RELATIONSHIP BETWEEN FEEDING, REPRODUCTIVE CONDITION, JAW SIZE AND DENSITY IN THE RED SEA URCHIN, *Strongylocentrotus franciscanus*

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Relationship between feeding, reproductive condition, jaw size and density in the red sea urchin, Strongylocentrotus franciscanus

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RELATIONSHIP BETWEEN FEEDING, REPRODUCTIVE CONDITION, JAWS SIZE AND DENSITY IN THE RED SEA URCHIN *STRONGYLOCENTROTUS FRANCISCANUS*.

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Abstract

The effects of starving and feeding on 3 size classes of red sea urchins (*Strongylocentrotus franciscanus*) were investigated in the laboratory for 5 mo. Starving led to a decrease in gonad index and an increase in relative jaw size while feeding led to large increases in gonad index and decreases in relative jaw size. Changes in relative jaw size occured due to different growth rates of the test and jaws. In starved urchins, jaws stayed the same size but the test shrank, whereas in fed urchins, jaws grew at a slower rate than the test. There were no differences in growth between *S. franciscanus* tagged with tetracycline and the untagged controls.

The relationships among urchin population density, feeding condition, jaw size and gonad condition were studied at 25 sites within 4 areas around Vancouver Island, British Columbia. Density indirectly influenced relative jaw size and gonad condition of red urchins due to changes in diet associated with increases in density. Food weight contained in urchin guts decreased with increasing density but did not influence relative jaw size. Maximum urchin test diameter in the population decreased with increasing population density, probably because low resource availability at higher densities could not support as large a body size. Exposure to surf and storms seemed to shift resource allocation from the gonads towards building a heavier skeleton.

A laboratory experiment was performed to determine the appearance of some potentially important food items in the diet, following ingestion and partial digestion by urchins. The diet of wild red sea urchins was then investigated for the 25 study sites. Variability in the diet occured on both small (< 2km at Tofino, <10km at Alert Bay) and large (>100km) spatial scales. *Nereocystis luetkeana* was the most abundant item in urchin guts in 3 areas out of 4, being second in abundance in the 4th area. At Tofino, seagrasses *Zostera marina* and/or *Phyllospadix scouleri* were the most abundant food items in urchin guts. Feeding seemed to be influenced by both food preferences and algal availability, as has been shown in several other species of sea urchins.

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Chapter 1

General Introduction

The red sea urchin, *Strongylocentrotus franciscanus* (Agassiz), is common in shallow rocky subtidal habitats throughout the west coast of North America (Bernard and Miller 1973), from the southern tip of Baja California, Mexico to Sitka and Kodiak, Alaska and on the Asiatic coast as far south as the southern tip of Hokkaido Island, Japan (Kato and Schroeter 1985). *S. franciscanus* is the largest and most abundant species of urchin found in British Columbia (B.C.) (Bernard and Miller 1973) and is important both ecologically and economically. The red sea urchin is fished commercially by divers, to about 15 m depth throughout the coast of B.C. (Campbell and Harbo 1991). Two other species of sea urchins, the green (*S. droebachiensis*) and purple urchins (*S. purpuratus*), close relatives of red urchins, are also present in B.C. but are less abundant. A fishery also exists for the green urchin (Campbell and Harbo 1991).

Urchin – Kelp Bed Interactions

Most sea urchin species are primarily herbivorous (Johnson and Mann 1982). They are often the determining factor regarding the abundance and distribution of marine plants in shallow water marine environments (Lawrence 1975). Echinoids have been held accountable for the complete deforestation of vast areas of well-developed kelp forest habitats in many different parts of the world (Harrold and Pearse 1987). Density of echinoids is an important factor in determining grazing intensity (Harrold and Pearse 1987). Under extreme grazing pressures, almost all algae are consumed except the most hardy species, such as the corallines and some opportunistic algae (Lawrence and Sammarco 1982), thus destroying kelp beds and leading to the formation of

"barren grounds" or "urchin barrens". Harrold and Pearse (1987) reviewed the interactions between urchins and kelp beds and suggested that the ecological impact of echinoids often seems to be all or none. Urchins will generally stay in cryptic habitats and feed on drift algae, having little impact on attached plants. When conditions change past some 'threshold', urchins leave their shelter and start feeding on attached algae, which eventually leads to the formation of barrens. The lower depth limit of kelp forests commonly coincides with high urchin densities (Druehl 1978, reviewed in Harrold and Pearse 1987), the upper limit of the urchins might be controlled by waves (reviewed in Harrold and Pearse 1987). Overgrazing (of macroscopic algae) is not necessarily followed by urchin population crashes for several reasons, primarily the urchins' ability to utilize alternate resources such as benthic diatoms, less-preferred foliose and encrusting algae, and detritus (Duggins 1980). Furthermore, detached drifting algae are frequently plentiful regardless of local urchin concentrations (Duggins 1980) and red urchins are very efficient at capturing drift algae (Duggins 1981). Barrens can therefore persist for a long time, despite the low algal standing stocks. The ability to feed at a high rate on a variety of both plant and animal foods, to move over large areas while foraging, and to persist despite low food levels make the regular echinoids a versatile and important biotic component of the marine environment (Lawrence and Sammarco 1982).

Where there are dense urchin populations, urchin grazing largely accounts for the very limited distribution of macroalgae in shallow water (Himmelman et al. 1983). Removal of *S. droebachiensis*, which is generally abundant in shallow subtidal rocky habitats on the east coast of Canada, caused a large increase in algal species diversity and, algal abundance increased about 125-fold after two years (Himmelman et al. 1983). Small urchins (< 10 mm) which had not been removed showed a high growth rate (compared to urchins of the same size in control areas with no removal) showing that there is strong intraspecific competition for food, and growth is markedly limited by algal resources (Himmelman et al. 1983). Urchins, by strongly limiting the distribution and abundance of macroalgae, greatly reduce benthic primary productivity (Himmelman et al. 1983). Paine and Vadas (1969 a) also observed increased algal abundance and species diversity

after removing *S. purpuratus* from tide pools and *S. franciscanus* from subtidal areas in Washington. Levitan (1988 a) showed algal biomass to increase 30-fold within 6 mo after a mass mortality event that killed 99% of the urchin *Diadema antillarum* in the U.S. Virgin Islands. A later increase in *Diadema* mean test diameter caused the urchin biomass to increase 42-fold causing algal biomass to decrease by 84% (Levitan 1988 a). Scheibling (1984) reported similar results after mass mortality of *S. droebachiensis*, due to disease, occurred on the Atlantic coast of Nova Scotia. Experimental removals of red, purple and green urchins in Torch Bay, Alaska, led to drastic increases in algal biomass and diversity which then decreased (but still stayed at levels higher than the pre-removal conditions) as succession progressed and *Laminaria groenlandica* Rosenvigne became dominant (Duggins 1980).

The importance of sea urchins to subtidal community structure has also been demonstrated by following community structure after arrival of sea otters (*Enhydra lutris*) along the coasts of the north-east Pacific. In British Columbia, sea otters are the most important predator of sea urchins, and possibly the only predator capable of regulating urchin abundance (see Breen 1980), with the possible exception of man. After arrival of sea otters in an area, either through expanding their range or by re-introduction, urchin abundance decreased and algal abundance increased (Breen et al. 1982. Watson 1993). Algal species diversity generally increases shortly after urchins are excluded. Succession then takes place and one or more competitive dominant species (generally perennials) come to exclude the competitively inferior (generally annual) species (Duggins 1980, Paine and Vadas 1969 a, Watson 1993). Where sea otter foraging was intense, red urchin-dominated communities on western Vancouver Island became algal-dominated within a year (Watson 1993). Elsewhere, the red sea urchin can dominate the subtidal zone, except for a shallow algal fringe to which kelps are restricted (Breen et al. 1982). Sea otters have been qualified as keystone predators in nearshore communities of the north Pacific Ocean (Estes and Palmisano 1974, Estes et al. 1978). By reducing sea urchin abundance, sea otters promote the growth of kelp beds, and this in turn may affect populations of other invertebrates, fishes, and predators of fish (Breen et al. 1982). The sea otters' great impact on community structure is

because they are preying upon organisms (sea urchins) that would otherwise overgraze basic resources (Duggins 1980). When sea otters are present, decreased abundance of sea urchins, the competitive dominant herbivores, leads to lower competition between herbivores (see Estes et al. 1978), whereas competition between macro-algae increases due to lower grazing pressures (Estes et al. 1978).

Although sea otter predation can sometimes strongly influence community structure, the effects are not all-or-none as the previous section may suggest and the "keystone" aspect of sea otter predation has been questioned (e.g., Foster 1990, Foster and Schiel 1988). Foster and Schiel (1988) showed that < 10% of sites surveyed in California outside the present sea otter's range (but within the sea otter's historical range) were deforested of kelps by sea urchins. Variability across a range of composition, rather than stability in one of two possible states over at least one turnover of kelp and urchin populations, is characteristic of kelp forest communities in California (Foster and Schiel 1988). Several other factors than sea otter predation can influence the presence of macroalgae and the structure of nearshore communities (Foster and Schiel 1988).

Juvenile Red Sea Urchin Ecology

Juvenile red sea urchins are often found under the spine canopy of adults (Breen et al. 1985, Tegner and Dayton 1977). The sheltering of the juveniles under adults has two advantages for the juveniles. First, hiding under the spine canopy of adults protects juveniles from predators (Breen et al. 1985, Duggins 1981, Tegner and Dayton 1977) thus increasing survival. Tegner and Levin (1983) showed predation on juvenile red urchins, by the rock lobster *Panulirus interruptus*, to be lower (<50%) when spine canopy shelter was present. Second, sheltering provides juveniles with access to food captured by adult urchins (Breen et al. 1985, Duggins 1981, Tegner and Dayton 1977). Juvenile green and purple sea urchins also occur under adult red urchins (Duggins 1981, pers. obs.) but rarely under adults of their own species (pers. obs.). Red urchins have longer spines and are larger than purple (Tegner and Levin 1983) and green urchins; therefore,

adult purple and green urchins cannot physically provide much shelter. Juveniles hiding under adults are smaller than those associated with the edge of adults or those in the open (Breen et al. 1985). As urchins grow bigger, they move towards the periphery of the spine canopy (Tegner and Dayton 1977) until they are too large to get any protection.

Cameron and Schroeter (1980) showed that urchin larvae do not settle preferentially under adults and suggested that the association of juveniles under the adults' spine canopy could result from differential mortality of exposed and sheltered juveniles, or from migration of the juveniles under the adults. Breen et al. (1985) showed the latter hypothesis to be true and that protection from predation, rather than access to food captured by adults, is the most important function of the adult-juvenile association. In California, almost all juveniles (>80%) are found associated with adults (Tegner and Dayton 1977). In British Columbia, however, about a third of all juveniles are found in the open (Breen et al. 1985). The lower number of juveniles protected in B.C. might be due to lower predation pressures since there are fewer fast moving predators of sea urchins in B.C. than in California (Breen et al. 1985). In B.C., there are no equivalent species for the spiny lobster (*Panulirus interruptus*), the senorita (*Oxyjulis californica*) or the sheephead (*Semicossphus pulcher*), three fast moving predators found in California (Breen et al. 1985). The longer spines of red, compared to purple urchins are also an advantage to large individuals. Tegner and Dayton (1981) showed that some urchin predators prefer purple urchins over red ones and associated this difference to the increased protection from predation offered by the longer spines of red urchins.

The Red Sea Urchin Fishery in British Columbia

In B.C., commercial, sports and native fisheries exist for the red sea urchin; the latter two are, however, much smaller (< 1% of landings) than the commercial fishery (Campbell and Harbo 1991). Commercial exploitation by divers started in the early 1970's (Bernard 1977). Landings increased during the 1980's and were moderated, in the south coast of B.C., by quotas. Later

increases in landings were due to the development of the fishery on the north coast (Campbell and Harbo 1991). Further regulations included minimum and maximum harvest size, area rotation closures, season closures and license limitations (Campbell and Harbo 1991). Demand for urchin roe has increased in recent years (Campbell and Harbo 1991). The fishery peaked in 1991, at over 12 000 tonnes landed, and decreased to slightly over 6 000 tonnes landed in 1992 (Rick Harbo pers. comm.). In 1993, landings, for the entire coast of B.C., reached 6 264 tonnes worth $ 5 271 000 to the fishers (Department of Fisheries and Oceans Landings Statistics) for an average price of $ 0.84 per kg. Nearly 95% of harvested sea urchins are exported to Japan (Fisheries Statistics, Vancouver). Urchin roe can be sold fresh, frozen, canned, salted (Mottet 1976) or preserved in alcohol (Bernard and Miller 1973).

The suggested minimal fishable density (for the fishery to be profitable) is ca. 5 urchins/m^2 but fishing very dense colonies (30 urchins/m^2) is not profitable because gonad yield is inversely correlated with density (Bernard 1977). The main possible effects of commercial harvesting on urchin populations are a decrease in the reproductive output, due to the lower number of individuals, and fertilization success, due to increased distance between spawning individuals. Aggregations of the urchins that remain after harvesting (Breen et al. 1978) might enhance reproductive success under lower densities. On the other hand, Levitan et al. (1992) argued that even if a small number of animals clump, fertilization success may still be low. Another possibly important effect of harvesting on urchin populations is the decrease in space available under adults for juveniles to shelter (Tegner and Dayton 1977), possibly leading to decreased juvenile survival that could threaten recovery of exploited stocks. Tegner and Dayton (1977) have also shown that recruitment to fished areas is lower than that to unfished urchin grounds.

Effect of Feeding Level and Diet on Sea Urchin Growth, Gonads and Jaws

The effect of feeding level and diet on urchin growth, gonads and jaws will be discussed in detail in the following chapters, only a brief introduction and overview are presented here.

Growth and Gonads

Test height (TH) of the red urchin's skeleton is roughly half the length of the test diameter (TD). The gonads (reproductive organs), also referred to as roe, are the parts of the urchins that are sold commercially. Factors influencing gonad condition are thus of interest both for ecological and economic reasons. Biologically, gonad size is probably their most important aspect; commercially, however, color (Kramer and Nordin 1975) and texture influence quality. Bright yellow and firm gonads are preferred over darker, softer roe.

Growth rates of any species (of echinoderms) can be greatly affected by the availability of resources (Lawrence and Lane 1982). Several studies have shown various food items to produce different growth rates in several species of urchins, including *S. franciscanus* (reviewed in Lawrence 1975). Foods that provide the best growth, generally a few species of kelps, are preferred by urchins over other foods (reviewed by Lawrence 1975, Keats et al. 1984, Vadas 1977). The bull kelp, *Nereocystis luetkeana* (Mertens) Postels *et* Ruprecht, is the preferred food of urchins on the Washington state coast (Vadas 1977) while in California, the giant kelp, *Macrocystis pyrifera* (L.) Agardh, is the preferred food of sea urchins (Leighton 1966). In general, foods that support somatic growth will also support gonadal growth (Lawrence and Lane 1982, Vadas 1977). The growth rates of several species of urchins, including the red urchin, are correlated with the degree of algal growth and the occurrence of drift algae (reviewed in Lawrence 1975), i.e., food quantity. Growth rate also changes with the age or size of the individuals. In echinoids, rapid growth rate of juveniles and a slow growth rate of adults generally occur (Ebert 1982, reviewed in Lawrence and Lane 1982, Vadas 1977).

The effect of food type, i.e., diet, on gonadal growth has been demonstrated for echinoids (Larson et al. 1980, reviewed by Lawrence and Lane 1982, Vadas 1977). Food quantity also affects gonad size. In sea urchins, there is an inverse relationship between reproductive effort and food ration (Thompson 1983). In *Evechinus chloroticus*, gonad size was lower at locations with low

food availability compared to locations with abundant food (Dix 1970). Druehl and Breen (1986) have shown that experimental reduction in algal abundance, by harvesting the giant kelp *Macrocystis integrifolia* Bory, leads to a decrease in gonad index and a darkening of gonad color, in *S. franciscanus* and *S. droebachiensis*; a decrease in the abundance of drift algae was also observed.

Different characteristics of food can affect 1) consumption rate, 2) digestibility, 3) absorption, and 4) composition (Lawrence and Lane 1982). Each of these can influence growth, although separating the effects of the different characteristics on somatic and gonadal growth is difficult (Lawrence and Lane 1982).

Jaws

Before discussing the different factors that influence jaw size in sea urchins, a review of the feeding apparatus of urchins is in order. The urchin's feeding system, the Aristotle's lantern (Fig. 1.1), is a complex system made of 40 skeletal parts: 5 teeth, 10 demipyramids, 10 epiphyses, 5 rotules and 5 double elements forming the compasses (reviewed in De Ridder and Lawrence 1982). The demipyramids, which are also referred to as jaws, are attached in pairs to form the pyramids (Fig. 1.2, 1.3). The pyramids have a groove running vertically through which the teeth pass (one tooth per pyramid). The teeth grow continually at the aboral end of the lantern and then slide through the pyramids, from which they emerge at the oral end. One epiphysis, serving for muscle attachment, is attached to the top of each demipyramid. Associated with this skeletal system is a network of muscles acting to raise and lower, and open and close the lantern (reviewed in De Ridder and Lawrence 1982).

Feeding condition of sea urchins influences the size of their jaws relative to test diameter (TD), i.e., the jaw length (JL) to test diameter ratio (JL/TD). Relative jaw size of several urchin species increases with low food levels in the laboratory (Chapter 2 and references therein). Differences in JL/TD between wild populations have generally been attributed to different food

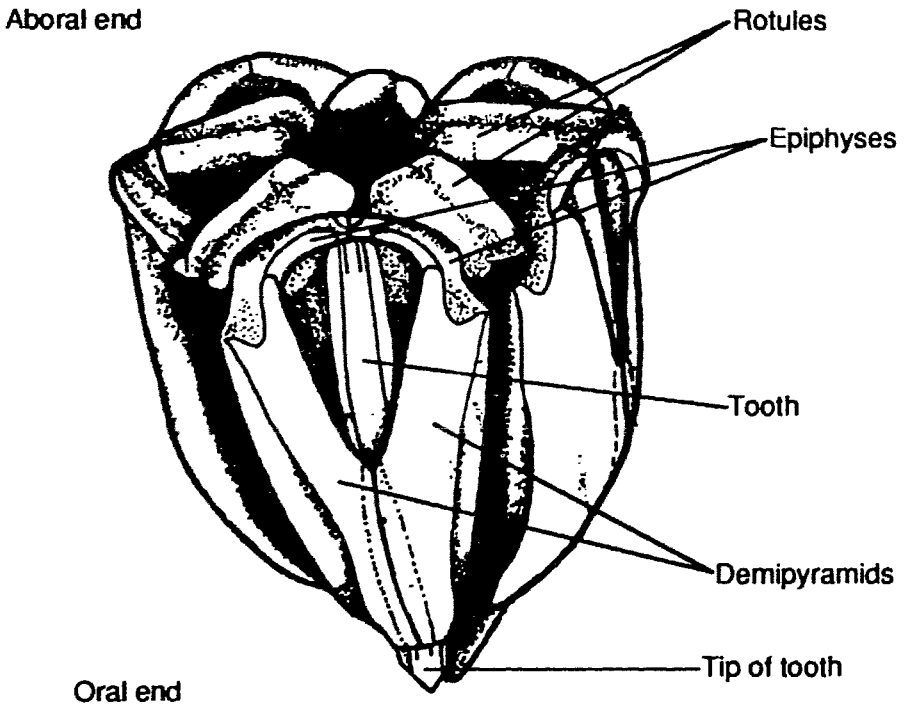

Figure 1.1: Red sea urchin Aristotle's lantern. Compasses (at the aboral end) are not shown.

