Effects of experimental harvest on red sea urchins (*Strongylocentrotus franciscanus*) in northern Washington

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Abstract—Commercial harvest of red sea urchins began in Washington state in 1971. Harvests peaked in the late 1980s and have since declined substantially in Washington and other areas of the U.S. west coast. We studied effects of experimental harvest on red sea urchins in San Juan Channel (SJC), a marine reserve in northern Washington. We recorded changes in density and size distribution of sea urchin populations resulting from three levels of experimental harvest: 1) annual size-selective harvest (simulating current commercial urchin harvest regulations), 2) monthly complete (non–size-selective) harvest, and 3) no harvest (control) sites. We also examined recolonization rates of harvested sites. The red sea urchin population in SJC is composed of an accumulation of large, old individuals. Juvenile urchins represent less than 1% of the population. Lower and upper size limits for commercial harvest protect 5% and 45% of the population, respectively. Complete harvest reduced sea urchin densities by 95%. Annual size-selective harvest significantly decreased sea urchin densities by 67% in the first year and by 47% in the second year. Two years of size-selective harvest significantly altered the size distribution of urchins, decreasing the density of legal-size urchins. Recolonization of harvested sites varied seasonally and occurred primarily through immigration of adults. Selective harvest sites were recolonized to 51% and 38% of original densities, respectively, six months after the first and second annual harvests. Yields declined substantially in the second year of size-selective harvest because of the fishing down of the population and because of low recolonization rates of harvested sites. We recommend that managers consider the potential efficacy of marine harvest refuges and reevaluate the existing upper and lower size limits for commercial harvest to improve long-term management of the sea urchin fishery in Washington.

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Red sea urchins (*Strongylocentrotus franciscanus*) are the most commonly harvested species of sea urchin on the west coast of North America. Sea urchin harvest in this region occurs primarily in California, Washington, and British Columbia. The commercial sea urchin fishery in Washington began in 1971, and landings were low through the early 1980s (Fig. 1). Landings increased dramatically in the late 1980s, peaking at over 4000 metric tons (t) in 1988. Landings have since declined. Approximately 387 t of sea urchins were harvested in 2000, valued at $699,052 (Ulrich[1]). Red sea urchins currently constitute approximately 60% of landings—the remainder being green sea urchins (*S. droebachiensis,* Ulrich[1]).

The Washington sea urchin fishery currently is managed by using harvest quotas, size limits, license restrictions, limited entry, and mandatory log books (Lai and Bradbury, 1998). Season length is not limited, but harvest occurs primarily during the winter when roe quality is highest (Bradbury[2]). A rotational harvest strategy was practiced from 1977 until 1995, in which each harvest district (Fig. 2) was harvested once every third year. In 1995 a U.S. federal court ruling on shellfishery management in Washington's coastal marine waters (Shellfish Subproceedings of United States vs. State of Washington, 873 F. suppl. 1422, 1994, known commonly as the "Rafeedie Decision") allotted one half of all harvestable shellfish to native tribes. As a result, rotational harvest was discontinued and replaced by annual harvest to ensure that all tribes had equal access to their usual and accustomed fishing areas each year.

Sea urchin harvests declined substantially in the early 1990s along parts of the west coast (Fig. 1). Quotas and season lengths were reduced in Washington because of overharvesting concerns (Bradbury[2]). Quotas were not reduced in California, and catches declined substantially (Kalvass and Hendrix, 1997). Sea urchin densities in some harvested areas in northern California are less than one quarter of those in nearby reserve areas (Kalvass and Hendrix, 1997). In Washington, densities and the proportion of legal-size sea urchins in the population have declined (Pfister and Bradbury, 1996). Harvesters may be maintaining catch per unit of effort at high levels by exploiting new populations, thereby masking stock declines (Pfister and Bradbury, 1996).

Experimental harvests may indicate potential effects of commercial harvest

[1] Ulrich, M. 2001. Personal commun. Washington State Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501.

[2] Bradbury, A. 2000. Personal commun. Washington State Department of Fish and Wildlife, Point Whitney Shellfish Laboratory, 1000 Point Whitney Road, Brinnon, WA 98320.

Table 1

Depth and area of study sites in San Juan Channel, Washington. Site numbers are those shown in Figure 2. Initial sea urchin densities are from sampling in permanently marked circular sampling areas in early March 1997.

Site	Abbreviation	Treatment	Depth (m)	Area (m^2)	Initial sea urchin density (no./m^2)
1. Mid San Juan Island	Mid SJI	complete harvest	6.6	428	1.15
2. South McConnell Island	South McConnell	complete harvest	10.4	405	1.13
3. O'Neal Island	O'Neal	complete harvest	5.8	430	1.36
4. Point Caution, San Juan Island	Point Caution	selective harvest	7.5	422	1.95
5. Upper San Juan Island	Upper SJI	selective harvest	9.1	421	1.27
6. North McConnell Island	North McConnell	selective harvest	9.1	415	0.37
7. Yellow Island	Yellow	control	6.9	404	2.05
8. Point George, Shaw Island	Point George	control	7.5	406	1.96
9. Shady Cove, San Juan Island	Shady Cove	control	10.2	447	0.94

on sea urchin populations in Washington. We examined changes in density and size distribution of red sea urchin populations resulting from two levels of experimental harvest. Our study site was San Juan Channel (SJC), one of two areas in Washington where commercial sea urchin harvest has been prohibited since the 1970s (Fig. 2). We compared density and size distribution data for sea urchins from experimentally harvested sites in SJC with similar data collected from 1) nearby control sites, and 2) 19 sites in the Strait of Juan de Fuca (SJDF), an area commercially harvested since the early 1970s. We also examined recolonization of harvested sites through recruitment and immigration. We discuss implications of our results for management of sea urchin harvest effort and the potential use of marine harvest refuges in enhancing Washington's sea urchin fishery.

