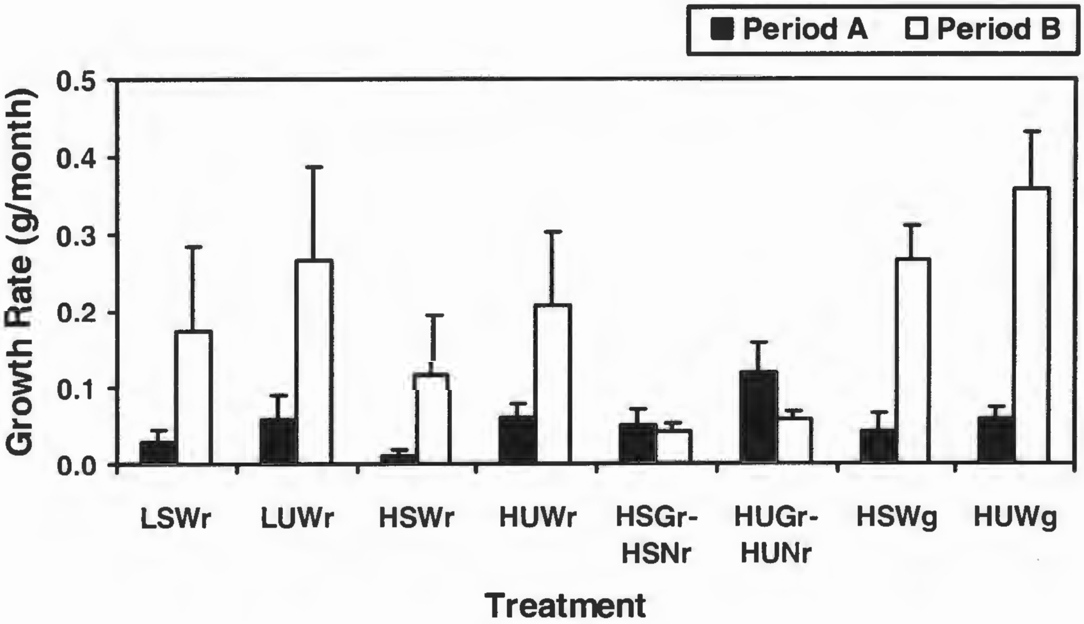


Figure 23. Black bars represent data from Period A and open bars represent data from Period B. Data are mean ± 1 SE for three replicate aquaria (each aquaria started with five juveniles). For a detailed list of treatment definitions, see Table 5. (A). Growth rate (change in test diameter) of juvenile sea urchins. (B). Average growth rates (change in mass) for juveniles from the growth experiment.

In Period A, the presence of adults led to generally lower juvenile growth rates (both test diameter and body mass) in all comparisons (see Tables 6 and 7 for results of ANOVA). Juveniles fed ground kelp grew faster than juveniles fed whole blades of kelp, though this difference was only significant in one case (Tables 6 and 7). Water motion and species were not found to be significant factors in determining juvenile growth in Period A (Tables 6 and 7).

Table 6. Summary of six separate two-way ANOVA examining the effects of adult presence and (i). water flow, (ii). algal form, and (iii). urchin species test diameter growth. Bold type indicates significant results.

Time	Comparison	Source	SS	df	F	Sig
Period A	I	Adult	$1.04 \cdot 10^{-3}$	1	10.90	**0.011**
		Kelp	$4.24 \cdot 10^{-4}$	1	4.45	0.068
		Adult*Kelp	$2.66 \cdot 10^{-6}$	1	0.03	0.871
	ii	Adult	$1.90 \cdot 10^{-3}$	1	22.83	**0.001**
		Flow	$6.33 \cdot 10^{-5}$	1	0.76	0.409
		Adult*Flow	$1.69 \cdot 10^{-4}$	1	2.04	0.191
	iii	Adult	$3.53 \cdot 10^{-4}$	1	4.46	0.068
		Species	$1.40 \cdot 10^{-4}$	1	1.77	0.220
		Adult*Species	$1.39 \cdot 10^{-4}$	1	1.76	0.222
Period B	i	Adult	$5.37 \cdot 10^{-4}$	1	8.11	**0.022**
		Kelp	$1.81 \cdot 10^{-3}$	1	27.44	**0.001**
		Adult*Kelp	$1.40 \cdot 10^{-3}$	1	21.16	**0.002**
	ii	Adult	$4.61 \cdot 10^{-3}$	1	57.70	**<0.001**
		Flow	$1.63 \cdot 10^{-5}$	1	0.20	0.663
		Adult*Flow	$5.38 \cdot 10^{-5}$	1	0.67	0.436
	iii	Adult	$2.21 \cdot 10^{-3}$	1	19.91	**0.002**
		Species	$3.38 \cdot 10^{-4}$	1	3.04	0.119
		Adult*Species	$1.85 \cdot 10^{-4}$	1	1.66	0.233

Table 7. Summary of six separate two-way ANOVA examining the effects of adult presence and (i). water flow, (ii). algal form, and (iii). urchin species on mass. Bold type indicates significant results.

Time	Comparison	Source	SS	df	F	Sig
Period A	i	Adult	$1.04 \cdot 10^{-3}$	1	6.14	**0.035**
		Kelp	$4.24 \cdot 10^{-4}$	1	3.75	**0.089**
		Adult*Kelp	$2.66 \cdot 10^{-6}$	1	0.14	0.719
	ii	Adult	$1.90 \cdot 10^{-3}$	1	4.28	**0.072**
		Flow	$6.33 \cdot 10^{-5}$	1	0.13	0.728
		Adult*Flow	$1.69 \cdot 10^{-4}$	1	0.29	0.604
	iii	Adult	$3.53 \cdot 10^{-4}$	1	3.65	0.093
		Species	$1.40 \cdot 10^{-4}$	1	0.50	0.502
		Adult*Species	$1.39 \cdot 10^{-4}$	1	1.01	0.344
Period B	i	Adult	$5.37 \cdot 10^{-4}$	1	0.99	0.350
		Kelp	$1.81 \cdot 10^{-3}$	1	4.80	0.060
		Adult*Kelp	$1.40 \cdot 10^{-3}$	1	1.30	0.287
	ii	Adult	$4.61 \cdot 10^{-3}$	1	1.10	0.325
		Flow	$1.63 \cdot 10^{-5}$	1	0.16	0.702
		Adult*Flow	$5.38 \cdot 10^{-5}$	1	0.06	0.818
	iii	Adult	$2.21 \cdot 10^{-3}$	1	2.44	0.157
		Species	$3.38 \cdot 10^{-4}$	1	1.84	0.212
		Adult*Species	$1.85 \cdot 10^{-4}$	1	0.01	0.921

In Period B, the presence of adults led to significantly smaller test diameters, but did not have a significant effect on body mass (Tables 6 and 7). Juveniles that were not fed any kelp (i.e. HSN_{red} and HUN_{red} treatments) had significantly smaller test diameters, and though they also had lower body masses, this difference was not statistically significant (Tables 6 and 7). Water motion and species were not found to be statistically significant factors in determining juvenile growth in Period B, though juvenile *S. droebachiensis* did attain slightly heavier body masses than *S. franciscanus* (Tables 6 and 7).

Juvenile urchins grown in the presence of adults showed consistently lower growth rates compared to juveniles alone with two exceptions: (a) Sheltered versus unsheltered *S. droebachiensis* in Period A and (b) The "starved" treatments of Period B, which both displayed no significant differences in test diameter growth. Not surprisingly, in Period B, starved juveniles (HSN_{red} and HUN_{red}) displayed lower growth rates than juveniles fed whole blades of kelp (LSW_{red}, LUW_{red}, HSW_{red}, HUW_{red}, HSW_{green}, and HUW_{green}).

Adult urchins increased in size between the November 3, 2000 and December 4, 2000 measurements (LSW_r = 141 ± 9 mm vs. 153 ± 2 mm, HSW_{red} = 147 ± 4 mm vs. 151 ± 6 mm, and HSG_{red} = 149 ± 0 mm vs. 150 ± 3 mm). However, by February 5, 2001 a decrease in average test diameter (LWS_{red} = 151 ± 2 mm, HSW_{red} = 148 ± 2 mm, and HSN_{red} = 141 ± 1 mm) was recorded. For adult *S. droebachiensis*, an increase in test diameter was recorded between the November 3, 2000 and the December 4, 2000 measurements (LSW_{red} = 51 ± 2 mm vs. 61 ± 2 mm).

There were no significant differences found in test diameter for adults in either of the whole kelp treatments (high water motion $F_{(2,6)} = 0.34$, $p = 0.721$; or low water motion $F_{(2,6)} = 1.37$, $p = 0.323$) over the course of the experiment (Figure 24). However, adults in the ground kelp treatment showed a significant decrease in test diameter in period B ($F_{(2,6)} = 7.31$, $p = 0.025$), which corresponds to the reduction in kelp supplied to those treatments. Adult *S. droebachiensis* experienced a significant increase in test diameter between periods A and B ($t = 5.86$, $p = 0.004$).

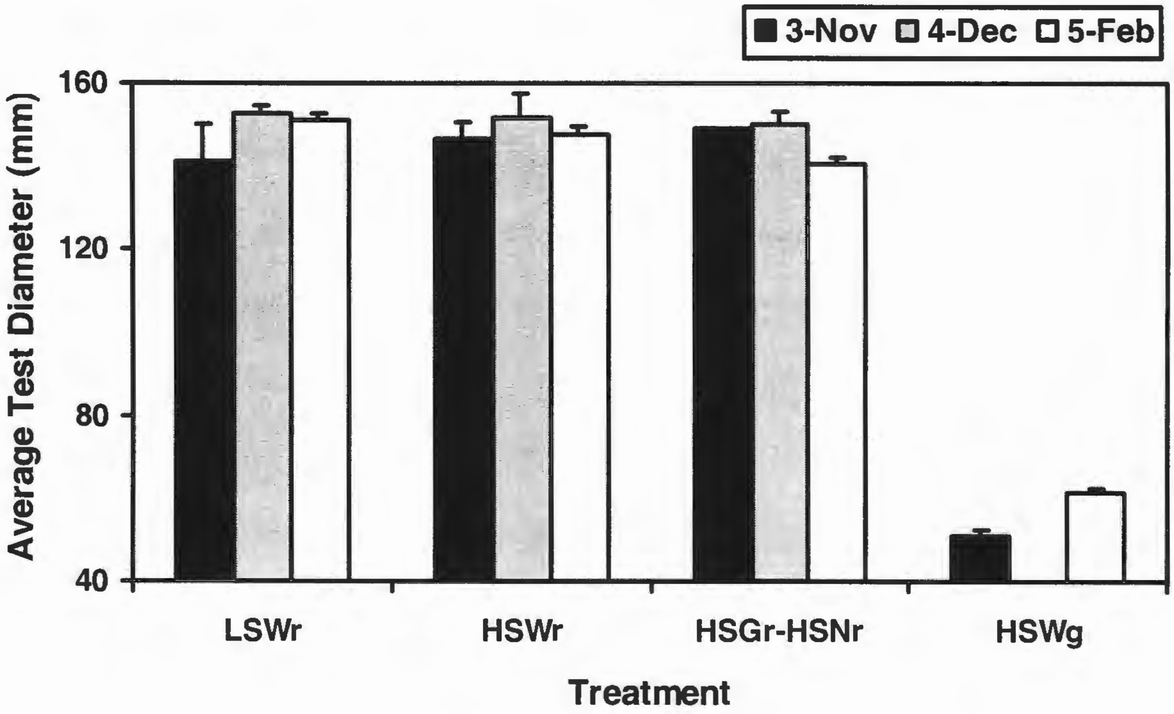


Figure 24. Changes in adult test diameter over time for growth experiment. The black and grey bars represent measurements taken in Period A (Nov. 3 and Dec. 4 respectively) whereas the open bars represent measurements taken in Period B (Feb. 5). Data are mean ± 1 SE for three aquaria (two adult red urchins per aquaria; four adult green urchins per aquaria). For a detailed list of treatment definitions, see Table 5.

Linear regression analysis indicated that growth rate (mm/day) could be related to initial test diameter. For *S. franciscanus*, a significant relationship between growth rate and initial test diameter was found both in November (Growth rate $_{(\text{Nov.} - \text{Dec.})}$ = (Test diameter$_{\text{Nov}}$) * (- 1.0 ± 0.3) + (150.4 ± 37.4); Adjusted $R^2 = 0.64$, p = 0.006) and December (Growth rate $_{(\text{Dec.} - \text{Feb.})}$ = (Test diameter$_{\text{Dec}}$) * (- 0.797 ± 0.312) + (115 ± 47); Adjusted $R^2 = 0.41$, p = 0.038).

Sheltering behaviour in the growth experiment

S. franciscanus juveniles fed whole kelp (HSW$_{\text{red}}$) showed an non-significant (p = 0.682, Kruskal-Wallis) increase in sheltering in Period B compared to Period A (77 ±

5 and 71 ± 3 respectively; Figure 25). Conversely, *S. franciscanus* juveniles in the ground kelp-no kelp treatment HSG_{red}-HSN_{red}) showed a decrease in sheltering in Period B (from 66 ± 10 % to 55 ± 1 %), though this difference was not significant (p = 0.263, Kruskal-Wallis). A significantly higher proportion of juveniles sheltering in the HS treatment compared to the HSG_{red}-HSN_{red} treatment (p = 0.025, Kruskal-Wallis).

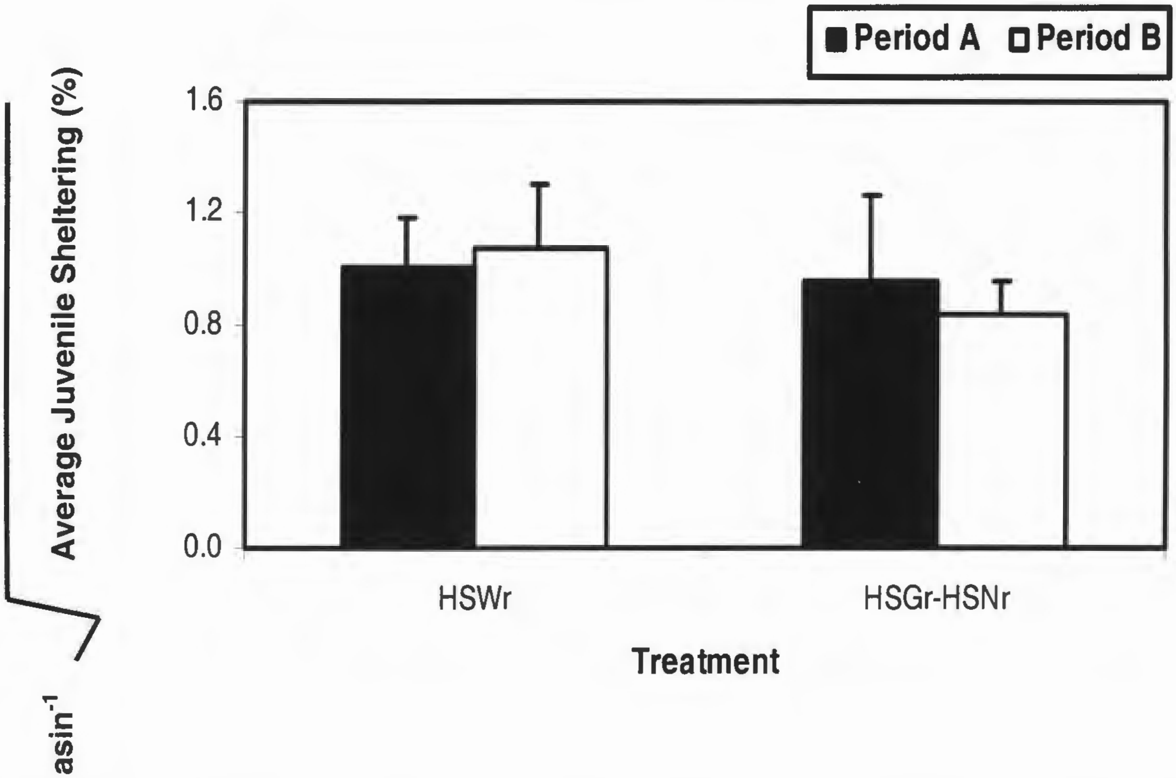


Figure 25. Average proportion of juvenile urchins found sheltering under adult urchins in growth experiment. Black bars represent averages from Period A and open bars represent average from Period B. Data are mean ± 1 SE for three replicate aquaria (each aquaria started with five juveniles).

Movement rates for all treatments were calculated from the 59 juveniles that remained unsheltered for the duration of the experiment (28 sheltering juveniles were obscured from view). Of the 59 juveniles observed, 41 showed no movement during the course of the experiment. Movement rates were low for both the HSW_{red} and HUW_{red} treatments (0.43 ± 0.55 body lengths/hour and 0.40 ± 0.40 body lengths/hour respectively; Figure 26). Juveniles exhibited higher movement rates for the HSN_{red} and HUN_{red} treatments (3.50 ± 1.92 body lengths/hour and 5.42 ± 1.71 body lengths/hour, respectively). Although juvenile movement rates were unaffected by adult presence ($p = 0.831$, Kruskal-Wallis), they were significantly higher in treatments without kelp ($p < 0.001$, Kruskal-Wallis).

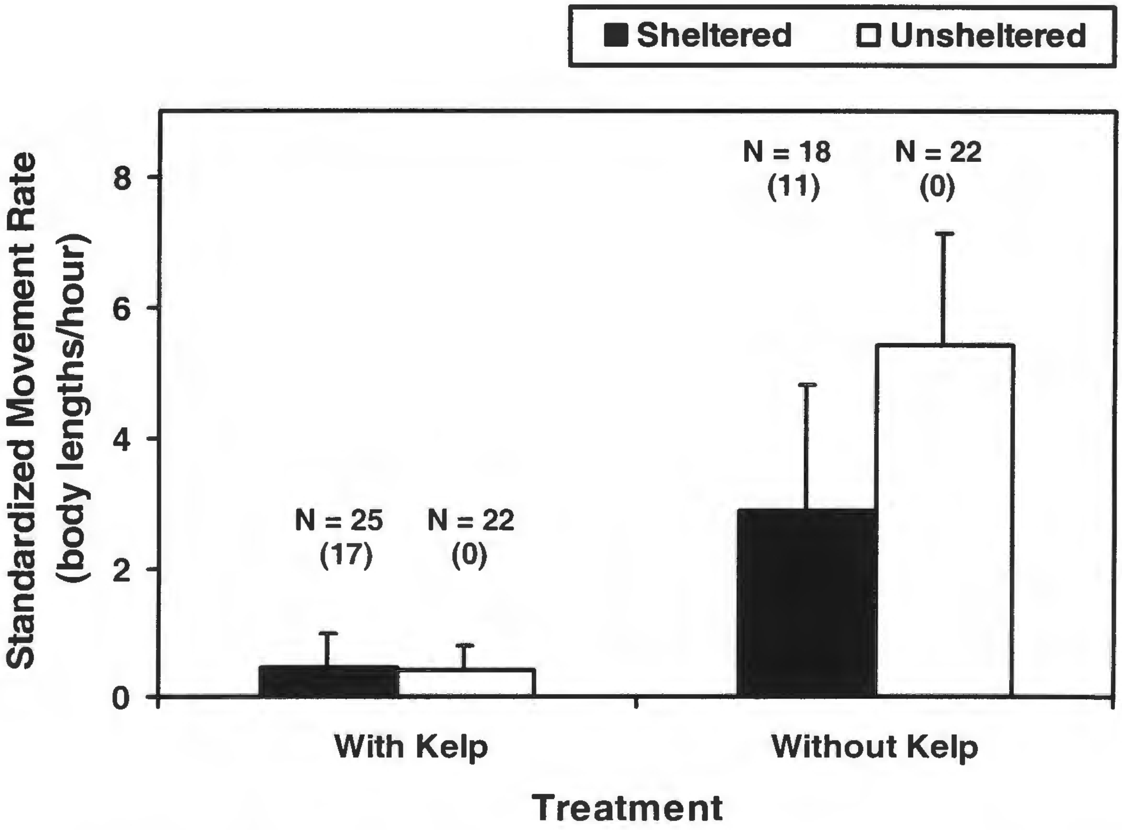


Figure 26. Movement rates of juvenile *S. franciscanus* in growth experiment. Black bars are treatments with juveniles and adults and open bars are treatments with juveniles alone with kelp treatment corresponding to HSW_r and HSW_r respectively and without kelp to HSN_r and HUN_r respectively. Data are mean ± 1 SE. N is the number of juveniles observed at the beginning of the experiment and the numbers in parentheses represent juveniles that moved under adults during the observation period and were thus obscured from view (not included in final analysis).

