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ARTICLE IN PRESS

Recruitment patterns and juvenile–adult associations of red sea urchins in three areas of British Columbia

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ABSTRACT

Red sea urchins, *Strongylocentrotus franciscanus*, form meta-populations which are connected by the dispersal of pelagic larvae. Local adult spawning biomass likely plays only a small role in the local recruitment in terms of larval supply, but larger adult red sea urchins provide protection to conspecific juveniles which are often found sheltered under their spines. Based on survey data collected for the past 15 years in three areas of British Columbia, we used generalized linear models to study the juvenile–adult association, the temporal and spatial variations in recruitment, and the effect of adult population density on recruitment success. The probability for a juvenile red sea urchin to be found under a larger red sea urchin decreased with increasing test diameter (TD) of the juvenile and with decreasing adult density. The probability fell from over 50% for juveniles less than 10 mm TD to almost 0% for juveniles at 40 mm TD. The probability for an adult red sea urchin to provide shelter to conspecific juveniles increased with increasing TD of the adult and with increasing juvenile density, but was generally low (<15%). Recruitment levels varied annually within each area, and differed between three surveyed areas. Adult densities, at least up to certain levels, had a positive impact on the recruitment. Intensive harvesting of red sea urchins in a location likely caused a reduction in the amount of recruitment to the location over the next number of years. Understanding the role of adults in the recruitment process is essential for assessing effectiveness of alternative management strategies for the red sea urchin fishery.

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1. Introduction

Red sea urchins, *Strongylocentrotus franciscanus*, are mostly found on rocky substrates from the intertidal zone to depths of approximately 50 m below chart datum. The red sea urchin is the largest and most abundant species of sea urchin in British Columbia (BC) (Bernard and Miller, 1973), and is a long lived and slow growing species (Ebert et al., 1999; Ebert and Southon, 2003; Zhang et al., 2008). Red sea urchins have been commercially harvested by divers since the 1970s in BC. A sound fishery management approach requires an understanding of the effects of harvest-related factors on recruitment, which is a key biological parameter for regulating the population production. The amount of red sea urchin (hereafter referred to as 'red urchin') recruitment in a given location is determined by the amount of larvae that settle and the subsequent survival rate to the age of recruitment, defined in this study as 3 years.

Individual red urchins mature at approximately 50 mm test diameter (TD) (Bernard and Miller, 1973) and usually spawn during May and June in BC (Kramer and Nordin, 1975). The larvae of red urchins remain pelagic for a period of 2–4 months before settlement (Strathmann, 1978) and are capable of dispersing great distances and recruiting into spatially separate communities (Mileikovsky, 1971; Strathmann, 1974). Thus, red urchins can form a meta-population that is connected by dispersal of larvae. Small red urchins (TD < 30 mm) are often found underneath the spines of larger individuals (Tegner and Dayton, 1977; Breen et al., 1985; Sloan et al., 1987), possibly for protection from predators (Tegner and Dayton, 1977; Duggins, 1981).

The relationship between the adult red urchin population and recruitment success seems to be complicated. Local adult spawning biomass likely plays only a small role in recruitment to the local population, in terms of larval supply. Genetic data from red urchins show no evidence of strong sub-structuring in BC waters (Miller et al., 2006). However, adult red urchins provide protected shelter to juveniles, and this protection may greatly enhance juvenile survival rate (Tegner and Dayton, 1981). Alternatively, a close association between juveniles and adults may cause an increase in intercohort competition for resources (Werner and Anholt, 1993). An exceedingly high adult density may impose a negative effect on recruitment due to the competition for food. A good understanding

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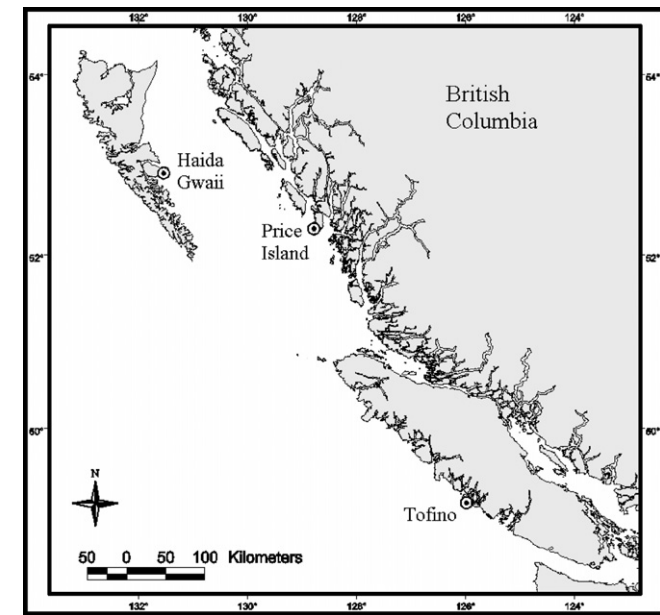*E-mail address:* zane.zhang@dfo-mpo.gc.ca (Z. Zhang).