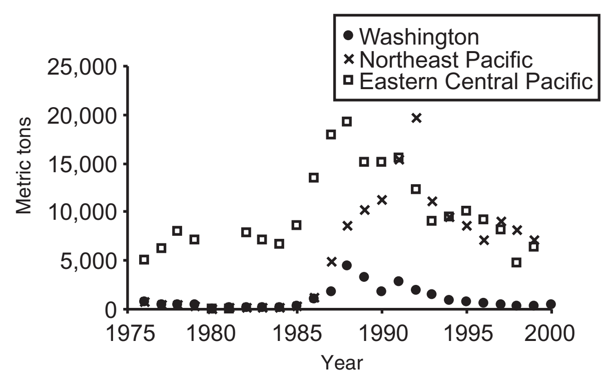

Figure 1

Annual harvest of red sea urchins (*Strongylocentrotus* spp.) in Washington state and in the larger Northeast Pacific and eastern Central Pacific areas of the west coast of the United States. Northeast Pacific includes the area north of 40°30′N (approximately Oregon-California border). Eastern Central Pacific includes the area south of 40°30′N. (Sources: Hoines, 1994, 1998; FAO, 1980, 1981, 1992, 2001; Bradbury.[2])

Methods

We established nine study sites in SJC from November 1996 to March 1997 (Fig. 2). Sites were 6–10 m in depth and approximately 10 m × 40 m, with the long axis of each site running parallel to the shoreline along the depth contour (Table 1). Eight permanently marked circular sampling areas (each 7.07 m^2) were located along the midline of each site along the depth contour. Site selection was based on high red sea urchin density (≥1.5/m^2 in preliminary surveys), substrate (primarily large cobble or bedrock) and safety considerations.

We applied one of three harvest treatments to each site. "Selective harvest" consisted of annual removal of all legal-size sea urchins (102–140 mm test diameter) each winter (March of 1997 and 1998). Selective harvest simulated the annual commercial harvest of a bed of sea urchins in the San Juan Islands (Pfister and Bradbury, 1996). "Complete harvest" consisted of removal of all sea urchins present in March 1997, and at monthly intervals thereafter through September 1998. The complete harvest treatment did not represent any current management strategy for commercial harvest. Rather, the complete harvest treatment represented one extreme (the control treatment being the second) against which effects of selective harvest may be compared. Sea urchin densities were not manipulated in the "control" treatment. Because of logistical constraints, control sites were located in smaller preserve areas within SJC where harvest of all invertebrates and fish is prohibited. Harvest treatments were randomly assigned to the remaining six sites. All sea urchins harvested were measured at the surface and released at other locations in SJC well away from the study sites.

In SJC, we sampled at large (sites) and small (circular areas within sites) spatial scales. Small-scale sampling was more frequent, allowing detection of potential short-