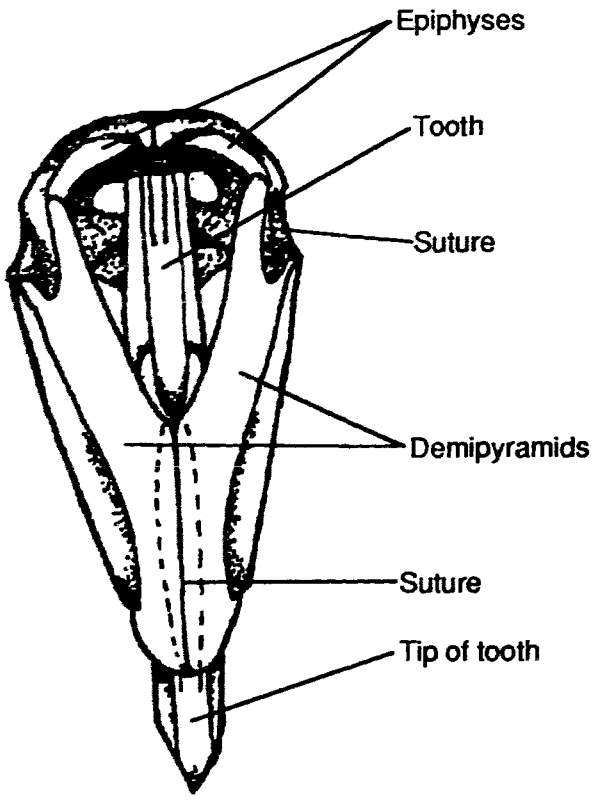

Figure 1.2: Single red sea urchin pyramid and tooth.

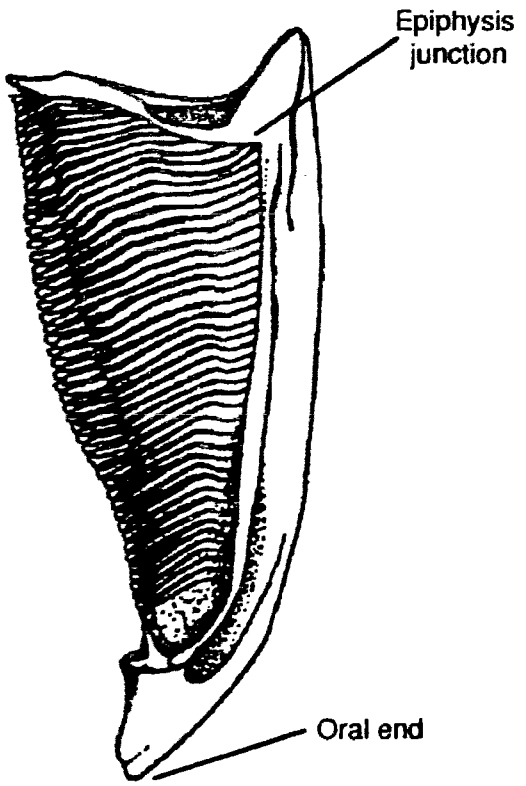

Figure 1.3: Red sea urchin demipyramid

levels between locations. Diet also influences jaw size (T. Morris and A. Campbell pers. comm., Chapter 3). Black et al. (1984) showed that larger jaws increase an urchin's grazing ability. The altered relationship between the size of the test and demipyramid under food limited conditions appears to be a general phenomenon (Levitan 1991 a).

Reproductive Biology of Sea Urchins and the Role of Density

The size at first reproduction in the red sea urchin is ca. 50 mm (Bernard and Miller 1973). Sea urchins are broadcast spawners, they release their gametes in the water where fertilization occurs (Campbell and Harbo 1991) and the sexes are separate (Bernard 1977). Spawning is episodic, involving limited groups, even in a continuous population (Bernard 1977) and takes place between May and June in British Columbia (Kramer and Nordin 1975).

Reproductive success is important for commercially exploited populations since this can influence population recruitment. Reproductive success is not only dependent on gamete production (i.e., reproductive output), but also on fertilization rates which are largely influenced by a variety of factors. Therefore, estimating reproductive success from gamete production alone can be inappropriate and misleading (Levitan 1991 b). Levitan et al. (1992) showed that group size, degree of aggregation, position within a spawning group and water flow all affect fertilization success, and therefore reproductive success in red urchins. Low gamete production, per individual, at high density can lead to similar or higher reproductive success (i.e., number of offsprings produced) than high (individual) gamete production at low density due to increased fertilization success at high density (Levitan 1991 b). Keats et al. (1984) showed that the percent body weight of spawn produced by green urchins decreases with depth. However, gamete production per unit area was highest at the algal-urchin zone interface, despite a lower gonad index, than in the algal zone itself where the gonad index was highest (Keats et al. 1984). The increased gamete production was due to higher urchin biomass (Keats et al. 1984). Density of

males affects fertilization rate in *Diadema antillarum* with the fertilization rate ranging from 7.3 to 45% at 1 and 16 males/m^2 respectively (Levitan 1991 b).

When population density decreases, distance between individuals generally increases, unless the individuals clump together. Levitan (1991 b) showed decreasing fertilization success with increasing distance between sperm source and eggs, due to the dilution of the sperm as it diffuses over larger volumes. Both the number and distribution of point sources of sperm release are important factors in fertilization success (Levitan 1991 b). Not only is the density of spawning individuals important but also the numbers of urchins spawning. When a few rare individuals clump, and spawn, the probability of fertilization increases slightly (Levitan 1991 b). When many individuals are at high density, and spawn, the probability of fertilization increases greatly (Levitan 1991 b). For this to happen, however, good synchrony of spawning between individuals in the population would be required. Temporary spawning aggregations would increase the likelihood of fertilization at low population density and reduce the nutritional costs of living at high density (Levitan 1991 b).

Fertilization decreases with increasing water flow due to rapid dilution of sperm (Levitan et al. 1992) and high turbulence quickly dilutes gametes below the concentration where fertilization is likely (see references in Levitan 1991 b). Under normal flow conditions associated with the spawning season of *S. franciscanus* on the west coast of Vancouver Island, the number and distribution of spawning conspecifics can have an important impact on fertilization (Levitan et al. 1992).

Levitan et al. (1991) showed, for *S. franciscanus*, that sperm concentration has the greatest effect on fertilization followed by sperm-egg contact time and sperm age. Fertilization rate dropped from 80% to 3% (in the laboratory) with a decrease in sperm concentration from 10^4 to 10^2 sperm/ml (Levitan et al. 1991). They argue that, since sperm becomes diluted very fast in the wild, only factors that change before sperm is too diluted to fertilize eggs are relevant to fertilization success; sperm age is therefore not important while sperm-egg contact time is.

After fertilization, development of the planktotrophic larvae begins and lasts until settlement and metamorphosis, the whole process lasting 62 to 131 days (Strathman 1978). This reproductive pattern (long pelagic larval life) ensures a wide distribution of new individuals (Bernard and Miller 1973) which is strongly affected by current patterns (Tegner 1989). Larvae may be carried hundreds or perhaps thousands of kilometers from their source (Ebert et al. 1994). Settlement in *Strongylocentrotus* spp. is sporadic and highly variable in time and space (Bernard and Miller 1973, Ebert et al. 1994, Kawamura 1973, Mottet 1976, Sloan et al. 1987). Recruitment to established populations and the establishment of new colonies are infrequent (Bernard 1977) and recruitment is generally low, averaging 7% (Breen et al. 1978) to 9.5% (Sloan et al. 1987) in British Columbia. However, Tegner (1989) stated that suitable substrate for settlement is not likely to be limiting as long as excessive sedimentation or pollution are not an issue. Sea urchin larvae settle on algal and bacterial films (Hinegardner 1969) which are ubiquitous in the sea (Cameron and Schroeter 1980). Larval survival can be influenced by the feeding condition of the mother since the lipid and energy contents of eggs are lower in urchins fed lower rations (Thompson 1983).

Scope of this Study

In view of the importance of diet, food abundance and density on gonad condition and jaw size of several species of sea urchins, the present study was conducted to investigate the relationships between these factors in *S. franciscanus* in British Columbia.

The first objective of this study was to investigate the effects of factors such as feeding or starving on growth of test, gonads and jaws of red sea urchins in the laboratory. Studies have shown effects of food level on somatic and gonadal growth (see previous sections and later chapters) of several urchin species but relatively little work has been done with the red urchin. Food abundance has also been related to gonad color and texture but little has been done to determine how gonad color and texture are affected by this factor, probably because these factors

are not of biological but rather of economic significance. The present study included determinations of gonad color and texture, along with the more traditional determinations of gonad size and gonad index. The dynamics of jaw and test growth rates were compared to determine the mechanisms underlying changes in relative jaw size under different feeding levels.

The second objective was to determine the relationship between urchin density in the wild, gonad condition, jaw size, amount of food and diet. I hypothesized that with increasing density, each urchin would obtain less food, which would theoretically reduce gonad condition and increase jaw size. Another possible effect of density is to change the urchins' diet which can in turn affect gonad condition and jaw size. Including quantitative estimates of diet and food abundance in the analysis thus allow separation of "true" density, i.e., crowding, effects from feeding related effects that are associated with density. The relationship between maximum TD and density in different populations was also investigated. Maximum TD should be lower in sea urchin populations with higher densities than with lower densities. For urchins under poor feeding conditions, the maximum body size that can be supported should be lower than for those under good feeding conditions.

The third objective of the study was to develop a methodology for identification of food items found in urchin guts and to quantitatively show differences in the diet of red sea urchins at small and large geographical scales. Large scale (>100 km) differences in diet were compared in four areas around Vancouver Island. Small scale (<10 km at Alert Bay, <2 km at Tofino) differences in diet were compared between 11 sites at Tofino and between 12 sites at Alert Bay. The data on relative abundance of the food items in the diet, at the different sites, was used to determine the effects of diet on wild red sea urchin gonad condition and jaw size.

Chapter 2

Growth of test, jaws and gonads of fed and starved red sea urchins

Introduction

Growth of sea urchins depends on the amount and quality of food provided (reviewed in Lawrence and Lane 1982). Feeding also affects jaw size of sea urchins. Relative jaw size, or jaw length to test diameter ratio (JL/TD), has been shown to be higher when food abundance is low than when food is abundant, in several species of urchins (Black et al. 1982, 1984, Ebert 1980, Levitan 1991 a). Ebert (1980) suggested that having a larger JL/TD allows urchins to gather more food. Black et al. (1984) showed that *Echinometra mathaei* with a larger lantern could obtain more food than those with smaller lanterns, thus demonstrating the functional significance of the relative size of the Aristotle's lantern. A large lantern is therefore an advantage for urchins under low food conditions. Several studies have shown that the test can shrink when urchins have little or no food (Ebert 1967, Levitan 1988 b, reviewed by Lawrence and Lane 1982). Three possible mechanisms could explain the increase in JL/TD under low food conditions: 1) the jaws could grow while the test remains the same; 2) the jaws could stay the same size while the test shrinks; 3) the jaws could grow while the test shrinks. Levitan (1991 a) showed that, in *Diadema antillarum*, demipyramids grow at a limited rate when food ration is low while the test shrinks; when no food is available, demipyramids stop growing (or might even shrink) while test size decreases. No studies have investigated which mechanism holds true in red urchins. Ebert and Russell (1992) suggested that growth of the jaws of *S. franciscanus* might be more canalized than in other species of sea

urchins and noted the need to obtain more information on the response of *S. franciscanus* to changes in food availability. Urchins provided with ample, good quality, food show a decrease in JL/TD. Similarly to starved urchins, three mechanisms could explain the decrease in JL/TD depending on test and jaw growth rates.

Gonad condition is also affected by feeding level and food quality in sea urchins (reviewed in Lawrence and Lane 1982). Gonads are small when urchins are fed little or poor quality food and larger when they are fed sufficient amounts of good quality food. Color and texture, important aspects of gonad quality for the fishery, are also influenced by feeding condition.

The purpose of the present study was to investigate the effects of feeding or starving on red sea urchins. Test growth, jaw growth, JL/TD and gonad condition, i.e., gonad index, color and texture, were studied. The experiment was conducted in the laboratory, over a 5 month period, with two size classes of juveniles and also adult urchins. To determine which mechanism governs the changes in JL/TD with more certainty, tetracycline tagging was used in the juveniles. Tetracycline binds to the calcium that is deposited in the skeleton during growth, thus providing a time mark (Edwards and Ebert 1991, Gage 1991, 1992, Ebert and Russell 1992). Tetracycline is incorporated in the skeleton shortly after injection, producing a tag line, seen under ultra-violet light (which causes fluorescence of the tetracycline). Any calcite seen past the tag line, e.g., on jaws, was deposited after tagging.

Materials and Methods

The effects of feeding and starvation on growth, gonad condition and jaw length to test diameter ratio (JL/TD) of red sea urchins from 3 size classes were investigated in the laboratory. Adult urchins, 70 - 110 mm TD, and two size classes of juveniles: 15 - 26 and 47 - 56 mm TD, were collected off Moser Point (Lat. 49°09'06" N Long. 125°57'35" W) on Vargas Island near Tofino (Figure 2.1) on October 26, 1993. A sample of urchins in each size class was measured for TD and test height (TH), weighed and dissected before the experiment to determine initial gonad

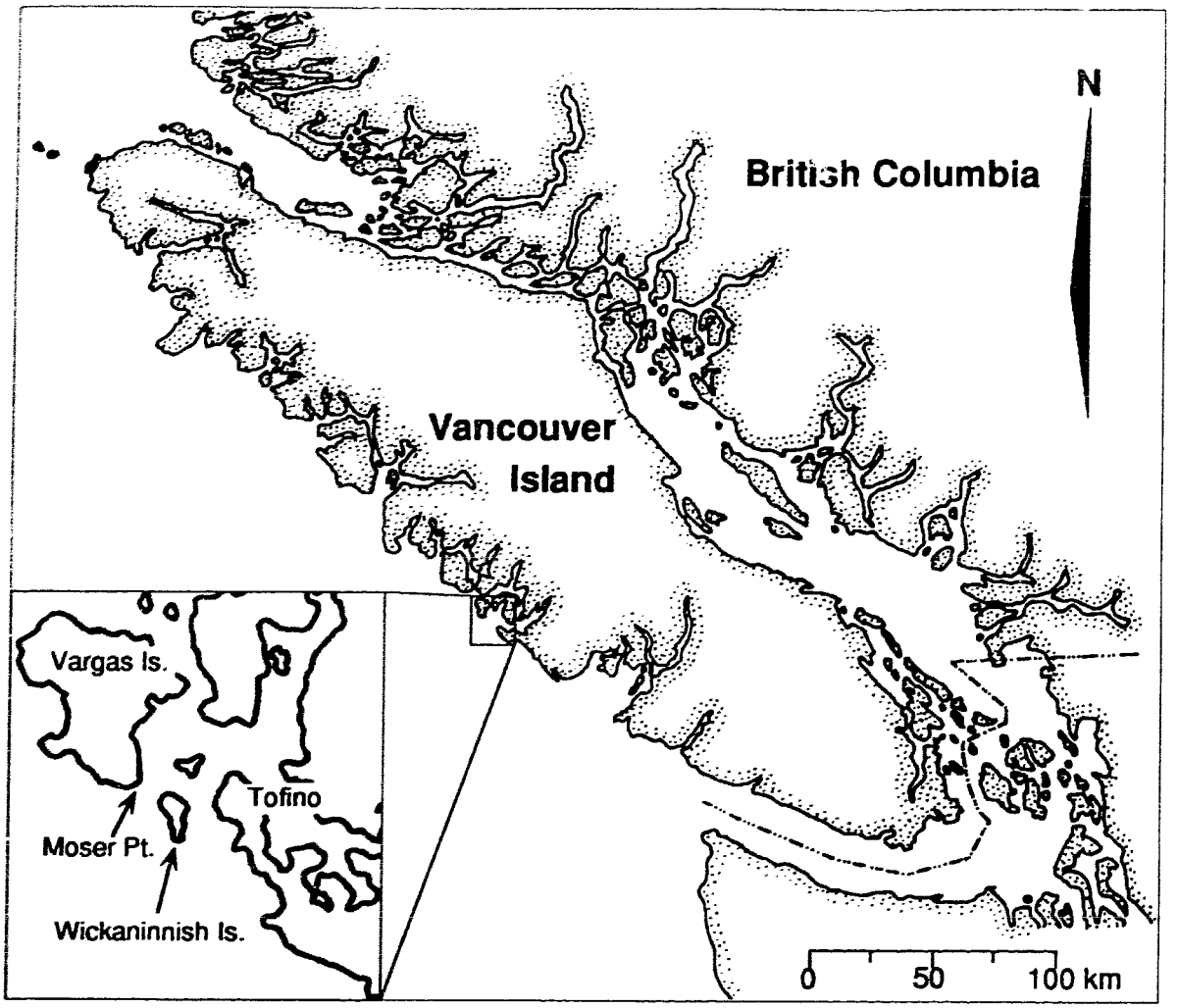

Figure 2.1: Map of Vancouver Island showing the location of Tofino and Moser Point

condition and JL/TD (see below for a description of gonad condition and JL/TD determination). Twenty adults, 26 juveniles in the smaller size class (later referred to as size class 1) and 11 of the larger juveniles (size class 2) were dissected. For each of the three size classes, half the urchins were randomly selected to be starved (total starvation) and the other half to be fed frozen *Nereocystis luetkeana ad libitum*. *Nereocystis* was chosen because it is a preferred food of sea urchins (Vadas 1977). Large quantities of *Nereocystis* blades were frozen because *Nereocystis* is an annual and dies off in late fall and no high quality alternate food source was available. TD and TH (measured with vernier calipers to the nearest 0.5 mm for adults and 0.05 mm for juveniles) and total weight (measured to the nearest 0.1 g) were recorded at the beginning of the experiment. Three measurements of TD (taken from the center of an ambulacrum to the center of the opposite interambulacrum) per individual urchin were taken to minimize possible differences due to slight test asymmetry. The experiment with adult urchins started on October 31, 1993, the one with juveniles started on November 16, 1993. The feeding/starving was conducted for 152 days after which the urchins were measured, weighed and dissected to determine gonad condition and JL/TD (see below). The adults were sacrificed on April 1 and 2 1994. Juveniles were sacrificed between April 17 and 20 1994.

Adult Urchins

Four groups of 15 randomly selected urchins were used in the experiment. Two groups were starved and the other two were fed (Figure 2.2). Each group was held in a ca. 800 l tank supplied with flowing filtered seawater and aeration. Approximately 1.5 kg of food per tank was provided every 4 to 5 days to ensure excess *Nereocystis* was always present in the fed treatment. All tanks were cleaned (of left-over food and feces) by siphoning each time the urchins were fed. Seawater temperature was ambient seasonal (8-9 °C) and the urchins were kept under normal photoperiod.