The results of the model analysis are presented in Figure 27. In this analysis, movement rates for treatments without adults remained stable throughout the analysis as no juveniles were obscured from view in these treatments (HUW_{red} = 0.40 ± 0.40 body lengths/hour and; HUN_{red} = 5.42 ± 1.71 body lengths/hour). Conversely, the average movement rates for juveniles in the HSW_{red} treatment ranged from 0.14 ± 0.15 body lengths/hour to 10.34 ± 1.52 body lengths/hour when obscured juveniles were assumed to move between 0 and 15 body lengths/hour ($y = 0.680x + 0.139$). For the HSN_{red} treatment, movement rates ranged from 1.36 ± 0.82 body lengths/hour to 10.53 ± 1.53 body lengths/hour when obscured juveniles were assumed to move between 0 and 15 body lengths/hour ($y = 0.611x + 1.363$). Significant differences in juvenile movement rates between the "with adult" and "without adult" treatments were found only when "unseen" juveniles were assumed to move 10 body lengths/hour or more (see Table 8 for full statistical results). In contrast, when comparing "with kelp" and "without kelp" treatments, significant differences in average movement rates were found when sheltered juveniles were assumed to move 10 body lengths/hour or less.

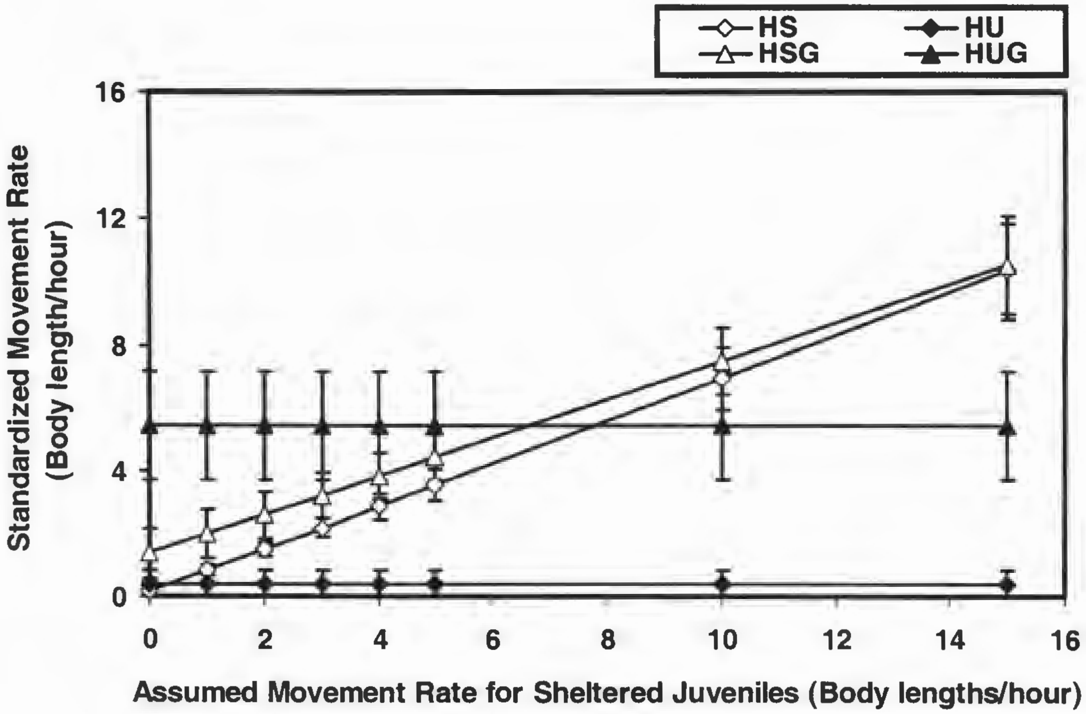


Figure 27. Modeled movement rates (normalized by body length), using assumed rates of movement for sheltering (unobserved) juveniles in addition to observed movement rates presented in Figure 29. Open symbols represent treatments with juveniles and adults and black symbols represent treatments with juveniles alone. Data are mean ± 1 SE for individual juveniles. N are as follows:, HSW_r = 25, HUW_r = 22, HSN_r = 18, and HUN_r =22.

Table 8. Summary of two-way ANOVA examining the effect of adult presence and algal form on juvenile movement rate. Bold type indicates significant results.

Assumed movement rate for sheltered juveniles (cm / hour)	Factor	χ^2	df	p
Not included	Adult	0.343	1	0.560
	Kelp	6.302	1	**0.015**
	Adult*Kelp	0.368	1	0.547
0	Adult	4.950	1	0.290
	Kelp	10.312	1	**0.020**
	Adult*Kelp	3.835	1	0.054
1	Adult	2.491	1	0.118
	Kelp	10.286	1	**0.002**
	Adult*Kelp	4.009	1	**0.049**
2	Adult	0.839	1	0.362
	Kelp	10.138	1	**0.002**
	Adult*Kelp	4.140	1	**0.045**
3	Adult	0.063	1	0.803
	Kelp	9.872	1	**0.002**
	Adult*Kelp	4.223	1	**0.043**
4	Adult	0.167	1	0.684
	Kelp	9.501	1	**0.003**
	Adult*Kelp	4.257	1	**0.042**
5	Adult	1.097	1	0.298
	Kelp	9.042	1	**0.004**
	Adult*Kelp	4.242	1	**0.043**
10	Adult	13.841	1	**< 0.001**
	Kelp	6.221	1	**0.015**
	Adult*Kelp	3.664	1	0.059
15	Adult	29.278	1	**< 0.001**
	Kelp	3.865	1	0.053
	Adult*Kelp	2.848	1	0.095

Question # 4 – Is sheltering behaviour affected by cues related to the adults?

(i). Interspecific sheltering behaviour.

There were also differences in sheltering behaviour between *S. franciscanus* and *S. droebachiensis* examined at high water motion (see Figure 28). When *S. franciscanus* juveniles were placed with adult *S. franciscanus*, 52 ± 7 % were found to shelter under adults. This proportion was lower, however, when the *S. franciscanus* juveniles were placed with adult *S. droebachiensis* (16 ± 5 %). *S. droebachiensis* juveniles exhibited low levels of sheltering regardless of the adult species with which they were placed (5 ± 2 % for adult *S. franciscanus* and 3 ± 2 % for *S. droebachiensis* adults).

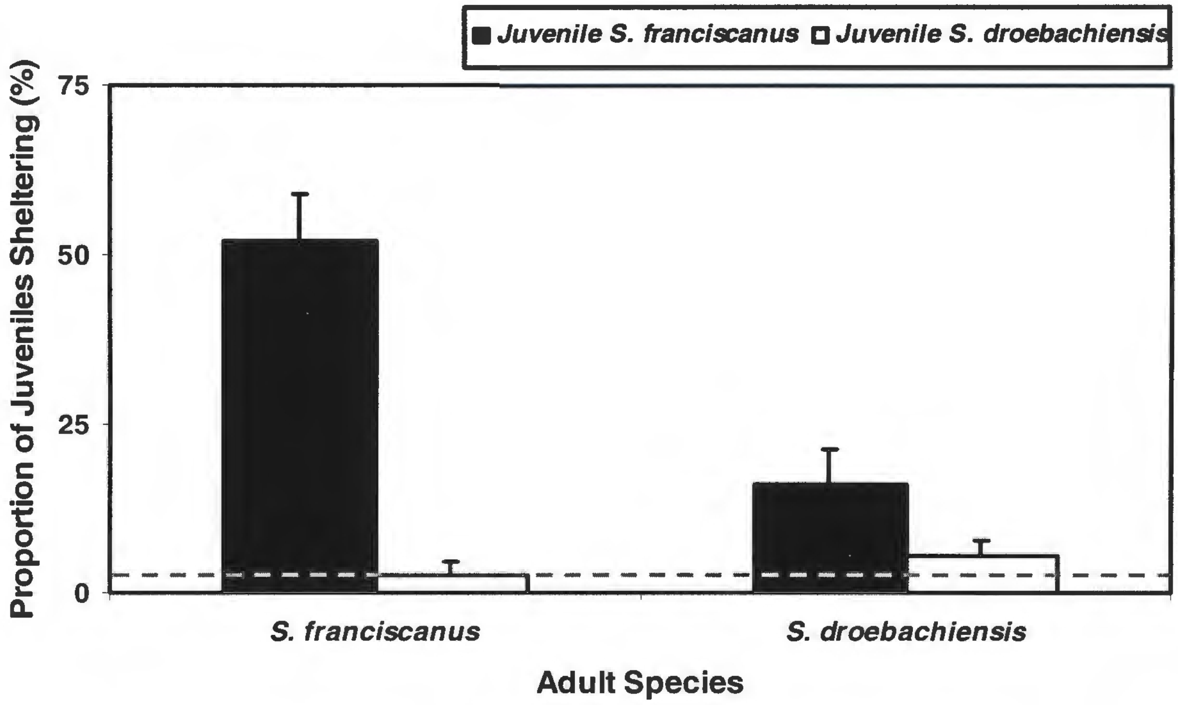


Figure 28. Mean percentage (± standard error) of juveniles sheltering when presented with different species of adult urchin at high flow. Black bars represent juvenile *S. franciscanus* and open bars represent juvenile *S. droebachiensis*. Dashed line represents the proportion of aquarium surface area (3 %) covered by adult targets. Bars are means of fifteen replicates (each replicate consisted of five juveniles).

Results of the two-way ANOVA showed that both main effects, juvenile species ($F_{(1, 56)} = 44.30$, $p < 0.001$) and adult species ($F_{(1, 56)} = 13.67$, $p < 0.001$), and their interaction, juvenile species x adult species ($F_{(1, 56)} = 18.40$, $p < 0.001$) all being significant.

(ii). The influence of juvenile-adult proximity on sheltering.

Figure 29 shows the frequency of juvenile sheltering when juveniles were placed under adults versus in the middle of the aquarium. Juveniles tended to shelter to a greater extent when placed under adults, and sheltering was higher for both cases at high levels of water motion. For example, when juvenile urchins were placed in the open, 56 ± 7 % were found sheltering under high flow conditions whereas 27 ± 7 % of the juveniles were found sheltering under low flow conditions. This result was more pronounced for juveniles placed under adult urchins, where 80 ± 4 % were found sheltering under high flow conditions, and 27 ± 4 % were found sheltering under low flow. Water motion has a significant effect on the proportion of juvenile sheltering, ($F_{(1, 39)}$ = 12.96, p = 0.002) but starting position does not ($F_{(1, 39)}$ = 1.66, p = 0.205).

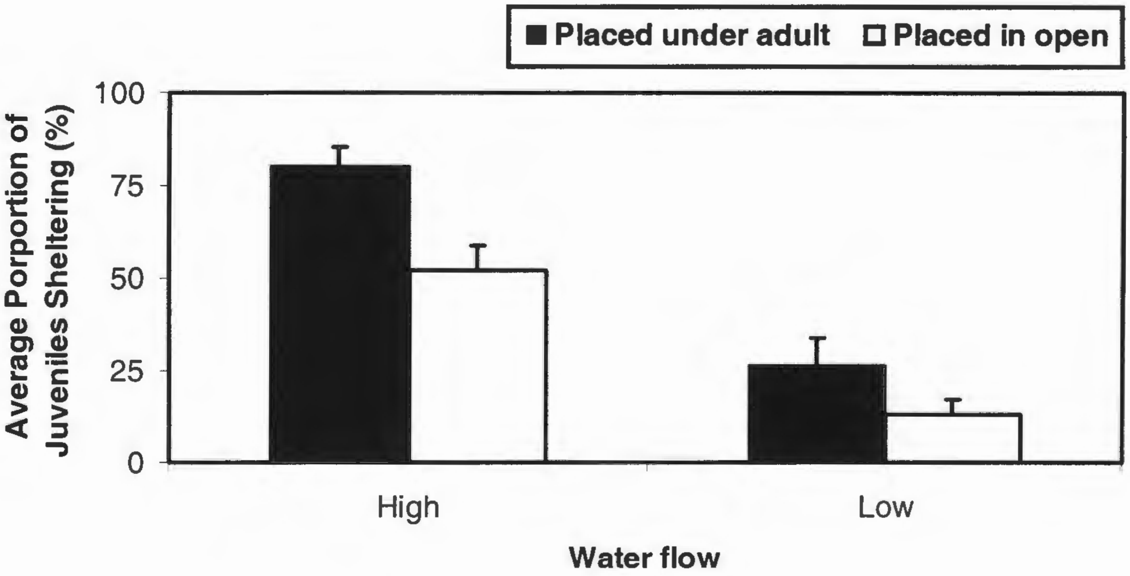


Figure 29. The effect of initial juvenile placement within the aquarium (in the open vs. under adults urchins; see Figure 16) on the proportion of juveniles sheltering. Black bars represent trials where juveniles were placed under adult urchins and open bars indicate trials when juveniles were placed in the open at the beginning of the trial. Open bars are means of fifteen replicates (each replicate consisted of five juveniles). Filled bars are means of six replicates (each replicate consisted of five juveniles). Data are mean ± 1 SE for 6 trials (started under adult) and 15 trials (started in open) with five juveniles per trial.

3.4. Discussion

In marine benthic systems, habitat use (i.e. refuges) for juveniles can differ from adults (Arsenault and Himmelman, 1996; Turon et al., 2000) and it has been proposed that these shifts are an optimal strategy that balances potential risks (i.e. predation, dislodgement) with growth. It is hypothesized that the sheltering behaviour of juvenile *S. franciscanus* is such a strategy in that it serves to: (a) Increase protection from predators; (b) Increase protection from water motion; and (c) Increase access to food (i.e. macroalgae).

Question # 1 – Does sheltering provide hydrodynamic protection?

A significantly higher proportion of juveniles were found sheltering in the spine canopy habitat provided by adults at higher water flows (Figure 19). These spine canopy habitats appear to offer juveniles hydrodynamic protection, as velocities were reduced 5 cm upstream and 20 cm downstream of an adult urchin (Figure 17). It has been long recognized that structural complexity in many natural systems influences hydrodynamic flow (Nowell and Jumars, 1984; Ackerman and Okubo, 1993; Weissberg and Zimmer-Faust, 1993; Keller et al., 2001) and the use of hydrodynamic refuges has been suggested for various marine benthic species (Arsenault et al., 1997; Figueiredo et al., 1997; Boulding and Harper, 1998; Vetter, 1998). This concept, often known as "current shading" describes the reduction in flow from the upstream to downstream side of an organism and has been demonstrated to influence community dynamics in freshwater (Cardinale et al., 2002), marine (Johnson, 1990; Okamura, 1992; Sebens et al., 1997) and terrestrial (Jones et al., 1997; Mulder et al., 2001) systems. Furthermore, Arsenault et al.,

(1997) demonstrated that growth rates for juvenile Iceland scallops *Chlamys islandica* decreased as a consequence of reduced water velocities in such hydrodynamic refuges. For marine benthic invertebrates, it is possible that these hydrodynamic refuges reduce the energetic requirements needed to maintain metabolic processes (e.g. Pace, 1975).

Question # 2 – Does sheltering provide protection from predation?

The risk of predation also influences the frequency of juvenile sheltering as juveniles exposed to predators were more likely to be found under adults rather than juveniles not exposed to predators (Figure 19). These results are consistent with field studies (Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987), which suggest that the spine canopy offers a refuge for juvenile urchins from predators such as *P. helianthoides.* In addition, this study supports the notion that benthic organisms are capable of detecting their risk of being preyed upon and can incorporate this information in making decision (Lima and Dill 1990). The frequency of juvenile sheltering under the risk of predation was roughly 50 % (Figure 19), which is lower than the 80 % reported by Breen et al. (1985). This difference could be attributed to the higher density of juveniles used, greater proportion of adult habitat provided, or the different species of predator (*Pycnopodia helianthoides* vs. *Solaster stimpsonii).* The most important difference however, may be that in the other study, predators were introduced directly into the urchin tank. This may influence the dispersion of a chemical cue or allow non-chemical interactions between predator and urchins. Regardless, these findings confirm that the presence of starfish-associated chemical signals result in the pattern of behaviour predicted by Breen et al. (1985).

The feeding preference experiments showed that whereas *S. droebachiensis* juveniles are less attractive to *P. helianthoides* than *S. franciscanus* juveniles, they remain potential prey items. Furthermore, juvenile *S. franciscanus* may gain protection from predation by sheltering under the spines of adult conspecifics. Conversely, juvenile *S. droebachiensis* do not appear to obtain such protection. It is predicted that the larger size of adult *S. franciscanus*, in particular the spines, provides greater protection for adults and sheltering juveniles. It should be noted however, that only one run of this experiment was conducted due to the limited number of juveniles that could be sacrificed to predators, and should be replicated to increase the confidence in the results.

Question # 3 – Does sheltering provide a nutritional benefit?

(i). What form of kelp is utilized by juvenile sea urchins?

Significant growth rates for smaller juveniles in the whole kelp treatment (0.28 ± 0.03 mm/month to 0.37 (without replication) mm/month for *S. franciscanus* and 0.61 ± 0.10 mm for *S. droebachiensis*) demonstrated the presence of functional jaws. Growth rates were lower for juvenile *S. franciscanus* compared to *S. droebachiensis*, however this may have been influenced by differences in initial test diameter (1.42 ± 0.02 mm and 2.57 ± 0.07 mm, respectively). Rowley (1990) reported similar growth rates for *S. purpuratus* (0.29 to 0.45 mm/month) during the first 50 days after larval settlement. High survival rates (53%) for the ground kelp treatment indicates that juveniles may also absorb dissolved organic material, as is the case for larval urchins (Manahan et al., 1983). However, growth rates for the ground kelp treatment were zero (0.00 ± 0.04 mm/month). Furthermore, many individuals in the control experienced negative growth (-0.04 ± 0.05 mm/month), which supports a similar field observation by Ebert (1967). It is clear that juveniles use kelp very early after settlement.

(ii). Does sheltering increase access to kelp for juvenile sea urchins?

Growth rates for larger juvenile *S. franciscanus* ranged between -0.21 to 1.00 mm/month in Period A and 0.17 to 1.71 mm/month in Period B (see Table 9). Growth rates for juvenile *S. droebachiensis* ranged from 0.29 to 0.41 mm/month in Period A and 0.73 to 0.96 mm/month in Period B. Rowley (1990) reported similar growth rates for *S. purpuratus* (0.29 to 0.45 mm/month) during the first 50 days after larval settlement. Table 9 presents growth rates for both *S. franciscanus* and *S. droebachiensis* found in the literature. Figure 30 summarizes these data and illustrates that growth rates reported here are comparable to those found in the literature.

Table 9. Comparison of growth rates for juvenile sea urchins.