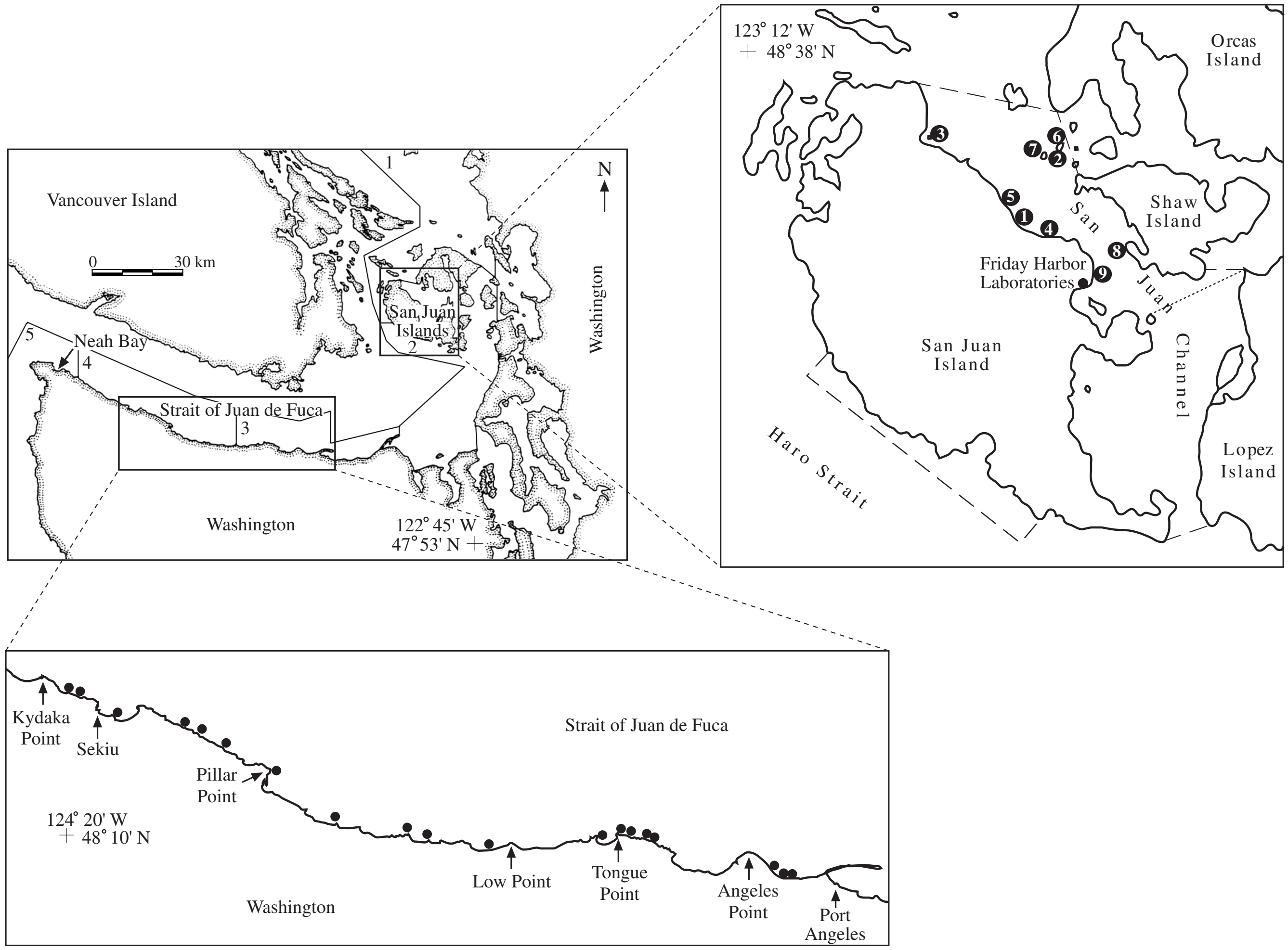

Figure 2

(**Upper left**) The commercial harvesting districts for sea urchins in Washington (after Lai and Bradbury, 1998). Harvest district numbers are shown in the upper left corner of each district. (**Right**) Enlargement of San Juan Channel, showing locations of study sites. Sites 1–3 are complete harvest sites, sites 4–6 are selective harvest sites, and sites 7–9 are control sites. Dashed lines represent the boundary of the areas on the west coast of San Juan Island and in San Juan Channel closed to commercial sea urchin harvest through fall 1998. The dotted line represents the modified southern boundary of the reserve area in San Juan Channel established in fall 1998. (**Lower left**) Enlargement of the Strait of Juan de Fuca sampling area. Black circles indicate locations of randomly chosen sampling sites.

term effects of harvest; whereas large-scale sampling better indicated how treatments affected the entire bed of sea urchins. We identify the scale of sampling (sites vs. circular areas within sites) for all results.

Size distribution

In SJC, we measured all sea urchins removed during the initial harvest of complete and selective harvest sites in March 1997, and all sea urchins removed during the second annual harvest of selective harvest sites in March 1998. In September of 1997 and 1998, we measured a minimum of 100 sea urchins *in situ* in all sites in randomly chosen 5 m × 5 m quadrats. We also measured sea urchins in the circular areas within sampling sites *in situ* in all sites five times per year: early March, mid March, April, June, and September. The sampling periods represented preharvest and 5, 30, 90, and 180 days after harvesting in each year for the selective harvest treatment.

Nineteen randomly chosen sites in the western SJDF were sampled in August and September 1997 (Fig. 2). All sites were 7–8 m below mean lower low water. At each site, we measured sea urchins *in situ* on 1–3 transects parallel to shore, each ≥30 m^2.

Lower and upper size limits for commercial sea urchin harvest are 102 and 140 mm test diameter in SJC, and 83 and 114 mm in SJDF (Pfister and Bradbury, 1996). Sea urchin measurements in SJC and SJDF were recorded to the nearest 5 mm (e.g. 130 mm=test diameters 130–134 mm), except during the initial sampling periods (March–June 1997), when sea urchins measured *in situ* only were recorded to the nearest 10 mm (e.g. 130 mm=test diameters

130–139 mm). Because of the measurement increment used, we could only estimate proportions of under-, legal-, and over-size sea urchins in SJC and SJDF. Asterisks (*) indicate estimated size classes. Estimated size classes are as follows: SJC—under*-size: 0–95 mm, legal*-size: 100–135 mm, and over*-size: 140–175 mm; SJDF—under*-size: 0–80 mm, legal*-size: 85–110 mm, and over*-size: 115–175 mm. Sea urchins less than 50 mm are less than two years old and were classified as juveniles (see Pfister and Bradbury, 1996).

Harvest and recolonization

Recolonization was determined for three periods: summer 1997 (March 1997 [postharvest]–September 1997), winter 1997 (September 1997–March 1998 [preharvest]), and summer 1998 (March 1998 [postharvest]–September 1998). In complete harvest sites, monthly recolonization for each time period was calculated as the sum of the number of sea urchins removed each month from each site during the time period divided by the number of months in the time period. A few sea urchins that divers did not harvest in March 1997 because they could not safely be removed from the substrate were excluded from the calculation of recolonization for the first time period. Size of recolonizers was based on sea urchins harvested from May 1997 to September 1998. In selective harvest sites where sea urchins were removed only once each year, we calculated monthly recolonization for each time period as the difference between the number of sea urchins counted in each site at the beginning and end of the time period, divided by the number of months in the time period.

At the end of the study (September 1998), divers sampled destructively for juvenile sea urchins in one 0.80-m^2 wedge within each circular area within a sampling site. Prior to this time, divers may not have seen very small sea urchins concealed underneath rocks or large sea urchins because sampling was not destructive to avoid disturbing other experiments. We include results on both red and green juvenile sea urchins sampled because of the very low number of red sea urchins sampled and to provide an indication of the microhabitats inhabited by juvenile sea urchins in general in SJC.