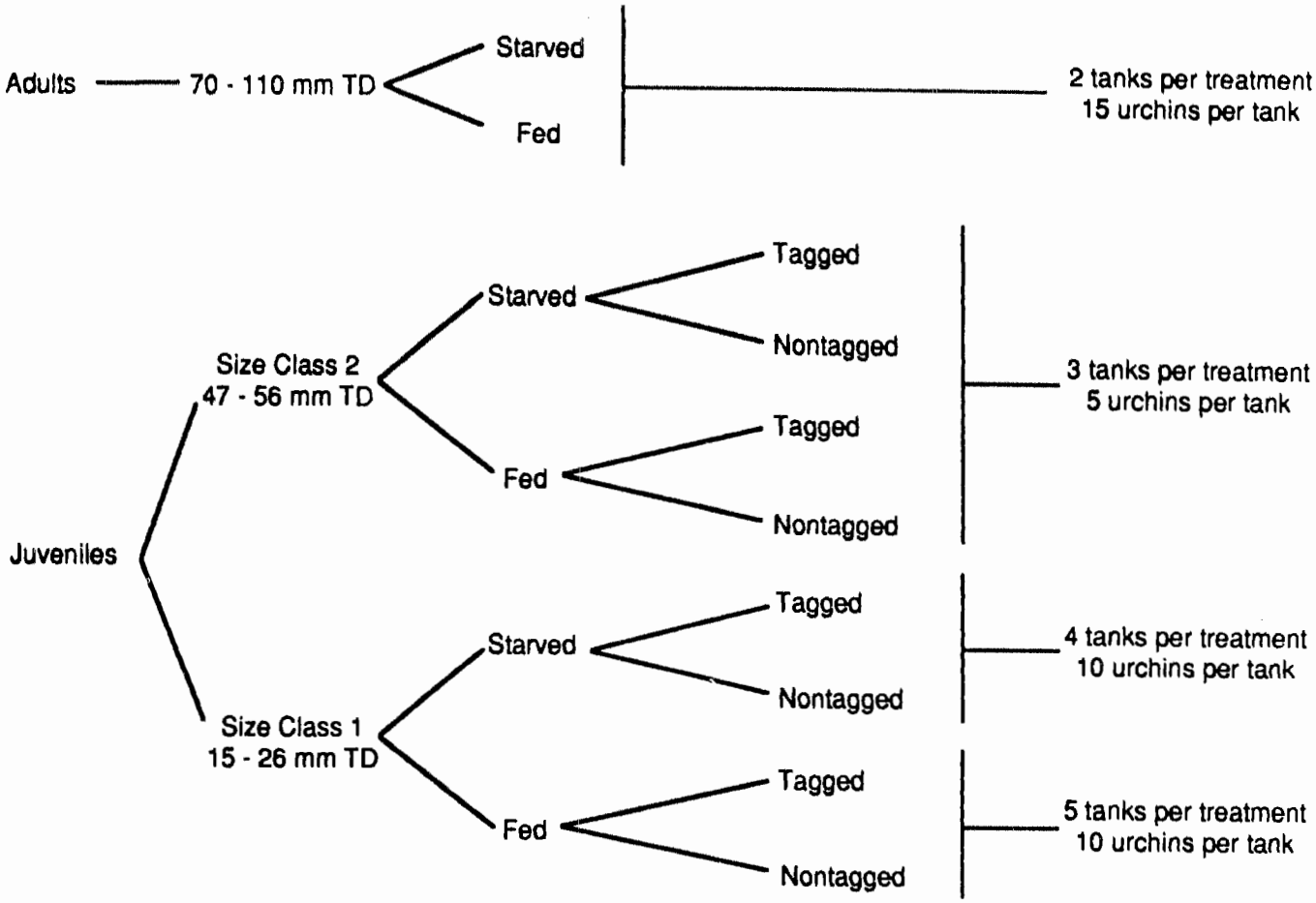

Figure 2.2: Schematic representation of the experimental design

Juvenile Urchins

Half the urchins in each size class were starved while the other half were fed. To investigate the dynamics of jaw growth, half the urchins of each feeding treatment and size class were tagged with tetracycline following the methods of Ebert (1980). The other half of the urchins were kept as nontagged controls (Figure 2.2). Tagging was performed by injecting 0.1 to 0.5 ml, depending on the urchin's size, of a solution of 20 g of tetracycline per liter of seawater through the anus using syringes with 22 or 25 gauge needles.

In size class 1, both fed (tagged and nontagged) treatments were randomly assigned 5 tanks while the starved treatments received 4 tanks, each tank containing 10 urchins. In size class 2, each of the 4 treatments (fed-tagged, fed-nontagged, starved-tagged, starved-nontagged) was randomly assigned 3 replicate tanks containing 5 urchins each. The urchins were held in 50 l tanks with flowing filtered seawater (at ambient seasonal temperature) and aeration. Fed treatments were provided ca. 0.4 kg of food per tank each 4 to 5 days to ensure excess food was present at all times. All tanks were cleaned before each feeding.

Gonad Condition and Jaw Length to Test Diameter Ratio Determination

Gonad condition was estimated using 3 variables, i.e., gonad index, color and texture. The gonad index of the urchins was calculated as:

$$\text{Gonad Index} = \frac{\text{Gonad Weight, g}}{\text{Gutted Weight, g}} \text{ X } 100$$

where Gutted Weight is the total weight of the urchin (including gonads) after draining the coelomic cavity and removing food from the gut. Color and texture of the gonads were both

recorded on a scale from 1 to 3: 1 = yellow or firm, respectively, (high quality), 2 = yellow with other colors or semi-firm, and 3 = brown or flimsy, respectively, (low quality) gonads.

The methods of Ebert (1980) were followed for jaw length to test diameter ratio determination. The Aristotle's lantern from each urchin was soaked in bleach (12% Sodium Hypochlorite) for 24 hours, to dissolve organic tissue. After bleaching, the calcified parts were rinsed and air dried. The length, i.e., the distance from the oral tip to the epiphysis junction (Ebert 1980, Figure 2.3 here), of all 10 demi-pyramids (jaws) from each urchin was measured to the nearest 0.01mm with digital vernier calipers. Jaw length to test diameter ratio was calculated as:

$$JL/TD = \frac{\text{Mean Jaw Length}}{\text{Mean Test Diameter}} \times 100$$

where the Mean Jaw Length is the mean length of all 10 demi-pyramids for each urchin and Mean TD is the mean of 3 TD measurements per urchin.

Jaw growth for tagged urchins, i.e., the distance between the tag line and the epiphysis junction (Figure 2.3), was measured with an ocular micrometer under a compound microscope using incident ultra-violet light. Jaw length was then measured, with digital vernier calipers, to the nearest 0.01 mm.

Statistical Analysis

Each of the 3 size classes were analyzed separately, in each case, the initial conditions of the experimental urchins were compared together (with a nested Anova, i.e., tank nested in treatment) and with the sample dissected initially (with a one-way Anova) to ensure that all treatments were similar at the beginning of the experiment. Tank effects within treatments, at the end of the experiment, were investigated using a nested Anova where tank was nested in treatment. Since no tank effects were present, urchins from all the tanks within each treatment

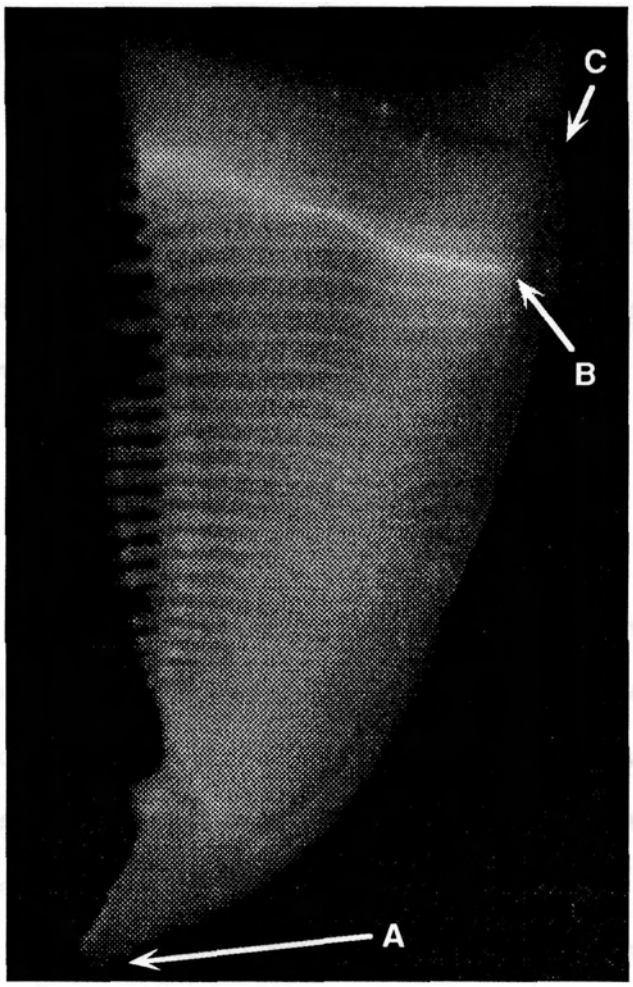

Figure 2.3: Demipyramid of red sea urchin tagged with tetracycline before 5 months of feeding. A) Oral tip, B) Tetracycline tag mark, C) Ephiphysis junction. Distance A-B is the jaw size at the time of tagging. Distance A-C is the jaw size at the end of the experiment.

were pooled together for later analyses. Gonad index and JL/TD were arcsine transformed since these variables are ratios (Sokal and Rohlf 1981). Two sample t-tests assuming unequal variances were used for some comparisons. They will later be referred to as 2 sample t-tests.

Adult Urchins

The final condition of fed vs. starved urchins was compared using 2 sample t-tests. The final condition of urchins in each feeding treatment was compared to the condition of the urchins dissected at the beginning of the experiment using 2 sample t-tests.

Juvenile Urchins

In size class 1, only nontagged urchins were used for growth data because the tagged ones suffered high mortality. Two sample t-tests were used to compare between fed and starved urchins at the end of the experiment. For size class 2, two-way Anovas were performed to investigate the effects of tagging and feeding. No tag effects were noted (see Results) so data for tagged and nontagged urchins were pooled for later analyses.

Two sample t-tests were used to compare the gonad condition and JL/TD at the end of the experiment, for each feeding treatment, with the samples dissected initially. The final vs. initial test diameter, test height and total weight for each feeding treatment were compared using paired t-tests where the average initial and final measurements for each tank were paired.

Differences in jaw growth between feeding treatments, for the tagged urchins, were compared using two sample t-tests. The tag mark allowed the measurement of initial and final jaw lengths for each urchin, a paired t-test was therefore used on jaw length for each feeding treatment. Since the data for initial and final jaw length were paired, size class 1 was included despite the high mortality rates.

Results

Growth

The nested Anovas showed no differences in the size of the urchins (TD, TH, total weight) between the tanks, at the beginning of the experiment, for any of the size classes. No differences in urchin size were found between the initial sample dissected and the experimental urchins for any size classes. The nested Anovas on the final measurements showed no tank effects. Therefore, data were pooled for subsequent analyses.

Adult Urchins

The final condition of fed vs. starved urchins is shown in Table 2.1. Fed urchins were significantly larger than the starved ones at the end of the experiment for test height and total weight; test diameter, however, was not significantly different (Table 2.1). Highly significant differences were found for the three variables measuring gonad condition (gonad index, color and texture). Gonads were larger, firmer and of a lighter color in fed urchins than in starved ones. Jaw length was not significantly different between the two treatments, but the JL/TD was significantly greater for starved urchins than fed ones.

The final measurements of the fed and starved urchins were compared to the initial sample dissected (Table 2.1). Starved urchin size (TD, TH, total weight) was slightly smaller than the initial sample but not significantly different. However, the gonad condition and JL/TD changed significantly during the experiment. Gonad index decreased, texture increased (gonads were softer at the end) and JL/TD increased. However, no significant changes in gonad color were found. Fed urchin size at the end was not significantly different from that of the initial sample dissected (Table 2.1) although it averaged slightly higher. Gonad index increased, color

Table 2.1: Adult red sea urchin test, gonad and jaw growth after 152 days of starvation or of feding on *Nereocystis luetkeana ad libitum* in the laboratory.

	Mean per treatment			2 sample t-Test p values		
	Initial Field	Final		Fed	Fed	Starved
	Sample	Starved	Fed	vs.	vs.	vs.
Variable	n = 20	n = 26	n = 27	Starved	Initial	Initial
Test Height (mm)	44.600	42.731	46.396	0.031	0.260	0.212
Test Diameter (mm)	91.400	85.961	91.006	0.067	0.880	0.066
Total Weight (g)	297.520	274.881	333.626	0.032	0.180	0.398
Drained Weight (g)	224.700	154.535	274.659	0.000	0.008	0.000
Gutted Weight (g)	175.495	146.304	247.096	0.000	0.000	0.031
Gonad Weight (g)	18.985	10.246	73.441	0.000	0.000	0.000
Gonad Color	2.350	1.855	1.074	0.000	0.000	0.076
Gonad Texture	2.100	2.577	2.074	0.002	0.880	0.005
Gonad Index (%)	10.736	6.518	29.599	0.000	0.000	0.000
Jaw Length (mm)	17.737	17.458	17.269	0.670	0.244	0.512
JL/TD (%)	19.487	20.399	19.004	0.000	0.141	0.012
Gonad Index (arcsine trans)	0.330	0.252	0.575	0.000	0.000	0.000
JL/TD (arcsine trans)	0.457	0.469	0.451	0.000	0.143	0.012

n = sample size

improved significantly (decreased) but no changes in texture were observed. Neither jaw length or JL/TD changed during the experiment.

Juvenile Urchins

In size class 1, final size of fed urchins was greater than that of starved urchins (Table 2.2). Gonad index was greater in fed urchins. Starved urchins had practically no gonads, i.e., each gonad was only a very thin thread and therefore no color or texture could be determined for them. Both jaw length and JL/TD were significantly different between feeding treatments. Jaw length was greater in fed urchins while JL/TD was smaller.

In size class 2, two-way Anovas were used to test for tag and food effects (Table 2.3) on the final condition of the urchins. Tagging did not affect any of the variables except gonad color. The interaction between food and tag (in the 2 way Anova) was significant meaning that the effect of tagging on gonad color depended on the feeding treatment. Tagging affected gonad color in starved urchins but not in fed ones. Gonad color of starved tagged urchins was darker than that of fed urchins -- tagged or not -- and that of starved nontagged urchins. Food effect was highly significant for all the variables studied. Fed urchins were larger with bigger and firmer gonads than starved urchins. Jaw length was shorter for starved urchins but JL/TD was higher than these in fed urchins.

Table 2.4 shows the comparisons between the starved urchins and the initial sample dissected, for gonad condition and jaw size, for size classes 1 and 2. For the smaller urchins, gonad index, jaw length and JL/TD remained the same. Gonad index did not change significantly because the index was already close to zero at the beginning of the experiment. For the larger size class, gonad index decreased, color did not change for nontagged urchins but deteriorated (increased) for tagged ones and texture remained the same. Neither jaw length nor JL/TD changed.

Table 2.2: Comparison of final test size, gonad condition and jaw length of juvenile red sea urchins (15 - 26 mm initial TD) after 152 days of starvation or of feeding on *Nereocystis luetkeana ad libitum* in the laboratory.

	Mean per treatment		p values *
Variable	Starved n = 23	Fed n = 49	Fed vs. Starved
Test Height (mm)	9.472	14.131	0.000
Test Diameter (mm)	20.568	34.472	0.000
Total Weight (g)	4.108	19.019	0.000
Drained Weight (g)	2.949	17.011	0.000
Gutted Weight (g)	2.707	15.489	0.000
Gonad Weight (g)	0.000	2.615	<0.001
Gonad Color	no data	1.000	-
Gonad Texture	no data	2.408	-
Gonad Index (%)	0.000	16.107	<0.001
Jaw Length (mm)	4.827	6.511	0.000
JL/TD (%)	23.570	18.932	0.000
Gonad Index (arcsine trans)	0.000	0.410	<0.001
JL/TD (arcsine trans)	0.507	0.450	0.000

*: two sample t-tests assuming unequal variances.
n = sample size

Table 2.3: Comparison of final test size, gonad condition and jaw size of tetracycline-tagged and nontagged juvenile red sea urchins (47 - 56 initial TD) that were fed *ad libitum* on *Nereocystis luetkeana* or starved for a 152 day period in the laboratory

	Mean per treatment						
	Fed		Starved		2 way Anova p values for effect of		
Variable	Tagged n = 15	Nontagged n = 15	Tagged n = 15	Nontagged n = 14	Tag	Food	Tag*Food
Test Height (mm)	24.667	23.833	21.333	22.125	0.976	0.000	0.236
Test Diameter (mm)	59.531	59.108	48.059	48.988	0.828	0.000	0.561
Total Weight (g)	90.359	86.101	48.843	53.359	0.976	0.000	0.301
Drained Weight (g)	76.359	74.783	28.621	31.359	0.857	0.000	0.504
Gutted Weight (g)	70.115	62.673	27.414	29.810	0.480	0.000	0.171
Gonad Weight (g)	18.224	19.061	0.401	0.539	0.655	0.000	0.749
Gonad Color	1.000	1.000	2.067	1.143	0.004	0.000	0.004
Gonad Texture	1.867	2.000	2.933	3.000	0.193	0.000	0.662
Gonad Index (%)	25.519	26.472	1.299	1.244	0.589	0.000	0.545
Jaw Length (mm)	11.359	11.225	10.354	10.592	0.809	0.000	0.398
JL/TD (%)	19.093	19.008	21.583	21.667	0.999	0.000	0.699
Gonad Ind. (arcsine trans)	0.529	0.540	0.093	0.085	0.946	0.000	0.525
JL/TD (arcsine trans)	0.452	0.451	0.483	0.484	0.999	0.000	0.699

Tag * Food is the interaction term in the 2 way Anova.
n = sample size

Table 2.4. Comparison of final vs. initial gonad condition and jaw size of juvenile red sea urchins fed *ad libitum* on *Nereocystis luetkeana* or starved for 152 days in the laboratory. Initial TD of urchins in size class 1 = 15 - 26 mm, initial TD of urchins in size class 2 = 47 - 56 mm. Data from tetracycline-tagged and nontagged urchins were pooled.