Species (location)	Initial Size (mm)	Density (per L)	*Growth rate (mm / month)*	Food Type(s)	Source
S. franciscanus	0.75 to 2.25	60	-0.04 to 0.28	*Macrocystis integrifolia*	This study
(British Columbia CAN)	7.36 to 8.24	0.12	-0.21 to 1.71	*M. integrifolia*	This study
S. franciscanus (Washington, USA)	26.5 to 31 46.5 to 52.5	32 32	45.0 to 59.3* 56.9 to 67.2*	*Nereocystis leutkeana*	Swan 1961
S. franciscanus (California, USA)	0.404 ± 0.038	No report	1.8	*Macrocystis pyrifera*	Rogers-Bennett et al. 1994
S. droebachiensis	1.19 to 4.96	60	0.22 to 0.29	*M. integrifolia*	This study
(British Columbia CAN)	7.40 to 8.01	0.12	0.29 to 0.96	*M. integrifolia*	This study
S. droebachiensis (Nova Scotia, CAN)	3 to 6	0.82	0.38 to 1.25	*Laminaria longicruris*	Raymond & Scheibling 1987
	3 to 6	52	- 0.02 to 0.62	*Lithothamnium glaciale*	Raymond & Scheibling 1987
	0.4 to 0.5	100	0.19 to 0.29	*L. longicruris; Lithothamnium glaciale*	Raymond & Scheibling 1987
S. droebachiensis (Maine, USA)	13 to 17	0.45 to 0.47	0.03 to 1.55	*Mytilus edulis; M. trossulus; L. longicruris; Laminaria digitata; L. glaciale; Phymatolithon laevigatum*	Meidel & Scheibling 1999
S. droebachiensis (Nova Scotia, CAN)	38 to 52	0.51	~ 2	*L. longicruris; L. digitata; Codium fragile*	Scheibling & Anthony 2001
S. droebachiensis (New Hampshire, USA)	8 to 10 24 to 26 40 to 42 50 to 52	87 89 83 34	23.1 to 31.6* 33.4 to 45.3* 45.3 to 54.1* 51.4 to 57.3*	*L. digitata; Ascophyllum nodosum*	Swan 1961
S. droebachiensis (Washington, USA)	26 to 32 55 to 57 76 to 78	26 21 9	47.2 to 59.7* 57.8 to 66.6* 77.2*	*N. leutkeana*	Swan 1961

* indicates range of sizes measured after 12 months (growth rates not known)

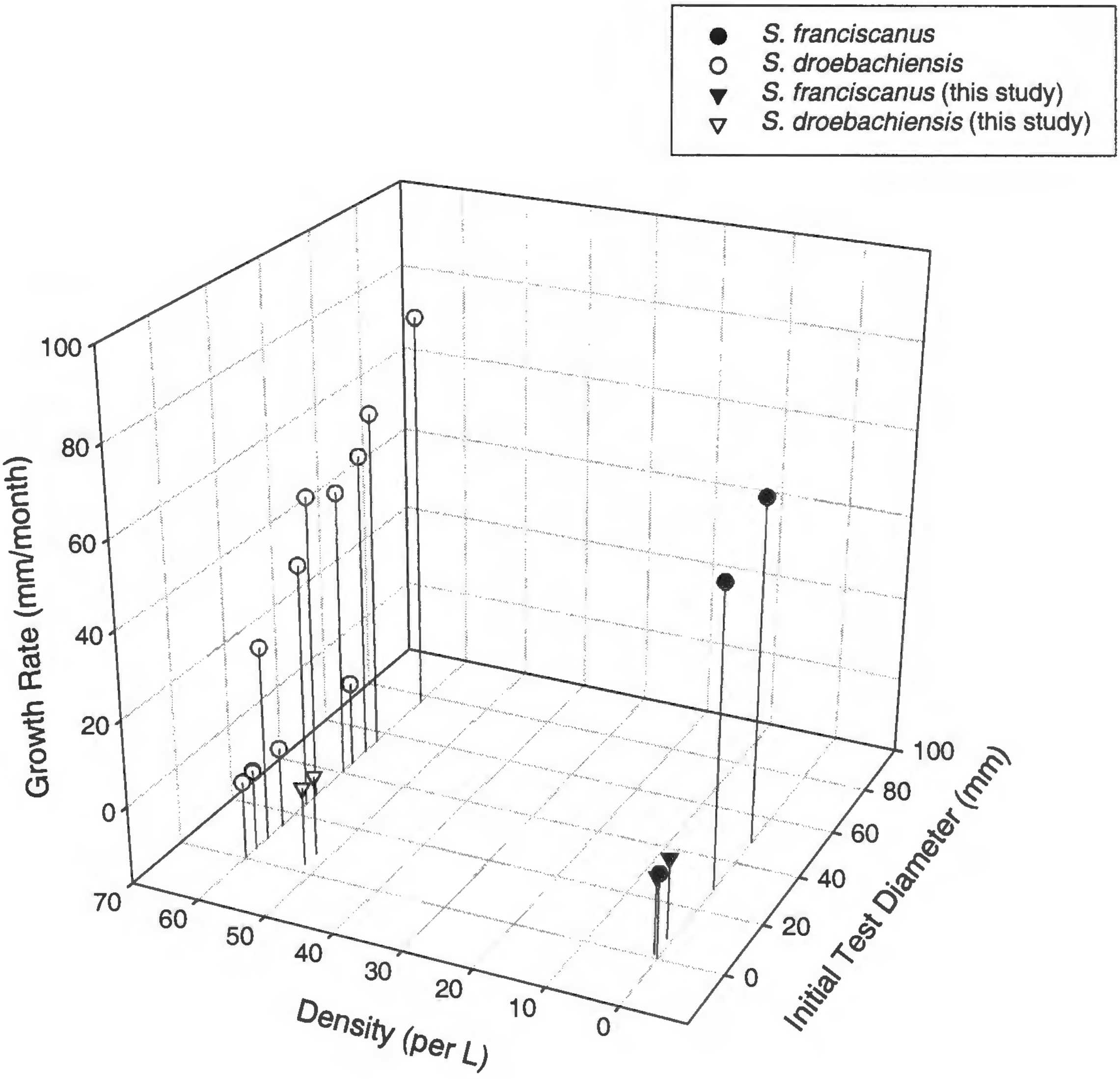


Figure 30. Three-dimensional plot of juvenile sea urchin (*S. franciscanus* and *S. droebachiensis*) growth rates in relation to initial size (i.e. test diameter) and density. Black symbols represent *S. franciscanus* and open symbols represent *S. droebachiensis.* Circles are data from the literature and triangles and data from this study.

The potential nutritional advantage of juvenile sheltering was addressed in the growth experiment in which juveniles cultured in the presence of adults had lower growth rates than juveniles grown alone, which was opposite to expectations. That the presence of adult urchins led to consistently lower growth rates for juvenile urchins regardless of flow rate, algal form, or urchin species, speaks to a competitive interaction between adults and juveniles. In Period A, growth and survival was significantly higher when juveniles were isolated from adults. This difference in juvenile growth could be attributed to competition with adults for kelp (Table 6 and 7) as suggested by Low (1975). This type of competition between adults and juveniles has also been reported for other marine invertebrates such as limpets (Fletcher, 1988). It is important to note however, that results from this study do not address the relative importance of other food sources (i.e. benthic microalgae) or the relative abundance of drift kelp resources under field conditions.

Kelp abundance is difficult to estimate since it refers to not only standing crop, but also the more ephemeral presence of drift kelp. Low (1975) indicates that detritus may in fact be the major food item for *S. franciscanus*. A benthic litter assessment on Vancouver Island determined that 41 g wet weight/m^2 of drift kelp accumulated over one week in the field (Smith and Foreman, 1984). This is lower than the 50 g wet weight of kelp (314 g wet weight/m^2) provided in the growth experiment three times a week. If adult urchins are better equipped to capture drift kelp (due to longer spines and tube feet) than juveniles, it may still benefit juveniles to shelter under adults when algal resources are scarce. Sheltered juveniles, although competing with adults, may experience nutritional gains compared to unsheltered juveniles. The results from this study however, indicate that juveniles sheltering under feeding adults have similar growth and survival rates as juveniles from both starved treatments. It would appear unlikely that juveniles under all except the most food-limited conditions would benefit nutritionally from sheltering under adults.

Juvenile urchins displayed significantly higher movement rates in treatments without kelp ($F_{(1,\ 60)} = 8.46$, $p = 0.005$; Figure 26). This supports the notion that some animals are capable of assessing not only predation risk, but also nutritive conditions when making behavioural decisions (Dill and Fraser 1997). While the validity of these results are limited by the lack of data on movement rates for sheltered juveniles, the model analysis suggests that the conclusions are valid assuming that sheltered juveniles move between 2 and 5 body lengths/hour.

If competition for food between juveniles and adults is intense, recruitment would be expected to occur in areas without adults. However, as Low (1975) hypothesized selective pressures from predators may remove juveniles that recruit into areas without adults. Results from this study are consistent with the idea that: (1) juveniles associated with adults experience lower growth rates; (2) when food was limited, juveniles sheltered under adults less frequently while increasing their movement rate; and (3) juveniles shelter in response to dangers such as predation and hydrodynamic disturbance.

Question # 4 – Is sheltering behaviour affected by cues related to adults?

(i). Interspecific sheltering behaviour.

Interspecific adult-juvenile associations have been reported for other echinoderms (Hendeler et al., 1999). However, no evidence was found that would suggest any behaviourally-mediated association between *S. franciscanus* and *S. droebachiensis.* Juvenile *S. franciscanus* appear to be more vulnerable to predators and they benefit from the protection of the spine canopy, which would explain the higher frequency of sheltering under adults of both species. Juvenile *S. droebachiensis* were found to be a less attractive food item to *P. helianthoides* relative to *S. droebachiensis*, which might help explain the lower frequency of sheltering for the less vulnerable species. Furthermore, the smaller spine length of adult *S. droebachiensis* may not provide as much protection as adult *S. franciscanus.* Although *S. droebachiensis* are known to use their podia and pedicellariae to manipulate objects and ward off predators, no interaction between adults and juveniles was observed.

(ii). Juvenile-adult proximity.

The proximity of a juvenile urchin to an adult had relatively little influence on the rate of juvenile sheltering whereas fluid conditions had a much more pronounced effect. Results do not support the notion that, in these experiments, juvenile sheltering is limited by the ability to locate adults, which may be related to the complex pattern of mixing in the aquarium. Although the type of cue used to locate adults remains unknown, results indicate that it is well distributed in this study. Revealing the type and source of cue(s) used by juvenile urchins to locate adults in this sheltering behavior remains a challenge.

Juvenile Behaviour

The results of this study show that: (a) Juvenile sheltering appears to be a strategy influenced by predation and hydrodynamic conditions; and (b) In the absence of predators and with moderate water motion, juvenile sheltering imposes a cost in the form of increased competition for food. This behaviour is a clear example of risk-balancing as described by Fraser and Huntingford (1986). Not unexpectedly, juveniles under low risk conditions (i.e. low water motion, no predators) tended to shelter under adults less frequently (Figure 19). Furthermore, in low risk situations, juveniles that associated with adults had significantly lower growth rates (Tables 6 and 7). Finally, when juveniles were placed under adults in low risk situations, juveniles were observed to emerge from underneath adults (Figure 29), further supporting the notion that sheltering behaviour is an inducible rather than a stereotypic response. The long spines of adult *S. franciscanus* appeared to prevent *P. helianthoides* from preying upon juveniles. Though not explicitly tested here, predation events on juveniles by *P. helianthoides* most assuredly decrease fitness and thus juvenile sheltering would be classified as an induced defense according to the criteria outlined in Table 3 (Karban and Myers 1989).

Whereas predation and water motion appear to strongly influence juvenile behaviour, limitations to the interpretation of these results must be noted. For example, Lima and Bednekoff (1999) noted that prey behaviour depends on the overall temporal pattern of risk. Their *risk allocation hypothesis* states that organisms that experience only brief periods of high risk will react differently to a predator than when exposed to frequent periods of high risk. This may cause a systematic overestimate the impacts of predation on behaviour. Given that both juvenile and adult urchins in this experiment were kept in the laboratory for several months under moderate flow conditions and without exposure to predators, it is possible that reactions from the sheltering experiments could overestimate the magnitude of the defensive response if this risk allocation hypothesis also applies to sea urchins.

Recruitment

It has been suggested that competition between juveniles and adults may set "general limits" to recruitment in populations of *S. franciscanus* in British Columbia (Low 1975). North (1971) however, provides a word of caution against generalizing such conclusions about urchins over a large geographic area. Furthering this view, Ebert (1983) proposed a “latitudinal cline of recruitment” citing low recruitment in British Columbia compared to more frequent recruitment in southern California. (see Table 10). Interestingly, Connolly et al. (2001) measured recruitment of barnacles (*Balanus* sp. and *Chthamalus* sp.) and mussels (*Mytilus* sp.) directly, thus minimizing the influences of post-settlement processes and found an inverse latitudinal cline with recruitment being between 19 to 98 times higher in northern sites (i.e. Cape Meares, OR, 46°28' N) compared to southern locations (i.e. San Simeon, CA, 35.5° N). Determining whether post-settlement processes play a role in explaining these relationships between latitude and recruitment is difficult as little is known about juvenile stages for many marine invertebrates.

For juvenile *S. franciscanus*, lower rates of sheltering have been reported in British Columbia (60 % to 76 %; see Table 11) and Northern California (73 %) compared to southern California (81 %). It should also be noted that the definition of “juvenile" was not consistent among studies. In the study from California (Tegner and Dayton 1977) individuals with test diameters < 20 mm were identified as juveniles whereas the studies from British Columbia used individuals < 50 or 60 mm

(Breen at al., 1985; Sloan et al., 1987; Rogers-Bennett et al., 1995). Thus, differences in juvenile sheltering frequencies between northern and southern locations may be underestimated. Furthermore, survival rates for *S. franciscanus* are also lower (0.77 per year) in Northern California, Oregon, Washington, and Alaska compared to Southern California and Mexico (0.93 per year; Ebert et al., 1999).

Table 10. Geographic variation in recruitment rates for *Strongylocentrotus franciscanus*.

Location	Latitude	Juvenile	Average ± SE (%)	Range (%)	Source
Queen Charlotte Islands	52° 30'	< 60 mm	18 ± 6[1]	3 - 35	Breen and Adkins 1982
Vancouver Island	48° 50'	< 60 mm	6 ± 2[2]	0 - 50	Adkins et al 1981
Vancouver Island	48° 30' to 50° 30'	< 50 mm	10	0 - 47	Sloan et al. 1987
Vancouver Island	~	< 30 mm	1	Up to 30	Low 1975
Northern California	38° 19.2' to 39° 21.5'	< 60 mm	24 ± 5	9 - 76	Morgan 1997
Point Loma, CA	32° 42'	< 60 mm	47 ± 3	32 - 61	Tegner & Dayton 1981

[1] - Average of 5 sites

[2] - Average of 27 sites

Table 11. Geographic variation in the proportion of juvenile *Strongylocentrotus franciscanus* sheltering under adults.

Location	Latitude	Juvenile	Average ± SE (%)	Range (%)	Source
Queen Charlotte Is.	52° 46.2'	< 50 mm	60	60	Breen et al. 1985
Vancouver Island	48° 52.3' to 49° 07.5'	< 50 mm	76 ± 7[1]	65 - 90	Breen et al. 1985
Vancouver Island	~ 48° 50' to 50° 50'	< 60 mm	73 ± 10[2]	19 - 100	Sloan et al. 1987
Northern California	38° 19'03"	5-50 mm	73	Not Given	Rogers-Bennett et al. 1995
Point Loma, CA	32° 42'	< 20 mm	81	Not Given	Tegner & Dayton 1977

[1] - Average of 3 sites

[2] - Average of 11 sites

3.5. Conclusion

The results of this study indicate that post-settlement processes play an important role in influencing the frequency of juvenile sheltering. Although juvenile mortality cannot be eliminated as a possible explanation for adult-juvenile associations, these results support the hypothesis that sheltering is a consequence of juvenile behaviour. Juvenile sheltering appears to be a behavioural strategy that reduces exposure to both predators and water motion, though juveniles under adults are subject to competition with adults for food (macroalgae). Juveniles may be able to move under adults over short distances, but further study is needed to determine the significance of this behaviour in the field. The early life history of benthic invertebrates should continue to be investigated in order to understand how events during these stages influence recruitment.

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Chapter IV. Secondary chemical cues facilitate juvenile-adult associations in red sea urchins (*Strongylocentrotus franciscanus*).

Abstract

Much progress has been made in understanding the adaptive value of chemical cue detection by marine organisms, many of which appear to be based on a single chemical signal. Here, the role of a secondary chemical cue in triggering an avoidance behaviour for juvenile sea urchins (*Strongylocentrotus franciscanus*) is demonstrated experimentally. Results indicate that: (a) juvenile sheltering behaviour is facilitated by chemical signaling ($F_{(2,\ 35)} = 10.29$, $p = 0.001$); and (b) a chemical signal produced by adult sea urchins only in the presence of a predatory sea star (*Pycnopodia helianthoides*) attracts juvenile urchins ($\chi^2 = 13.74$, $p = 0.003$). This indirect "secondary" cue may allow juvenile sea urchins to balance trade-offs between competitive ability and predator avoidance. Under natural conditions, it is probable that organisms are faced with a complex mosaic of chemical signals, underscoring the importance of considering multiple cues.

Strongylocentrotus | chemical cue | spine canopy | juvenile | sea urchin

4.1. Introduction

Many defenses employed by marine organisms to minimize predation may be categorized as either morphological or behavioural. Morphological defenses can involve spines (Harvell, 1984), armor (Peichel et al., 2001), or coloration (Lindberg and Pearse, 1990). Three common behavioural responses to predators are: (a) fleeing (Snyder and Snyder, 1970); (b) aggregation (Maruck and Harkless, 2001); and (c) refuge use (see Tomba et al., 2001). Such behaviour however, may bring with it a cost in the form of lower access/utilization of resources (Tomba et al., 2001). It has been shown that organisms have the capacity to assess their risk to predation and use this information in decision-making (Lima and Dill, 1990). Thus, it should be advantageous for individuals to assess environmental factors in an expeditious and accurate manner to make decisions that optimally balance growth and predation risk. Environmental information may be gathered using visual, tactile, hydrodynamic, electrical and chemical cues. In marine systems, visual cues may be limited when light is limited by depth and/or turbidity (Smith, 1992). Tactile cues, while more reliable, do not allow an organism to detect a predator over distance. It is unknown, though unlikely that marine invertebrates possess the anatomical and physiological features to utilize electrical cues. Chemical cues however, may provide a more reliable cue (though see Weissburg and Zimmer-Faust, 1993) that also provides advance warning of danger.

Organisms in a fluid environment often possess morphological, physiological and behavioural features that rely on the detection of chemical cues/signals. In both freshwater and marine environments, there are examples of organisms using chemical cues to locate predators, (Phillips, 1978; Sih, 1986; Appelton and Palmer, 1988; Crowl and Covich, 1990; Hazlett, 1990; Hazlett, 1994; Marvin and Hutchison, 1995; Schonle and Bergelson, 1995; McCollum and Leimberger, 1997; Leonard et al., 1999; Relyea, 2000; Toth and Pavia, 2000) prey, (Weissburg and Zimmer-Faust, 1993; Rochette et al., 1994; Zimmer-Faust and Finelli, 1995) conspecifics, (Atema and Engstrom, 1971; Zimmer-Faust et al., 1985; Jensen, 1991; Schneider and Moore, 2000) and food (Chivers et al., 2000). Defensive chemical cues can be delineated into three major categories: (a) avoidance cues; (b) alarm cues (von Frisch, 1941); and (c) stress cues (Chivers and Smith, 1998; Schneider and Moore, 2000). Avoidance cues involve chemicals released directly from predators that induce defensive responses from prey (Phillips, 1978; Sih, 1986; Appelton and Palmer, 1988; Crowl and Covich, 1990). Alarm cues originate from injured conspecifics, and have also been widely reported (Snyder and Snyder, 1970; Marvin and Hutchison, 1995; Huryn and Chivers, 1999; Chivers et al., 2000; Jacobsen and Stabell, 2000; Toth and Pavia, 2000). Conversely, descriptions of stress cues involving chemicals from disturbed, yet undamaged conspecifics are less common (Schneider and Moore, 2000, but see Hazlett, 1985; Schonle and Bergelson, 1995).

To date, studies of stress signals have used physical agitation of the sender to induce stress. However, it is unknown if stress signals can be induced through chemically mediated vectors alone. For example, Montgomery, (1966) collected mucous produced by abalone (*Haliotis assimilis*) exposed to “sea star seawater” and found that this mucous elicited defensive behaviour in abalone that had not been exposed to the predatory sea star. While not experimental, these results suggest that a cascade of chemical cues may provide information about a source through an indirect pathway.

Juvenile red sea urchins (*Strongylocentrotus franciscanus*) have been found to reside under the spines of the adults (Low, 1975; Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987; Nishizaki and Ackerman, 2001). Recent work indicates that juvenile *S. franciscanus* may be protected from predation and water motion by the adult urchin spine canopy (Nishizaki and Ackerman, 2001). It has been postulated that this sheltering behaviour represents a trade-off for juvenile urchins between increased predatory and hydrodynamic protection versus increased competition for food with adults (Chapter III). A juvenile, therefore, must be able to both locate adult urchins and assess potential environmental risks. Chemical communication may provide reliable cues to track these targets in the marine environment.