Data analysis

Size-frequency data were grouped into discrete size classes and compared by using chi-square analysis. Sea urchin data collected at each site were correlated over time. Therefore, we used a paired t-test to analyze the effect of harvest on the total number of sea urchins in sites and on the density of sea urchins in each size class. Similarly, we analyzed sea urchin densities in permanent circular areas over time by using repeated measures analysis of variance. In the analysis, site was treated as a random factor and was nested within treatment, which was treated as a fixed factor. Densities of juvenile sea urchins in September 1998 were analyzed by using analysis of variance. Sea urchin densities were log-transformed to improve the variance structure for analysis (Zar, 1984). Mean values generally are followed by one standard deviation in the text. The level of significance for all tests was $\alpha = 0.05$.

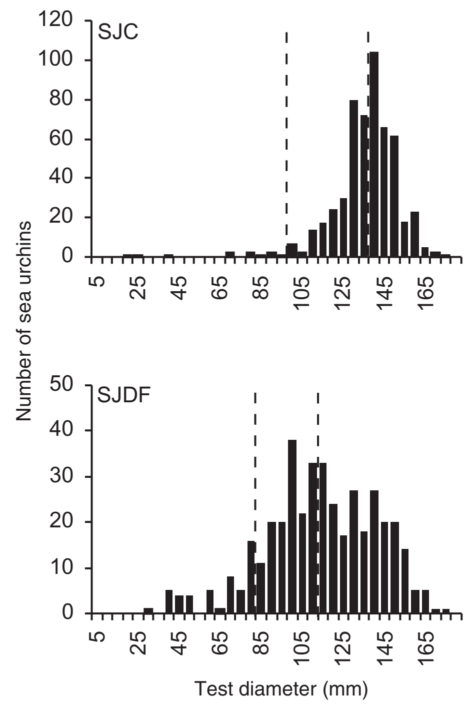

Figure 3

Size-frequency distribution of red sea urchins sampled in the three control sites combined in San Juan Channel (SJC) in September 1997 (n=537) and in the western Strait of Juan de Fuca (SJDF) in August 1997 (n=405). Dashed lines indicate minimum and maximum size limits for commercial harvest in each location.

Results

Size distribution of sea urchins in SJC and SJDF

Size distributions of red sea urchins in SJC were strongly skewed to the right and had a modal size of 140 mm (range 20–175 mm, Fig. 3). 4.8% (±3.1%) of sea urchins in circular areas in all sites in early March were <100 mm (under*-size), 50.0% (±13.0%) were 100–139 mm (legal*-size), and 45.2% (±12.5%) were ≥140 mm (over*-size). Juveniles represented 0.3% (±0.4%) of the population.

The modal size of red sea urchins in SJDF was 100 mm (range 30–175 mm, Fig. 3). 12.1% of the red sea urchin population was under*-size, 35.6% was legal*-size, and 52.4% was over*-size. Juveniles represented 2.5% of the population.

Effect of harvest on size distribution

Sea urchins harvested in the initial size-selective harvest in 1997 were 90–160 mm in diameter (mode 135 mm,

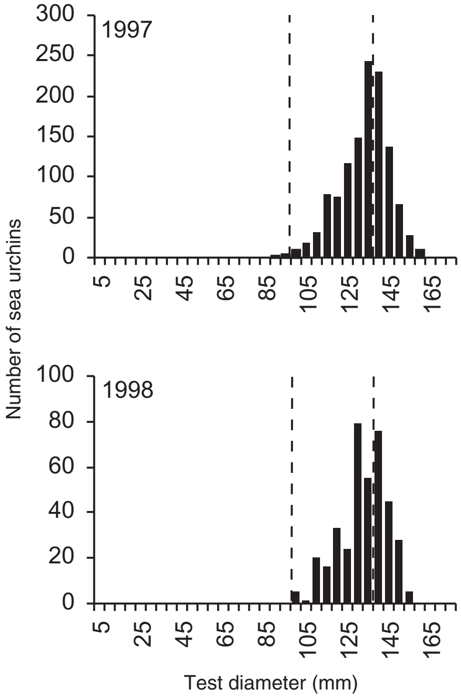

Figure 4

Size distribution of red sea urchins harvested from the three selective harvest sites combined in San Juan Channel (SJC) in March 1997 (n=1194) and March 1998 (n=387). Dashed lines indicate minimum and maximum size limits for commercial harvest in SJC.