Fig. 1. Geographic locations of the three study areas in British Columbia.

of the effects of adult density on the recruitment is important for developing sound fishery management. We are not aware of any studies that quantitatively examine the impact of various adult red urchin densities on recruitment.

Field surveys have been conducted almost annually on red urchin populations at three study areas in BC over a 15 year period. The purpose of the long term studies was to quantify the variable biological characteristics of red urchin growth, natural mortality and recruitment for use in stock assessments in BC. We reported on the growth and natural mortality rates for red urchins in Zhang et al. (2008). The purpose of the current study was to (1) examine temporal and spatial variation in red urchin recruitment, (2) quantitatively describe the relationship of TD, juvenile density, and adult density on probabilities for juveniles to receive protection from adults and on probabilities for adults to provide protection to juveniles, and (3) to determine the positive and negative impact of different adult densities on the subsequent recruitment to the red urchin population.

2. Materials and methods

2.1. Study areas

We used survey data from three areas in BC: Haida Gwaii (HG, formerly Queen Charlotte Islands (QCI)), Price Island (PI), and Tofino (TO) (Fig. 1). The three areas were each divided into nine experimental sites, six of which sustained some level of harvesting in 1995 and/or 1996. In 2005, an intensive harvest of over 80% of all red urchins to a depth of 10 m chart datum was conducted in five sites in HG (two of which had also been harvested in 2004). We used the four sites which were not harvested in 2005 (two of which had been harvested minimally in 1996, relative to the harvest in 2005) as control sites for HG, and the three sites which were not harvested in 1996 as control sites for PI. In TO, one of the three no-harvest sites was not surveyed after 2001, and therefore only the remaining two controls were used in the current study.

2.2. Surveys

Field surveys were conducted in the three areas since 1994, generally on an annual basis. Surveys were conducted in May of 1994–1999 and in August thereafter in HG, in September in PI, and in June in TO. In HG, 8–10 1 m-wide transects of variable length were randomly placed perpendicular to the shoreline in each site. In PI and TO, typically 5 transects were randomly placed in each site. Each transect consists of many quadrats of 1 m^2 each. Data were collected in every 1 m^2 quadrat of each transect in the early years (1994 and 1995), and in alternate quadrats in later years. TDs of red urchins in all surveyed quadrats were measured with vernier calipers, from which the total number was counted. Juvenile red urchins observed associated with spines and or underneath larger red urchins were noted. Other data recorded include substrate type and algae type and percent cover of algae.

2.3. Density estimation

We calculated four red urchin densities in each site: total density for all sizes, density of adults defined as individuals $\geq$70 mm TD, density of juveniles defined as individuals $\leq$40 mm TD, and density of recruitment defined as individuals three years old. For recruitment age, we relied on the growth models established by Zhang et al. (2008), where the midpoint of TDs for ages 2 and 3 and for ages 3 and 4 were used as the lower and upper size limit for age 3 red urchins. The TD ranges for age 3 red urchins were 27–38 mm for HG, 33–45 mm for PI and 28–39 mm for TO. We chose age-3 to represent recruitment because too few smaller red urchins were observed and because there would be a problem with increasing overlap of size-ranges with older age-classes.

The red urchins occur most often on rock (hard) substrates and rarely on sand or mud (soft) substrates. The number of quadrats on soft substrates varied between years. To reduce the bias associated with substrate preference, quadrats on soft substrates were not included in the density estimates. The total density of all sizes by site and year was estimated as the average number of red urchins found in all surveyed quadrats in the site (excluding soft substrates) and in the year. Adult, juvenile and recruitment densities, by site and year, were estimated as the products of the corresponding total density and, respectively, the observed proportion of adults, juveniles and recruits in the surveyed population, by year. The density of a given size group for each study area was calculated as the mean of the estimated site densities in the area.

2.4. Juvenile–adult association

In this study, large red urchins having smaller ones underneath their spines or tests were defined as "protecting" red urchins, and smaller individuals receiving protection from adults were defined as "protected" red urchins. Data on these juvenile–adult associations were not recorded for all years. We used the survey data from years 2001–02, 2004, 2006–10 for HG; 1997, 2001–02, 2007–08 for PI; and 1998, 2001, 2003, 2005–06 for TO. Data from the control sites were used in modelling the juvenile–adult association.