Here, a chemical signal produced by adult urchins in response to a predator cue is shown to evoke a sheltering behaviour in juvenile urchins. This sequential chemical signaling appears to be one of the first accounts of a secondary chemical cue.

4.2. Materials and Methods

Sea Urchins

Adult *S. franciscanus* were collected by SCUBA and held in tanks with flowing seawater (temperature = 8.80 to 13.20 °C, salinity = 25.93 to 34.66 ppt, pH 7.50 to 8.30, Dissolved oxygen = 43.20 to 100 % saturation) at the Bamfield Marine Sciences Centre (BMSC). Juvenile *S. franciscanus* were obtained from an experimental hatchery (Island Scallops; Qualicum Beach, British Columbia, Canada) and were maintained in separate tanks with flowing seawater.

Juvenile Sheltering Experiment

Laboratory experiments were undertaken to address how juvenile urchins locate the adults under whom they shelter. The goal of this “juvenile sheltering” experiment was to determine if juveniles used chemical and/or tactile cues to locate adults.

All experiments were conducted according to the methods outlined in Chapter III, though a brief explanation of the protocol will be provided below. Experiments occurred in a glass aquarium (60 cm × 30 cm × 30 cm) using water from the BMSC seawater system, which provided unfiltered seawater from a depth of 25 meters at a constant temperature of 10 - 12 °C throughout all of the experiment. Water flow was supplied via two nozzles (15 L/min each), with one nozzle placed above the left and right sides of the aquarium (see Figure 16).

Cages were placed in each of the four quadrants of the aquarium (large circles in Figure 16a). Adult urchins, rocks, and model urchins were placed in the cages as potential “targets” for juveniles to shelter under. Three comparisons were designed to address the relative importance of chemical and tactile cues: (a) adult urchins versus rocks; (b) adult urchins versus urchin tests; and (c) urchin tests versus rocks. Rocks of similar size as the adults were boiled and cleaned before use. Urchin tests were created by air-drying eviscerated urchins and covering with several layers of marine epoxy (Industrial Formulators, Burnaby, BC, Canada) thinned with methylene chloride (Industrial Plastics, Victoria, BC, Canada) until the mixture applied evenly to urchin spines. Tests were then dried at 60 ºC for 6 hours. The models were then placed in distilled, de-ionized for several days before use to minimize any chemical leaching from the epoxy during the experiment.

To begin each trial five juvenile urchins (7.60 ± 0.11 mm test diameter; mean ± standard error) were placed in the centre of the aquarium floor ("x" in Figure 16a). The position of each juvenile was noted after 12 hours (i.e. under adult urchin tests, under/on rock, on bottom of aquarium, on glass walls of aquarium, or on wood cages). Each comparison was replicated 15 times (with five different juveniles per replicate). A one-way ANOVA was used to test the null hypothesis that juvenile sheltering was unaffected by the types of targets presented.

Y-maze Experiment

Experiments were conducted to determine the response of juvenile and adult urchins to chemical cues emanating from: (a) conspecifics; (b) predators (sea stars, *Pycnopodia helianthoides*); and (c) Food (kelp, *Macrocystis integrifolia*). A control was employed through the use of rocks (boiled for > half hour). A "Y-maze" (Figure 31) was designed to identify whether chemoreception is a mechanism through which juvenile sheltering may occur. This Y-shaped choice chamber was filled to a depth of 3.5 cm and fluorescene dye was used to ensure that flow was uniform on both sides of the chamber. The mean chamber velocities were recorded as 3.3 cm/sec and 2.1 cm/sec. Caged targets (i.e. five juvenile urchins, an adult urchin, a predator, or kelp) were placed alternately in one of the arms near the inlet end of the chamber (denoted by "T" in Figure 31). Test subjects (i.e. three juveniles or one adult) were placed on the centre-line of the chamber 15 cm from the outlet end (on the "x") and the position of the subject was recorded after 45 minutes for adult test subjects or 12 hours for juvenile test subjects. The following comparisons were examined for juvenile urchins: (a) kelp vs. rock; (b) adult vs. rock; (c) predator vs.

rock; (d) predator vs. adult; (e) adult upstream of predator vs. rock; (f) adult downstream of predator vs. rock; and (g) rock vs. rock (control). In addition one comparison (the adult downstream of predator vs. rock treatment) was tested using adult urchin subjects. It should be noted that although Y-maze experiments are suitable for examining the orientation of organisms, they are less suitable for measuring the speed of the response due to potential wall encounters (Dale, 1997).

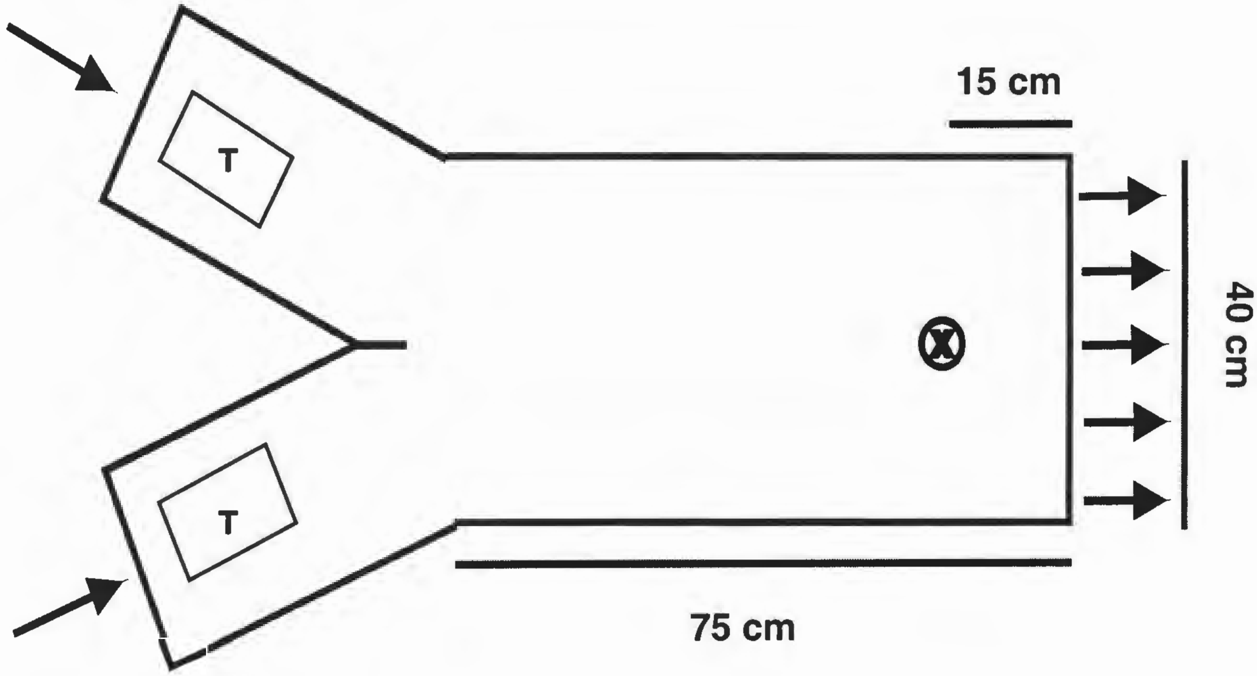

Figure 31. Y-shaped flow chamber (filled to 3.5 cm depth). Arrows indicate direction of water flow. "T" represents target areas. Individuals being tested were placed on the "x" at beginning of each trial.

Urchin movement was categorized under one of the following: (a) upstream and to the same side as the target; (b) upstream and to the opposite side (away) of the target; (c) downstream and to the same side as the target; and (d) downstream and to the opposite side of the target. A Chi-squared test was used to test the null hypothesis that urchins would distribute evenly in each of the four quadrants.

4.3. Results

Juvenile Sheltering Experiment

In all cases, juvenile urchins were found under targets (i.e. adults, models, or rocks) at rates higher than would be predicted by chance alone. Whereas targets accounted for only 6 % of the space available in the aquarium, 21 - 61 % of the juveniles tested were found sheltering in the various treatments. Figure 32 illustrates the differences in the proportion of juvenile urchins sheltering in response to various targets. When presented a choice between adult urchins and rocks, 52 ± 7 % of the juveniles were found to shelter under adults compared to only 8 ± 3 % found under rocks. When given a choice between urchin tests and rocks however, 9 ± 3 % of the juveniles were found under the tests, whereas 13 ± 4 % were found under the rocks. Finally, when offered a choice between adult urchins and urchin tests, 27 ± 8 % of the juveniles were found under the adults and 27 ± 4 % were found under the urchin tests, which is comparable to the adult-rock choices.

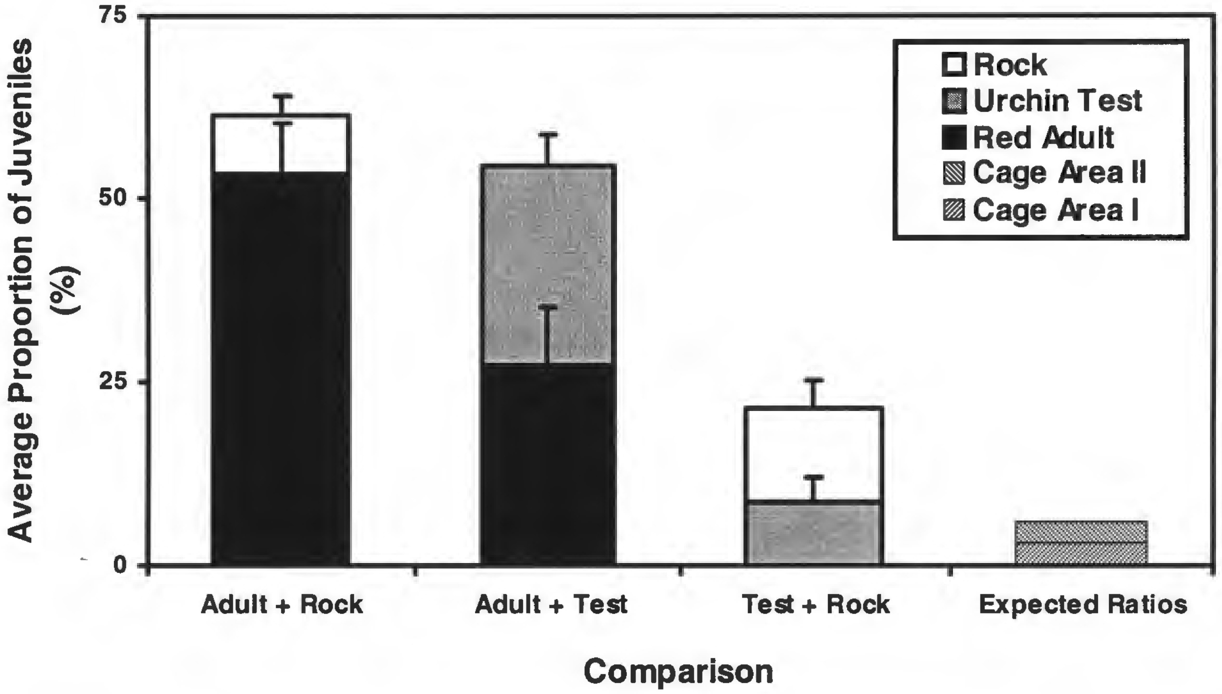

Figure 32. Proportion of juvenile urchins sheltering in different habitats after twelve hours. Black bars represent adult urchins, open bars represent rocks, grey bars represent model urchins, and hatched bars represent the proportion of area covered by targets (see "Expected ratios" for explanation below). Remaining juveniles were found in other habitats (i.e. on glass/wood/open floor). Bars represent 15 replicates (12 for test + rock) consisting of five juveniles per replicate. The "Expected Ratios" bar represents the expected juvenile distribution in each type of habitat as calculated by surface area. The two hypothetical "targets", or cage areas, cover equivalent surface area as two urchins, rocks, or model urchins.

The proportion of sheltering juveniles varied significantly between treatments ($F_{(2, 35)} = 10.293$, $p = 0.001$). Planned comparisons (Bonferroni test) indicated that significantly fewer juveniles sheltered in the urchin tests vs. rock treatment compared with both the adult versus rock ($p < 0.001$) and adult urchins vs. urchin tests ($p = 0.020$) treatments. The analysis also showed that the adult urchins vs. rock and adult urchins vs. urchin tests treatments were not significantly different ($p > 0.999$).

Y-Maze Experiment

A number of general patterns were evident in the Y-maze experiments. Juvenile urchins showed no directional bias in the control treatment (Figure 33) as 14, 24, 29, and 33 % of the juveniles were found in each of the four quadrants. In all treatments with the exception of the kelp treatment, at least one juvenile urchin was found in each of the four quadrants. When kelp was presented as a target, 78 % of the juveniles moved upstream and to the arm containing kelp and no juveniles were found in the quadrant downstream and away from the arm containing kelp. Juveniles were split between the other two quadrants (9 and 13 %). When an adult urchin was placed downstream of a predator, 56 % of the juveniles moved towards the target arm (i.e. the adult) while the remaining juveniles were found distributed evenly among the other three quadrants (e.g. 11, 15, and 19 % each). This was the strongest response of juvenile urchins towards adults of all comparisons using adult urchins.

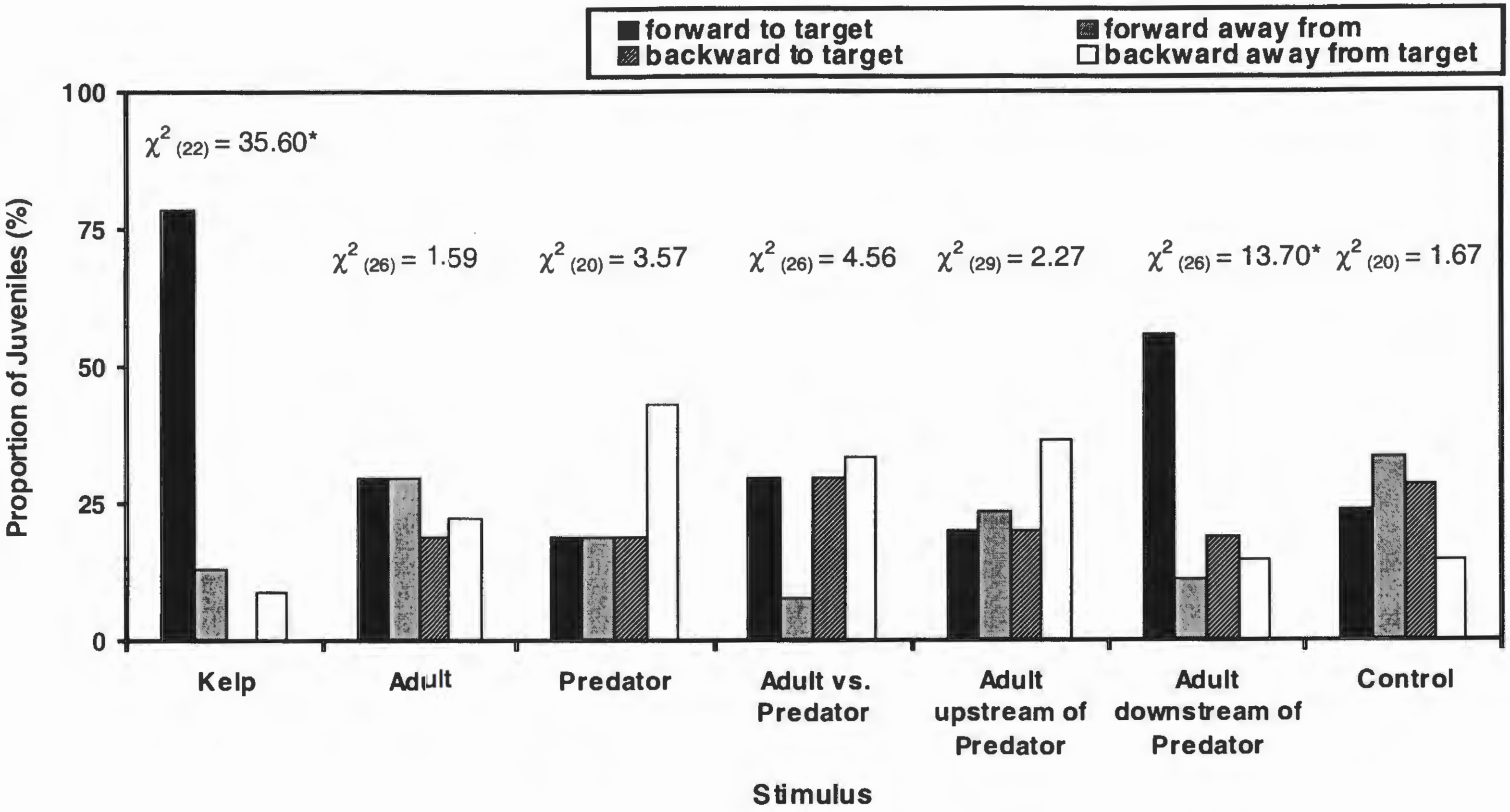

Figure 33. Distribution of juveniles in the Y-maze in response to different chemical stimuli. Black bars represent juveniles moving upstream and to the side towards the target stimulus (e.g. the adult in the adult vs. predator treatment), open bars represent juveniles moving upstream and to the opposite side of the target (e.g. the predator in the adult vs. predator treatment), hatched bars represent juveniles moving downstream and towards the side with the target, and grey bars represent juveniles moving downstream and to the opposite side of the target. Asterisk indicates a significant chi-square statistic (i.e. $p < 0.05$).

For all other treatments, a lower proportion of juveniles (19 to 30 %) showed an orientation towards the target arm. In particular, relatively few juveniles moved towards the arm containing predators in the (a) predator vs. adult; (b) predator; and (c) adult upstream of predator treatments (e.g. 30, 19, and 20 % respectively). In these treatments, juveniles tended towards the quadrant downstream and away from the predator (e.g. 33, 43, and 37 %), although these differences were not found to be significant. In all three treatments, juveniles distributed relatively evenly between the remaining two quadrants (e.g. 7, 30; 19, 19; and 20, 23 %; Figure 33).

Juvenile red urchins exposed to kelp moved significantly ($\chi^2 = 35.61$, $p < 0.001$) towards kelp (Figure 33). Conversely, when an adult urchin was used as a target, juveniles showed no directional movement ($\chi^2 = 1.59$, $p = 0.662$). A non-significant bias away from the predator was observed in the predator, ($\chi^2 = 3.57$, $p = 0.312$) and adult vs. predator ($\chi^2 = 4.56$, $p = 0.207$) treatment. As mentioned above however, juveniles were attracted towards the arm with an adult downstream of a predator ($\chi^2 = 13.74$, $p = 0.003$), but not when adults were upstream of the predator ($\chi^2 = 2.27$, $p = 0.943$). Juveniles in the control treatment, (rock vs. rock) did not display a predictable pattern of movement ($\chi^2 = 1.67$, $p = 0.644$). The results of the Y-maze experiment are presented in Table 12.

Adults did not respond to juveniles in any manner. Although there were similarities in the response of adult and juvenile urchins towards kelp (Figure 32), other responses of adults were different than those of juveniles. In the adult urchin downstream of a predator treatment, test adults primarily (71 %) moved upstream and away from the arm containing the targets (Figure 34). In contrast to juvenile urchins, adults showed an aversion from the arm containing adults downstream of predators ($\chi^2 = 17.43$, $p < 0.001$). The results of the Y-maze experiment are presented in Table 12.

Table 12. Summary of Chi-square analysis for Y-maze experiment. Bold indicates significant differences.