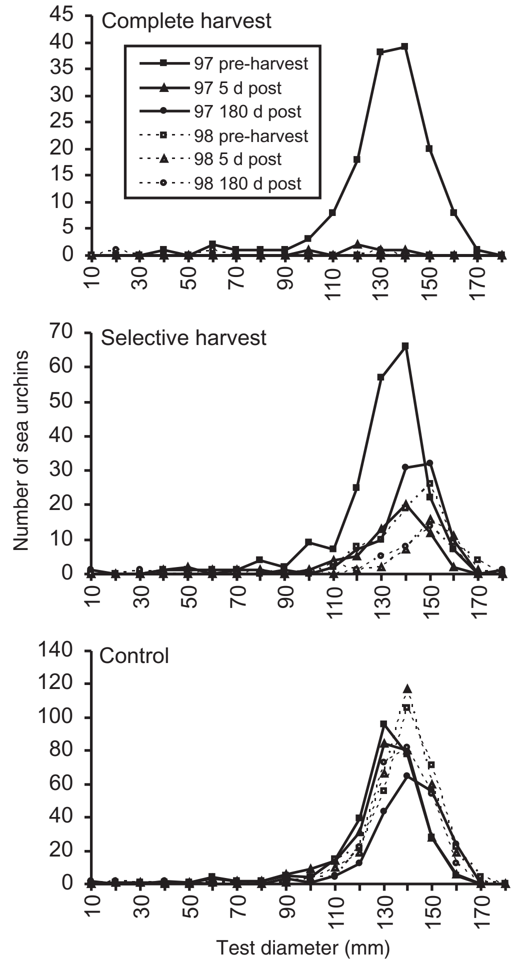

Figure 5

Size distribution of red sea urchins in the complete harvest, selective harvest, and control treatments in San Juan Channel (SJC) in early March (before harvest), mid-March (five days after harvest), and September (180 days after harvest) of 1997 and 1998. Solid lines represent sampling periods in 1997, and dashed lines represent sampling periods in 1998. Cumulative sample sizes for the three sites within each treatment and for all sampling periods illustrated are n = 149, 518, and 1627 for the complete harvest, selective harvest, and control treatments, respectively. Samples are from urchins measured *in situ* in sampling circles. One site (mid SJI) was excluded from the 1997 early March sampling period for the complete harvest treatment.

Fig. 4). The harvest consisted of 0.5% (±0.4%) under*-size sea urchins, 59.5% (±6.6%) legal*-size sea urchins, and 39.9% (±9.2%) over*-size sea urchins. Sea urchins harvested in the second annual size-selective harvest in 1998 were 100–155 mm in diameter (mode 130 mm). The composition of the harvest was similar: 0.0% (±0.0%), 57.1% (±18.7%), and 42.9% (±18.7%) of sea urchins were under*-, legal*-, and over*-size, respectively.

The initial size-selective harvest did not significantly alter the size distribution of the population (P=0.18, Fig. 5) but did significantly reduce the density of legal*-size sea urchins (P=0.05, Table 2). The cumulative effect of two annual size-selective harvests on the size distribution of the population was highly significant (P<0.0001, Fig. 5) and significantly reduced the density of legal*-size sea urchins (P=0.03, Table 2). The modal size of sea urchins in selective harvest sites increased to 150 mm after the second annual harvest (Fig. 5). Six months after the second annual harvest, the size distribution of the population remained significantly different from the original (1997 preharvest) size distribution (P=0.0001). Size distributions of sea urchins in selective harvest sites did not differ between fall 1997 and fall 1998 according to large-scale sampling (P=0.06), averaging 5.8%, 34.3%, and 60.0% for under*-, legal*-, and over*-size sea urchins, respectively (n=756). Size distributions of sea urchins in control sites, based on small-scale sampling, were similar throughout the study (Fig. 5) and did not differ between fall 1997 and fall 1998 according to large-scale sampling (P=0.10).

Table 2

Changes in the density (no./m^2) of under*-, legal*- and over*-size sea urchins as a result of selective harvests in March of 1997 and 1998. Values are averages (±SD) of the three selective harvest sites and are based on sea urchins sampled in permanent circular sampling areas within each site. See text for explanation of size categories.

	1997			1998		
	Preharvest	5 days after harvest	180 days after harvest	Preharvest	5 days after harvest	180 days after harvest
Under*-size	0.06 (±0.06)	0.03 (±0.04)	0.01 (±0.02)	0.00 (±0.00)	0.01 (±0.01)	0.01 (±0.01)
Legal*-size	0.62 (±0.37)	0.14 (±0.10)	0.18 (±0.24)	0.14 (±0.18)	0.04 (±0.06)	0.07 (±0.05)
Over*-size	0.52 (±0.39)	0.20 (±0.13)	0.37 (±0.18)	0.32 (±0.06)	0.19 (±0.08)	0.15 (±0.10)

Table 3

Total number of sea urchins (±SD) in San Juan Channel study sites over time. Harvests occurred in early March of 1997 and 1998. "Postharvest" data were collected immediately after the harvest by divers performing the harvest. SJI = San Juan Island.

	1997			1998		
Site	Preharvest	Postharvest	180 days after harvest	Preharvest	Postharvest	180 days after harvest
Complete harvest						
O'Neal Island	511	19				
Mid SJI	639	40				
South McConnell	641	37				
Average	597 (±74)	32 (±11)				
Selective harvest						
North McConnell	261	100	173	181	113	147
Upper SJI	560	206	229	207	92	139
Point Caution	907	228	421	430	226	290
Average	576 (±323)	178 (±68)	274 (±130)	273 (±137)	144 (±72)	192 (±85)
Control						
Yellow Island			547			646
Point George			823			859
Shady Cove			347			266
Average			572 (±239)			590 (±300)

Effect of harvest on density

Sea urchin densities in the SJC sites initially averaged 1.35/m^2 (±0.55, Table 1). Differences in initial sea urchin density between sites were marginally significant (P=0.05) because of the low density of sea urchins at North McConnell. Because of the difference in initial density, we expressed changes from preharvest to postharvest densities in SJC sites as percentages of the original population.

Initial harvest in March 1997 decreased the number of sea urchins in complete harvest sites by 94.7% (range: 93.7–96.3%) and in selective harvest sites by 66.6% (range: 61.7–74.9%, Table 3). Reharvest of selective harvest sites in March 1998 reduced sea urchin numbers 46.9% (range: 37.6–55.6%). All decreases were significant (P≤0.04). Yields from selective harvest sites averaged 0.95 sea urchins/m^2 in 1997, and 0.31 sea urchins/m^2 in 1998. The number of sea urchins in control sites did not differ between 1997 and 1998 (P=0.77, average 1.41/m^2).