We used a generalized linear model with the Bernoulli probability distribution to study the impact of test diameters, juvenile and adult densities on the probability of juvenile–adult association:

$$I_{i,j,k} \sim bern(p_{i,j,k}) \tag{1}$$

where I was either 1 if the individual was in an association or 0 if otherwise, p is the probability for this individual to receive or provide protection, and the subscripts, i, j, and k refer to Year, Site and Individual, respectively. We used the logit link function to model the probability, based on TD (TD), juvenile density (JD), and adult density (AD):

$$\log it(p_{i,j,k}) = a + b \times TD_k + c \times AD_{i,j} + d \times JD_{i,j} \tag{2}$$

where a, b, c and d are the model parameters for intercept, test diameter, adult density and juvenile density, respectively, whose

values are to be estimated. The logit link function is simply the log function of odds, $p/(1-p)$, namely the ratio of probability of having the juvenile–adult association to the probability of not having such association. The red urchins with TD between 40 and 70 mm were occasionally found receiving protection from larger individuals and in other instances providing protection for smaller individuals. The binary association data (1 for association and 0 for non-association) for red urchins < 70 mm TD were used to model probability of receiving protection, and the binary association data for red urchins > 40 mm TD were used to estimate probability of providing protection.

2.5. Recruitment variation

The observed amount of recruitment varied between years and sites in all study areas. To examine the degree of variation in the density of recruitment (R) to an area, we used a generalized linear model with the gamma distribution:

$$R_{i,j} \sim gamma(s_{i,j}, r) \qquad (3)$$

where s and r are, respectively, the parameters of shape and rate of the gamma distribution, and the subscripts i and j refer to Year and Site. The mean of the gamma distribution of recruitment density ($\hat{R}_{i,j}$) is $s_{i,j}/r$. The amount of observed recruitment also varied with adult density, with each area having a different relationship. Recruitment increased with adult density in all areas when density was relatively low, while at higher densities, recruitment continued to increase in HG, remained unchanged in PI and decreased in TO. Based on these observations, we examined the impact of adult density on recruitment, using a quadratic function for PI and TO, and a linear function for HG. $\hat{R}$ was modelled as:

$$\begin{cases} \log(\hat{R}_{i,j}) = u + YE_i + SE_j + \alpha \times AD_{i,j} & \text{(for } HG) \\ \log(\hat{R}_{i,j}) = u + YE_i + SE_j + \alpha \times AD_{i,j} + \beta \times AD_{i,j}^2 & \text{(for } PI \text{ and } TO) \end{cases} \qquad (4)$$

where u is the intercept, YE_i and SE_j are the effects of Year i and Site j, respectively, $AD_{i,j}$ is adult density in Year i for Site j, and α and β are coefficients for the effect of the adult density. Only the data from the control sites were used in these models. For a given site and year, $\exp(\alpha \times AD)$ (for HG) and $\exp(\alpha \times AD + \beta \times AD^2)$ (for PI and TO) would mean the amount of change in recruitment relative to the expected recruitment when adult density is zero.

To examine the impact of intensive harvesting on subsequent recruitment in HG, we modelled the harvesting effect, HE, as follows:

$$\log(\hat{R}_{i,j}) = u + YE_i + SE_j + HE \times I_{i,j} \qquad (5)$$

where $I_{i,j}$ is an identification parameter which was set to 1 if Year i was later than 2005 (the harvesting year) and if Site j was a harvesting site in 2005, and set to 0 if otherwise. The data from all nine sites were used in this model. The expected recruitment density for the harvested site in post-harvesting year was $\exp(u + YE_i + SE_j + HE)$ and would have been $\exp(u + YE_i + SE_j)$ if the harvesting had not been conducted. Therefore, $\exp(HE)$ represents a relative difference or percentage change in recruitment density caused by the harvesting.

2.6. Bayesian analyses

We used the WinBUGS software program (Spiegelhalter et al., 2003) to conduct the Bayesian analyses, which requires that all model parameters have prior probability distributions. We assigned uninformative priors to all parameters in order to force the model to estimate these parameters using the information from the data. Specifically, a, b, c, d, u, α, β, and HE were each assigned a normal distribution with mean = 0, and variance = 10,000 ($\sim N(0, 100^2)$), and r was assigned a gamma distribution: $r \sim Gamma(0.001, 0.001)$ where 0.001 and 0.001 represent the parameters of shape

and rate of the gamma distribution. Sum-to-zero constraints were applied to the categorical variables of Year effect and Site effect, namely: $\sum_i YE_i = 0$ and $\sum_j SE_j = 0$. Each Year effect and Site effect, except for the 1st Year and Site effects, were assigned a normal distribution with mean = 0 and variance = 10,000 (($YE_i \sim N(0, 100^2)$, $i > 1$) and ($SE_j \sim N(0, 100^2)$, $j > 1$)). The 1st Year and Site effects were calculated based on the effects of other years and sites: $YE_1 = -\sum_{i=2} YE_i$ and $SE_1 = -\sum_{j=2} SE_j$.