Size Class	Variable	Mean per treatment			2 sample t-Test p values	
		Initial Field Sample	Final		Starved vs Initial	Fed vs. Initial
			Starved	Fed		
1		n = 26	n = 23	n = 49		
1	Gonad Weight (g)	0.008	0.000	2.615	>0.20	0.000
1	Gonad Color	1.000	no data	1.000	-	*
1	Gonad Texture	3.000	no data	2.408	-	<0.001
1	Gonad Index (%)	0.059	0.000	16.107	>0.20	0.000
1	Jaw Length (mm)	4.731	4.827	6.511	0.688	0.000
1	JL/TD (%)	23.990	23.570	18.932	0.137	0.000
1	Gonad Index (arcsine trans)	0.006	0.000	0.410	>0.20	0.000
1	JL/TD (arcsine trans)	0.512	0.507	0.450	0.133	0.000
2		n = 11	n = 29**	n = 30		
2	Gonad Weight (g)	2.158	0.468	18.643	0.022	0.000
2	Gonad Color	1.000	1.143	1.000	>0.200	*
2	Gonad Texture	2.727	2.966	1.933	0.255	0.002
2	Gonad Index (%)	6.613	1.273	25.995	0.003	0.000
2	Jaw Length (mm)	10.687	10.469	11.292	0.328	0.004
2	JL/TD (%)	21.333	21.624	19.050	0.541	0.000
2	Gonad Index (arcsine trans)	0.248	0.089	0.534	0.000	0.000
2	JL/TD (arcsine trans)	0.480	0.484	0.452	0.525	0.000

*: t-test could not be performed since all urchins have the same value.

**: n=14 for gonad color, values in table are for nontagged urchins. For tagged urchins, n=15, color = 2.067, $p < 0.002$. Tagged and Nontagged urchins were analysed separately since taging has significant effects on gonad color (see Table 2.3).

n = sample size

Differences between the fed samples and initial samples for gonad condition and jaw size are presented in Table 2.4. For both size classes, final gonad index was higher and texture lower (better) than at the beginning. Gonad color did not change. Jaw length was higher but JL/TD was lower for fed urchins at the end of the experiment than for the initial samples dissected.

Final sizes of the urchins were compared by using paired t-test pairing the average measurements by tank (Table 2.5). Starved urchins in size class 1 did not differ in size at the beginning and the end of the experiment. On the other hand, starved urchins in size class 2 were significantly smaller at the end of the experiment. Fed urchins in both size classes were significantly larger at the end except for test height in size class 2. The lack of difference in TH is believed to be an artifact since TH at 107 days -- after two thirds of the experiment -- was larger than initial (data not presented here) and then decreased while both TD and total weight kept increasing steadily. The lack of evidence for shrinkage in size class 1 might be due to high mortality rates of the smallest urchins in that size class (see next section), which would bias the mean up and thus mask any shrinkage. The urchins that died were mostly <20 mm TD.

The tagged jaws provided the opportunity to investigate the dynamics of jaw growth in more detail (Table 2.6). Jaw growth of fed urchins was significantly higher than that of starved urchins. No growth could be seen on any but two of the starved urchins suggesting that the jaws did not grow. Growth for the two starved urchins was negligible compared to that of fed urchins. Absence of jaw growth in the other starved urchins cannot be ruled out since no tag line could be seen.

The decrease in JL/TD observed in fed juvenile urchins (both size classes) is due to a slower growth rate of the jaws relative to the growth rate of the TD (Table 2.5). Although JL/TD did not change significantly for starved urchins in size class 2, the urchins shrunk while the jaws did not change size suggesting that, given enough time, the JL/TD would probably increase. The observed increase in JL/TD would then be attributable to a shrinkage of the test while jaws stay the same size, rather than to an increase in jaw size. In size class 1, TD, jaw length and JL/TD of starved urchins did not change during the experiment, however total weight decreased suggesting

Table 2.5: Growth of test and jaws of juvenile red sea urchins fed *ad libitum* on *Nereocystis luetkeana* or starved for 152 days in the laboratory. Measurements in mm, weights in g. Initial TD of urchins in size class 1 = 15 - 26 mm, initial TD of urchins in size class 2 = 47 - 56 mm. Data from tetracycline-tagged and nontagged urchins were pooled.

		Mean per treatment				Mean per treatment			
Size Class	Variable	Starved		p values*	Percent Growth	Fed		p values*	Percent Growth
		Initial	Final			Initial	Final		
1		n = 4				n = 5			
1	Test Height	9.325	9.435	0.654	1.177	9.302	14.126	0.000	51.856
1	Test Diameter	20.380	20.486	0.839	0.518	20.488	34.467	0.000	68.232
1	Total Weight	4.217	4.012	0.546	-4.847	4.160	19.016	0.000	357.165
1	Jaw length **	5.175	5.198	0.189	0.444	5.281	6.151	0.000	16.474
2		n = 6				n = 6			
2	Test Height	24.260	21.760	0.001	-10.303	24.020	24.250	0.668	0.958
2	Test Diameter	51.160	48.565	0.001	-5.073	51.657	59.319	0.000	14.834
2	Total Weight	55.068	51.269	0.029	-6.899	55.026	88.230	0.000	60.344
2	Jaw Length **	10.367	10.367	***	0.000	10.722	11.347	0.000	5.829

*: Paired t-test with mean measurements per tank paired together

**: Paired t-test with initial and final jaw length paired for each tagged urchin; n = 9 and 10 for size class 1 starved and fed respectively, n = 15 for size class 2 fed and starved

***: Cannot perform paired t-test since mean difference =0 and standard deviation difference =0

n = number of replicate tanks for each treatment

Table 2.6: Analysis of jaw growth parameters in tetracycline-tagged juvenile red sea urchins that were fed *ad libitum* on *Nereocystis luetkeana* or starved for 152 days in the laboratory. Initial TD of urchins in size class 1 = 15 - 26 mm, initial TD of urchins in size class 2 = 47 - 56 mm.

		Means per treatment		
Size Class	Variable	Starved	Fed	p values*
1		n = 9	n = 10	
1	Initial Length (mm)	5.175	5.281	0.737
1	Final Length (mm)	5.198	6.151	0.014
1	Growth (mm) **	0.023	0.870	0.000
1	% Growth ***	0.508	16.586	0.000
1	% Growth (arcsine trans)	0.031	0.412	0.000
2		n = 15	n = 15	
2	Initial Length (mm)	10.367	10.722	0.166
2	Final Length (mm)	10.367	11.347	0.000
2	Growth (mm) **	0.000	0.625	< 0.001
2	% Growth ***	0.000	5.898	< 0.001
2	% Growth (arcsine trans)	0.000	0.244	< 0.001

*: 2 sample t-tests assuming unequal variances

**: Average final - average initial jaw length for each tagged urchin

***: Growth / Initial size X 100, calculated for each urchin

n = sample size

that shrinking might have started which could later lead to an increase in JL/TD. Fed adult urchin JL, TD and JL/TD remained the same during the experiment (Table 2.1). The TD and JL of starved adults were not significantly different at the end of the experiment but JL/TD ratio was higher at the end than at the start. Since no differences in TD were found for adults, describing the dynamics of jaw vs. test growth is difficult. However, starved urchins shrank in TD (difference was not significant) and fed urchins' total weight increased (again not significantly) suggesting that the dynamics of jaw growth vs. test growth are the same in adults as in juveniles. The absence of significant shrinkage in adults may be due to energy reserves in gonads that would initially reduce changes in TD until the reserves are depleted.

Comparison of JL vs. TD regressions, pooling all laboratory urchins, (Figure 2.4) shows that JL of wild urchins was between that of fed and starved urchins. However, the slope for wild urchins was significantly lower than that of both fed ($p = 0.005$, Ancova) and starved ($p = 0.004$, Ancova) urchins. Jaw length in wild juveniles was close to that of starved urchins but, as TD increased, jaw length of wild urchins approached that of fed urchins. Fed and starved urchins had the same slope ($p = 0.587$, Ancova), however, the intercept was higher ($p = 0.000$) for starved urchins meaning that, for a given TD, starved urchins had larger jaws than fed urchins.

Mortality

Initial mortality, in the first 2 weeks of the experiment, was relatively low (Table 2.7) except for tagged urchins in size class 1. The high initial mortality in tagged urchins of size class 1 was likely a result from the tagging and handling procedure. During tagging, the test of some of the smaller urchins (ca. < 20 mm TD) was cracked when inserting the needle through the anus which is believed to have caused the high mortality. Tetracycline injection through the anus is therefore not recommended for urchins < 20 mm TD. Alternate tagging methods that can be used for such small urchins are calcein tagging (T. Morris and A. Campbell pers. comm.) or injecting tetracycline through the peristomial membrane (Rowley 1990). None of the tagged urchins in size class 2 died,

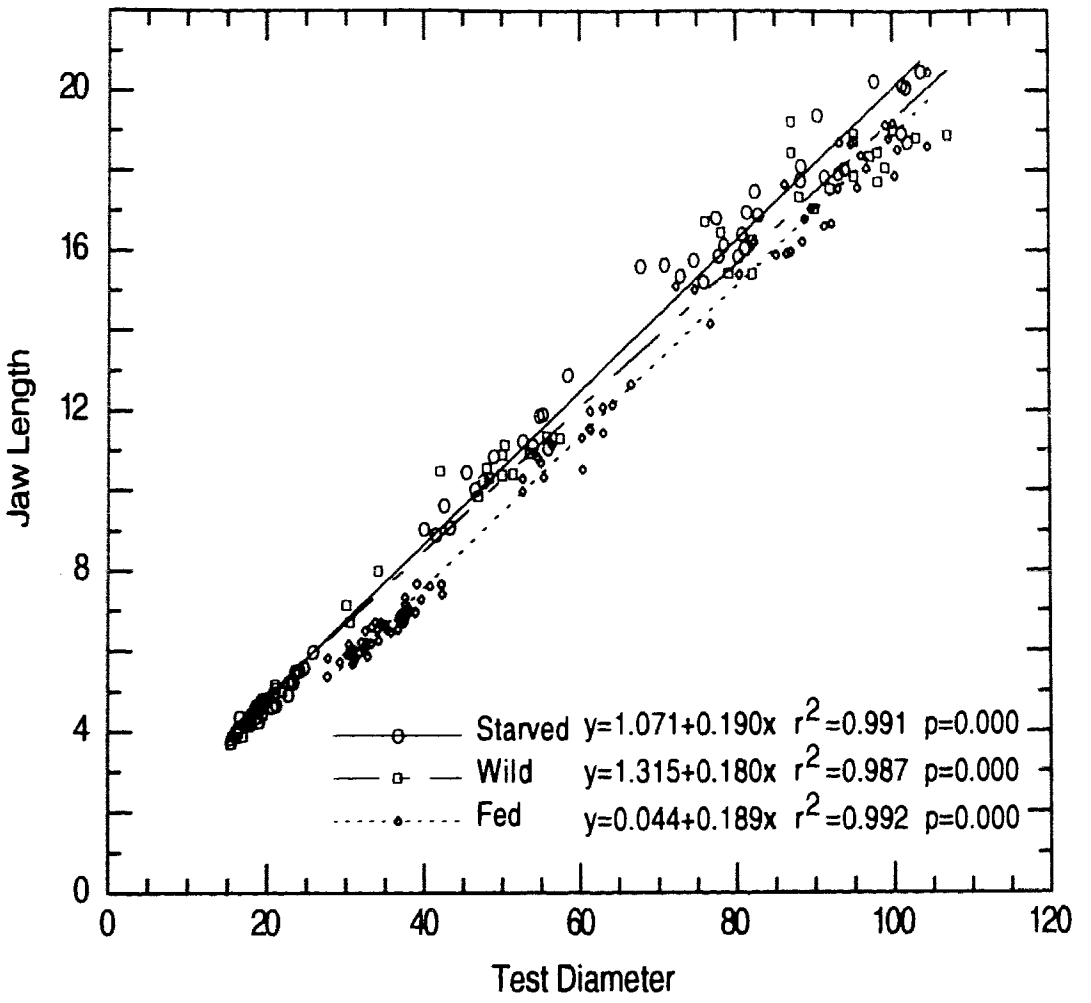

Figure 2.4: Jaw length of starved, wild, and fed red sea urchins in relation to test diameter. Urchins in the two feeding treatments were fed *ad libitum* on *Nereocystis luetkeana* (n = 91), or starved (n = 63), in the laboratory for 5 months. Wild urchins (n = 57) are a sample, coming from the same population as the experimental urchins, that was dissected at the beginning of the experiment.

Table 2.7: Percent mortality of red sea urchins for different periods of the laboratory experiments, for each size class, feeding (fed *ad libitum* on *Nereocystis luetkeana* or starved) and tagging (tetracycline-tagged or nontagged) treatments. Initial TD of urchins in size class 1 = 15 - 26 mm. Initial TD of urchins in size class 2 = 47 - 56 mm. Initial TD of adult urchins = 70 - 110 mm.

			% Mortality *		
			Period		
Size Class	Treatment		1 -14 d	14 - 152 d	0 - 152 d
1	Nontagged	Starved	0	42.5	42.5
1	Nontagged	Fed	0	2	2
1	Tagged	Starved	55	20	75
1	Tagged	Fed	80	2	82
2	Nontagged	Starved	0	6.7	6.7
2	Nontagged	Fed	0	0	0
2	Tagged	Starved	0	0	0
2	Tagged	Fed	0	0	0
Adults	Nontagged	Starved	3.3	10	13.3
Adults	Nontagged	Fed	10	0	10

*: Number of urchins that died during the given period / number of urchins at the start of the experiment X 100

which supports the hypothesis that the high mortality in size class 1 was due to damage done to the urchins while tagging and not an effect of the tetracycline itself. A few adult urchins died within the first 2 weeks of the experiment. Those deaths are believed to result from the handling and measuring stresses at the beginning of the experiment.

Mortality after the first 2 weeks of the experiment was low (< 2%) for fed urchins but high for starved urchins (Table 2.7). Mortality of starved adults and large juveniles (size class 2) was relatively low, i.e., < 10%, compared to that of small juveniles (size class 1) which was between 20 and 42.5% for the last 138 days of the experiment.

Discussion

Effect of tetracycline tagging

The effect of tetracycline on urchin growth seems to vary with species. Tetracycline did not affect growth of the purple urchin (Ebert 1988), but Gage (1991) found that *Psammechinus miliaris* tagged with tetracycline were significantly smaller than nontagged controls after 1 year of growth, the difference later decreased and was afterwards non-significant. Tetracycline tagging did not influence growth of *S. franciscanus* significantly. One negative effect of tetracycline was a deterioration of gonad color in starved urchins. The reason for this darkening of the gonads was unknown. Although initial mortality was high in size class 1, the tagging procedure (i.e., the injection, rather than tetracycline itself) was believed to have caused the mortality since none of the size class 2 tagged urchins died.

Gage (1991) reported problems in tagging urchins with tetracycline, some urchins did not incorporate the tag in the skeleton. Here, only starved urchins did not incorporate the tag in their jaws suggesting that the urchins and/or their jaws were not growing at the time of tagging. Observation of the jaws of starved urchins that died shortly after the beginning of the experiment showed no tag line supporting this hypothesis. The fact that final jaw size of starved urchins was

not different from that of the initial sample also supports this assumption. The lack of the tag mark in starved urchins could result from the 2 weeks starvation period the urchins were subjected to before the start of the experiment. Edwards and Ebert (1991) also reported near-starved *S. purpuratus* not showing the tetracycline tag line.

Somatic and gonadal growth

Limited food has a strong influence on the overall growth of sea urchins (Edwards and Ebert 1991). Test shrinkage under starvation has been shown for *S. purpuratus* (Ebert 1967, Edwards and Ebert 1991) and *Diadema antillarum* (Levitan 1989), and here for *S. franciscanus* between 46 and 57 mm initial TD. Shrinking body size under low food conditions can be an advantage since metabolical costs are decreased allowing longer survival (Levitan 1989). Although there is evidence for shrinkage in size class 2 under laboratory conditions, negative growth might not occur in the wild. The shrinkage observed was relatively minor (-5% TD) and urchins were completely starved for 5 months, such a long period of total starvation might not occur in the wild.

Levitan (1988 b) refers to size regulation as a proportional size adjustment (positive or negative) including skeletal elements, other body tissues, as well as nutrient reserves, while starvation is referred to as a loss of nutrient reserves and/or a disproportionate reduction of gonad size. In size class 2, starved urchins lost 7% of their body weight but gonad weight decreased by 78%. No significant test shrinking was found in adults but gonad weight decreased by 46%. These results suggest that *S. franciscanus* does not regulate size (*sensu* Levitan 1988 b) but rather reacts to low food level with starvation. In *Diadema antillarum* however, size regulation occurs, the ability to reduce body size and its associated metabolic costs allows these organisms to survive and allocate the appropriate amount of energy for reproduction at a given food level (Levitan 1989). Members of the family Strongylocentrotidae have slow growth rates while Diadematidae

have rapid growth rates (Lawrence and Lane 1982). This could explain why size regulation occurs in *D. antillarum* while starvation occurs in *S. franciscanus*.

The alteration of body size in response to altered nutritional levels is of great significance to urchins (Lawrence and Lane 1982). Benefits should accrue from an increase in size, while the ability to decrease in size provides an additional supply of reserves while reducing the body size to one that can be maintained at the lower level of food supply (Lawrence and Lane 1982). Phenotypic plasticity may have a high adaptive value to rapid and extreme changes in environmental conditions (Edwards and Ebert 1991).

Growth rate of urchins changes with size. Ebert and Russell (1993) reported, for *S. franciscanus*, an exponential phase early in growth followed by a maximum growth rate and a decline with very slow growth for large individuals. Here, after 5 months of feeding, urchins in size class 1 increased in test diameter by 68%, from 20.5 to 34.5 mm. In size class 2, the increase was lower at 14.8%, from 51.7 to 59.3 mm TD, while adults (mean initial TD = 91.4 mm) did not grow significantly. Both relative and absolute growth rates decreased with increasing size. This supports the results of Ebert and Russell (1993) and shows that the maximum growth rate is reached below 51.7 mm TD, i.e., by the time urchins reach 51.7 mm TD their growth rate has already started slowing. Not enough data was available to know precisely the TD at which the maximum growth rate is reached in *S. franciscanus*, growth experiments involving more size classes of urchins under 50 mm TD would be required.

Growth estimates for wild urchins at Saltspring Island, B.C., suggest slow growth which implies that size is 13.3 mm TD at 1 yr, 25.7 mm TD at 2 yr and 37.2 mm TD at 3 yr (Ebert and Russell 1992). However, the urchins used to estimate growth at Saltspring Island were either tagged with invasive tags that can reduce growth, or held in cages that may alter natural conditions (Ebert and Russell 1992). Ebert and Russell (1993) estimated that red urchins from subtidal populations would take about 12 yr to attain 100 mm TD, in California, and that red urchins take 4 yr to grow from 20 to 80 mm TD. Although the results presented here show a higher growth rate than the ones observed by Ebert and Russell (1992, 1993), e.g., from 20.5 to 34.5 mm

TD in 5 mo, growth rates are most likely lower in the field where food abundance can be limiting. The growth rates reported by Ebert and Russell (1993) were estimated from wild populations and may be better estimates of growth in the field than laboratory experiments. However, Bernard and Miller (1973) reported that red sea urchins from British Columbia could attain 100 mm TD in 4 to 5 yr. Knowing growth rates is important to determine recovery rates of exploited populations. The present minimum size limit for the fishery on the south coast of B.C. is 100 mm (Campbell and Harbo 1991). The range of growth rates presented above varies greatly and suggests that growth may be slow. Although growth rates are most likely dependent on local conditions in the wild, more studies of the growth rate of wild red sea urchins from different areas of British Columbia are desirable to obtain better estimates of growth rates of urchins and recovery rates of exploited stocks.