Small-scale sampling also demonstrated significant changes in sea urchin density as a result of the experimental harvest treatments (Table 4). Initial harvest reduced sea urchin densities by 97.6% and 69.5% in complete and selective harvest sites, respectively. Mid-March (5 days after harvest) densities averaged 0.03/m^2 (±0.07/m^2) and 0.37/m^2 (±0.45/m^2) in complete and selective harvest sites, respectively. Sea urchin densities in complete harvest sites remained low for the duration of the study (<0.04/m^2). Sea urchin densities in selective harvest sites increased slight-

Table 4

Summary of repeated measure analysis of variance results for red sea urchin density. In cases where the degrees of freedom for the tests of significance for the within-subjects effects were adjusted by the Huynh-Feldt epsilon, the unadjusted degrees of freedom are given in parentheses. Asterisks in column five indicate factors significant at the 0.05 level. Power was estimated by using graphs in Zar (1984). (—) indicates that power was very low for the effect but could not be computed exactly (Sokal and Rohlf, 1995).

Source	Degrees of freedom	Mean square	F-ratio	P-value	Observed power
Within-subjects effects					
Year	1	0.24	1.88	0.22	<0.20
Year × treatment	2	0.11	0.88	0.46	—
Year × site (treatment)	6	0.13			
Season	3.56 (4)	0.28	14.34	* 0.000	>0.99
Season × treatment	7.11 (8)	0.055	2.78	* 0.033	0.44
Season × site (treatment)	21.34 (24)	0.020			
Year × season	3.72 (4)	0.12	9.42	* 0.000	0.98
Year × season × treatment	7.45 (8)	0.070	5.32	* 0.001	0.86
Year × season × site (treatment)	22.34 (24)	0.013			
Between-subjects effects					
Intercept	1	22.11	214.92	0.000	1.00
Treatment	2	6.79	14.99	* 0.005	0.95
Site (treatment)	6	0.45			

Table 5

Monthly recolonization (no. of sea urchins/site) for complete and selective harvest sites from April 1997 through September 1998. The summer and winter time periods are April–September and October–March, respectively. SJI = San Juan Island.

Treatment	Site	Summer 1997	Winter 1997	Summer 1998
Complete harvest	O'Neal Island	22.7	11.7	16.0
	Mid SJI	29.5	13.8	34.2
	South McConnell	16.3	4.7	6.3
	Average	22.8	10.1	18.8
Selective harvest	North McConnell	12.2	1.3	5.7
	Upper SJI	3.8	3.7	7.8
	Point Caution	32.2	1.5	10.7
	Average	16.1	0.3	8.1

ly in the summer following each harvest (see next section). Sea urchin densities in control sites changed little over time, averaging 1.61/m^2 (±1.4/m^2) over the study period.

Recolonization of harvested sites

Recolonization of complete harvest sites averaged 17.2 sea urchins per month (range: 0–68), or 0.04/m^2·month. The average size of sea urchins recolonizing complete harvest sites was 129 mm (±19 mm, range: 35–175 mm, n=824). Recolonization of complete harvest sites was higher during the summer of each year than during the winter and decreased slightly but not significantly over time (P=0.31, Table 5).

Recolonization of selective harvest sites was lower than observed in complete harvest sites (average 7.9 sea urchins/month or 0.02/m^2·month, Table 5). Recolonization was highest during summer 1997, followed by summer 1998. There was no net recolonization during winter 1997. Sites were recolonized to 51.2% of original densities by September 1997 (range: 40.9–66.3%, Table 3). In September 1998, after two annual harvests, sites averaged 37.7% of original densities (range: 24.8–56.3%).

Juvenile recruitment

Juvenile sea urchins were rare in all SJC study sites in March 1997 (0.4% (±0.6%) of sea urchins sampled in

Table 6

Modal size and proportion of juveniles in red sea urchin populations along the west coast of North America.

Location	Modal size (mm)	% of juveniles	Source
Southeast Alaska, shallow habitats	100–120	~35% <60 mm	Carney, 1991
Southeast Alaska, deep habitats	140–160	~8% <60 mm	Carney, 1991
Vancouver Island, BC	100–120	<5% <30 mm, ~50% <100 mm	Watson, 1993
Vancouver Island, BC	100–150*	~7% <50 mm*	Breen et al., 1978
Vancouver Island, BC	80–150*	0–11% <50 mm*	Breen et al., 1976
Strait of Georgia, BC	100–139*	9.5% <50 mm*	Sloan et al., 1987
San Juan Channel, Washington	140–144	0.3% <50 mm, 4.8% < 100 mm	This study
Strait of Juan de Fuca, Washington	100–104	2.5% <50 mm, 24.7% <100 mm	This study
Northern California	~107	~8–12% <50 mm	Rogers-Bennett et al., 1995; Smith et al., 1998
San Nicolas Island, Southern California	100–120	~7% < 50 mm	Cowen, 1983
Southern California	25 and 110	39% < 30 mm	Tegner and Dayton, 1981

* Commercially harvested populations.

circular areas). Over the entire study period, juvenile red sea urchin densities in circular areas averaged 0.005/m^2 in control sites (0.6% of the population), 0.001/m^2 in selective harvest sites (0.9% of the population), and 0.0006/m^2 in complete harvest sites. Sampling at the larger spatial scale revealed similar results. Juvenile sea urchin density averaged 0.002/m^2 in control sites in September of both 1997 and 1998. Juvenile sea urchin density averaged 0.001/m^2 and 0.005/m^2 in selective harvest sites in September of 1997 and 1998, respectively.