For executing the juvenile–adult association model, the first 50,000 samples from the posterior distribution were treated as a burn-in period. To reduce autocorrelation, every 10th sample from the posterior distribution was selected after the burn-in period. Visual examination showed that the autocorrelation was low at this sampling interval. For the recruitment models, ten million samples from the posterior distribution were treated as a burn-in period. Every 1000th sample from the posterior distribution was selected after the burn-in period to reduce the autocorrelation. For each model run, 10,000 samples were saved. Two chains were used with different initial values for the Gelman–Rubin diagnostics convergence test (Gelman and Rubin, 1992). This test provided no evidence for lack of convergence because the two independent chains virtually overlapped each other for both the juvenile–adult association model and the recruitment model.

Estimated values of coefficients pertain to the effects of the corresponding explanatory variables on the expectation of the response variable. To evaluate the importance of the effect of an explanatory variable, we examined whether the posterior distribution for the corresponding coefficient was scattered around zero. The posterior distribution away from the zero value would mean that this explanatory variable has an important contribution in the prediction of the response variable. In this paper, "significance" was generally used to indicate that there is only a small probability (≤ 0.05) for the coefficient value to be smaller or larger than zero based on the posterior distribution. To evaluate differences in the coefficients of the juvenile–adult association models between different study areas, we calculated the probability that the model predicted parameter value for one area is as great or greater than the model predicted corresponding parameter value for another area. A "significant" difference means that this probability is either as small or smaller than 0.025 or as large or larger than 0.975.

3. Results

Red urchins receiving protection from larger individuals were predominantly juveniles (<40 mm TD), whereas those providing protection to smaller ones were primarily adults (≥ 70 mm TD) (Fig. 2). There were relatively few small (<15 mm TD) protected red urchins recorded because those individuals are difficult to detect in the field surveys.

Model-predicted probabilities of juvenile–adult association agreed well with the observed data (Fig. 3). The model predicted that more than half of small red urchins (<10 mm TD) were receiving protection in HG and TO and over 90% of these small red urchins were under protection in PI (Fig. 3). The proportion of red urchins being protected fell quickly with increasing size to <20% at sizes greater than 30 mm TD, although the rate of decrease was variable (Fig. 3). The probability for red urchins providing protection increased with their sizes, although this probability was generally small. Less than 15% of red urchins at any observed size group provided protection to the smaller ones (Fig. 3).

The probability of juvenile–adult association was consistently and significantly affected by TD and may also be significantly affected by adult and juvenile densities (Table 1). The probability of being a protected red urchin decreased significantly with increasing juvenile TD (b) ($p < 0.05$) in all three areas, as indicated by the
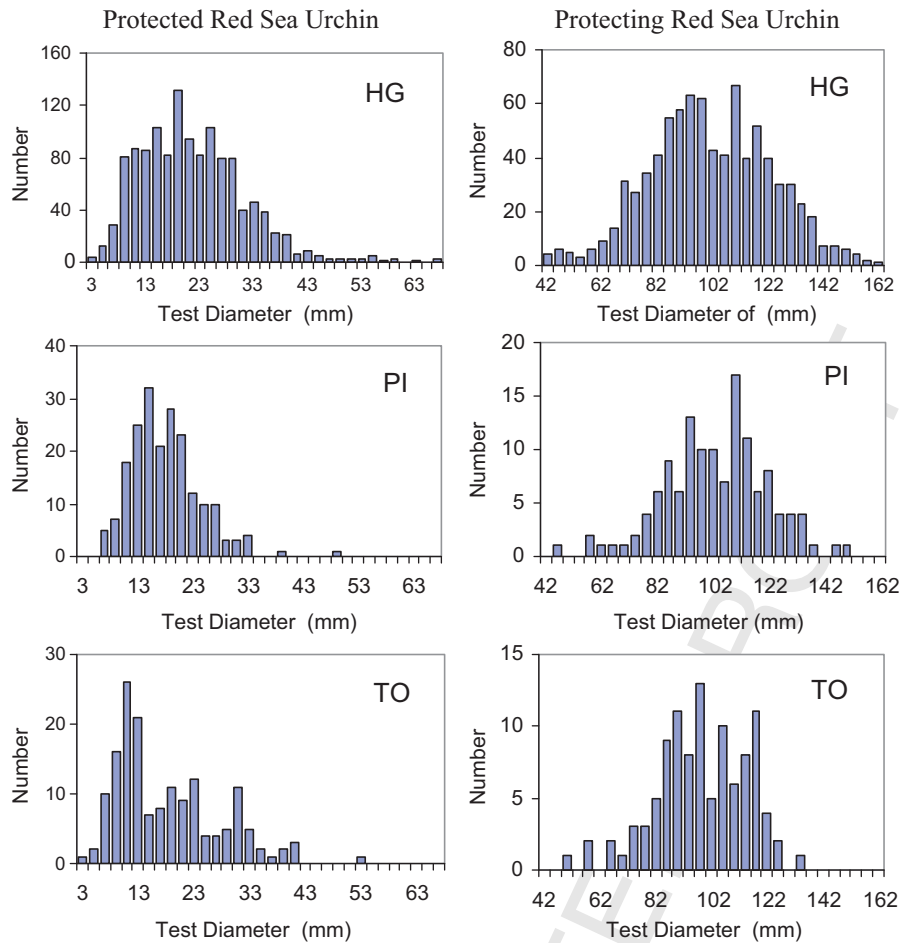
Fig. 2. Size frequency distributions for protected (left panel) and protecting (right panel) red sea urchin in the control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO).