The slow test growth observed in adults might be caused by a shift in energy allocation from somatic to gonadal growth. In echinoids, the relative amount of gonad produced increases with age and then stabilizes (Lawrence and Lane 1982). In *S. droebachiensis*, annual production increases linearly with dry weight of the soft tissues, for somatic production this increase is very small, since most of the additional energy available in larger urchins is channeled into reproductive output (Thompson 1979). Here, gonad index of fed adults increased to 29.6% while, that of urchins in size class 2 increased to 26.0%, and that of size class 1 urchins increased to 16.1%, after 5 mo of feeding, suggesting that relatively more energy is devoted to gonadal growth as size increases in *S. franciscanus*.

A second possible reason for slow growth of large individuals is decreasing growth efficiency with size. In most echinoid species, relative production or net growth efficiency decreases with increasing age (Lawrence and Lane 1982). The increased gonad production with age is usually not sufficiently great to offset the declining productivity of body growth and therefore, total productivity declines with age (Lawrence and Lane 1982).

Although no evidence of test growth or shrinkage was evident in adults, the effects of feeding or starving on gonad condition are very important. The gonad index in fed urchins

increased about 3-fold (from 10.7 to 29.6%) while that of starved urchins decreased from 10.7 to 6.5%. At the end of the experiment, the gonad index of starved urchins was 5 times lower than that of fed urchins. The two experimental treatments are probably extremes of feeding levels; in the wild, urchins are not likely to get so little or so much food, for such a long period, as the starved and fed treatments respectively. These extremes of feeding might occur in the wild but probably not for such long periods. Gonad index of wild urchins would then be expected to vary between these 2 values. Such a large variation in gonad index, depending on feeding condition, can have important effects on wild urchins. Gonad production and growth (somatic) are a function of food rations in green urchins (Thompson, 1983) and gamete output is directly related to the weight of soft tissue (Thompson 1979). The individual gamete output might therefore be low in populations that are not well fed. Low gamete output can then translate in low reproductive success due to low fertilization rate (discussed in Chapter 1). However, high density often seems the cause of poor feeding in urchins; the influence of density on fertilization success might therefore offset the decrease in individual gamete output. In *Diadema antillarum*, per capita zygote production is relatively constant across densities because the decrease in gonad size -- and thus gamete output -- with increasing density is offset by higher fertilization success (Levitan 1991 b). Feeding similarly led to drastic increases in gonad indices of urchins in size classes 1 and 2.

Optimum feeding improves not only gonad index but also gonad color and texture. The importance of the effects of feeding on these variables is not ecological but rather an economic one, since urchins with firmer, lighter colored gonads get a higher price than ones with soft brown gonads. In adults, gonad index and color improved while texture stayed the same. The situation is a little different for smaller urchins, gonad index and texture improved while color -- which was good at the start -- remained the same. The improvement of roe yield and quality associated with good feeding conditions suggests that there might be a potential for short term aquaculture where urchins would be collected from the wild and fed for a few months to improve roe quality. Keats et al. (1983) investigated the possibility for short term aquaculture of green urchins. In a period of 2-3 mo, urchins fed good quality foods increased their gonad index from about 2 to 15-20%.

Red sea urchins are mature at ca. 50 mm TD (Bernard and Miller, 1973). However, fed urchins in size class 1 (mean final TD = 34.5 mm) showed gonad growth (from 0.1 to 16.1% gonad index) indicating that feeding can influence size at maturity or can lead juveniles to store energy in gonads. The gonads are the main nutrient storage organs in sea urchins (Bernard 1977, Giese 1966, Lawrence and Lane 1982, Mottet 1976). However, spawning age is dependent on food availability (Bernard and Miller 1973). Some gametogenic activity was observed (histologically) in red sea urchins as small as 30 mm by Bernard and Miller (1973). Size at first reproduction changes in populations of *S. intermedius* (Kawamura and Taki 1965, Kawamura 1973), *S. purpuratus* (Kenner and Lares 1991), *Evechinus chloroticus* (Dix 1970) and *Echinocardium cordatum* (Buchanan 1966) from different habitats, possibly due to differences in food abundance. I did not know if the urchins in my experiments were mature or not so neither hypothesis can be ruled out. It is likely that a combination of the two occurred. Lawrence et al. (1992) also noted that gonadal production can be induced in small individuals of *Paracentrotus lividus*, at a size at which production is usually only somatic, when food availability is high.

Relative jaw size

Large relative jaw sizes have been shown under food limitation in the laboratory and under high densities in the field in several urchin species (*Strongylocentrotus purpuratus* and *Diadema setosum* [Ebert 1980], *Echinometra mathaei* [Black et al. 1982], *Diadema antillarum* [Levitan 1991 a]). Relative jaw size can thus be used to estimate feeding condition (Ebert 1980, Levitan 1991 a). Ebert and Russell (1992) compared two wild populations of red urchins but did not find significant differences in JL/TD between the two. Black et al. (1984) showed that *Echinometra mathaei* with relatively large jaws grazed about 3.75 times more food than urchins with smaller jaws in a 3 day period and noted that relatively large-jawed urchins are better at both scraping and biting food.

Here, in *S. franciscanus*, starving made JL/TD increase in adults but feeding did not change JL/TD. In juveniles, however, starving did not affect JL/TD, but feeding made JL/TD decrease. This agrees with the results shown in Figure 2.4 which suggest that juveniles were almost starved in the wild whereas adults were relatively well fed. One would not expect the JL/TD of almost starved urchins to increase a lot or, conversely, that of relatively well fed urchins to decrease. The juveniles were probably less well fed than adults, at the time of collection, because of their distribution in the field. Adults were found in shallow water at the edge of the algal fringe but few juveniles were found at that depth. Juveniles were more abundant ca. 12 m from the algal fringe in a barren area where little food was available.

In *Diadema antillarum*, the increase in JL/TD is primarily due to a decrease in size of the test (Levitan 1991 a). Although more growth occurs in the demipyramids than in the test when food is limiting, demipyramid growth decreases, on an absolute scale, with decreasing food (Levitan, 1991 a). The dynamics of jaw and test growth are similar in red urchins. Comparison of final jaw length with that of urchins dissected initially, as well as data from tagged urchins, showed no evidence of jaw growth for starved urchins in any of the size classes. Although starved urchins did not incorporate the tetracycline tag, T. Morris and A. Campbell (pers. comm.) successfully tagged starved juvenile red sea urchins, with calcein, and found no jaw growth after a 90 d starving period. Here, negative growth of the test occurred in size class 2 and a slight decrease was also observed in adults. Negative growth of the test, while jaws stay the same size therefore seems to be the most probable mechanism by which relative jaw size increases. Conversely, a jaw growth rate slower than test growth rate is the mechanism leading to lower relative jaw size when urchins are well fed. Significant jaw growth was observed in size classes 1 and 2 but the jaw growth rate was lower than the test growth rate.

Mortality

The survival rates of newly settled to mid-sized red sea urchins appear to limit the size of fishable stocks in some populations (Tegner 1989). The high mortality rate of starved urchins smaller than 26 mm TD, over the last 4.5 months of the experiment, implies that they do not endure starvation as well, or cannot endure it as long, as larger urchins. This might have repercussions in the wild if long periods of starvation occur. A large number of juveniles could die from starvation, possibly threatening stock recovery for the fishery. When estimating feeding condition from JL/TD, the smallest juveniles appeared to be starved, suggesting that such starvation related mortality might occur in the wild. This could happen on high density urchin beds during winter months when food abundance is low.

Conclusions

Tetracycline does not affect growth of red urchins and can be used for mark-recapture experiments to estimate growth rates in the wild, as has been done by Ebert and Russell (1992, 1993). As in other species of urchins, feeding influences both somatic and gonadal growth to a large extent, and possibly the size at maturity. Growth rate decreases with increasing size and is very low in adults. The maximum growth rate is reached before 50 mm TD. Jaw plasticity under different feeding conditions occurs in red urchins, the mechanism for increases in relative jaw size (under poor feeding conditions) is a shrinking of the test while jaws stay the same size while the mechanism for decrease (under good feeding conditions) is slower growth rate of the jaws compared to that of the test. Urchins smaller than 26 mm TD are more subject to mortality from starvation than larger (>46 mm TD) urchins.

Chapter 3

Feeding and reproductive conditions of wild red sea urchins at different densities

Introduction

Several studies have shown that urchins can influence the flora around them depending on their density, often creating urchin barrens, typically with little food, when densities are high (Chapter 1, reviewed by Harrold and Pearse 1987). Urchin population density may influence the quantity and quality of food that urchins feed on and consequently, the condition of their gonads. The effects of density might be indirect, due to other variables that change with density, rather than true density (crowding) effects. The effects of density are generally attributed to lower food available *per capita* as density increases (reviewed in Lawrence and Lane 1982). Thus, diet and food availability are likely to change with density and, since these factors affect gonad condition and relative jaw size (Chapter 2 and references therein), might be the direct cause of density effects. Here, I studied the relationship between red urchin density and amount of food and diet composition on urchin gonad condition and relative jaw size, at 25 sites within 4 areas around Vancouver Island, British Columbia. A hypothesis was tested that sea urchin density was related to food abundance and quality, resulting in urchins that have large jaws and poor gonads in high urchin density areas and small jaws and good quality gonads in lower urchin density areas.

Density can possibly affect the body size that can be supported in a population. If poor feeding is associated with high density, the body size that can be supported in the population should decrease with increasing density. This relationship has been shown for several species of

sea urchins (reviewed in Lawrence and Lane 1982, Levitan 1988 b) and was investigated here for *Strongylocentrotus franciscanus*.

Exposure to waves and storms can possibly influence urchin test thickness (i.e., thickness of the test wall). Species of urchins with a relatively heavier body wall can withstand higher exposures than species with lighter body walls (Ebert 1982). Urchins in high exposure areas would thus be expected to have a thicker, heavier test to enable them to withstand waves whereas urchins in sheltered areas would not need as strong a test. If differences in relative size of the test exist, differences in the relative size of other body components might also be present since a higher allocation of resources to the test would translate in less resources available for other body parts. This effect might be compounded with higher amount of resources allocated to spine repair in exposed areas (Ebert 1968). Gonads are the most likely organs to suffer from such a change in resource allocation between different body parts. The relationships between exposure and skeleton weight and, between skeleton weight and gonad index, were therefore investigated.

Materials and methods

Experimental Areas and Sites

The relationship between feeding condition, diet, reproductive condition and urchin density was investigated in 4 areas around Vancouver Island, B.C. in July 1994. In the first area, Tofino (Figure 3.1), on the West coast of Vancouver Island, 11 sites were surveyed off Vargas Island, Wickaninnish Island and the La Croix Group. The other 3 areas were on the East side of Vancouver Island. At Alert Bay (Figure 3.1), the second area, 12 sites were surveyed off Cormorant Island, the Pearse Islands and Plumper Islands. At Campbell River (Figure 3.1), the third area, one site was surveyed off Quadra Island near Yaculta. Last, one site was surveyed off Kendrick Island near Nanaimo (Figure 3.1). The location and description of each site are provided in Table 3.1.

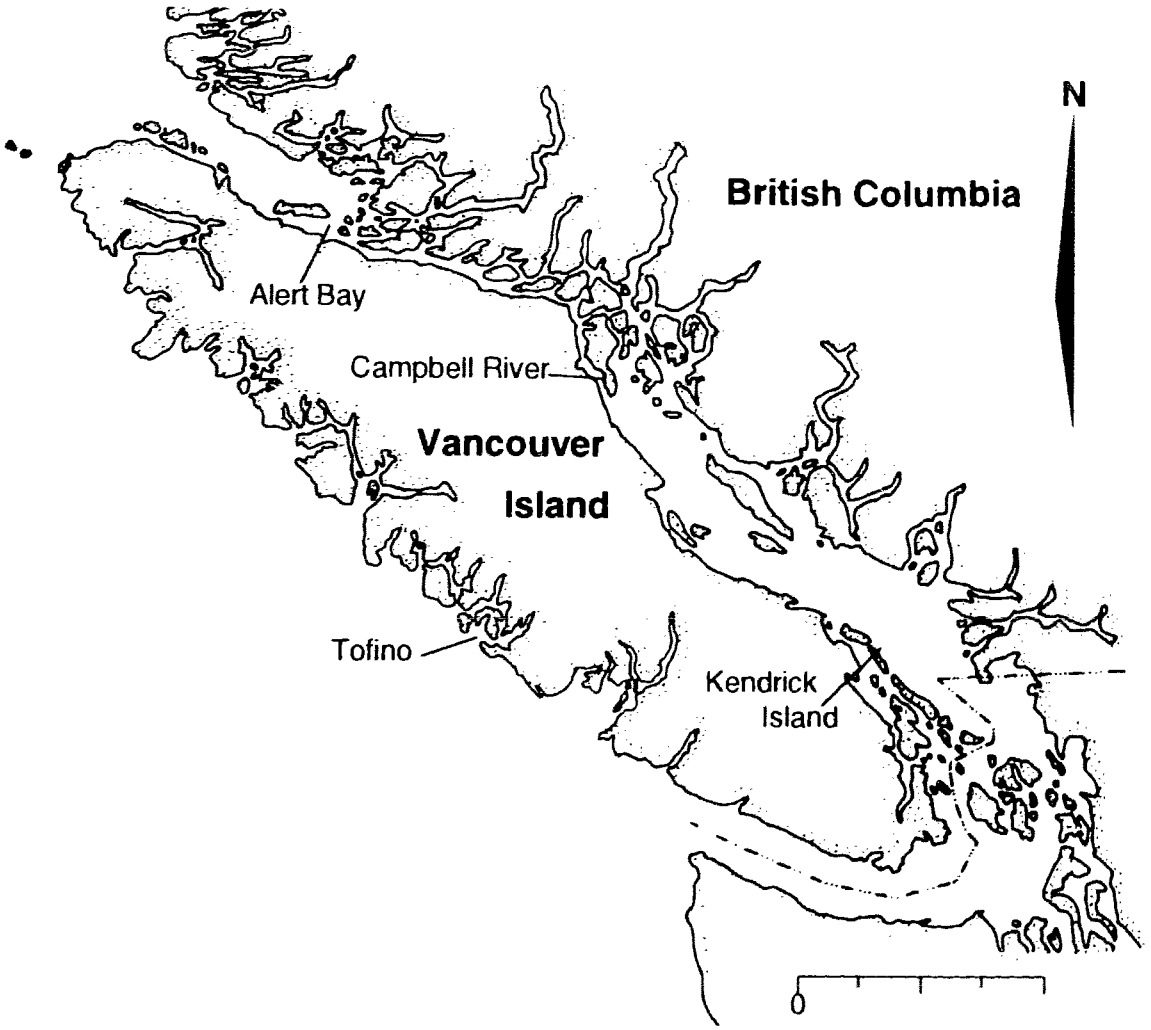

Figure 3.1: Map of Vancouver Island showing the location of the 4 experimental areas.

Table 3.1: Description and location of the experimental sites

Area	Site	Latitude	Longitude	Exposure	Substrate	Slope	Density*
Tofino	1	49°09'45" N	125°57'36" W	Strong tidal flow	Bedrock + sand	20°	6.75
	2	49°09'21" N	125°57'36" W	Moderate exposure	Bedrock + boulders	50°	10.50
	4	49°08'36" N	125°58'30" W	High surge	Bedrock + sand	40°	31.95
	5	49°08'50" N	125°57'06" W	Moderate exposure	Bedrock + cobble	60°	15.45
	6	49°08'36" N	125°57'09" W	High surge	Bedrock with crevices	30°	19.75
	7	49°08'30" N	125°57'00" W	High surge	Bedrock + sand	40°	18.35
	8	49°08'50" N	125°58'03" W	High exposure	Bedrock with crevices	40°	19.47
	9	49°08'52" N	125°58'14" W	High exposure	Bedrock with crevices	10°	13.68
	10	49°08'44" N	125°58'48" W	High surge	Bedrock + boulders	20°	26.70
	11	49°08'36" N	125°58'48" W	High exposure	Bedrock + boulders	50°	19.65
	12	49°08'49" N	125°58'38" W	Moderate exposure	Bedrock, smooth	10°	23.10
Alert Bay	1	50°35'15" N	126°57'06" W	Moderate exposure	Bedrock + cobble + gravel	10°	12.88
	2	50°34'30" N	126°54'28" W	Strong tidal flow	Bedrock + cobble + gravel	0°	5.64
	3	50°35'46" N	126°50'50" W	Strong tidal flow	Bedrock + boulders	30°	6.22
	4	50°36'00" N	126°51'36" W	Strong tidal flow	Bedrock + boulders + cobble	20°	2.86
	5	50°35'40" N	126°48'28" W	Strong tidal flow	Bedrock + boulders	30°	6.00
	6	50°35'10" N	126°50'06" W	Strong tidal flow	Bedrock + boulders	10°	7.18
	7	50°34'50" N	126°50'12" W	Strong tidal flow	Bedrock + boulders	10°	7.42
	8	50°34'28" N	126°49'40" W	Moderate exposure	Bedrock + cobble + gravel	10°	8.55
	9	50°33'15" N	126°51'15" W	Moderate exposure	Bedrock + boulders + cobble	50°	3.35
	10	50°34'30" N	126°41'00" W	Moderate exposure	Bedrock + boulders + cobble	30°	8.16
	11	50°35'15" N	126°46'40" W	Strong tidal flow	Bedrock + boulders + cobble	20°	3.04
	12	50°34'52" N	126°49'50" W	Strong tidal flow	Bedrock + boulders + cobble	10°	8.07
Campbell River	1	50°01'48" N	125°12'06" W	Strong tidal flow	Boulder + cobble + sand	10°	3.30
Kendrick Island	1	49°07'26" N	123°41'24" W	Moderate exposure	Bedrock + cobble	30°	13.45

*: Density refers to red sea urchin density (number of urchins per m^2)

At Tofino, sites were generally more exposed and had lower algal abundance than sites in the other areas. Algal abundance at Tofino was low because the slope was steep and a dense urchin band limited the lower distribution of the algae. At the most exposed sites, *Postelsia palmaeformis* Ruprecht was found in the intertidal and *Lessoniopsis littoralis* (Tilden) Rienke in the shallow subtidal. All sites in that area generally had similar algal communities; the shallowest part of the subtidal zone was dominated by surf grass (*Phyllospadix scouleri* Hooker), followed by a zone of *Laminaria setchellii* Silva, *Nereocystis luetkeana*, *Calliarthron* sp. (an articulated coralline), and *Pterygophora californica* Ruprecht. *Egregia menziesii* (Turner) Areschoug was also present in the shallow subtidal at some sites. *Nereocystis* was found at all sites, *Pterygophora* however was less abundant or absent at the most exposed sites. At most sites, the zone below the algal fringe was a typical urchin barren with very little algae except for red corallines. However, *Desmarestia* sp. was sometimes present below the algal fringe. Drift material was not very abundant and consisted largely of sea grasses (*Zostera marina* or *Phyllospadix scouleri*).