Invasive sampling in September 1998 confirmed that juvenile sea urchins were rare in SJC sites during the study. One juvenile (13 mm) red sea urchin and 45 juvenile (2–12 mm) green sea urchins were found in a search of 6.4 m^2 of substrate in each site (57.6 m^2 total). Density of juvenile green sea urchins sampled did not differ between treatments (P=0.79; average 0.79/m^2 [±0.86]). Only 4.3% of the juvenile green sea urchins were associated with (found within 8 cm of) an adult red sea urchin. 26.7% of juvenile green sea urchins were found in cryptic microhabitats (algal holdfasts), and the remainder were found on algal blades or on top of cobble, boulders, or bedrock.

Discussion

Size distribution of sea urchins in SJC and SJDF

The modal size of sea urchins in SJC is larger than observed in most other locations on the west coast (Table 6). The size distribution of red sea urchins in SJC sites is strongly skewed toward large individuals. The slow growth rate of sea urchins in Washington (Lai and Bradbury, 1998), combined with the fact that SJC was, at the time of our study, a reserve area that has never been subject to significant harvest, indicates that the sea urchin population in SJC is composed primarily of older individuals. Fewer juveniles are present in SJC and SJDF than in most other areas on the west coast (Table 6). Large recruitment events appear to be rare for red sea urchins in SJC, evidenced by the lack of peaks in the size distribution at small test diameters.

Effect of harvest on size distribution

The first annual size-selective harvest only slightly affected the size distribution of sea urchins in SJC. The cumulative effect of two annual size-selective harvests was significant, however, significantly reducing the density of legal*-size sea urchins in the population and increasing the modal size of the population. Commercial fisheries elsewhere along the west coast have also affected the size distribution of sea urchin populations. Three commercial harvests in the San Juan Islands (outside the SJC reserve) over a nine-year period decreased the proportion of legal-size sea urchins by about 73% (Pfister and Bradbury, 1996). In southern California, two years of harvest reduced the proportion of legal-size sea urchins in shallow waters by 15% (Tegner and Dayton, 1981). In northern California, the modal size of sea urchins in unharvested reserve sites was 108 mm, whereas the modal size of sea urchins in nearby heavily harvested sites with a 76-mm minimum size limit was 73 mm (Smith et al., 1998). On the east coast of Vancouver Island, however, the modal size of sea urchins remained above the legal size limit after 3+ years of significant harvest (Sloan et al., 1987).

The modal size of the sea urchin population and the upper size limit for legal harvest coincided in SJC. Small errors in the measurement of sea urchins by divers led to an incomplete harvest of legal-size sea urchins and inadvertent "poaching" of many over-size sea urchins (41% of the catch, likely a slight overestimate because sea urchins

140 mm in diameter were incorrectly classified as over-size). Both actions would tend to minimize effects of our experimental size-selective harvest. Commercial harvesters take a much smaller proportion of over-size sea urchins (11.2% of catch) and harvest a higher proportion of legal-size sea urchins (Pfister and Bradbury, 1996). Thus commercial harvest should produce larger differences in size distribution than observed in our study.

Effect of harvest on sea urchin density

Commercial harvest in nonreserve habitats of the San Juan Islands for over two decades has significantly decreased sea urchin densities (Pfister and Bradbury, 1996). Both harvest treatments in our study reduced sea urchin densities dramatically and immediately, as expected. The accumulation of older larger individuals in the SJC population led to high yields in selective harvest sites in 1997. Yields in selective harvest sites declined by more than two thirds in 1998 owing to the fishing down of the population (Hilborn and Walters, 1992), low immigration of legal-size sea urchins, and the presence of few under-size sea urchins in the population with a potential of growing to legal size.

Recolonization of harvested sites

Recolonization of harvested sites occurred primarily by immigration of adult red sea urchins. Recolonization began within one month of harvest and continued for the next 18 months. In northern California sites at 11 m in depth, red sea urchins also immigrated into harvested sites within a short time period (Rogers-Bennett et al., 1998). Complete and selective harvest sites in California were recolonized to 32% and 86% of their original densities, respectively, within nine days. These recolonization rates are much higher than those observed in SJC, possibly because of high sea urchin movement (up to 10 m/h, Rogers-Bennett et al., 1995, 1998) and smaller study plots (64 m^2 per site) in the northern California location. Sea urchins move less (~1 m/day) in areas with abundant food, such as in SJC, than in areas with little food (Mattison et al., 1977; Carney, 1991).

Seasonally high recolonization rates observed each spring in both harvest treatments may be related to feeding activity. Spring and summer are seasons when sea urchins feed more frequently (Vadas, 1968) and densities of algae preferred by sea urchins in SJC (e.g. *Laminaria, Nereocystis*, *Alaria*, and *Costaria*; Vadas, 1968, 1977) are highest (Carter, 1999). Both factors may have stimulated movement of sea urchins from deeper waters (with lower algal densities) into our sites.

On a monthly basis, selective harvest sites were recolonized at about half the rate at which complete harvest sites were recolonized. Sea urchins recolonizing complete harvest sites were removed monthly, whereas those recolonizing selective harvest sites were not. The presence of sea urchins, however, did not inhibit immigration in another study (Watson, 1993). Differences in sea urchin densities in adjacent habitats or food availability may have contributed to the observed differences in recolonization rates both within and between treatments.

Recolonization of selective harvest sites was insufficient to maintain sea urchin populations at the densities and size distributions observed prior to harvest under an annual harvest scenario. A site in Washington was recolonized to preharvest density and size distribution after 2.5 years (Bradbury, 1991). Recolonization of SJC sites varied substantially in the first year following harvest (range 1–202 sea urchins per site). One year, after harvest, sites varied between 37% and 69% of their original densities. Such variability in recolonization between sites may be common and should be considered when estimating recolonization rates for commercially harvested areas.