credible intervals all being in the negative (Table 1A). The probability of being a protected red urchin increased with increasing adult density (c), significantly in HG and PI and nearly significantly ($p < 0.1$) in TO (Table 1A). The correlation between the probability of being protected and juvenile density (d) was significantly negative in HG but not significant in PI and TO (Table 1A). The probability of being a protecting red urchin increased significantly with increasing TD and juvenile density (shown by the credible interval being in the positive) in all three areas (Table 1B). The correlation between the probability of providing protection and increasing adult density was significantly negative in HG, significantly positive in PI and did not change significantly in TO (Table 1B).

Estimated values of the coefficients of the logit link function were in most cases significantly different among the areas (Table 2). For the protection-receiving function, the value of the intercept (a) was larger for PI than for HG or TO, and was statistically not different for HG and TO (Table 2A). The value of the coefficient for TD (b) was larger for HG than for PI or TO, and was larger for TO than for PI. The value of the coefficient for adult density (c) was larger for PI than for HG or TO, and was statistically not different for HG and TO. The value of the coefficient for juvenile density (d) was larger for TO than for HG or PI and was statistically not different for HG and PI. For the protection-providing function, the value of the intercept (a) was larger for HG than for PI or TO and was larger for PI than for

Table 1
Estimated values of the coefficients of the logit link function (see Eq. (2)) for receiving protection (A) and providing protection (B), together with 95% credible intervals (CI) in Haida Gwaii, Price Island, and Tofino, using data from the control sites only. Parameter a is the intercept, b is the coefficient for test diameter, c is the coefficient for adult density and d is the coefficient for juvenile density.