Test organism	Water Velocity (cm/sec)	Treatment	N	χ^2	P
Juvenile Urchins	3.3	Kelp	23†	35.61	< **0.001**
	3.3	Adult	27	1.59	0.662
	3.3	Predator	21	3.57	0.312
	3.3	Adult vs. Predator	27	4.56	0.207
	3.3	Predator upstream of Adult	27	13.74	**0.003**
	3.3	Adult upstream of Predator	30	2.27	0.943
	3.3	Control	21	1.67	0.644
Adult Urchins	3.3	Predator upstream of Adult	14	17.43	**0.001**
	2.1	Kelp	24	39.00	< **0.001**
	2.1	Predator	23	11.00	**0.012**
	2.1	Juvenile	20	1.20	0.753
	2.1	Control	15	1.80	0.615

† - indicates one juvenile escaped Y-maze and thus not included in analysis

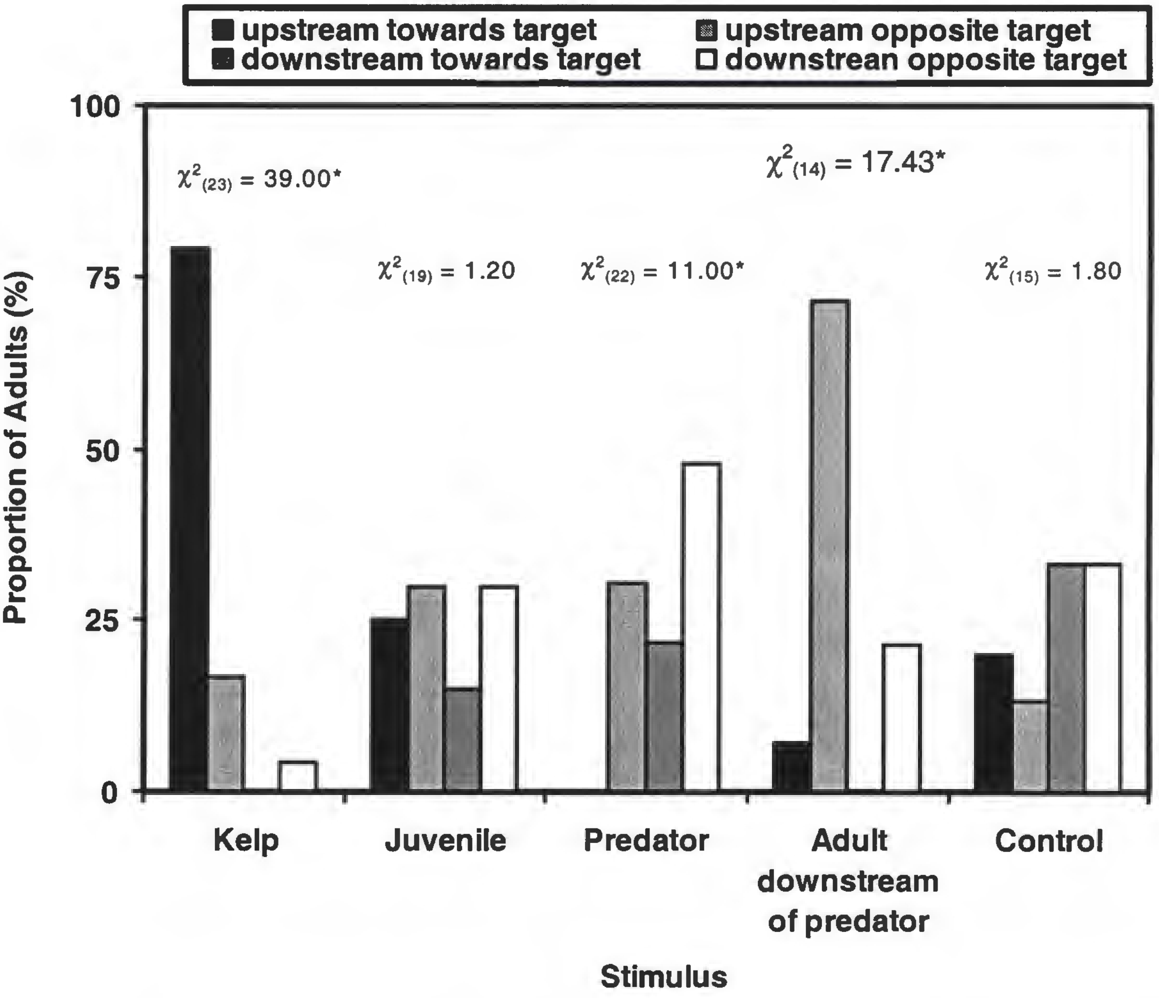

Figure 34. Distribution of adult urchins in the Y-maze in response to different chemical stimuli. Black bars represent adults moving upstream and to the side of the target stimulus, clear bars represent adults moving upstream and to the opposite side of the target, dotted bars represent adults moving downstream and towards the side with the target, and grey bars represent adults moving downstream and to the opposite side of the target. Asterisk indictes a significant chi-square statistic (i.e. $p < 0.05$).

4.4. Discussion

It is evident that water-borne chemical communication facilitates the association between juvenile and adult urchins when adult urchins are downstream of predators (Figures 35 and 36). It is interesting to note that water-borne chemical communication may be only one type of cue that juveniles use to locate refuge habitats in that juveniles sheltered under urchin tests in the presence of adults indicating that there may be an interaction between tactile and chemical cues. Furthermore, the possibility of visual cues cannot be discounted. While it is well known that echinoderms react to light (Hyman, 1955), it has been assumed that they are not capable of the type of image formation that the compound eye produces. Recently however, it has been shown that ophiuroids (brittlestars) employ lens-like calcite crystals to aid in photoreception, possibly with the ability to form images (Alzenberg et al., 2001). If this ability exists in juvenile urchins, it would be a potential method of location.

These results confirm the existence of a chemical cue emanating from threatened adults (i.e. stress signal). Juvenile urchins were attracted to adults only when adults were downstream of water containing chemical signals from *P. helianthoides*. While there are reports of defensive strategies triggered by chemical signals emanating from damaged (Rosenberg and Selander, 2000), or physically disturbed (Nevitt et al., 2000) conspecifics there are no experimentally confirmed reports of an indirectly stimulated stress signal. The only account of a secondary chemical cue is from observations involving two individuals of the threaded abalone *Haliotis assimilis* (Montgomery, 1966).

Traditionally, investigations of chemical communication have tested a single chemical cue. In many instances, repellant chemical cues are used to avoid potential dangers, (Rosenberg and Selander, 2000) whereas attractant chemical cues are often used to form aggregations with conspecifics (Côté and Jelnikar, 1999; Nevitt et al., 2000). Juvenile sheltering behaviour however, appears to be a more complex balance between increased protection (i.e. lower predation and water flow) and decreased foraging opportunity due to competition with adults (Chapter III). Therefore, juvenile urchins would benefit most by being able to discriminate between periods of danger, when sheltering is favored and periods of relative safety, when foraging would be favored. Balancing these factors requires that juveniles sense cues indicating when conditions are dangerous (i.e. predation or high water flow) simultaneously with cues to locate adult urchins to shelter under. A more parsimonious strategy however, would allow juveniles to sense whether adult urchins are safe or in danger. This would mean that juveniles could use a single cue to (a) sense danger; and (b) find a safe refuge.

As Harris and Foster (1995) indicate, single stimulus studies are often not sufficient to explain patterns of behaviour. For example, it has been shown that crayfish react more strongly when two chemical cues (an alarm cue and a predator cue) are presented together rather than each individually (Hazlett, 1999). Juvenile sheltering behaviour in sea urchins however, does not appear to be a result of a synergism between two chemical cues, but rather the sequential release of chemical cues by predator and adult. Juveniles did not respond when adults and predators were placed in separate arms or when adults were placed upstream of the predator. It was only when adults were downstream of a predator that juveniles displayed consistent directionality in their movement and in this case always towards adults.

Results from the Y-maze experiment indicate that adults do not respond to chemical cues from stressed adults in a similar manner. Rather, adults displayed a fleeing response whenever predator cues were present and never more towards predators. This suggests that juvenile behaviour is not simply a form of aggregation behaviour displayed by all urchins regardless of size or age.

For adult urchins, releasing chemical signals as a warning for unrelated juveniles should not be favored. However, using chemical cues from an adult to detect potential dangers should benefit slow-moving juvenile urchins (kairomone). Whereas it is possible that adult urchins are producing an alarm signal for juveniles, it is more likely that juvenile urchins have developed an ability to detect some metabolic byproduct from stressed adults. The chemical constituency of such a signal is an interesting question that remains unanswered.

The results of the Y-maze experiment indicate that adult urchins respond to water-borne cues (i.e. kelp, predators) more strongly than juveniles. Grasso et al. (1996) indicate that wider spacing between chemical sensors (i.e. antennae in lobsters) should be favored when orienting with respect to turbulent odor plumes. Sea urchins lack specialized sensory structures, with epidermal sensory cells spread over the entire body (Ruppert and Barnes, 1994). Sensory cells therefore, may be spread over the total diameter of an adult urchin, (test + spines) which may reach up to 340 mm (Bureau, 2000). Thus, it would be advantageous for the much smaller juveniles to "follow the lead" of adult urchins who may be able to sense danger more readily than the juveniles.

It has also been shown that interspecific chemical cues exist for both fish (Smith, 1982; Mathis and Smith, 1993) and kelp (Maier and Muller, 1986; Maier et al., 2001). With many invertebrates sheltering under the spines of adult urchins (Rogers-Bennett, 2001) it would be interesting to investigate whether this stress cue is recognized by other species.

4.5. Conclusion

These results suggest that secondary chemical cues are of importance in benthic marine ecosystems. Further study and re-evaluation of existing data are therefore warranted. In the case of juvenile red urchins, secondary chemical cues provide a mechanism whereby juvenile urchins can identify danger and locate the safety of the spine canopy. Both of these events are significant to the early life history of marine benthic invertebrates. In the case of juvenile *S. franciscanus*, secondary chemical cues provide a mechanism whereby juvenile urchins can identify danger and locate the safety of the spine canopy. Both of these events are significant to the early life-history of benthic marine invertebrates.

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Chapter V. The influence of adult sheltering on the abundance of juvenile red sea urchins (*Strongylocentrotus franciscanus*): A field study.

Abstract

The recruitment of juvenile red sea urchins (*Strongylocentrotus franciscanus*) is a variable process both spatially and temporally. Field surveys have found juvenile *S. franciscanus* primarily under the spines of adults, and three mechanisms for this adult-juvenile association have been suggested: (1) protection from predators; (2) protection from fluctuations in water velocity and; (3) access to food (i.e. macroalgae). The primary objective of this chapter is to determine whether, and to what extent adult sheltering affects the recruitment of juvenile *S. franciscanus* in the environment. This was achieved with the use of an underwater vacuum device that successfully sampled newly settled individuals (< 4 mm diameter). The abundance of juveniles was found to be influenced most strongly by the presence of adult *S. franciscanus* and increased water motion using principal components analysis (PCA) and multiple regression methods. Significantly higher juvenile frequencies were found at sites with adult *S. franciscanus* relative to those without ($\chi^2_1 = 39.39$ using Yate's correction for continuity, $p < 0.001$). Although these factors should be described in a more rigorous manner over larger spatial and temporal scales in the future, it is evident that there is a strong juvenile-adult association in *S. franciscanus*.

Strongylocentrotus | juvenile | sheltering | spine canopy| refuge |

5.1. Introduction

Recruitment rates for *S. franciscanus* are variable both spatially and temporally with juveniles (≤ 50 mm) comprising 0.8 to 24.0 percent of the population (Sloan et al., 1987) in British Columbia. Though the source of such variation remains largely unknown (Campbell and Harbo, 1991; Gosselin, 1997), three processes have been proposed to influence recruitment in sea urchins: (a) larval supply; (b) larval settlement; and (c) post-settlement mortality (Cameron and Schroeter, 1980). Larval supply represents the availability of larvae competent to settle in an area, while settlement is the conversion of free-swimming larvae into benthic juveniles, after which post settlement mortality or migration occurs (Harrold et al., 1991). For example, regions in Oregon with predictable upwellings are characterized by offshore advection and thus experience low recruitment (Ebert and Russell, 1988). However, in California upwelling events bring cold, nutrient-rich water which increases both productivity and recruitment (Ebert, 1983). It has been suggested that minor upwelling (typical of California) enhances recruitment by delivering nutrients, whereas more intense upwelling inhibits recruitment by advecting larvae away from shore (Ebert and Russell, 1988). Although juvenile density has been found to be higher in urchin barrens compared to kelp beds (Pearse et al., 1970; Tegner and Dayton 1981), larval settlement in both habitats was comparable (Rowley, 1989). Recently, Harris and Chester (1996) reported that recruitment of green sea urchins (*S. droebachiensis*) was not associated with larval supply. Results from both laboratory experiments and field sampling indicate that larvae settled preferentially in response to corraline algae, but did not respond to any adult-associated cues (Cameron and Schroeter, 1980; Rowley, 1989; Harrold et al., 1991). As Rowley (1989) concluded, neither larval supply nor larval settlement processes adequately predict the observed spatial distribution of juvenile urchins and the most likely explanation lies in post-settlement processes (e.g. mortality, migration).

Many mobile benthic marine organisms aggregate and potentially benefit from the presence of conspecifics (Shepherd, 1986; Stone et al., 1993; Rogers-Bennett 1989; Erlandsson et al., 1999; Childress and Herrnkind, 2001). Furthermore, ontogenetic changes in aggregating behaviour are common as: (1) vulnerable juvenile stages aggregate with conspecifics for protection; (2) individuals move apart as they attain some size refuge from mortality (i.e. predation) and; (3) aggregation occurs again as adults for reproductive purposes (Butler et al., 1999). Aggregation occurs in many species of sea urchin independent of an individual's size (Andrew and Choat, 1982; Himmleman, 1986), but in the red sea urchin (*Strongylocentrotus franciscanus*) small juveniles have been found aggregated primarily under much larger adult conspecifics (Ebert, 1968; Low, 1975; Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987; Morgan et al., 2000). There have been three benefits suggested to explain why juveniles shelter under adults: (1) protection from predation; (2) protection from fluid dynamic forces and; (3) access to macroalgae (Low, 1975; Pace, 1975; Tegner and Dayton, 1977; Duggins, 1981; Lissner, 1983; Breen et al., 1985; Kawamata, 1998'; Nishizaki and Ackerman, 2002).

Whereas the existence of juvenile-adult associations has been documented, there is little data pertaining to the potential role of environmental variables. This chapter therefore, addresses the ecological factors that are associated with *S. franciscanus* in the field. Specifically, results are presented from a field survey that assessed the degree to which juvenile *S. franciscanus* abundance is related to the presence of adults along a gradient of physical and biological variables

5.2. Materials and Methods

A field study was conducted in Barkley Sound, near Bamfield, British Columbia, between January and March 2001. Three islands, of differing levels of wave exposure were examined including: (a) a sheltered island (Dixon Island; 48 49.551°N; 125 11.819°W); (b) a moderately exposed island (Ohiat Island; 48 51.328°N; 125 11.000°W); and (c) an exposed island (Taylor Island; 48 49.647°N; 125 11.839°W; Figure 35). At each island, SCUBA divers set three parallel transect lines along the depth gradient between 10 m and 15 m apart. A 1 m^2 quadrat was placed at each of three depths (1.0 m, 3.0 m, and 4.7 m below chart datum; see below) adjacent to each transect line providing three replicates at each of three depths for the three locations (27 quadrats total). Depth was recorded as distance below chart datum, where the chart datum was Mean Lower Low Water as measured by the Canadian Hydrographic Service (Bamfield Harmonic Station at 48 50°N; 125 8°W). The substrate within each quadrat was classified using a numerical classification based on the Canadian Fisheries and Oceans scheme (D. Brouwer – Pacific Biological Station, personal comment): 1 - bedrock; 2 - boulder (material > 10 cm diameter); 3 - cobble (material > 4 cm); 4 - gravel (material < 4 cm); 5 - pea gravel (sand and gravel); 6 - sand; 7 - shell hash; and 8 - mud. An ecological survey of the quadrats was undertaken using the following species/functional categories: (1) Invertebrates – adult and juvenile *S. franciscanus*, adult and juvenile *S. purpuratus*, adult and juvenile *S. droebachiensis*, abalone, gastropods, mussels, clams, crabs, starfish, nudibranchs, sea cucumbers, polychaetes, brittlestars, limpets, chitons, annelids, anemones, scallops, and fish; and (2) Algae - red algae, green algae, brown algae, and corraline red algae. All adult *S. franciscanus* were measured by divers who also searched the substrate carefully for juvenile *S. franciscanus*. Following the survey, a specially designed airlift (see Coyer, 1999; Heine, 1999, 2000; Joiner, 2001) equipped with a 335 µm mesh Nitex holding bag was used to vacuum the surface of the quadrat (Figure 36). A 33 cm long brush (Justman Brush Co., Omaha, NE) was used to gently dislodge material from the bottom of the quadrat. All material trapped within the bag was transported to the laboratory for identification.

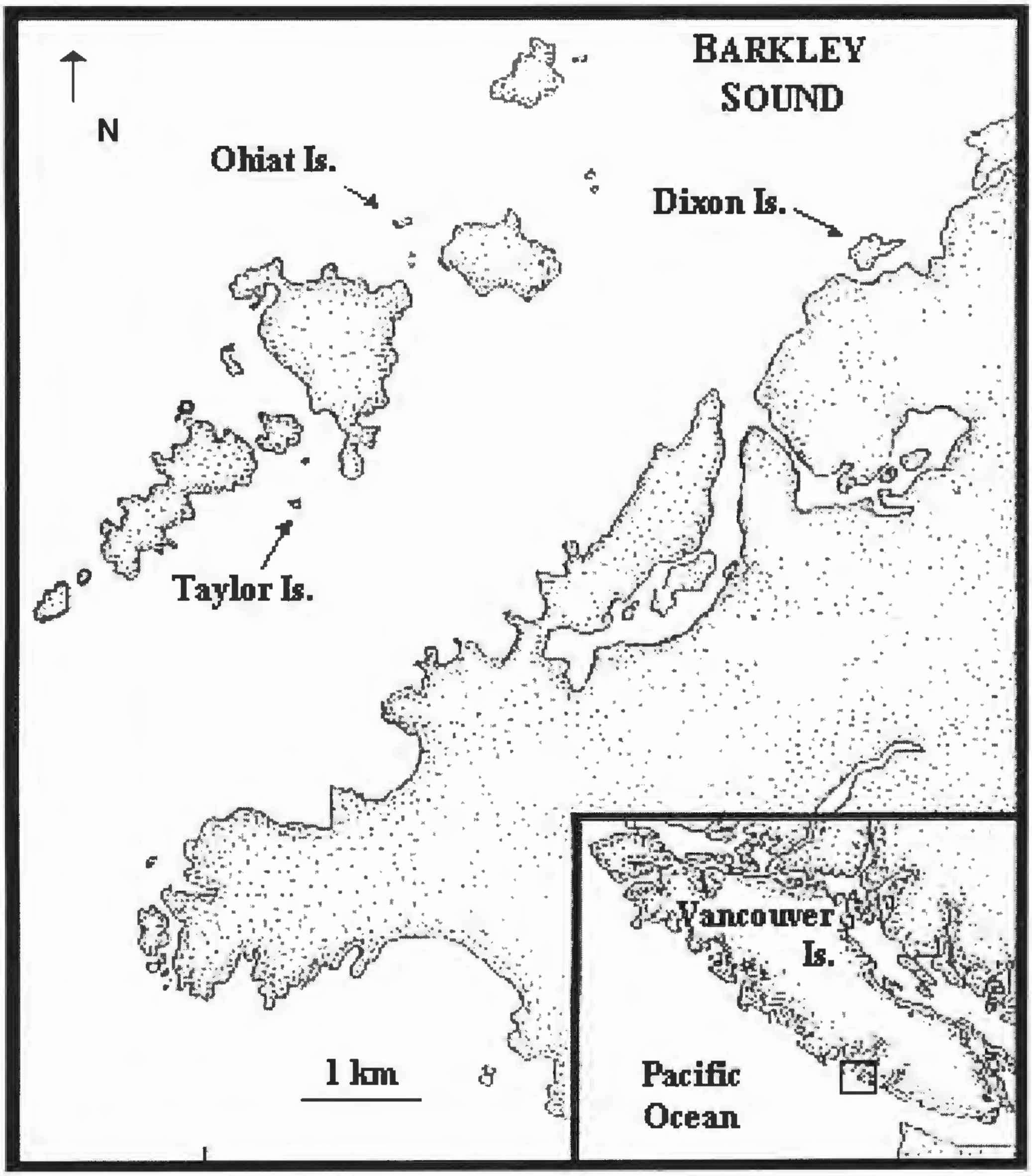

Figure 35. Map of research sites in Barkley Sound, British Columbia, Canada

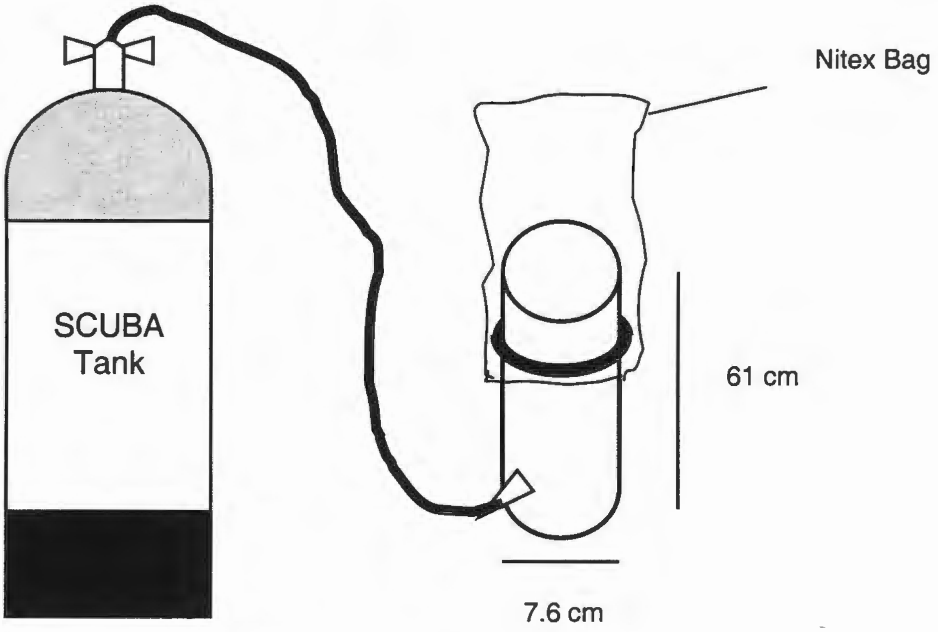

Figure 36. Schematic of the airlift device used to vacuum the seafloor for juvenile sea urchins (not to scale). SCUBA air tank was connected to a 7.62 cm diameter PVC pipe with a Nitex bag (335 µm mesh-size) fastened.