Recolonization rates observed in this study should be considered maximum estimates for recolonization of commercially harvested areas. SJC study sites were small, and sea urchins were relatively abundant adjacent to sites. Commercial fishermen harvest entire beds of sea urchins before moving on to the next bed and prefer to harvest at shallow depths (Pfister and Bradbury, 1996; Kalvass and Hendrix, 1997; Bradbury[2]). Thus sea urchins in adjoining habitats at the same depth would likely be harvested, and only sea urchins inhabiting deeper waters would be available for recolonization.

Juvenile recruitment

The unimodal size distribution of red sea urchins and the rarity of juvenile red sea urchins in SJC suggest variable and infrequent red sea urchin recruitment in northern Washington. In central California, red sea urchin recruitment was also rare; no major recruitment events occurred during a ten-year period (Pearse and Hines, 1987). Size structures of other sea urchin populations north of Point Conception also suggest low red sea urchin recruitment (Table 6).

Commercial harvest may negatively affect juvenile recruitment in several ways. Commercial harvest decreases sea urchin densities in northern Washington (Pfister and Bradbury, 1996; our study), potentially decreasing fertilization rates and larval supply (Levitan et al., 1992). A reduction in adult sea urchin density might also negatively affect juveniles in benthic habitats because adult sea urchins may provide associated juveniles with protection from predators (Duggins, 1981; Breen et al., 1985) and provide an increased food source (Tegner and Dayton, 1977, but see Andrew and Choat, 1985). In southern and northern California, 81% and 73%, respectively, of juvenile red sea urchins were found under the spine canopy of adults (Tegner and Dayton, 1977; Rogers-Bennett et al., 1995). In southern California, juvenile sea urchins were less abundant in harvested sites than in control sites (Tegner and Dayton, 1977). In northern California, juvenile red sea urchins were rare or absent in completely harvested sites but were present in similar numbers in selectively harvested and control sites (Rogers-Bennett et al., 1998). In British Columbia, 69% of juvenile red sea urchins were associated with adults (Breen et al., 1985). Adults may be less important to juveniles in SJC than in other west coast areas because few (4.3%) juvenile green sea urchins were found to be associated with adult red sea urchins (our study), juvenile abundance did not differ by harvest treatment (our study), refuge habitats (cobble, crevices, kelp holdfasts) are abundant, and fast moving sea urchin predators (e.g. fish, lobster) are rare or absent (Breen et al., 1985; Sloan et al., 1987).

Management implications

The current harvest strategy in Washington, applied to sea urchin beds in SJC, results in low yields in the second year of harvest owing to the fishing down of the population and slow recolonization of harvested areas. Annual commercial harvest of a single location is probably not economically viable. Commercial harvests in Washington and other areas of the west coast are well below levels observed in the late 1980s, and biomass estimates are not available to evaluate the status of stocks in Washington (Bradbury[2]). In such circumstances, options for managing the fishery to conserve, and possibly increase, stocks over the long term include artificially enhancing stocks, redirecting or reducing harvest, and establishing marine harvest refuges (Tegner, 1989; Quinn et al., 1993; Rogers-Bennett et al., 1995). Stock enhancement efforts often confer limited success (e.g. Tegner, 1989) and may negatively impact behavioral and genetic diversity of wild populations (Rogers-Bennett, 1997).

Sea urchin harvest in Washington is currently controlled by using harvest quotas, limited entry, and size limits; seasonal closures and rotational harvests were also employed until relatively recently (Pfister and Bradbury, 1996; Lai and Bradbury, 1998). Washington also has two marine harvest refuges (Fig. 2). Both rotational harvests and marine harvest refuges increase the probability of long-term survivorship of populations, particularly when recruitment is low and variable, as it appears to be in SJC (Botsford et al., 1993; Quinn et al., 1993; Pfister and Bradbury, 1996). Rotational harvests were discontinued in Washington in 1995, and the size of one of the two marine harvest refuges was reduced substantially in 1998 (Fig. 2). Additional marine harvest refuges in Washington might be established in areas difficult for harvesters to access (e.g. areas hazardous to navigation and far from port) with little decrease in the actual size of harvested areas (Starr, 1998). Critical to the effectiveness of marine harvest refuges in enhancing recruitment and fishery yields outside of refuge areas is the ability of larvae produced in refuges to recruit to areas outside of the refuge (Carr and Reed, 1992). The extended period that sea urchin larvae spend in the plankton (9–19 weeks, Strathmann, 1978) and the short residence time of water in SJC (Thomson, 1981; Hickey et al., 1991) suggest that larval dispersal from this and other refuge areas to areas outside of the refuge is highly likely, probably occurring on a scale of tens to hundreds of kilometers. Research on sea urchin recruitment patterns (including larval dispersal, settlement, and juvenile survival) in this region is needed to assess the potential for marine harvest refuges in Washington to contribute to recruitment of fished stocks in Washington.

The current size limits in SJC protect a substantially smaller proportion of the population than in SJDF (50% vs. 63%, respectively). Because there are very few small sea urchins in SJC, the lower size limit protects less than 5% of the population. The upper size limit, established to protect larger "broodstock," currently protects 45% of the population. Size limits in Washington were originally established to protect the lower and upper 20% of the population and to allow some individuals to grow through the legal-size "window" under a three-year rotational harvest policy (Pfister and Bradbury, 1996). Considering the small number of juveniles in the population and the return to an annual harvest in 1995, the existing size limits should be reevaluated for their efficacy at protecting local stocks in the context of other harvest control techniques.

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