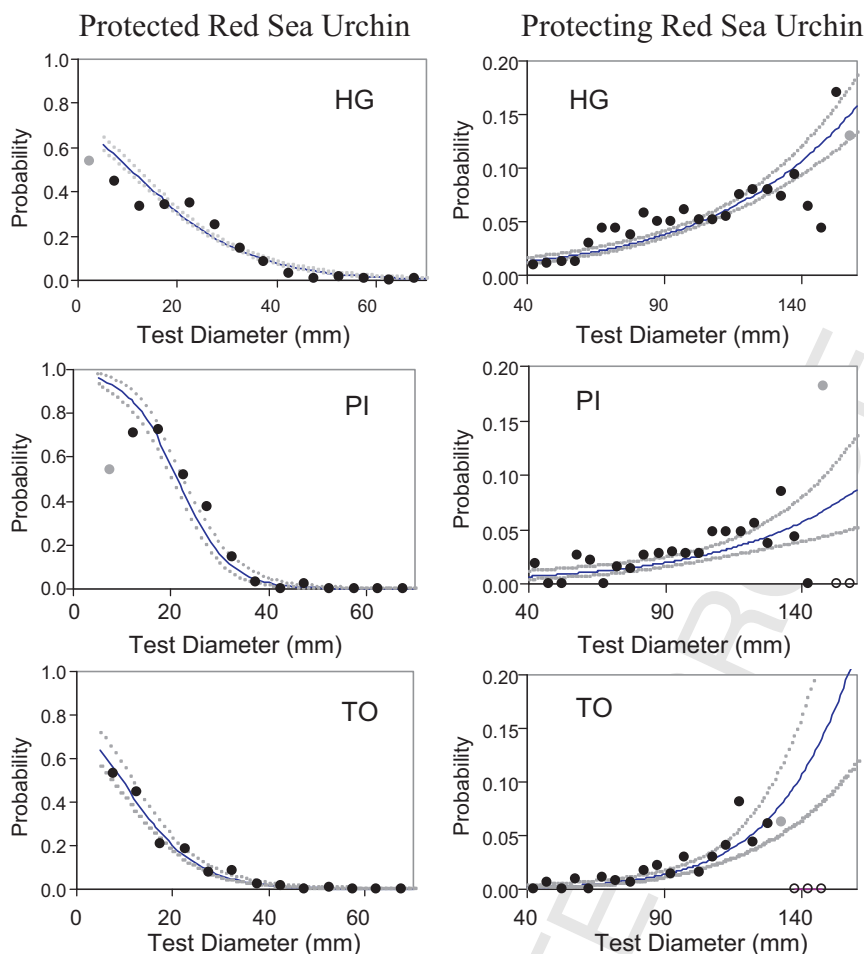| Parameter	Haida Gwaii		Price Island		Tofino	
	Mean	CI	Mean	CI	Mean	CI
(A) – Receiving protection						
a	0.426	0.236–0.618	2.396	1.662–3.152	0.202	−0.592 to 0.982
b	−0.085	−0.09 to −0.079	−0.195	−0.232 to −0.161	−0.131	−0.15 to −0.113
c	0.131	0.094–0.168	0.295	0.215–0.381	0.068	−0.008 to 0.143
d	−0.088	−0.131 to −0.044	−0.152	−0.361 to 0.055	0.084	−0.072 to 0.245
B – Providing protection						
a	−5.353	−5.780 to −4.907	−6.733	−7.709 to −5.792	−8.833	−10.25 to −7.466
b	0.022	0.019–0.026	0.022	0.014 to 0.031	0.043	0.032–0.055
c	−0.107	−0.155 to −0.058	0.074	0.026–0.122	−0.034	−0.116 to 0.045
d	0.351	0.303–0.398	0.49	0.352–0.625	0.409	0.254–0.577

Fig. 3. Probabilities of juvenile–adult association for protected (left panel) and protecting (right panel) red sea urchin in the control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO). The broken lines represent 95% credible intervals of the probabilities, and the dots are observed proportions of the association within each 5 mm test diameter interval based on the sample sizes (n) (○: $n < 10$; ⬤ : $10 \le n < 25$; ●: $n \ge 25$).

TO (Table 2B). The value of the coefficient for TD (b) was larger for TO than for HG or PI and was statistically not different for HG and PI. The value of the coefficient for adult density (c) was larger for PI than for HG or TO and was statistically not different for HG and TO. The value of the coefficient for juvenile density (d) was larger for PI than for HG and was statistically not different between PI and TO or between HG and TO (Table 2B).

Table 2
Probabilities of differences (>0) in estimated coefficients of the logit link function (see Eq. (2)) for receiving protection (A) and providing protection (B) among Haida Gwaii (HG), Price Island (PI) and Tofino (TO), based on data from the control sites. Parameter a is the intercept, b is the coefficient for test diameter, c is the coefficient for adult density and d is the coefficient for juvenile density.

Parameter	HG–PI	HG–TO	PI–TO
A – Receiving protection			
a	0.000**	0.706	1.000**
b	1.000**	1.000**	0.000**
c	0.000**	0.932	1.000**
d	0.717	0.018*	0.037^
B – Providing protection			
a	0.994*	1.000**	0.994*
b	0.529	0.000**	0.001**
c	0.002**	0.800	0.979*
d	0.025*	0.253	0.808

^ Nearly significant ($p \le 0.05$ or $p \ge 0.95$).
* Significant ($p \le 0.025$ or $p \ge 0.975$).
** Highly significant ($p < 0.005$ or $p \ge 0.995$).

Observed mean red urchin recruitment densities prior to 2007 were highest in TO, and higher in HG than in PI (Fig. 4). Annual range of recruitment densities were 0.25–3.14 per m² in TO, 0.07–2.24 m² in HG, and 0.05–0.55 per m² in PI. Recruitment densities, together with adult and juvenile densities, in TO have, however, declined drastically to virtually zero in the most recent years, since sea otters (*Enhydra lutris*) started to prey on large red urchins in 2006.

Variation in model-estimated Year effects on recruitment generally conformed to the variations in the observed mean recruitment densities, after adjusting for Site effects and adult density effects (Fig. 5). Relative to the mean Year effect over all the studied years, Year effects were significantly higher for some recruitment years and significantly lower in some other years. Higher or lower Year effects generally did not occur consistently over the areas (Fig. 5). Specifically, estimated Year effects made a significantly higher contribution to the recruitment in HG during 1998, 2001 and 2009, and a significantly lower contribution in 2007 and 2008; a significantly higher contribution in PI during 1998, 2001, 2002, 2004 and 2008, and a significantly lower contribution in 1996, 1997, and 2000; and a significantly higher contribution in TO during 1995 and 1996, and a significantly lower contribution in 2003 and 2004 (Fig. 5).