At Alert Bay, *Nereocystis* was the dominant algal species at all sites. *Laminaria saccharina* (L.) Lamouroux, *Alaria* sp. and *Costaria costata* (Agardh) Saunders were common in the shallow subtidal and at greater depths, *Agarum* spp. was abundant. There was relatively little variation in the algal community between sites. Total algal abundance was much greater at Alert Bay than Tofino. *Nereocystis* was not only more abundant but also larger and the algal zone was wider since the slope was generally gentler and the upper limit of the urchins deeper at Alert Bay than Tofino. Drift kelp, mostly *Nereocystis*, was very abundant at Alert Bay (observation by diving on the sites) and urchins were often seen, during the survey, feeding in areas where drift kelp was trapped.

At Campbell River, the urchins were found in a dense *Nereocystis* bed rather than at the kelp bed's margin. *Nereocystis* was therefore readily available. *Alaria* sp., *Sargassum muticum* (Yendo) Fensholt, *Ulva* sp. and *Ulvaria obscura* (Kutzing) Gayral were also abundant. The substrate was almost flat, at ca. 9 m deep, at Campbell River so algal abundance was high.

At Kendrick Island, *Nereocystis* was again the dominant species. *Alaria* sp., *L. saccharina*, *Agarum* spp. and the red algae *Gigartina* sp. were also common. The algal band was relatively wide so algal abundance was high.

At all sites, exposure to waves and storms and/or water movement was estimated on a semi-quantitative scale: 1) moderate exposure, 2) strong tidal flow, 3) high surge, 4) high exposure (Table 3.1). Although strong tidal flow might involve more water movement than moderate exposure, the latter involves more wave action. Exposure to waves and storms and/or water movement will later be referred to as exposure.

Survey Methods

At each site, urchin density, i.e., number of urchins per square meter, was measured by SCUBA divers using 1 m^2 quadrats along a 20 m transect line set perpendicular to the shoreline. The survey started at the shallow end of the urchin distribution. The divers worked their way down until reaching either a distance of 20 m from the start of the survey, or, the end of the urchin distribution (most often this occurred when the substrate changed from rock to sand). At the end of the survey, the divers came back up to the shallow end of the urchin distribution (the feed line) and collected a sample of urchins. Five urchins in each 10 mm size class between 70 mm TD and the largest size present at the site (ca. 120 - 140 mm TD) were collected and brought to the laboratory for dissections. All sites in the 4 areas were sampled between July 4 and July 27, 1994.

Dissection Methods

In the laboratory, the urchins were measured, TD and TH (to the nearest millimeter), and weighed (to the nearest 0.1 g). The urchins were then cracked open, with an urchin cracker (used in urchin processing plants), and flipped upside down to drain out the coelomic fluid. After ca. 1 min the drained weight was measured and the food was removed from the guts, placed in labeled

plastic bags and frozen for later diet analysis. The gutted weight was measured and the Aristotle's lantern taken out, placed in a labeled bag and frozen for later determination of jaw length. The food weight in the urchin was calculated as the difference between the drained weight and gutted weight. The gonads were removed from the urchin, weighed, and their color and texture were determined. Gonad color was recorded on a scale from 1 to 3: 1 = yellow (high quality); 2 = yellow with other colors, and 3 = brown (low quality) gonads. Texture was also recorded on a scale from 1 to 3: 1 = firm (high quality); 2 = semi-firm, and 3 = flimsy (low quality) gonads.

For each site, 10 urchins within the sample dissected were randomly subsampled for estimation of the relative abundance of the different food items constituting the diet (see Chapter 4 for detailed methods). Diet items were grouped in 7 categories: (1) *Nereocystis*, (2) other brown algae, (3) total brown algae, (4) eel grass, (5) foliose green algae, (6) foliose red algae and (7) other food items. The categories were chosen as the food items believed to have an important role in urchin nutrition based on their prevalence in the diet at one or several of the sites. The eel grass category includes both the eel grass *Zostera marina* and the surf grass *Phyllospadix scouleri* but is referred to as eel grass since *Phyllospadix* abundance was relatively low (see Chapter 4).

Bleaching of the Aristotle's lanterns and later measurements of demipyramid (jaw) length followed the same methodology used in the laboratory experiments (Chapter 1).

Statistical Analyses

The relationship between density and the amount of food contained in urchins was studied with a bivariate regression of the $\log_e$ of food weight vs. TD and density.

The effects that density, TD, food weight and relative abundance of the different food items have on jaw length and gonad weight were analyzed with backwards stepwise regressions, using $p > 0.1$ to remove and $p < 0.05$ to enter (Sokal and Rohlf 1981). Residuals were plotted and when necessary, i.e., in the case of gonad weight, the $\log_e$ transformation was used. The backwards stepwise regressions were first run without taking diet into account, thus allowing all

653 urchins (from the 4 areas) to be included in the analyses. They were then run, including diet related variables, which included 250 urchins. These analyses did not take into account area and site effects. A nested Anova, where sites were nested within area, was used to test for area and site effects.

Gonad color and texture are rank data and are therefore not continuous so non parametric tests were used. The Spearman correlation coefficients and their p values, between color and density, TD, TH, total weight, gonad index, jaw length, JL:TD, food weight and relative abundance of the food items were calculated to determine which variables influenced color. The same analysis was conducted for gonad texture.

Results

Regression analysis of the $\log_e$ of food weight against density and TD showed food weight to increase significantly ($p=1x10^{-13}$) with TD and decrease significantly with density ($p=1x10^{-13}$); supporting the hypothesis that urchins have less food available to them as density increases. Diet also tends to change with density, e.g., *Nereocystis* abundance in the diet decreased with increasing density (Spearman correlation coefficient = -0.580, $p < 0.0001$) while eel grass abundance increased with density (Spearman correlation coefficient = 0.696, $p < 0.0001$).

The regression analysis, without taking diet into account, showed jaw length to be positively correlated with density and test diameter and negatively correlated with gonad index (Table 3.2). When the abundance of the different food items in the diet was included in the model, test diameter and gonad index were still correlated with jaw length but density did not have any effects. However, the relative abundance of all brown algae was negatively correlated with jaw length, i.e., jaw length decreased with increasing amounts of brown algae in the diet. Food weight was one of the variables included in the models (with and without including diet) before running the stepwise process. In both cases, food weight was dropped out of the model since it did not influence jaw length significantly.

Table 3.2: Backwards stepwise regression models, for jaw length and $\log_e$ of gonad weight of wild red sea urchins, from 25 populations located in 4 areas around Vancouver Island, with or without taking diet into account in the analyses. Stepwise process run using $p < 0.05$ and $p > 0.10$ to enter or remove, respectively, a variable from the model.

	Jaw Length			$\log_e$ Gonad Weight		
	Variable*	Regression Coefficient	p value	Variable*	Regression Coefficient	p value
Without taking diet into account	Constant	5.275	10^{-15}	Constant	2.198	$2x10^{-10}$
	Density	0.020	0.003	Density	-0.009	0.0003
	Test Diameter	0.135	10^{-15}	Test Diameter	0.030	10^{-15}
	Gonad Index	-0.051	$7x10^{-9}$	JL/TD	-0.077	$3x10^{-7}$
				Food Weight	-0.002	0.018
	n= 650 r^2= 0.764 **p= 10^{-15}			n= 648 r^2= 0.633 **p= 10^{-15}		
Taking diet into account	Constant	5.878	10^{-15}	Constant	1.643	0.003
	Test Diameter	0.135	10^{-15}	Test Diameter	0.031	10^{-15}
	Gonad Index	-0.050	0.0007	JL/TD	-0.053	0.016
	Total Brown Algae	-0.005	0.024	Food Weight	-0.003	0.0004
	Foliose Red Algae	-0.023	0.058	*Nereocystis*	0.002	0.022
				Eel Grass	-0.006	0.0001
				Other Foods***	-0.003	0.035
	n= 246 r^2= 0.770 **p= 10^{-15}			n= 245 r^2= 0.699 **p= 10^{-15}		

*: Refers to variables that the backwards stepwise regression model kept. See text for a list of the variables included in the model at the beginning.

**: Refers to the p value for the whole model.

***: See text for a description of what is included in "Other Foods".

r^2 = coefficient of determination, indicates the proportion of variation explained

n = sample size

Regression analyses showed the $\log_e$ of gonad weight to be negatively correlated with density and JL/TD and positively correlated with TD (Table 3.2). Food weight effect was significant but the relationship between gonad weight and food weight was negative rather than the expected positive relationship. Similarly to the situation with jaw length, density drops out of the model once diet is taken into account. Gonad weight increases with the amount of *Nereocystis* in the diet and decreases with increasing amounts of eel grass and "other foods" (see Materials and methods). The relationships between gonad weight and test diameter, JL/TD and food weight are still significant when diet is taken into consideration.

Gonad color increased with urchin size, i.e., TD, TH and total weight (Table 3.3). Color increased with jaw length but not with JL/TD, suggesting that the effect of jaw length was related with urchin size. Color decreased (improved) with gonad index indicating that when gonad index was low, color was poor and good color was associated with high gonad indices. Color was positively correlated with texture. Diet also influenced color, increasing amount of *Nereocystis* and total brown algae consumed improved color whereas increasing amounts of eel grass in the diet caused color to deteriorate. Texture was negatively correlated with gonad index, i.e., urchins with a low gonad index had softer gonads while urchins with a high gonad index had firmer gonads. Texture was influenced by diet in a similar manner as color was. All three indicators of gonad quality thus improve together.

The nested Anova, testing for area and site effects (Table 3.4) showed highly significant effects of both area and sites on jaw length and the $\log_e$ of gonad weight. The area and site effects were hard to separate from the effects of the variables included in the stepwise regressions since some of these variables are correlated with area and site, e.g., high densities, high importance of eel grass and lower importance of *Nereocystis* occurring mainly at Tofino. The fact that the stepwise regressions showed significant effects of some food items, etc., in spite of not taking area and site effects into consideration, suggests that the effects shown in the stepwise regressions must be important.

Table 3.3: Spearman correlation coefficients between gonad color and gonad texture of wild red sea urchins, from 25 populations located in 4 areas around Vancouver Island, and the variables affecting them.

Color			Texture		
Variable	Correlation Coefficient	p value*	Variable	Correlation Coefficient	p value*
Test height	0.261	0.0001	Gonad index	-0.242	0.0001
Test diameter	0.230	0.0002	Gonad color	0.192	0.0013
Total weight	0.233	0.0001	*Nereocystis*	-0.190	0.0015
Gonad index	-0.216	0.0004	Total brown algae	-0.243	0.0001
Gonad texture	0.192	0.0013	Eel grass	0.192	0.0013
Jaw length	0.325	0.0001	Other food items	0.194	0.0012
Nereocystis	-0.153	0.0084			
Total brown algae	-0.191	0.0014			
Eel grass	0.197	0.0011			

*: Using the normal approximation, n = 245.
A negative correlation coefficient means that color, or texture, improves (decreases) with an increase in the associated variable.

Table 3.4: Nested analysis of covariance of jaw length and $\log_e$ gonad weight of wild red sea urchins, from 25 populations (sites) located in 4 areas around Vancouver Island, to test for effects of test diameter, area and site (nested within area).

Dependant Variable	Source of Variation	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	P Value
Jaw Length	Test Diameter	3229.9	1	3229.9	3531.3	10^{-15}
	Area	268.3	3	89.4	97.8	10^{-15}
	Site {Area}	259.5	21	12.4	13.5	10^{-15}
	Error	580.8	635	0.9		
$\log_e$ Gonad Weight	Test Diameter	160.5	1	160.5	1550.0	10^{-15}
	Area	8.7	3	2.9	27.9	10^{-15}
	Site {Area}	62.3	21	3.0	28.7	10^{-15}
	Error	66.0	637	0.1		

Site {Area} refers to site effects with site nested in area.

Maximum TD in the population at each site was obtained from size-frequency distributions of ca. 450 individuals per site (Alan Campbell pers. comm.). There was a weak (r^2= 0.219) but significant (p= 0.018) relationship between maximum TD in the population and population density (Figure 3.2).

The effect of exposure on skeleton weight was studied with a One-way Ancova (Table 3.5). Wet weight of the skeleton was calculated as the gutted weight minus the gonad weight and therefore includes the test, spines, lantern and gut. Skeleton weight was $\log_e$ transformed to normalize the data. There were highly significant effects of exposure and TD on skeleton weight. Adjusted means and Bonferroni pairwise comparisons (Table 3.5) showed that the skeleton weight at the two highest exposure levels were not significantly different while other pairwise comparisons were. Skeleton weight generally increased with exposure, except for exposure 2 (strong tidal flow) where it was lower than at exposure level 1 (moderate exposure). However, moderate exposure involved more wave action than strong tidal flow.

The relationship between gonad index (arcsine transformed) and TD and skeleton weight showed that gonad index increased with TD but decreased with increasing relative test weight (Table 3.6). However, this relationship was quite weak (r^2= 0.139).

Discussion

Jaw Length

Previous studies have associated increases in relative jaw size with decreasing food availability, without always measuring the latter, e.g., Black et al. (1982). In wild red sea urchins, food quality affected jaw size rather than food quantity. T. Morris and A. Campbell (pers. comm.) showed, in the laboratory, that JL/TD was higher in juvenile red urchins fed low quality food (eel grass, *Zostera marina* L.) -- even when food was provided in excess -- compared to that of urchins fed good quality food (*Nereocystis*). In this study, there was a negative relationship between jaw

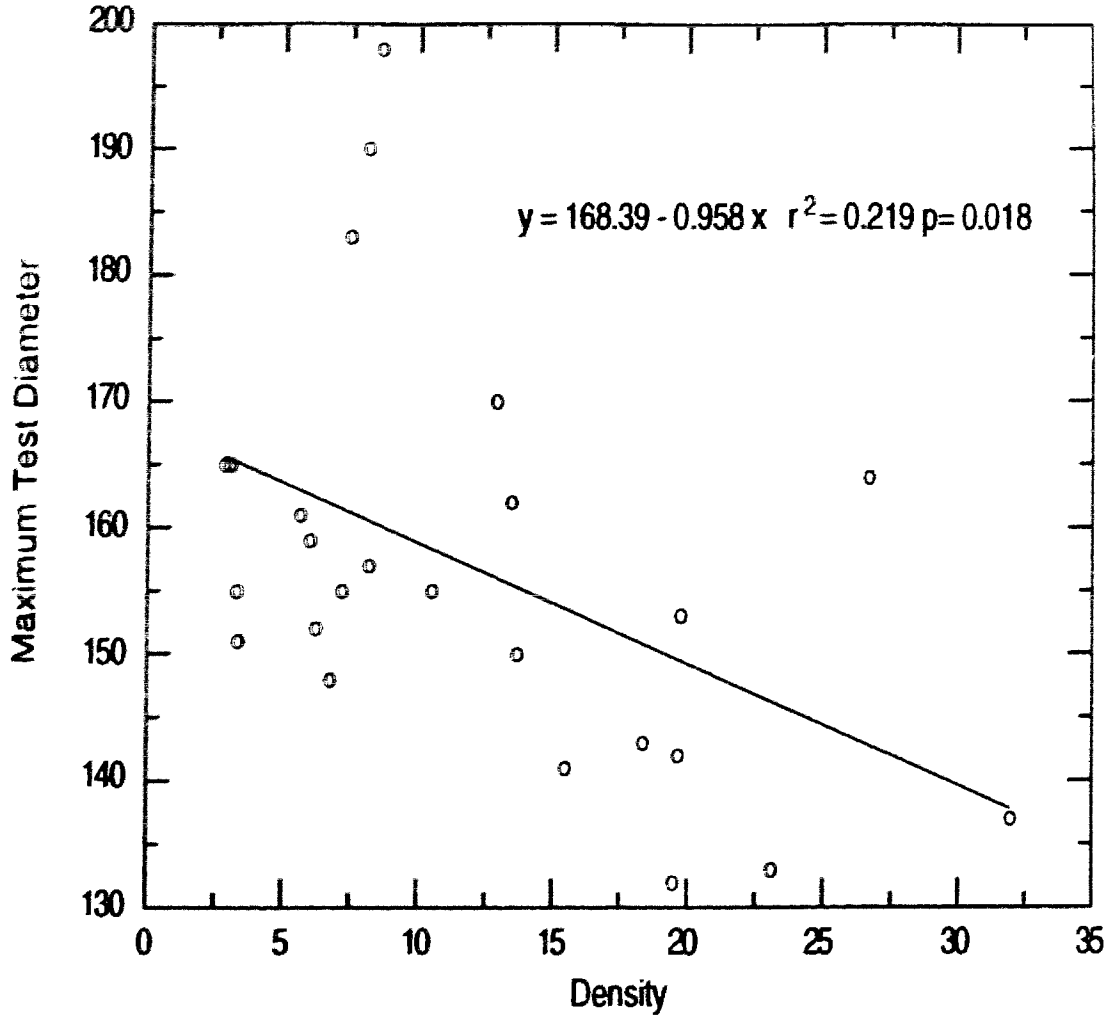

Figure 3.2: Maximum test diameter (mm) of wild red sea urchins, in each of 25 sites located in 4 areas around Vancouver Island, in relation to population density (urchins/m^2).

Table 3.5: Analysis of covariance and Bonferroni pairwise comparisons to test for effects of exposure and test diameter on the $\log_e$ of skeleton weight of wild red sea urchins from 25 populations located in 4 areas around Vancouver Island.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Squares	F Ratio	P Value
Exposure	2.883	3	0.961	37.825	0.000
Test Diameter	114.521	1	114.521	4507.559	0.000
Error	16.514	650	0.025		
n= 655					

Exposure Level	Adjusted Mean Skeleton Weight (g)*	Significance Test**
1 Moderate	191.713	b
2 Strong Tidal Flow	181.278	a
3 High Surge	211.030	c
4 High Exposure	216.372	c

*: Adjusted means of log-transformed data were back transformed to the original units, i.e., grams.

**: Bonferroni pairwise comparisons, exposure levels with different letters are significantly different from one another at p= 0.001.

Table 3.6: Bivariate regression of gonad index (arcsine transformed) of wild red sea urchins, from 25 populations located in 4 areas around Vancouver Island, as a function of test diameter and skeleton weight.

Variable	Regression Coefficient	p value
Constant	0.132	$4x10^{-6}$
Test diameter	0.004	10^{-15}
Skeleton weight	-0.0005	$5x10^{-9}$
n= 655, r^2= 0.139, F= 52.830, p= 10^{-15}		

length and the relative abundance of "total brown algae" (mostly *Nereocystis*) in the diet, which supports the findings of Morris and Campbell (unpublished data).

Food weight contained in the urchins did not have a significant effect on jaw length, despite the fact that food weight decreased with density. However, the amount of food in the guts is probably highly variable in time and the samples taken are only a "snapshot" (instantaneous) view whereas jaw length is a parameter that changes over longer periods. The evidence from other species and the results of my laboratory experiments (Chapter 2) show that the amount of food available undoubtedly influences relative jaw size of urchins. The results presented here, however, show that diet is another factor that can influence relative jaw size, as shown by T. Morris and A. Campbell (unpublished data), and that in the wild, diet might influence relative jaw size to a larger extent than food availability does, at least for the red sea urchin.

The only other study of jaw size in wild red sea urchins is that of Ebert and Russell (1992) in which they did not find differences in jaw size between two locations, despite differences in growth rates. They suggested that available food was the same or that development of Aristotle's lantern in these animals is more canalized than it appears to be in other species of echinoids that have been studied. Jaw plasticity in red sea urchins had not been studied in the laboratory at the time of Ebert and Russell's (1992) paper, but the present study (Chapters 2 and 3) clearly shows that jaw plasticity occurs in red sea urchins.