The degree of exposure was measured at each depth at each site using the dissolution rate of plaster of Paris cubes. The cubes were poured into a 3 cm x 3 cm x 4 cm mould using one part plaster and two parts cold water that was allowed to dry for 24 hours. Cubes were calibrated in a flow chamber (Figure 14) using an both an Acoustic Doppler Velicometer (ADV) and by timing the downstream transport of dye. Cubes were suspended 5 cm above the bottom of the chamber and the amount of mass lost over a 24 hour period was recorded. Linear regression analysis was used to determine the relationship between water velocity and the dissolution rate of the cubes ($y = (2.014 \pm 0.513)x + (15.686 \pm 4.319)$, N =

33, $r^2 = 0.32$, $p < 0.001$). A field tripod unit made out of steel rebar was deployed at each depth within a site for at least 24 hours (Figure 37). One cube was fixed at 5 cm and the other was fixed at 20 cm above bottom of each leg of the tripod. This technique is designed to integrate the energy in the water column directly above and near the seafloor (e.g. 5 cm and 20 cm respectively). A simultaneous deployment was also undertaken to determine among-site variation at one depth (1.0 m below chart datum) for 24 hours.

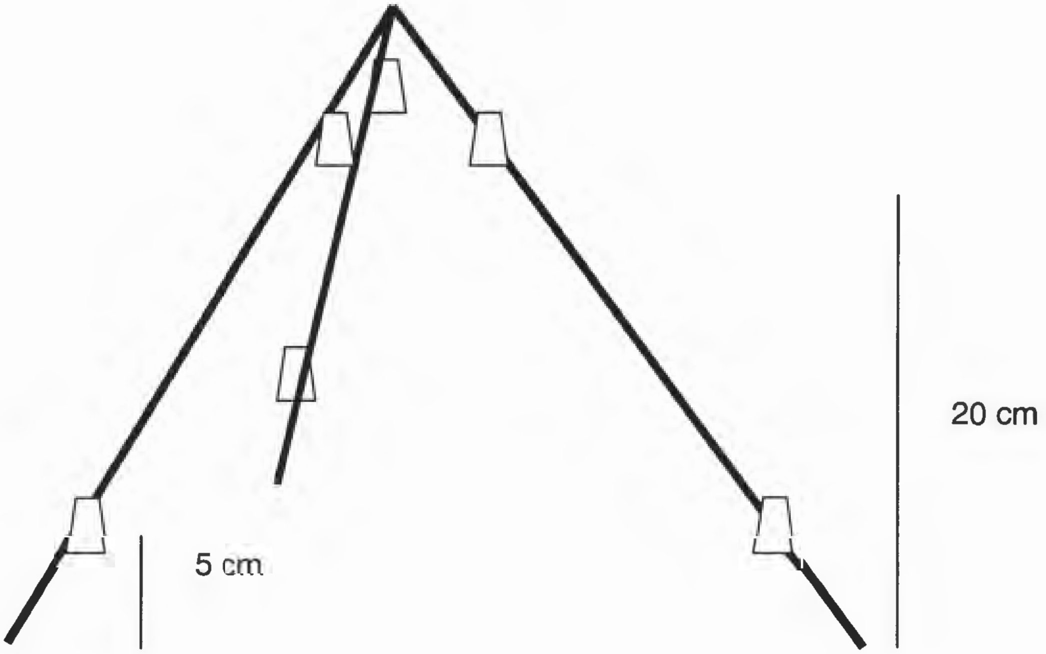

Figure 37. Schematic of tripod unit with plaster cubes (3 x 3 x 4 cm) at 5 cm and 20 cm above the bottom. Each leg of the tripod is 70 cm long.

Statistical Analysis

Data that were normally distributed or could be normalized by standard techniques, were analyzed using ANOVA, followed by a Bonferonni test for multiple comparisons (Underwood, 1981). If data could not be normalized, the Kruskal-Wallis non-parametric ANOVA as used (significance level of $p = 0.05$ used).

The abundance of twenty animal and four algal groups were collected for each quadrat. In addition, substrate type, depth, water motion (at 5 cm and 20 cm above substratum), and site location were measured. Three quadrats (one each at 1.0, 3.0, and 4.7 m depth for Ohiat Island) were missing measurements of water motion, so replacement values based on average values from the same depth within the same site were used. These measured variables were then reduced to six nontrivial dimensions using principal components analysis (PCA) and applying the broken-stick criterion to determine the relative interpretive value of each component (Frontier, 1976; Jackson, 1993). The final principal components were rotated using the Varimax method to interpret component loadings.

Juvenile *S. franciscanus* abundance was compared against each of the six principal components mentioned above using six separate simple linear regressions. A multiple linear regression was employed to examine the relationship between juvenile abundance and a combination of habitat-related variables. All six principal components were entered into a stepwise linear regression to identify the most parsimonious model predicting juvenile abundance.

Spatial associations between juvenile and adult *S. franciscanus* were also assessed with a two-way contingency table using presence-absence data for both juvenile and adult *S. franciscanus*. Data were adjusted using the Yate's correction for continuity (Zar, 1999). All statistical analysis was conducted using SPSS 10.0.5 for Windows$^{©}$ software (SPSS Inc., Chicago, IL).

5.3. Results

The substrate conditions varied among sites with the exposed site being composed primarily of bedrock versus a combination of bedrock, boulders, and cobble at the sheltered and moderately exposed sites (Figure 38). The average substrate index for the sheltered and moderately exposed sites was 2.7 ± 0.5 and 2.7 ± 0.4, respectively. In contrast, the average substrate index at the exposed site was 1.2 ± 0.1. Similar assessments of substrate type were made at the shallow, mid, and deep depths (2.2 ± 0.6, 2.2 ± 0.4, and 2.3 ± 0.4 respectively). Differences among sites were significant ($F_{(2,24)} = 5.34$, $p = 0.012$) and Bonferroni multiple comparisons revealed two pairwise differences between the exposed site versus the sheltered and moderately exposed sites ($p = 0.028$ in each comparison). No statistical differences were found when substrate type was considered across depths ($F_{(2,24)} = 0.02$, $p = 0.981$; Figure 39).

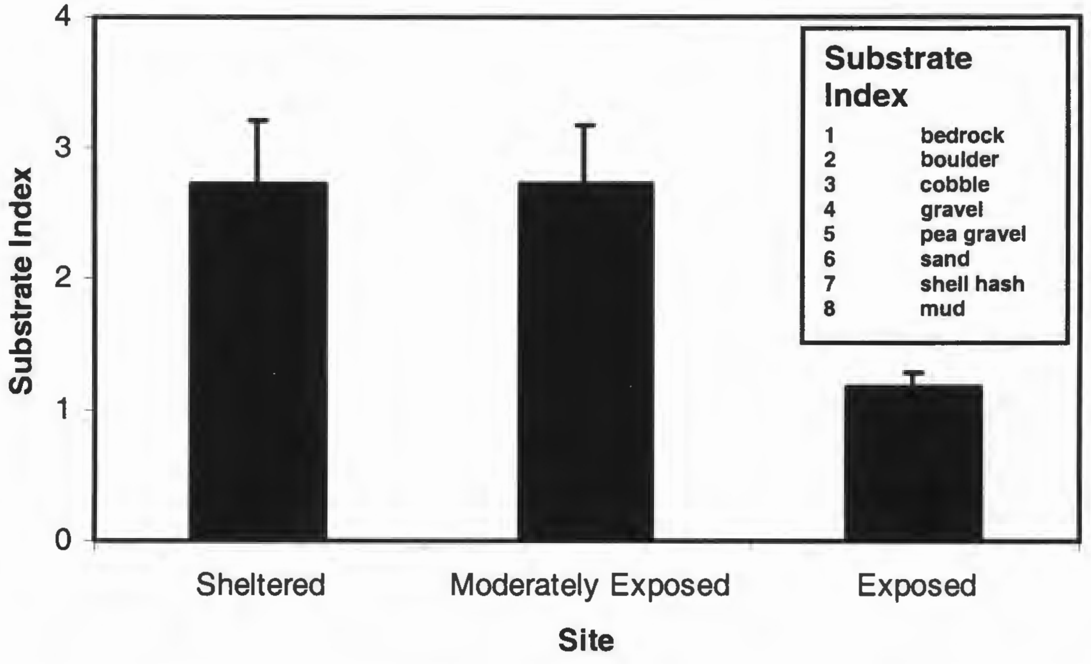

Figure 38. Substrate conditions at sheltered (Dixon Island), moderately exposed (Ohiat Island), and exposed site (Taylor Island). The substrate index, which is defined in the text, ranges from bedrock (1) through mud (8). Bars represent the mean ± 1 SE for three replicate samples at each of three sites. Note there was no variation in the index at the Exposed site.

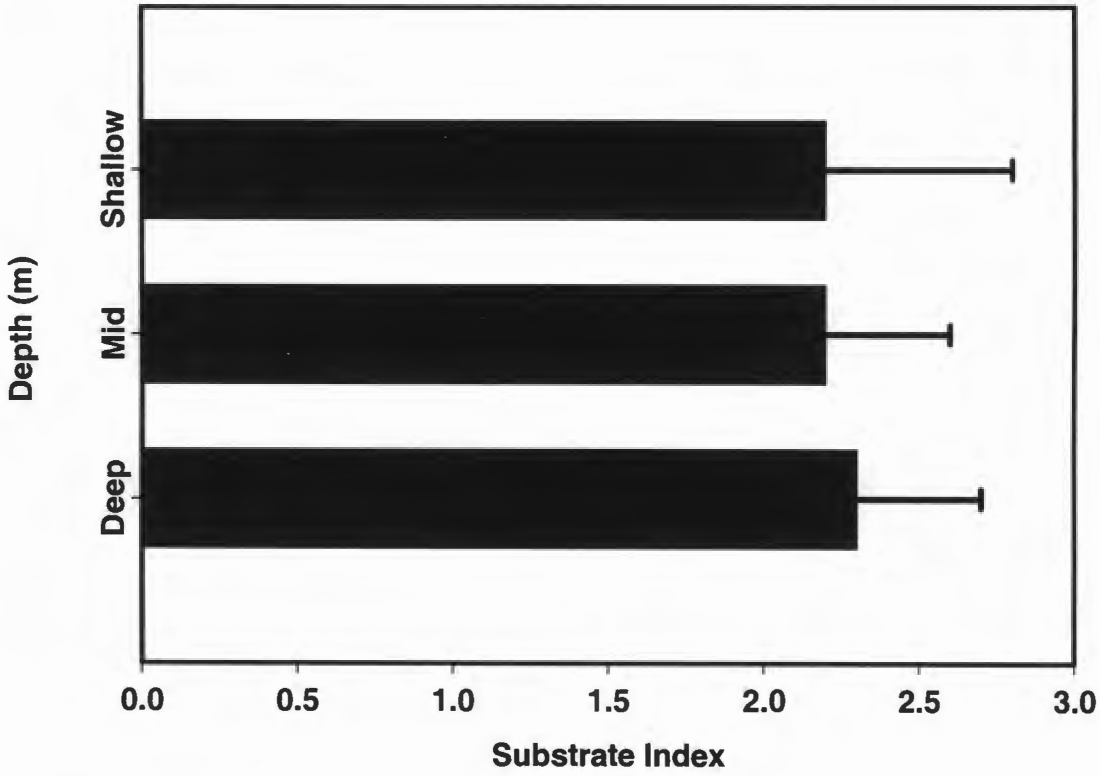

Figure 39. Substrate conditions at shallow depths (0.98 ± 0.23 m), mid depths (3.05 ± 0.14 m depth), and deep depths (4.69 ± 0.21 m). The substrate index, which is defined in the text, ranges from bedrock (1) through mud (9). Bars represent the mean ± 1 SE for three replicate samples at each depth.

Two velocities were determined (or estimated) from the measured dissolution rates of the plaster cubes for each site, at 5 cm and 20 cm above substratum. There was little variation in water velocity among sites (Figure 40): sheltered site 9 ± 3 cm/sec (5 cm height), and 10 ± 3 cm/sec (20 cm height); moderately exposed site 10 ± 2 cm/sec, and 10 ± 3 cm/sec; and exposed site 13 ± 4 cm/sec, and 13 ± 4 cm/sec. Shallow sites appeared to show slightly higher velocities than intermediate and deep depths (Figure 41): shallow site averaged 12 ± 4 cm/sec and 12 ± 4 cm/sec for the 5 cm and 20 cm heights, whereas velocities were lower at both the intermediate depth (11 ± 3 cm/sec, 10 ± 3 cm/sec) and the deep depth (10 ± 3 cm/sec, 10 ± 3 cm/sec).

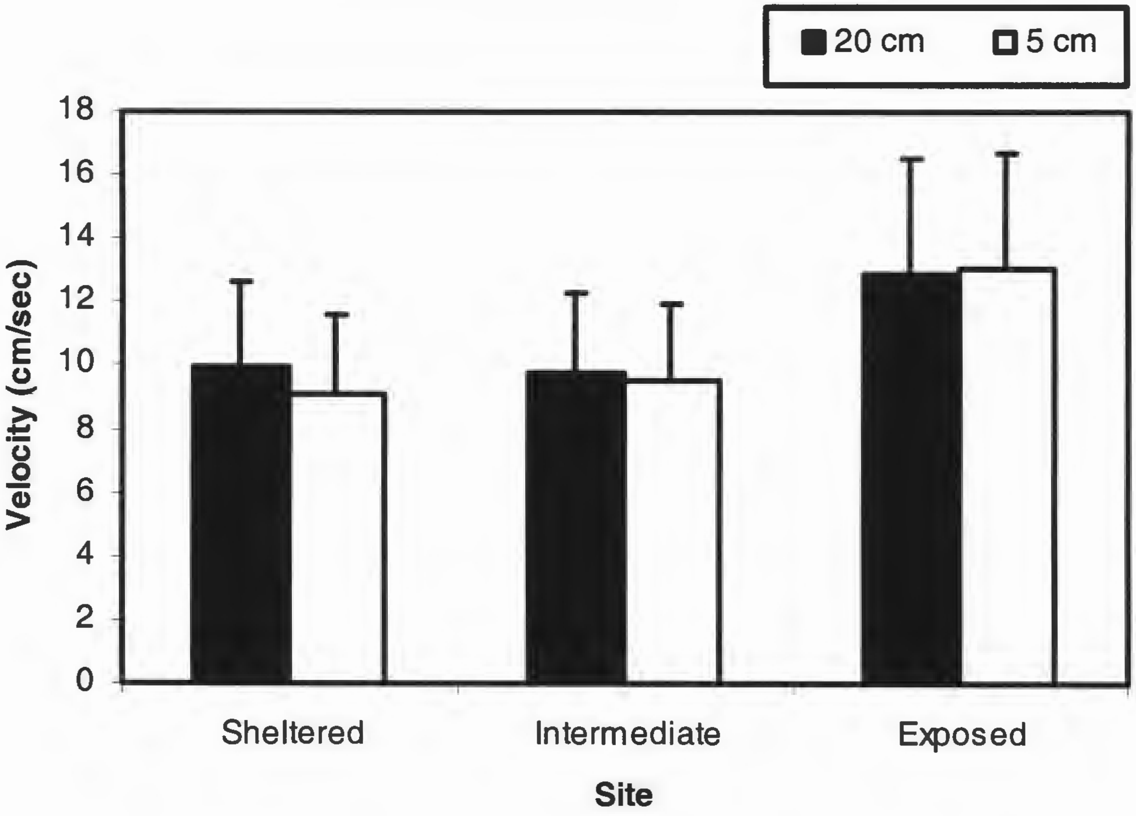

Figure 40. Fluid dynamic conditions as inferred from the dissolution of plaster cubes in sheltered site (Dixon Island), "Moderately Exposed" site (Ohiat Island), and exposed site (Taylor Island). Water velocities are presented for 5 cm (black) and 20 cm (open) above the substratum. Bars represent the mean ± 1 SE for nine replicate samples at both the "Sheltered" and "Exposed" sites and six replicate samples at the "Moderately Exposed" site.

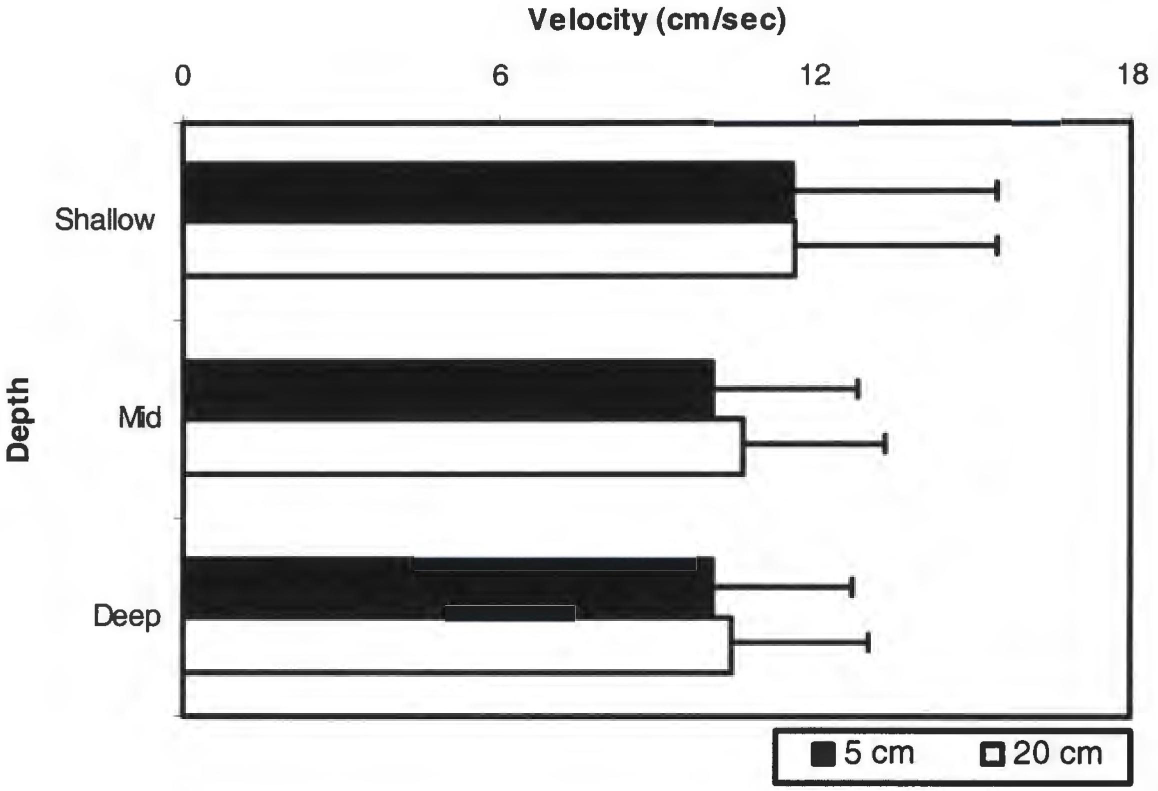

Figure 41. Fluid dynamic conditions as inferred from the dissolution of plaster cubes at shallow depths (0.98 ± 0.23 m), mid depths (3.05 ± 0.14 m), and deep depths (4.69 ± 0.21 m). Water velocities are presented for 5 cm (black) and 20 cm (open) above the substratum. Bars represent the mean ± 1 SE for eight replicate samples at each depth.