Site effects on recruitment were variable among the four control sites in HG and the three sites in PI, but constant between the two sites in TO (Fig. 6). When effects of all other influencing factors remain the same, higher Site effect would, expectedly, produce higher recruitment density for the site. Compared to the overall mean for HG, the recruitment density was expected to be
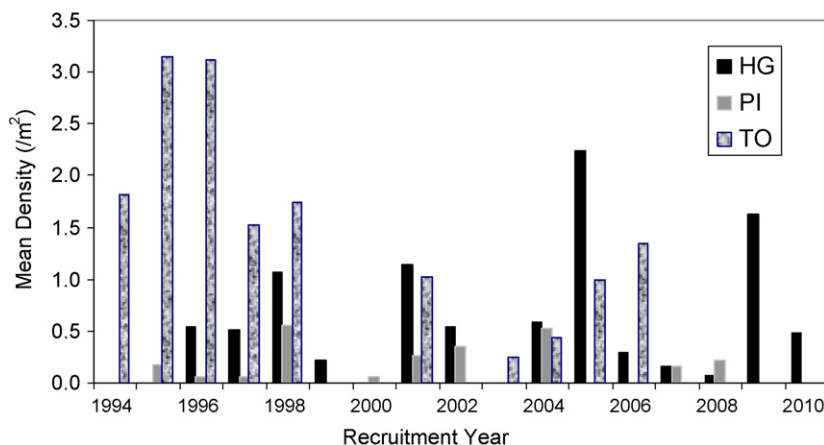
Fig. 4. Mean recruitment densities over the control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO).

significantly higher in one site, significantly lower in another, and intermediate and not significantly different in the other two sites in HG. Compared to the overall mean for PI, the recruitment density was expected to be significantly higher in one site, and not significantly different in the other two sites in PI. The Site effects alone did not affect recruitment densities significantly between the two sites in TO (Fig. 6).

The adult density had a positive impact on the recruitment, at least up to a certain level (Table 3 and Fig. 7). The estimated impact was the highest in PI, and higher in TO than in HG. The positive impact increased with adult density up to about 10 per m^2 for PI at which, given the other influencing factors remaining unchanged, recruitment would be enhanced approximately by 450 times relative to that with zero adult density. When the adult density increased further in PI, the amount of recruitment decreased. In TO, the positive impact increased with adult density up to the maximum observed density of about 19 adults per m^2, at which
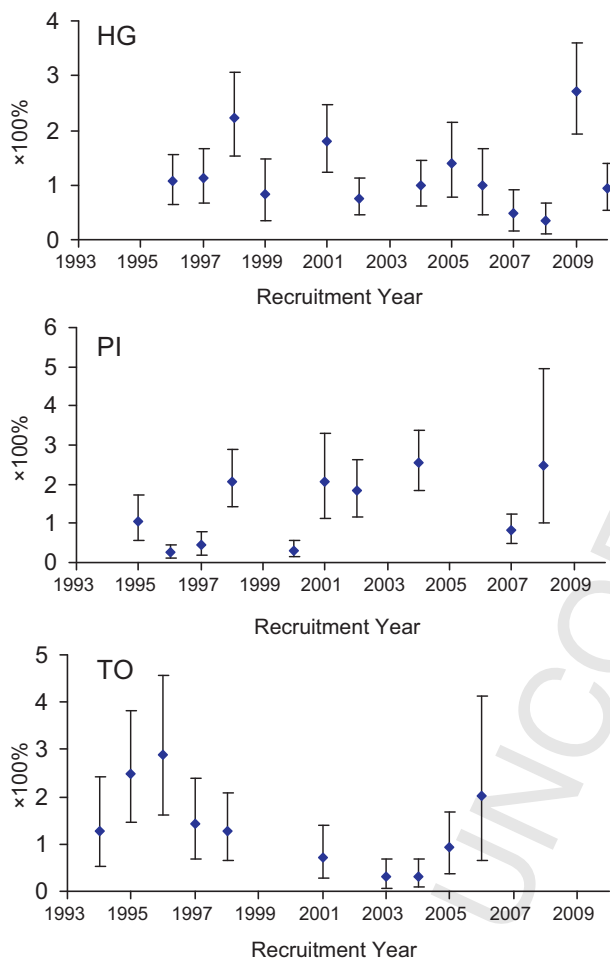