Gonad Condition

Gonad size has been shown to be dependent on food supply and/or diet (Frantzis and Gremare 1993, Gonor 1973, Keats et al. 1983, 1984, Chapter 2) in the wild and in the laboratory. Diet influenced the gonad weight of red urchins; gonad weight increased with increasing amounts of *Nereocystis* in the diet but decreased with increasing amounts of eel grass and "other foods" (see Materials and Methods). Possible reasons for diet effects are discussed below.

Druehl and Breen (1986), Harrold and Reed (1985), Pearse (1980) and others showed differences in gonad indices between locations, associated with feeding conditions for the red urchin. Gonad index generally decreases with low food abundance. A significant effect of food weight in the guts of the urchins was found here but the relationship between food weight and gonad weight was negative when a positive one was expected. However, the regression coefficient for food weight (-0.002 or -0.003 depending on the regression model) is relatively small. Keats et al. (1984) noted that as the gonads develop, there is less room in the test for food material. This seems like the only explanation for the decrease in food weight with increasing gonad weight observed here. As noted previously, the estimate of food weight might not be very reliable. If the amount of algae present at each site is used as an indicator of food abundance, the results are more typical. Gonad weight decreased with density and generally high density sites had much less food available than lower density ones (pers. obs.).

The nutritional state of echinoids is reflected in their gonadal development (Kenner and Lares 1991). The negative relationship observed between jaw length and gonad index, or similarly between gonad weight and JL/TD, shows that when jaws are larger, due to poor feeding, gonads are small in the field and confirms the laboratory results. Black et al. (1984) similarly showed gonads to be smaller in urchins (*Echinometra mathaei*) with larger lanterns from wild populations with different densities and suggested that the food supply of animals with relatively large lanterns may be poor, because they also have small gonads.

Color of the gonads is largely affected by the type of food eaten (Mottet 1976) and food supply (Bernard and Miller 1973). Gonad color and texture both improve with increasing amount of *Nereocystis* and total amount of brown algae in the diet, and decrease with amount of eel grass. Gonad color is better in smaller urchins, as noted by the fishers, which is one of the reasons why the west coast fishers are asking for the lower size limit to be lowered (A. Campbell pers. comm.). Texture however is independent of size. Color and texture are positively correlated and therefore tend to improve together. They also improve with increasing gonad index showing a trend for all aspects of roe quality to improve together. Targeting harvest sites with abundant brown algae and

little eel grass would therefore be a good strategy for the fishers to obtain a high quality product. Bernard (1977) reported that texture changed at different times of the year in a population of red urchins from Amphitrite Point, B.C. However, I do not have any data to confirm this finding.

Analyses without taking diet into account showed density effects, for both jaw length and gonad weight. However, once diet was included in the analyses, density did not have significant effects while the abundance of some food items (in the diet) did. The effects of density were thus not direct but rather indirect, due to the change in diet at high density. As density increased, the amount of *Nereocystis* in the diet decreased while that of eel grass increased. These changes in the diet, associated with changes in density, in turn affected jaw length and gonad weight. The effects of density were therefore not due to crowding. Levitan (1989) showed in the laboratory that food level affected TD and gonad volume in *Diadema antillarum*, but that density (crowding) did not.

The effects of diet on gonad index and relative jaw size can be explained by urchin feeding behavior and physiology. This study and the one by T. Morris and A. Campbell (unpublished data) showed seagrasses to produce low somatic and/or gonadal growth in red urchins. Surf-grass (*Phyllospadix* spp.) is not a preferred food of urchins (see Lawrence 1975, Paine and Vadas 1969 b). Feeding rates are generally correlated with food preference (Frantzis and Gremare 1993, Larson et al. 1980, Vadas 1977). Low feeding rates on less preferred foods often translate to lower caloric intake (Larson et al. 1980, Vadas 1977) and thus less resources for growth and reproduction.

Another factor that can be of influence is difference in quality of the different food items. Quality can be considered to be all characteristics of food that affect its use as a nutrient (Lawrence and Lane 1982). These characteristics include those which affect 1) consumption rate, 2) digestibility, 3) absorption and 4) composition (Lawrence and Lane 1982). Paine and Vadas (1969 b) showed that the surf grass *P. scouleri* has a slightly higher energy content than *Nereocystis* (4.41 vs. 4.38 kcal/ash-free g dry weight). Therefore, caloric content cannot be the cause of differences in quality. However, there are large differences in absorption rates of

echinoids fed different macrophytes (Frantzis and Gremare 1993). *S. intermedius* shows considerable ability to digest the main components of the kelp *Laminaria longissima* except for crude fiber (Yano et al. 1993). There is little digestion and absorption of structural carbohydrate (Lawrence and Lane 1982). Seagrasses probably contain much more crude fiber and/or structural carbohydrates than kelp which could explain why they produce low growth despite their high caloric content. Absorption efficiency of seagrasses is lower than that of several species of kelps (see Table 7 in Lawrence 1975), supporting this hypothesis.

The poor gonad condition and large relative jaw size, at high densities, could thus result from low feeding rate -- and consequently low caloric intake -- on eel grass, or from the lower quality of eel grass as a nutrient (compared to *Nereocystis*), or from a combination of these two factors. The reproductive success of *S. droebachiensis* appears to be contingent more upon quality rather than the availability of food (Vadas 1977). My results suggest that this is also true for wild populations of red urchins.

Maximum Test Diameter

Maximum size of *S. franciscanus* decreased with density. Differences in maximal and/or mean sizes of urchins in wild populations have been interpreted as the result of differences in food levels (Ebert 1968, reviewed in Lawrence and Lane 1982, Levitan 1988 b). Maximum body size is variable since a given quantity and quality of food should have a limit to the size of individual it can support (Lawrence and Lane 1982). Maximum body size in a population can therefore be used as an indicator of the potential for growth of individuals of that populations. The maximum body size indicates the size that individuals can attain under the local conditions. For urchins, food is not a limiting factor to numbers but only to biomass (Ebert 1968), i.e., high numbers of urchins can persist despite low food availability. Within dense populations, urchins compete for the sparse quantity of food available and, as a result the urchins' growth rate is extremely reduced

(Himmelman et al. 1983). Since less food is available per individual at high density, the maximum size that can be supported decreases.

Effect of Exposure

Ebert (1982) showed that survival rates, and consequently longevity, of urchins are influenced by exposure; species of urchins with a larger relative body wall have better survival -- for a given exposure -- than species with relatively smaller body walls. It is likely that within-species' differences in relative body wall size under different exposure regimes, as presented here, similarly influence survival.

Building a relatively larger body wall requires more resources for both growth and maintenance (see Ebert 1982). A larger proportion of available resources would thus be invested in the body wall. Furthermore, urchins in high surf areas might have less energy available to them for two reasons. First, surf action may affect available feeding time (Swan 1961). Second, urchins in shallow water on exposed shores are generally much harder to remove from the substrate than urchins in deeper or sheltered waters (pers. obs.), suggesting that they spend more energy to hold on to the substrate. Thus, if urchins in exposed areas have less resources and spend a relatively larger amount of them towards the body wall, one would expect that less resources would be available for other functions, including reproduction. The observed decrease in gonad index associated to increases in skeleton weight supports this hypothesis.

Caution must be taken when drawing conclusions from these results since my measurements of skeleton weight included both Aristotle's lantern and gut weight, in addition to test and spine weight. Using only test-and-spine weight would give more convincing results but the trend of decreasing gonad index with increasing skeleton weight, along with the increase in skeleton weight with exposure, does suggest that the shift in resource allocation described above takes place.

Conclusions

The effects of density on sea urchin jaws and gonads are indirect effects due to the changes in diet associated with increasing urchin densities. As expected, relative jaw size increases while gonad weight decreases with increasing population density. Although food weight contained in the urchins decreased with density, jaw size was not affected by food weight. The effects of diet on gonad weight and jaw size are probably related to differences in the value of the foods eaten at different densities.

Maximum TD of red sea urchins decreases with increasing population density. Poor feeding conditions at high densities cannot support as large a body size as the better feeding conditions found at lower densities.

Results suggest that exposure increases relative skeleton weight of red urchins. The shift in resource allocation towards the skeleton decreases energy available for reproduction as seen in the decreasing gonad index. Further investigations of this relationship would be desirable since the methods used here are possibly biased since "skeleton" weight included the lantern and gut.

Chapter 4

Diet of red sea urchins in southern British Columbia

Introduction

Harrold and Reed (1985), Irvine (1973) Mattison et al. (1977) and Vadas (1977) studied the diet of the red sea urchin. Harrold and Reed (1985) and Vadas (1977) showed differences in the diet and gonad index of red urchins between sites and associated the latter with differences in food quantity and quality. Studies comparing differences in diet between sites (Harrold and Reed 1985, Irvine 1973, Mattison et al. 1977, Vadas 1977) were done on a small spatial scale (< 50 km, sometimes < 1 km). No study, to my knowledge, has investigated large scale differences in diet of the red urchin and, despite the number of studies of diet from different areas, comparisons are somewhat difficult since methods used to estimate diet are often not the same, e.g., field observations vs. gut contents. Also, the number of sites where diet was investigated in each of the previous studies is generally limited.

The objectives of this study were, first, to develop a methodology for identification of the food items found in red sea urchin guts. Second, to obtain quantitative estimates of the relative abundance of food items, in the red sea urchin's diet, to determine which food items are the most important and, how diet changes spatially (between 25 sites) at two scales: large scale, between areas, and small scale, between sites within an area. Third, to determine the effects of the relative abundance of the different food items, in the red sea urchin's diet, on the gonad condition and jaw size of wild red sea urchins (Chapter 3).

Materials and Methods

Urchins generally cut their food in small pieces (pers. obs.) making the identification of the partly digested food items difficult, especially for food items with a similar structure. A laboratory experiment was conducted before the analysis of diet of wild urchins to increase the accuracy of species identification.

Laboratory Experiment

The appearance of the presumed main food items, after their ingestion and partial digestion by urchins, was investigated in the laboratory. Ten species of brown algae were chosen: (1) *Agarum* spp., (2) *Alaria* sp., (3) *Desmarestia* sp., (4) *Egregia menziesii*, (5) *Laminaria saccharina*, (6) *Laminaria setchellii*, (7) *Macrocystis integrifolia*, (8) *Nereocystis luetkeana*, (9) *Pterygophora californica*, (10) *Sargassum muticum*. The choice of these species as potentially important diet items was based on two criteria. First, if direct observations of urchins feeding on a given species of algae were made in the field or, second, if a species was relatively important at any of the field sites surveyed. Each selected species was fed to two starved (for 5 to 7 months) urchins (73 - 98 mm TD) for 5 days. On the fifth day, the urchins were dissected to remove the gut contents. The partially digested food was then diluted in seawater and observed under a dissecting microscope. General appearance, color, thickness, structure, i.e., layering of cells seen in a cross section, and firmness of the algae were recorded for each species. Photographs under different magnifications were taken for later reference and the gut contents of each urchin were frozen for later reference as well.

Diet of Wild Urchins

For each of the 25 field sites surveyed (see Chapter 3), 10 urchins, from the sample dissected, were randomly chosen for analysis of their gut content. During the field dissections, gut contents of all urchins were kept in individual plastic bags and frozen for later analysis. In the laboratory, samples were thawed and sorted to remove any pieces of gut wall or other urchin parts from the food. The gut contents were then mixed thoroughly and a subsample was taken. Enough food was taken in the subsample to cover the bottom of a petri dish with a uniform layer of food -- one food item thick -- after spreading the subsample with seawater. The petri dishes had a grid with 37 intersection points on the bottom. Quantitative estimation of the relative abundance of each food item was performed, under a dissecting microscope, by identifying the food items present at each intersection point of the grid. The relative abundance of each food item was then calculated as:

$$\text{Percent Relative Abundance} = \frac{\text{Count for Food Item}}{\text{Total Count}} \times 100$$

where the Total Count is the total number of all food items counted, i.e., 37 minus the number of blank intersection points.

Statistical Analysis

The differences in abundance of the various food items within an area and in different areas were compared using non parametric tests because the data were not normal and could not be brought to normality by transformation. The abundances of all diet species were compared together, to establish if any species were more important than others, using a Kruskal-Wallis test. This was performed for all areas together and each area individually. Mann-Whitney U tests were

then used for pairwise comparisons between food item pairs to determine which food items were more important, again, for all areas together and for each area individually.

A second analysis was performed, for each food item individually, using a Kruskal-Wallis test to see if the importance of food items changes with area. The same analysis was also performed to see if the importance of food items changes between sites within an area. The latter analysis was done for Tofino and Alert Bay only since these are the only areas with several sites (See Chapter 2). For the analysis between areas, Mann-Whitney U tests were then used for pairwise comparisons, between area pairs, to determine at which area each food item was more important.

Results

The laboratory experiment allowed the presumed main food items to be identified after they have been ingested and partly digested. Most species had characteristics that enabled relatively easy identification although several pairs of species were very similar and thus harder to identify accurately. For example, *Alaria* sp. and *Agarum* spp. were very similar to one another but very different from all other species. Knowing the appearance of main food items after their ingestion allowed for more accurate identification of the food items present in wild urchins.

A total of 44 food items were identified in wild urchins (Table 4.1); in several cases, identification to species level was impossible because only part of an organism was present or because of partial digestion. Unidentified foliose red algae probably included *Porphyra* sp., *Iridaea* sp. and *Smithora naiadum* (Anderson) Hollenberg which grows abundantly on surf grass at Tofino. Coralline algae included *Calliarthron tuberculosum* (Postels *et* Ruprecht) Dawson, *Melobesia mediocris* (Foslie) Setchell *et* Mason, which grows on eel grass, and encrusting species. The crabs found in urchins were generally small unidentified crab legs only. The eel grass category included both *Zostera marina* and *Phyllospadix scouleri.* No attempt was made to separate these species from one another. However, most of the seagrass found in urchin guts (mainly at Tofino)

Table 4.1: List and frequency of occurrence (% of urchins that had the type of food in their guts) of food items found in the gut contents of wild red sea urchins in 4 areas around Vancouver Island. Sub-categories with a + denote food items that were found in the diet at a given location but for which the frequency of occurrence was not separated from that of the other items in the given category.

	Area			
Food Item	Tofino	Alert Bay	Campbell R.	Kendrick Is.
	n= 110	n= 120	n= 10	n= 10
Brown Algae				
• *Agarum* sp.	-	15.0	-	10.0
* *Alaria* sp.	21.7	4.2	80.0	50.0
Costaria costata	-	0.8	-	-
* *Desmarestia* sp.	27.5	-	-	-
• *Egregia menziesii*	5.0	-	-	-
• *Laminaria saccharina*	-	5.8	-	-
• *Laminaria setchellii*	12.5	0.8	-	-
• *Nereocystis luetkeana*	39.2	99.2	90.0	70.0
* *Pelvetiopsis limitata*	3.3	-	-	-
* *Pterygophora californica*	20.8	-	-	-
• *Sargassum muticum*	9.2	36.7	60.0	20.0
Unidentified filamentous	-	0.8	-	-
Green Algae				
* Foliose	43.3	48.3	100.0	30.0
Ulva sp.	+	+	+	+
Ulvaria obscura	-	+	+	-
Enteromorpha sp.	+	+	+	+
• Filamentous				
Cladophora sp.	-	0.8	-	-
Unidentified	20.0	-	-	-
Red Algae				
• Foliose	39.2			80.0
Gigartina sp.	+	-	-	+
Unidentified	+	14.2	-	+
* Branched	53.3	20.0	10.0	20.0
Sarcodiotheca sp.	+	-	-	-
Endocladia muricata	+	-	-	-
Polysiphonous	+	+	+	+
Unidentified	+	+	+	+
* Corallines	49.2	6.7	-	-
* Eel grass	77.5	3.3	-	-

continued on next page

Table 4.1 *continued*

Food Item	Area			
	Tofino	Alert Bay	Campbell R.	Kendrick Is.
	n= 110	n= 120	n= 10	n= 10
* Terrestrial plants	7.5			
Unidentified leaf	+	2.5	-	-
Tree bark	+	-	-	-
Wood	+	-	-	-
* Invertebrates				
Bryozoa	4.5	20.0	90.0	40.0
Membranipora membranacea	+	+	+	+
Unidentified bryozoans	+	+	+	+
Cructacea	29.1**	13.3**		
Amphipods	2.7	-	-	-
Cirripeds (barnacles)	+	+	-	-
Crabs	17.3	1.7	-	-
Crab megalops larvae	0.9	-	-	-
Cumaceans	-	0.8	-	-
Unidentified crustaceans	+	+	-	-
Gastropods, unidentified	0.9	0.8	-	-
Hydrozoans	37.3	3.3	-	20.0
Polychaetes, unidentified nereid	0.9	-	-	-
Sipunculid (peanut worms)	0.9	-	-	-
Ascidians (tunicates)	0.9	-	-	-
* Unidentified	84.2	30.0	100.0	20.0
Diatoms	-	+	+	-
Eggs	0.9	-	-	-

The food item categories with an * were those used in the statistical analyses.
**: Frequencies of occurrence of barnacles and unidentified crustaceans pooled.
- denotes a food item that is absent in the diet in an area.
n = number of urchins whose gut content was analysed.

was probably drifting *Zostera* that was carried to the sites by tidal currents from the abundant *Zostera* beds in Clayoquot Sound. The *Laminaria setchellii* category might also have included some *L. groenlandica* Rosenvigne which is very similar in appearance to *L. setchellii*.

Food diversity, i.e., number of different food items found in an area, was higher at Tofino than Alert Bay and much lower at Campbell River and Kendrick Island than in the first two areas. However, 10 urchins only were analyzed at Campbell River and Kendrick Island while 110 were analyzed at Tofino and 120 at Alert Bay so the differences in food diversity might be due to sample size rather than to true differences. For Tofino and Alert Bay the large and similar sample sizes suggest that the differences between these two areas are true differences in diet diversity in red sea urchins. Overall, 13 out of the 44 food items identified were invertebrates, 24 were algae and 7 were in other categories, showing that red sea urchins in British Columbia eat a wide variety of food items including several types of invertebrates.

Differences in the abundance of food items in the diet within areas

For the analyses of relative abundance of each food type, the number of categories was reduced to 19 by grouping some food items together (Table 4.1). Kruskal-Wallis analyses were used to check if some food items were more abundant than others in the diet of red sea urchins. Significant differences were found for all areas together and each area individually ($p = 0.000$ for areas pooled, Tofino and Alert Bay, $p = 0.003$ for Campbell River and $p = 0.005$ for Kendrick Island). This indicates that at least one of the food items is more important in the diet than the other ones. Pairwise comparisons were used to determine which food items were more important than others for all areas grouped and for Tofino and Alert Bay individually. Pairwise comparisons were not performed for Campbell River and Kendrick Island since only 10 urchins were analyzed in these areas; the mean percent relative abundance of the food items only is presented (Table 4.2). Overall, i.e., when grouping areas (Table 4.2), *Nereocystis luetkeana* was the dominant food item, followed by eel grass. Unidentified food items ranked third although their abundance was not

Table 4 2: Mean percent relative abundance of each food item found in the guts of wild red sea urchins from 4 areas around Vancouver Island. Data presented for all areas pooled and each area individually. Pairwise comparisons between food items were made by Mann-Whitney U test.