After transforming the data (natural logarithm), no significant differences were found in water velocity among depths ($F_{(2, 36)} = 0.860$, $p = 0.860$) or between heights above substratum ($F_{(1, 36)} = 0.787$, $p = 0.381$). There were however, significant differences in water velocities among sites ($F_{(2, 36)} = 19.22$, $p < 0.001$), with the exposed site being significantly higher than the other two sites ($p < 0.001$ in both cases).

The examination of the spatial variation among sites was conducted through the simultaneous deployment of plaster balls at each site (all at shallow depths) revealed similar rates of dissolution (Figure 42; sheltered site 18 ± 7 cm/sec, 18 ± 7 cm/sec and; moderately exposed site 18 ± 7 cm/sec, 18 ± 7 cm/sec; and expose site 17 ± 7 cm/sec, 18 ± 7 cm/sec). Significant differences in water velocity were not detected in relation to site ($p = 0.926$, Kruskal-Wallis) or height above substratum ($p = 0.875$, Kruskal-Wallis).

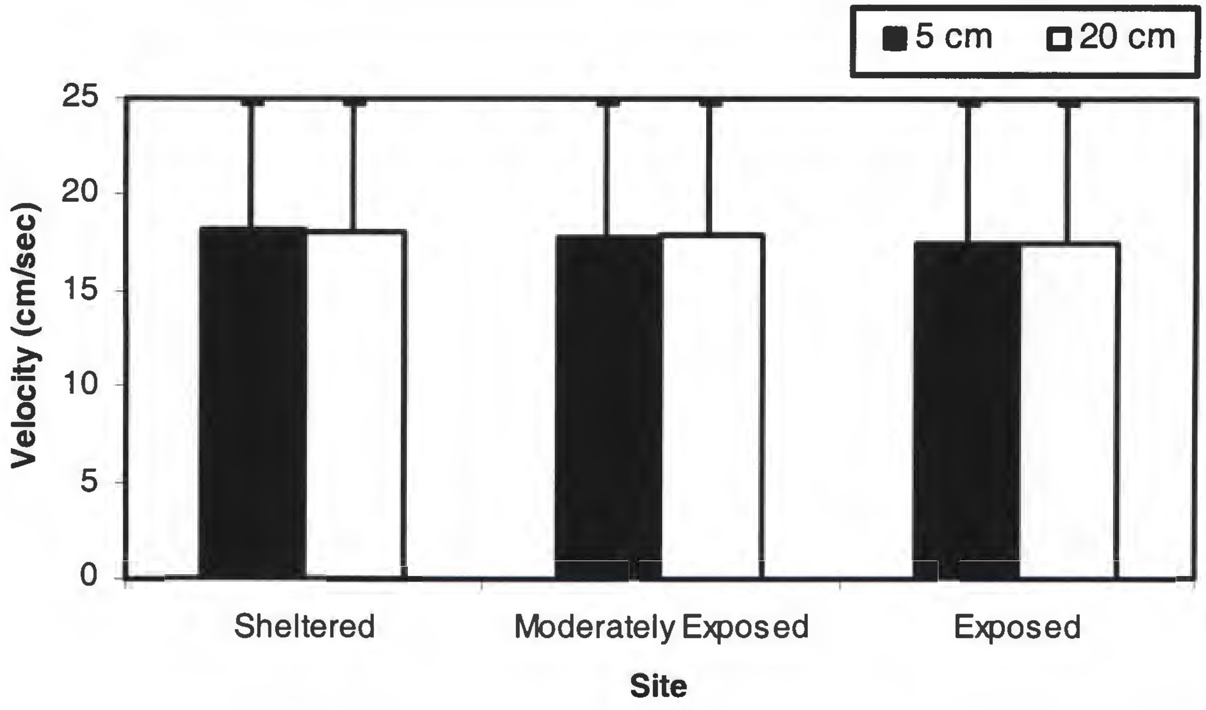

Figure 42. A simultaneous measurement of the water velocity from the dissolution of plaster cubes in sheltered sites (Dixon Island), moderately exposed sites (Ohiat Island), and exposed site (Taylor Island). Black bars represent data from 5 cm above substratum and open bars 20 cm above substratum. Data are mean ± 1 SE for nine replicate samples (each sample an average of three plaster blocks).

The algal community was composed primarily of corraline red algae (often 100 % coverage) with less brown algae (up to 50 % coverage) and no fleshy red or green algae (0 % each) recorded (Figures 43 and 44). Corraline algae varied little as depth increased (67 ± 13 %, 61 ± 16 % and 66 ± 15 % for the shallow, mid, and deep depths, respectively), and significant differences among depths were not detected ($p = 0.941$, Kruskal-Wallis). There was little variation in the abundance of corraline algae between sites (57 ± 14 %, 67 ± 14 % and 69 ± 14 % for sheltered, moderately sheltered, and exposed sites respectively) and significant differences in the abundance of corraline algae were not detected among sites ($p = 0.732$, Kruskal-Wallis). The abundance of brown algae decreased with depth (17 ± 8 %, 1 ± 1 %, and 0 % with no measured variance), although there was no pattern among sites (7 ± 6 %; 4 ± 6 %; and 6 ± 6 % for sheltered, moderately sheltered, and exposed sites respectively). Differences in algal abundance were not significant among depths ($p = 0.058$, Kruskal-Wallis) or sites ($p = 0.582$, Kruskal-Wallis).

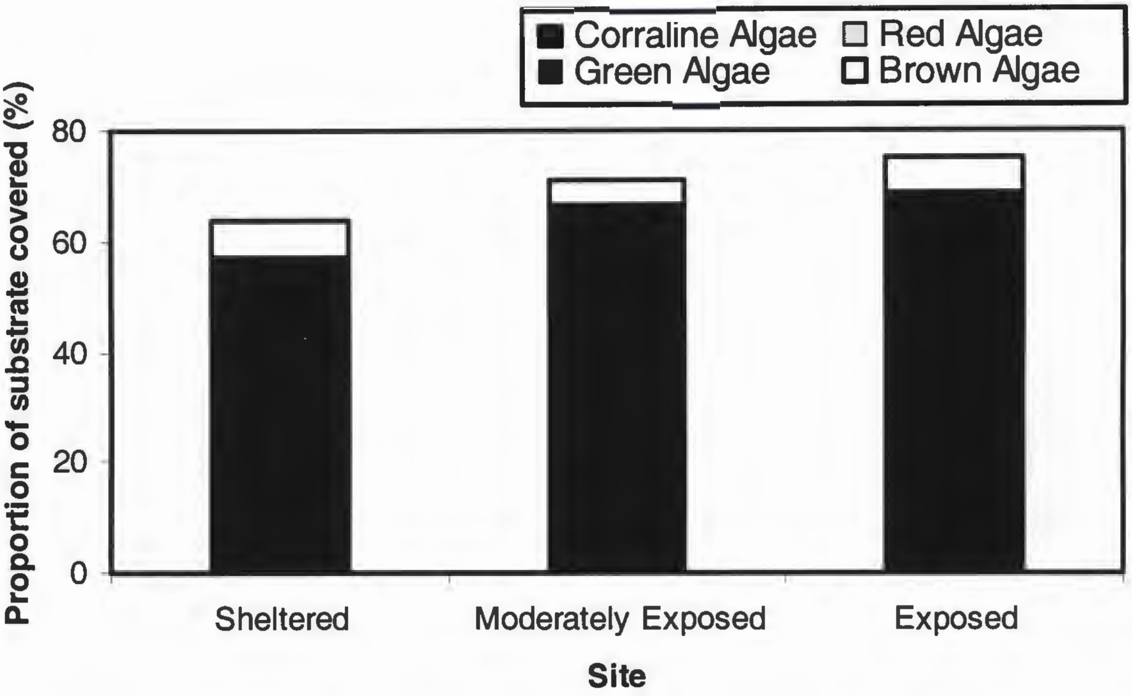

Figure 43. Algal composition in sheltered sites (Dixon Island), moderately exposed sites (Ohiat Island), and exposed site (Taylor Island). Black bars represent corraline algae, dotted bars represent red algae, hatched bars represent green algae, and open bars represent brown algae. Data are mean ± 1 SE for nine replicate samples at each site.

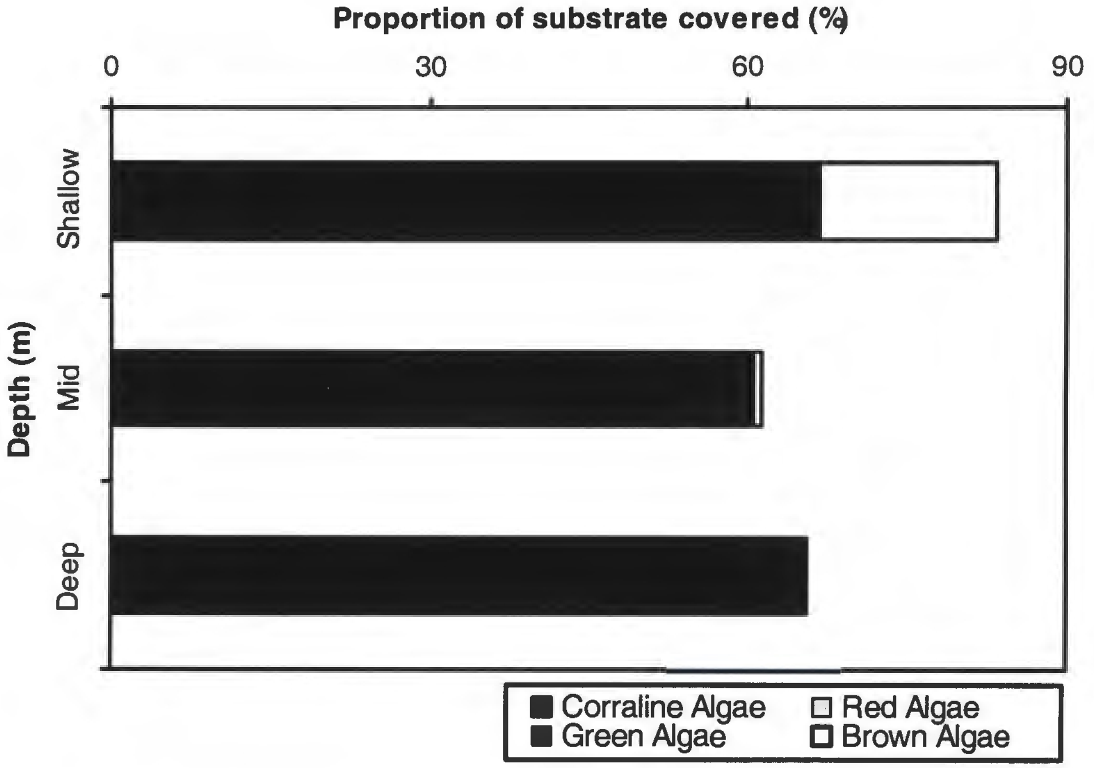

Figure 44. Algal composition at shallow depths (0.98 ± 0.23 m), mid depths (3.05 ± 0.14 m), and deep depths (4.69 ± 0.21 m). Black bars represent corraline algae, dotted bars represent red algae, hatched bars represent green algae, and open bars represent brown algae. Data are mean ± 1 SE for nine replicate samples at each depth.

The diversity of animals at the field sites revealed several patterns of abundance in that some groups remained relatively constant with depth while others varied (Figure 45). For example, the abundance of mobile organisms such as starfish, polychaetes, and fish were similar at each depth, whereas the abundance most other animals (e.g. gastropods, adult *S. franciscanus*, mussels, and brittlestars) decreased with depth. In contrast, the abundance of some species increased with depth (e.g. clams, crabs). Sites for all three depths were dominated by gastropods, which ranged from 2 to 223 individuals per quadrat. Hermit crabs (0 to 17), annelids (0 to 29), and adult *S. franciscanus* (0 to 28) were the other common animals. The distribution of most groups (anemones, brittlestars, polychaetes, gastropods, annelids, and all urchin species) was patchy, with high densities in a low number of quadrats.

S. franciscanus juveniles were found in lower abundance at the 3 and 5 m depths (e.g. 0.0 % and 0.6 %, respectively). It is important to note that juvenile *S. franciscanus* were not found visually by divers even though they were looking for them intensively and had experience observing them in the laboratory. The juveniles were, however, recovered through the vacuum filtration of the bottom via the airlift unit (Figure 36). The number of adult *S. franciscanus* recovered ranged from 0 to 28 individuals per quadrat with an average of 4.8 ± 1.1 individuals per quadrat, while the range for juvenile *S. franciscanus* was from 0 to 10 individuals per quadrat averaging 0.67 ± 0.38 individuals per quadrat. The observed range for juvenile *S. droebachiensis* was 0 to 6 individuals per quadrat with an average of 0.29 ± 0.25 individuals per quadrat (no adults were found) and the number of *S. purpuratus* adults ranged from 0 to 11 individuals per quadrat with an average of 0.46 ± 0.46 individuals per quadrat (no juveniles were found). At least one adult was counted in 25 of the 27 samples (93 %) and juveniles were found in 6 of the 27 samples (22 %). In other words, juveniles were found in 24 % of the samples where adults were present.

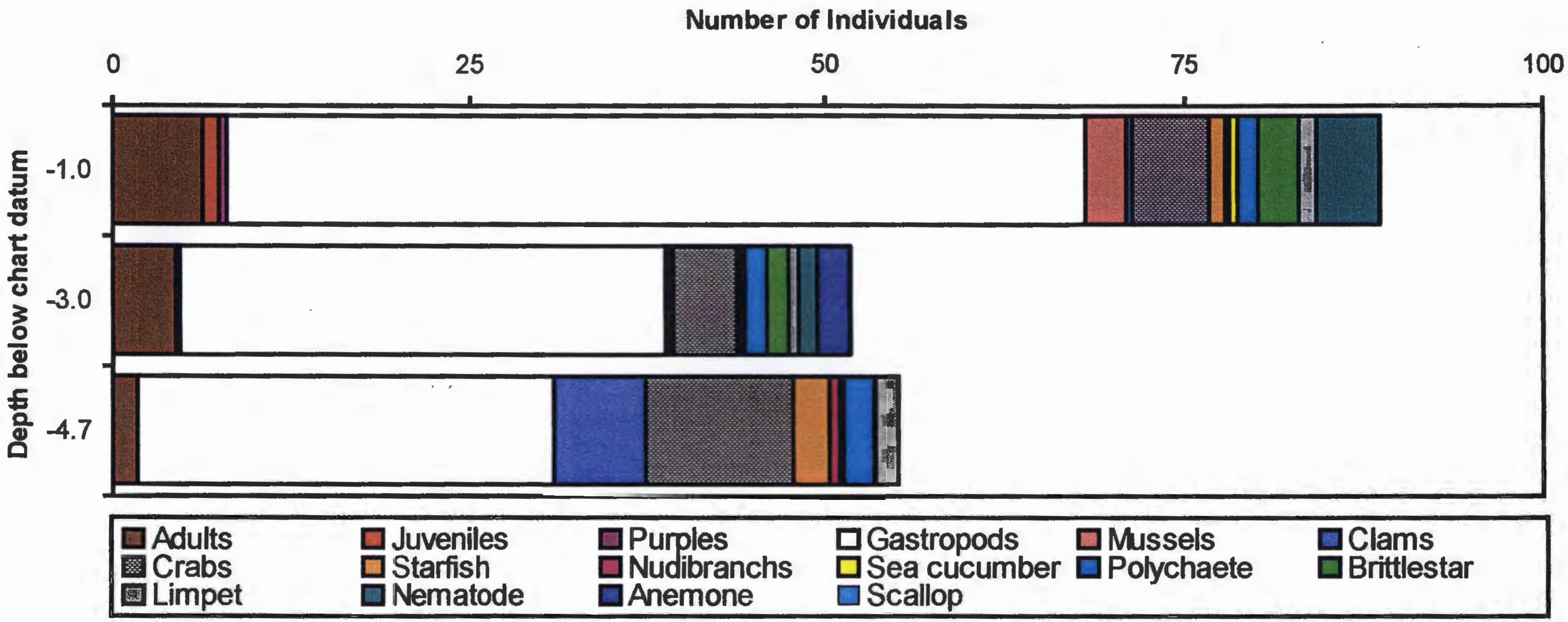

Figure 45. Species composition (animals only) at shallow depths (0.98 ± 0.23 m), mid depths (3.05 ± 0.14 m), and deep depths (4.69 ± 0.21 m). Data are mean ± 1 SE for nine replicate samples at each depth.

The results of the contingency table chi-square analysis presented in Table 13 indicate that no juvenile *S. franciscanus* were found in quadrats lacking adults. While most sites lacked juveniles (21 of 27 quadrats), all six times juveniles were found where adults were also present. There was a significant positive association between the occurrence of juvenile and adult *S. franciscanus* ($\chi^2_1 = 39.39$ using Yate's correction for continuity, $p < 0.001$; Table 13).

Table 13. Two by two contingency table assessing juvenile *S. franciscanus* distributions in relation to adult *S. franciscanus.*

	Adult Urchins	
Juvenile Urchins	Present	Absent
Present	6	0
Absent	19	2
Total	25	2

The twenty-nine measured variables were reduced to six principal components (Table 14). Measured variables with one or fewer observations (six variables) were discarded from the analysis, though their inclusion/exclusion did not alter the conclusions reached from either the PCA or subsequent regression analysis. The first principal component (PCA1) was interpreted to represent *benthic grazers* as gastropods and hermit crabs loaded highly. *Adult urchins* (both *S. franciscanus* and *S. purpuratus*) were most closely related to the PCA2, whereas PCA3 represented a gradient of *water motion* (both 5 cm and 20 cm above the substratum). Brittlestars and annelids loaded highly for PCA4 *detritus feeders* whereas PCA5 represented *sedimentation*. Brown algae were represented by PCA6, which was interpreted as a *food factor*.

Table 14. Principal components from individual counts (N = 27); missing values of energy dissipation are filled with average values at the same depth, within a site.

Component	Eigenvalues	Cumulative Variance (%)	Variables loadings in component	Interpretation
1	4.05	18.40	Gastropod (0.95), Hermit Crab (0.85)	Grazers
2	3.23	33.08	Red Adult (0.88), Purple Adult (0.86)	Adult Urchins
3	2.99	46.68	Dissipation at 20 cm (0.95); Dissipation at 5 cm (0.93)	Water Motion
4	2.26	56.96	Brittlestars (0.93); Annelids (0.88)	Detritus feeders
5	1.64	64.42	Clams (- 0.81)	Sedimentation
6	1.39	70.72	Brown Algae (0.92)	Food

The results of the simple linear regression (see Table 15A.) indicate that PCA2 (adult urchins) was the only component that had a statistically significant relationship with juvenile abundance ($R^2 = 0.80$, $p < 0.001$). PCA3 (water motion) accounted for 5.3 % of the variation in juvenile abundance and PCA4 (food) accounted for 2.0 %. All other principal components accounted for very little variation each (< 1 %). The stepwise multiple regression model predicting juvenile abundance contained only PCA 2 (adult urchins) and PCA 3 (water motion) as independent variables ($R^2 = 0.85$, $p < 0.001$; Table 15B). As the data in Figure 46 illustrates, peak juvenile abundances occurred at the very high end of PCA 2 (adult abundance) and in the mid-low end of PCA 3 (water motion). Furthermore, Figure 47 shows an unstructured distribution of standardized residuals indicating aptness of the linear model. A positive trend was observed between juvenile abundance these residuals (Figure 48).