All areas		Tofino		Alert Bay		Campbell River		Kendrick Island	
n=250		n=110		n=120		n=10		n=10	
Nereocystis	46.423	Eel grass	25.115	*Nereocystis*	75.623	*Nereocystis*	41.998	*Nereocystis*	41.953
Eel grass	11.117	*Nereocystis*	15.377	Fol. green algae	8.016	Fol. green algae	25.653	*Alaria*	21.443
Unidentified	7.895	Unidentified	13.943	*Agarum*	3.964	Unidentified	10.331	Fol. red algae	15.941
Fol. green algae	7.562	Branch. red algae	8.062	*Sargassum*	3.818	Invertebrates	9.287	*Agarum*	10.000
Branch. red algae	4.285	*Desmarestia*	7.142	Unidentified	2.734	*Alaria*	7.625	Branch. red algae	4.000
Invertebrates	3.978	Fol. green algae	5.903	Invertebrates	1.997	*Sargassum*	4.821	Fol. green algae	2.279
Desmarestia	3.154	Invertebrates	5.862	Branch. red algae	1.181	Branch. red algae	0.286	*Sargassum*	1.818
Agarum	2.303	Coralline algae	4.726	*L. saccharina*	0.789			Invertebrates	1.708
Sargassum	2.256	*L. setchellii*	4.558	Fol. red algae	0.775			Unidentified	0.857
Coralline algae	2.255	Fol. red algae	2.621	Coralline algae	0.366				
Alaria	2.234	*Alaria*	2.100	*Alaria*	0.306				
Fol. red algae	2.163	Filam. green algae	1.684	Terrestrial plants	0.175				
L. setchellii	2.039	*Pterygophora*	0.977	Eel grass	0.138				
Filam. green algae	0.752	*Pelvetiopsis*	0.811	*L. setchellii*	0.069				
Pterygophora	0.430	*Egregia*	0.495	*Desmarestia*	0.025				
L. saccharina	0.379	*Sargassum*	0.359	Filam. green algae	0.023				
Pelvetiopsis	0.357	Terrestrial plants	0.267						
Egregia	0.218								
Terrestrial plants	0.201								

Food items in a same vertical bracket are not significantly ($p > 0.01$) different from one another. No tests were done for Campbell River and Kendrick Island since only 10 urchins were analyzed for these areas.

n = number of urchins whose gut content was analysed.

significantly higher than that of any of the other less abundant food items. Foliose green algae, branched red algae and invertebrates then followed. At Tofino, eel grass was more abundant than *Nereocystis* but not significantly; all other food items were significantly less abundant than the first two. Unidentified foods ranked third, followed by branched red algae, *Desmarestia* sp. and foliose green algae. Invertebrates ranked seventh. At Alert Bay, *Nereocystis* was significantly more important in the diet than all other food items. Foliose green algae, although significantly less important than *Nereocystis*, were more important than other food items except for *Agarum* spp. and *Sargassum*. Invertebrates ranked sixth but were not significantly different from *Sargassum* at the fourth rank. At Campbell River, *Nereocystis* ranked first, followed by foliose green algae and unidentified food items. Invertebrates were the fourth most important item in the urchins' diet. At Kendrick Island, *Nereocystis* was again the dominant food item, followed by *Alaria* and foliose red algae, primarily *Gigartina* sp. Invertebrates came in eighth.

Differences in the abundance of food items in the diet between areas and sites

Kruskal-Wallis analyses were used, taking each food item individually, to determine if the abundance of each food item in the diet changes with area, and with site (within an area) for Tofino and Alert Bay (Table 4.3). The abundance of 15 out of 19 food items changed from one area to the next, meaning that a food item that is abundant in the diet in one area is not necessarily abundant in other areas. Site effects within areas were present, however the extent of the variability between sites was greater at Tofino than Alert Bay. At Tofino, the abundance of 13 food items was influenced by site effects whereas at Alert Bay, the abundance of only 6 food items changed from site to site, showing that small scale (< 10 km) variability is not constant in different areas. The variability between sites at Tofino was almost as high as the variability between areas. While at Alert Bay, the variability between sites was lower than the variability between areas. These results show that variations in urchin diet occur on both small and large (several 100 km) spatial scales.

Table 4.3: Kruskal-Wallis analyses to test for differences in the relative abundance of individual food items, in the diet of wild red sea urchins, between the 4 experimental areas, and between sites within areas (i.e., at Tofino and Alert Bay).

	p values for effect of		
		Site	
Food Item	Area	Tofino	Alert Bay
Eel Grass	0.000	0.000	0.695
Nereocystis	0.000	0.000	0.000
Pterygophora	0.000	0.000	1.000
Alaria	0.000	0.001	0.779
Agarum	0.000	1.000	0.000
Desmarestia	0.000	0.000	0.443
L. saccharina	0.051	1.000	0.125
L. setchellii	0.001	0.000	0.443
Foliose Greens	0.001	0.000	0.000
Coraline Algae	0.000	0.000	0.006
Foliose Reds	0.000	0.099	0.006
Branched Reds	0.000	0.000	0.165
Unidentified	0.000	0.003	0.147
Sargassum	0.000	0.125	0.000
Terrestrial Plants	0.157	0.698	0.608
Filamentous Greens	0.000	0.000	0.443
Egregia	0.051	0.212	1.000
Pelvetiopsis	0.161	0.000	1.000
Invertebrates	0.000	0.000	0.057

Pairwise comparisons were used to determine differences in the abundance of each food item between areas (Table 4.4). Four areas give 6 pairwise comparisons so the significance level was reduced to $p = 0.0083$ ($p = 0.05/6$) so that the overall significance level for each food item was 0.05. The abundance of 14 food items is different at Tofino and Alert Bay. There are fewer differences between Tofino and Campbell River (7) and between Tofino and Kendrick Island (6). Similarly, there are few differences between Alert Bay and Campbell River (5), between Alert Bay and Kendrick Island (3) and between Campbell River and Kendrick Island (3). The low number of differences between Campbell River or Kendrick Island and the other areas might be due in part to the fact that only 10 urchins were used for the analysis at Campbell River and Kendrick Island while 110 were analyzed at Tofino and 120 at Alert Bay. Nevertheless, there are more differences between Tofino vs. Campbell River and Kendrick Island than between Alert Bay vs. Campbell River and Kendrick Island.

Table 4.2 compares the abundance of food items with each other, within an area, to see which food items are more important in the diet in that area. On the other hand, Table 4.4 compares the abundance of each food item in an area with its abundance in the other areas to determine if the abundance of each food item changes between areas.

Eel grass was more important in the diet at Tofino than in the other areas (Table 4.4). *Nereocystis* was most important at Alert Bay, followed by Campbell River, Kendrick Island and Tofino. Foliose greens were more important at Campbell River than in all other areas. Generally, food items that were more important in the diet in an area than in another were more readily available in the area where they were more important (see description of algal communities at the different areas in Chapter 3). Testing this hypothesis statistically was not possible because no quantitative data on algal abundance were available.

Table 4.4: Pairwise comparisons (Mann Whitney U test) to determine differences in the relative abundance of individual food items in the diet of wild red sea urchins between the 4 experimental areas.

	Area			
Food Item	Tofino	Alert Bay	Campell R.	Kendrick Is.
Eel Grass	1	2	2	2
Nereocystis	3	1	2	2, 3
Pterygophora	1	2	1, 2	1, 2
Alaria	2	3	1	1
Agarum	2	1	1, 2	1
Desmarestia	1	2	1, 2	1, 2
L. saccharina	1	1	1	1
L. setchellii	1	2	1, 2	1, 2
Foliose Greens	2	2	1	2
Coraline Algae	1	2	2	2
Foliose Reds	2	3	2, 3	1
Branched Reds	1	2	2	1, 2
Unidentified	1	2	1	2
Sargassum	2	1	1	1, 2
Terrestrial Plants	1	1	1	1
Filamentous Greens	1	2	1, 2	1, 2
Egregia	1	1	1	1
Pelvetiopsis	1	1	1	1
Invertebrates	1	2	1	1, 2

Areas with lower numbers have a higher abundance for the given food item.

Areas with the same number are not significantly different ($p > 0.0083$, see text) from one another.

Field observations

Feeding observations in the field were also made by SCUBA diving. At Tofino, several urchins were seen eating drift material of various types including seagrasses, *Nereocystis* blades and stipes, *Pterygophora* stipes, and wood. Urchins were also observed feeding on *Laminaria setchellii* at the algal fringe and on *Desmarestia* sp. which was generally the only fleshy algae found below the algal fringe in the barren areas. At Alert Bay, almost all feeding observations were of urchins eating drift or attached *Nereocystis*. When eating attached *Nereocystis*, a group of urchins would typically start eating blade tips, which presumably reached the bottom at low tide, while pulling the alga down as they were eating their way towards the pneumatocyst. The urchins would thus proceed to eat all the blades off an alga, probably over several days. Irvine (1973) described a similar phenomenon when urchins catch drifting *Nereocystis* and noted that 100 urchins could be found feeding on a single plant.

Discussion

The method of using intersection points for determining the relative importance of the different food items is a modification of the numerical method for food analysis described in Hyslop (1980) and Windell (1971). This method allows for a nonsubjective estimation of abundance, as opposed to estimation by eye (see Hyslop 1980) or the points method (Windell 1971), which are more subjective. A drawback of the numerical method is that it gives the same importance to food items of different sizes. It can thus overemphasize the importance of small prey items taken in large numbers (Hyslop 1980). However, most food items found in urchin guts are roughly the same size (pers. obs.), so this bias is probably minimal. Hyslop (1980) stated that the numerical method may be the most appropriate where prey items of different species are in the same size range. It is therefore believed that the method used was the one providing the best estimate of

relative abundance with the least bias. The choice of 37, as the number of points to look at, was based on preliminary trials showing that using 26 or 52 intersection points gave very similar results (not presented here); using 37 points allowed a good estimate and was not too time consuming. Vasquez et al. (1984) used a similar method to estimate urchin diet.

Diet Description

Overall (for all areas pooled), *Nereocystis* was the most abundant food item in the red sea urchin's diet. Vadas (1977) also found *Nereocystis* to be the dominant part of the diet of *S. franciscanus* at 7 sites in the San Juan Islands, followed by the ulvoids (*Monostroma-Ulva* spp.). However, the diet at Tofino shows that *Nereocystis* was not always the most abundant type of food in urchin guts. Urchins at Tofino ate mostly eel grass (25%) which was also found in the diet of several other urchin species (Gonor 1973 [S. purpuratus], Kawamura and Taki 1965 [*S. intermedius*], Ogden 1976 [*Tripneustes ventricocus*, *Echinometra lucunter* and *Diadema antillarum*]). *Nereocystis* was the second most abundant food item. The relatively high abundance of unidentified items in Tofino is due mainly to one site where urchins appeared to be feeding on sediment which was classified as unidentified items. *Nereocystis* was generally the only kelp to consistently form an important part of the diet, even when other kelps were present at the site/area. There is an exception to this trend at Kendrick Island, where *Alaria* made up 21% of the diet. *Macrocystis*, which is a preferred food of urchins (Leighton 1966), was not found in the diet. However, absence of *Macrocystis* in the diet was due to absence of this alga at all field sites in the study. Green and red algae were also an important part of the red sea urchin's diet around Vancouver Island. These items ranked fourth and fifth overall. Coralline algae, which sometimes constituted a large part of urchin diet (Kenner 1992), were generally not abundant (< 5%).

Red sea urchins are not strict herbivores. Invertebrates ranked as the sixth most important food item, constituting from 2 to 6% of the diet, higher than the 0.56% reported by Vadas (1977) for the San Juan Islands. The most abundant invertebrates were barnacles and the

bryozoan *Membranipora membranacea*. Invertebrate abundance in this study was underestimated, for when urchins ate *Nereocystis* covered with the bryozoan *M. membranacea*, the food item was counted as *Nereocystis*, rather than as invertebrates. Although eating *Membranipora* might be incidental to eating the kelp on which *Membranipora* grows, the bryozoan may be an important source of nutrients for the urchins. Vadas (1977) also noted the potentially important role of *Membranipora* in urchin diets. Barnacles were also found in the diet of 2 species of urchins in Chile (Vasquez et al. 1984). Invertebrates were found in the diet of many urchin species (reviewed in Lawrence 1975). Although invertebrate abundance in the diet was not very high, their importance to the urchins could be larger than their abundance suggests. Protein level was more important than caloric levels for the growth of *Tripneustes ventricocus*; measuring the value of animals as food for echinoids is thus important (Lawrence and Lane 1982). If protein levels are important for the growth of *S. franciscanus*, invertebrates and other animal foods could play an important role in the urchin's diet.

Spatial variability

Spatial variability in diet of *S. franciscanus* was observed on both large (between areas) and small (between sites within areas) spatial scales. The extent of small scale variability changed with area and could be almost as great as large scale variability (Area effect vs. Site effect at Tofino in Table 4.3). Spatial variability observed in the diet, between areas and between sites within an area, was probably caused by differences in the diversity and availability of food items from one area/site to the next. The algal community was more variable at Tofino than at Alert Bay, explaining why a greater variety of food items were found at Tofino and why between-site variability was higher at Tofino than at Alert Bay. Although the sites at Tofino were closer together than the ones at Alert Bay, the range of conditions encountered between sites was larger at Tofino, due mainly to important differences in the degree of exposure to surf and storms between sites. Changes in diet on a small spatial scale have also been reported by other authors (Kenner

1992 [*S. purpuratus*], Mattison et al. 1977 [*S. franciscanus*], Ogden et al. 1989 [*Echinometra mathaei*]). Small-scale patchiness in food availability may tend to overshadow larger scale patterns (Kenner 1992). However, large scale patterns seem to be present here. The diet in each area on the east side Vancouver Island was dominated by *Nereocystis* (> 42%) and there were fewer differences in the abundance of individual food items between areas on the east side of the Island than between these areas and Tofino.

Small scale variability in the diet could also occur with increasing depths and/or distance from shore (Mattison et al. 1977, Ogden et al. 1989). However, I do not have any data to confirm this hypothesis for the red sea urchin's diet in southern B.C.

Temporal Variability

Nereocystis was the most abundant diet item in summer. However, *Nereocystis* dies off in late fall suggesting that urchins must change their diet at various times of the year. Urchins also depend on drift algae to a large extent (Irvine 1973, Keats et al. 1984, Mattison et al. 1977, Ogden 1976, Ogden et al. 1989, pers. obs.). Drift algae abundance also changes during the year, being most abundant in summer and fall (Druehl and Breen 1986, Harrold and Reed 1985) since drift algae abundance is related to local kelp abundance (Harrold and Reed 1985). The decrease in abundance of annual species of kelps and the associated decrease in the availability of drift in late fall suggests a shift in diet in winter. Vadas (1977) observed such a shift, after the disappearance of annual kelps, urchins increased feeding on *Agarum*, a readily available although not preferred perennial.

Selective Feeding vs. Food Abundance

Feeding preferences in urchins are well developed (Larson et al. 1980, Leighton 1966, Vadas 1977). For *S. droebachiensis*, food preference is not correlated with caloric content but,

because of higher feeding rates on preferred foods, caloric intake is positively correlated to food preference (Larson et al. 1980, Vadas 1977). Food preference and absorption efficiencies are correlated in red and green urchins (Vadas 1977). Absorption efficiency is highest for *Nereocystis* (84-91%), the preferred food, and low (36-56%) for *Agarum* spp., a non-preferred food (Vadas 1977). Despite strong food preferences, urchins do not always feed on their preferred foods. Diet of urchins in the wild is generally a compromise between food preference and food availability (Vadas 1977). Urchins are generalists (Lawrence and Sammarco 1982), or opportunistic (Ebert 1968, Irvine 1973, Kenner 1992) feeders eating less preferred foods when only those are available and switching to preferred foods once the latter become available (Irvine 1973, Kenner 1992, Leighton 1966). Therefore, urchin diet often corresponds more to local food availability than to food preferences (Kawamura 1973, Lawrence and Sammarco 1982, Ogden 1976). Urchins will clearly eat non-preferred foods when there is no choice (Lawrence 1975). Grazing of *S. purpuratus* and *S. franciscanus* is selective under conditions of abundant food supply, but selectivity disappears when grazing pressures become extreme (Leighton 1966). Preferential feeding results in optimal growth and reproduction while the generalist behavior extends or assures survival even in overgrazed environments (Larson et al. 1980). The generalist behavior might be expected to evolve where food availability is unpredictable or where competition for food is especially keen (i.e., overgrazed areas) (Larson et al. 1980).

The high dominance of *Nereocystis* (75.6% of the diet) at Alert Bay suggests that urchins feed selectively when there is abundance of preferred high quality foods. Other species of kelps (*L. saccharina, Alaria, Costaria* and *Agarum*) were present but the urchins were not eating much of them. Red urchins prefer *Nereocystis* over *L. saccharina* and *Alaria* (Vadas 1977). The abundance of *Agarum* at Alert Bay and Kendrick Island was relatively high. At some sites at Alert Bay, percent cover approached 100% at depths past the distribution of other kelps but where urchins were present (pers. obs.). *Agarum* spp. is usually avoided by *Strongylocentrotus* spp. despite its high caloric content, possibly due to the presence of a grazing-deterrent chemical defense (Larson et al. 1980, Vadas 1977). Herbivores avoid certain algal species and the most

likely possibility to explain this avoidance is some form of chemical or structural defense (Ogden 1976). Brown algal polyphenolics deter purple urchin feeding (Steinberg 1988). Still, *Agarum* spp. ranked 4th at Alert Bay and 3rd at Kendrick Island; however, *Agarum* abundance was always lower than 10% of the diet. Presence and relatively high rank of *Agarum* in the diet, considering *Agarum* is one of the least-preferred algae by urchins, might be due to high abundance of *Agarum* in the areas where the urchins were present. *Agarum* was thus readily accessible to urchins.

The fact that urchins eat mostly eel grass, showed to produce slow growth (T. Morris and A. Campbell, unpublished data) and poor quality gonads (Chapter 3), at Tofino shows that when food is scarce, red urchins will readily eat lower quality food items. *Desmarestia* is not a preferred food of sea urchins because *Desmarestia* contains sulfuric acid (Irvine 1973, Paine and Vadas 1969 b). Nevertheless, *Desmarestia* ranked fifth at Tofino and urchins were often seen eating *Desmarestia* on the areas barren of other fleshy (non coralline) algae, further showing that they will eat low quality foods when food is scarce.

Despite the lack of quantitative estimates of algal abundance, the results presented here support the hypothesis that urchin diet is mainly dependent on food availability and, when preferred foods are abundant (e.g., *Nereocystis* at Alert Bay), selective feeding can occur.

Conclusions

Red sea urchin diet is broad and varies considerably on both small and large spatial scales. The results also suggest that red sea urchin diet changes at different times of the year. As has been shown previously for this species and a variety of others, feeding appears to depend on local food availability with the possibility of selective feeding when preferred foods become available.

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