The results of the multiple linear regression contained one highly influential data point (Cook's distance = 5.74). This datum represented the highest abundance of both juvenile and adult *S. franciscanus* and attempted data transformations did little to reduce its impact. When this point was removed from the analysis, no significant relationship could be detected ($R^2 = 1.72$, $p = 0.115$). No evidence however, identified this point as an anomaly in terms of biological or ecological factors and was therefore, considered to be sampled from the target population.

Table 15. Results of: A. Simple linear regressions between principal components and the abundance of juvenile *S. franciscanus*; B. Best-subsets multiple regression predicting juvenile abundance from the most parsimonious combination of eight principal components. Stepwise criteria: probability of F to enter ≤ 0.05; probability of F to remove ≥ 0.10.

A.

	Beta	**R^2**	**p-value**
PCA1 – Grazers	0.161	0.007	0.687
PCA2 – Adult Urchins	**1.771**	**0.800**	**< 0.001**
PCA3 – Water Motion	0.455	0.053	0.249
PCA4 – Detritus feeds	- 0.015	< 0.001	0.970
PCA5 – Sedimentation	0.115	0.003	0.774
PCA6 – Food	- 0.280	0.020	0.482

B.

Dependent	Step	Components	Interpretation	R	Cumulative R^2	p-value
Juvenile	1	2	Adult Urchins	0.894	0.800	< 0.001
	2	2 + 3	Adult Urchins + Water Flow	0.923	0.852	< 0.001

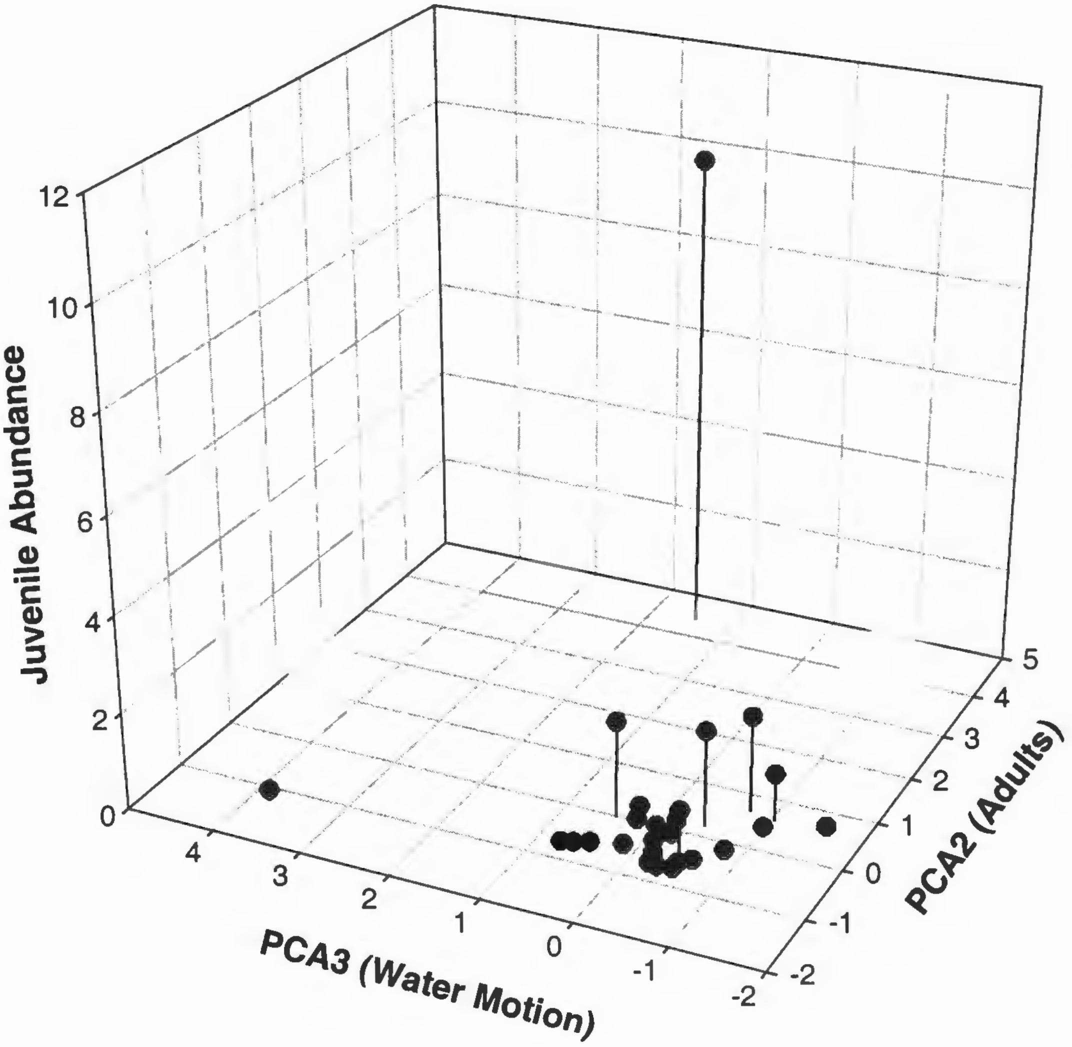

Figure 46. Juvenile *S. droebachiensis* abundance in relation to PCA2 (Adult presence) and PCA3 (Water motion). Data represent 27 quadrats.

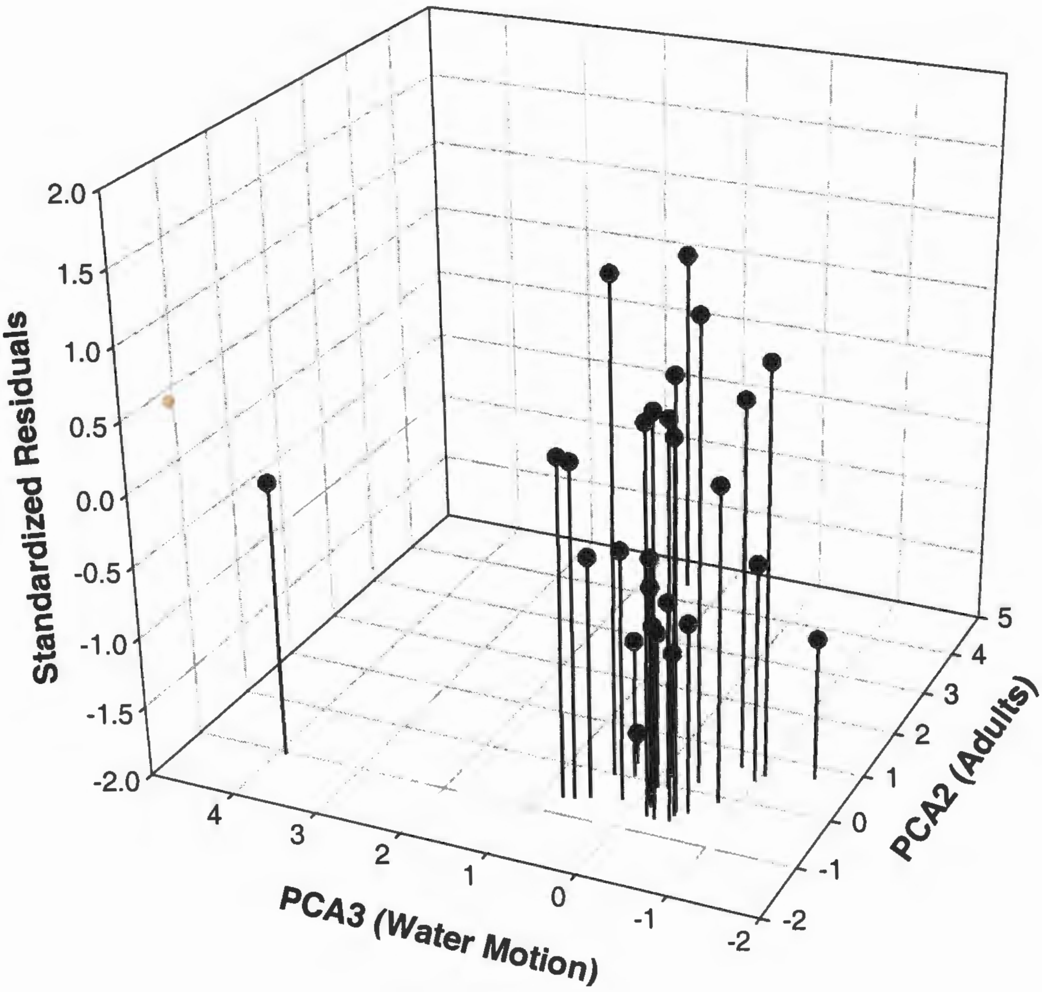

Figure 47. Standardized residuals in relation to PCA2 (Adult presence) and PCA3 (Water motion). Data represent 27 quadrats.

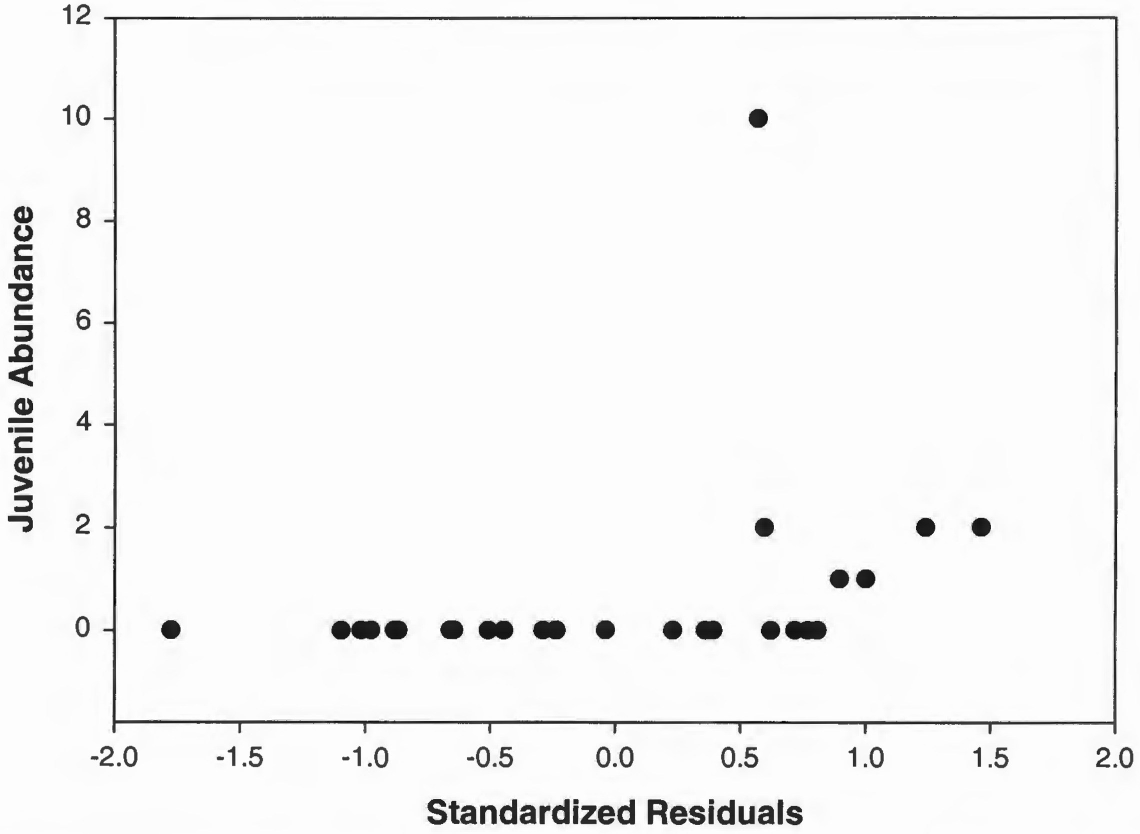

Figure 48. Juvenile abundance vs. standardized residuals for PCA 2 (Adults) and PCA 3 (Water motion).

5.4. Discussion

Results from this study (Table 13) indicate that juvenile abundances were positively associated with the presence of adults. Further analysis using PCA and simple linear regressions (Table 15A) suggest that the only significant variable predicting higher juvenile abundances was the presence of adults (PCA2). This is in accordance with findings of previous field surveys where positive juvenile-adult associations have been reported (Tegner and Dayton, 1977; Breen at al., 1985; Sloan et al., 1987). These surveys however, used visual identification of juveniles by underwater SCUBA divers to measure juvenile abundance. Results of our survey demonstrate that a number of small juvenile *S. franciscanus* found in the field using vacuum filtration were missed by traditional dive survey techniques supporting the findings of Runnels (1985).

Juvenile abundances showed positive trends with higher water motion (PCA3) and lower food abundance (PCA6; Table 15A), but they were not significant. Areas of higher water motion may limit the distribution of predators (i.e. crabs, starfish), deliver more drift algae whereas juveniles are able to take advantage of hydrodynamic refuges under adults (Chapter III). While PCA 6, *Food* did not significantly predict juvenile abundances (Table 15 A and B), assessments of algal community composition (Figures 46 and 47) in this study were limited to the winter season. These species, which are potential food sources for *S. franciscanus* (including preferred species *Macrocystis integrifolia* and *Nereocystis leutkeana*) would be expected to be reduced in abundance or absent during the sampling period reported here. Predators did not load highly on any of the principle components, due perhaps to the high mobility of such species (i.e. crabs, starfish).

The results of the multiple linear regression model converged to include the following variables in order of importance: (1). Adult urchins and; (2). Water motion (Table 15B). Juvenile abundances, though highly variable, were highest at sites with high adult abundance and high levels of water motion (Table 15 and Figure 46).

Measurements of water motion via the dissolution rate of the plaster of Paris cubes indicated that there was little variation between sites, which was supported by simultaneous measurements at all three sites (Figures 45). It is important to note that water motion measured via this method is dependent on whether conditions are characterized by steady versus fluctuating flow (Porter et al., 2000).

More detailed flow field measurements over a longer time period would help determine whether differences in water motion exist between sites. Recent evidence indicates that selection on intertidal snails related directly or indirectly to wave action may be most intense during storm events (Trussel, 1997). Our measurements did not include any major storm events, which may influence the pattern and intensity of water motion at each site differently.

Rogers-Bennett et al., (1995) suggest that adults in shallow habitats might enhance juvenile recruitment. Though depth did not load highly on any of the principle components, it is important to note that the highest density of juveniles (10 per m^2) was found 0.18 m above chart datum and no juveniles were found below 2.87 m. This is in contrast to the adults, whose distribution extended to the deepest sample at 5.03 m depth.

Given that urchins are mobile and recruitment in sea urchins varies temporally as well as spatially (Ebert 1983) repeated surveys should be conducted to verify the findings of this study.

5.5. Conclusion

The use of an underwater vacuum allowed for the collection of a valid, quantitative samples of recently settled *S. franciscanus* juveniles. This study emphasizes the notion that the adult spine canopy is an essential element in the early life history of juvenile *S. franciscanus.* Other ecological and physical factors such as water motion, food abundance and depth may also be of importance for juvenile *S. franciscanus.* This study supports laboratory-based findings that highlight the importance of juvenile sheltering in the early life-history of sea urchins (*S. franciscanus*).

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Chapter VI. Summary and conclusions.

Two main questions were proposed to be examined in this thesis: (1) why are juvenile sea urchins found primarily under adults and; (2) how did they get there? The behaviour experiments described in Chapter III combined with the field survey of Chapter V addressed the first question of why. Results indicate that juvenile *S.* franciscanus shelter at higher rates in response to predators and energetic water flow, whereas juvenile *S.* droebachiensis show generally low rates of sheltering regardless of predation risk or fluid conditions. Furthermore, juveniles of both species showed lower growth rates in the presence of adults compared to treatments without adults. The experiments in Chapter IV indicate the a mechanism whereby juvenile behaviour mediated by secondary chemical signals explains how juveniles locate shelter.

In marine systems, there is a growing appreciation of the role post-settlement processes have in recruitment (Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Menge, 2000). It appears that juvenile *S. franciscanus* react to potential dangers such as predation and hydrodynamic disturbance by sheltering under adults at higher rates. Results of the behaviour experiments confirm the notion that juvenile sheltering is in part a response to predators (Tegner and Dayton, 1981).

However, these results show that the sheltering behaviour in *S. franciscanus* is not controlled by any single factor. Increased sheltering rates under conditions of energetic water motion suggest a role for hydrodynamic flow in this behaviour. Very few studies have examined the influence of water motion on post-settlement stages for any benthic marine invertebrates (review Hunt and Scheibling, 1997; but see Arsenault and Himmelman, 1996).

It has also been speculated that sheltering juvenile *S. franciscanus* benefit from gaining access to macroalgal resources (Tegner and Dayton, 1977; Rogers-Bennett et al., 1995). The results of the growth experiment in this study however, do not support this hypothesis, and in contrast, indicate the existence of competition between juveniles and adults. This confirms the idea by Low (1975), whereby competition for food may exist between juveniles and adults, but that other selective pressures such as predation limit juveniles to adult-associated refuge habitats.

Of particular interest is the finding that juvenile *S. franciscanus* can actively move under adults. Low (1975) describes the sheltering of juveniles by adults as a "parental behaviour". Although post-settlement mortality may also contribute towards the observed pattern of recruitment, juvenile behaviour remains a potentially important mechanism. Rowley (1989) suggested that juvenile migration was unlikely to affect recruitment given the small size of recruits and the relative importance of juvenile behaviour under field conditions requires further investigation.

Results indicate the existence of a secondary chemical signal, a unique finding with respect to benthic marine systems. The complex manner in which juveniles utilize chemical cues to locate adults underlines the importance of incorporating individual behaviour into models of recruitment.

Finally, the results of the field survey support the findings of the lab-based experiments. Specifically that there is a strong association of juveniles sheltering with adults and with water motion. These results are in agreement with previous field studies (Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987), which found juvenile *S. franciscanus* associated with the presence of adults and increased water motion.

It should be noted however, that some fundamental questions remain. For instance, the validity of any generalization from the conclusions of the growth experiment is weak as densities of juveniles, adults, and macroalgae vary under natural conditions. In addition, the identity of the chemical cue used by juvenile *S. franciscanus* to locate adults is unknown. All *S. franciscanus* used in the behaviour experiments were starved, and it would be interesting to examine whether and how behaviour changes as both juveniles and adults are fed more. Specifically, it would be interesting to pursue whether juveniles are attracted more strongly to adults that are well fed. Other questions may include whether fed juveniles shelter more than starved juveniles, and whether juveniles shelter less in the presence of danger (i.e. predators, water motion) when food is readily available. Finally, more work must be conducted to confirm the conclusions of the field survey. Recruitment may vary widely among years (Ebert, 1983), thus sampling should be repeated to determine the generality of the conclusions presented here. Increased spatial and temporal resolution in measurements of water motion would also give a more accurate picture of the fluid environment facing juvenile sea urchins.

Though the association between juvenile and adult *S. franciscanus* has been recognized for over twenty years, how and why this phenomenon occurs has remained unknown. This thesis presents evidence concerning three factors (predation, water motion, and food) as they relate to juvenile sheltering. Juvenile *S. franciscanus* were observed to shelter under adults in response to increased predation risk and water motion, though juveniles associated with adults attained lower growth rates relative to juveniles without adults. Juvenile behaviour, which is influenced by chemical signals, was shown to be a possible explanation for how juvenile *S. franciscanus* come to dwell under adults.

In contrast, juvenile *S. droebachiensis* showed no positive behaviour (i.e. movement towards) adults or chemical signals released by adults. Growth of juveniles was reduced in the presence of adult, presumably due to competition for kelp. Furthermore, the survival of *S. droebachiensis* was not enhanced through association with adults.

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