Fig. 5. Variations in annual recruitment of red sea urchin in the control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO). The y-axis denotes the percentage of recruitment relative to the mean recruitment over all the years, and the vertical lines represent 95% credible intervals.
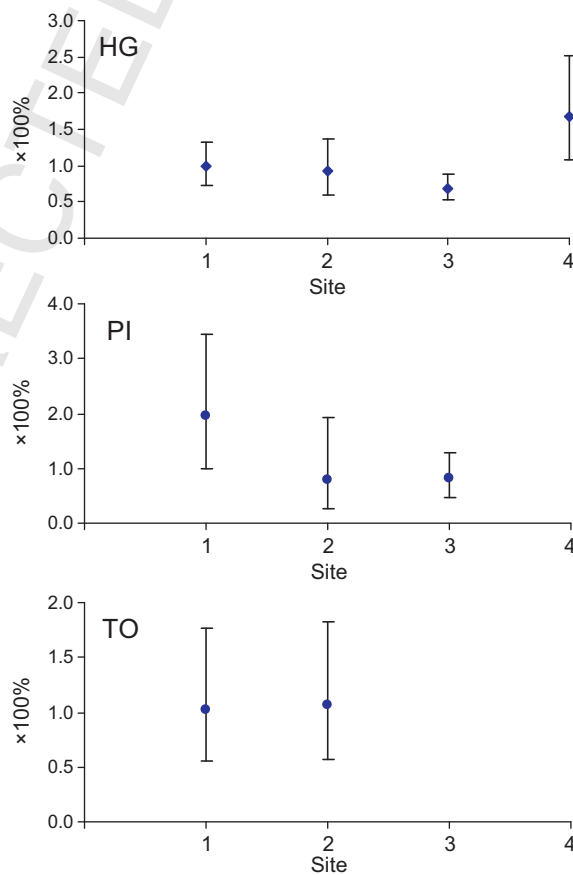

Fig. 6. Variations in recruitment of red sea urchin in different control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO). The y-axis denotes the percentage of recruitment relative to the mean recruitment over all the sites, and the vertical lines represent 95% credible intervals.

Table 3
Estimated values of the coefficients for adult densities in Eq. (4), together with 95% credible intervals (CI) in Haida Gwaii, Price Island, and Tofino, using data from the control sites only. Parameters α and β are the linear and quadratic coefficients for adult density, respectively.

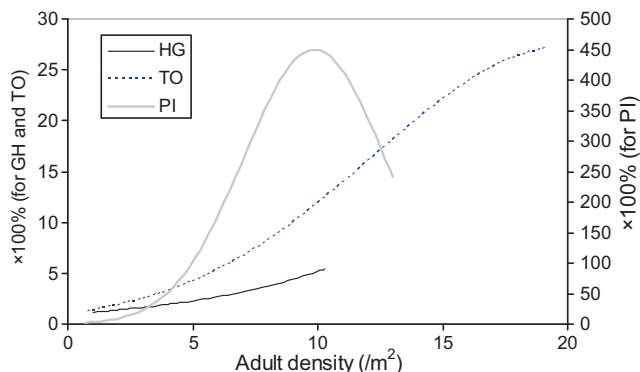| Parameter	Haida Gwaii		Price Island		Tofino	
	Mean	CI	Mean	CI	Mean	CI
α	0.165	0.047–0.278	1.239	0.703–1.810	0.330	0.005–0.744
β			−0.063	−0.092 to −0.035	−0.008	−0.022 to 0.003

Fig. 7. Effect of adult density on recruitment of red sea urchin in the control sites of Haida Gwaii (HG), Price Island (PI), and Tofino (TO). The y-axis denotes the amount of improvement in recruitment in terms of multiples of recruitment density when adult density is zero, given all the other factors are unchanged. Graphs were plotted between the minimum and maximum adult densities observed in each area.

recruitment would be enhanced approximately by 27 times relative to that with zero adult density given the other influencing factors remaining unchanged. In HG, the recruitment also increased with adult density up to the maximum observed density of about 10 adults per m^2, at which recruitment would be enhanced approximately by 5 times relative to that with zero adult density, given the other influencing factors remaining unchanged (Fig. 7).

Intensive harvesting at the HG sites likely caused a negative impact on the annual recruitment for the next five surveyed years. The probability was 0.89 for the recruitment density to be less than 100% of the "expected" recruitment density if the harvesting had not been conducted (Fig. 8). The probability was small, only 0.11, for intensive harvesting to actually have had a positive impact on recruitment density (Fig. 8). The highest probability occurred when the recruitment density was around 75% of the "expected" density. Therefore, the most likely reduction in the amount of annual recruitment was about 25% (Fig. 8).
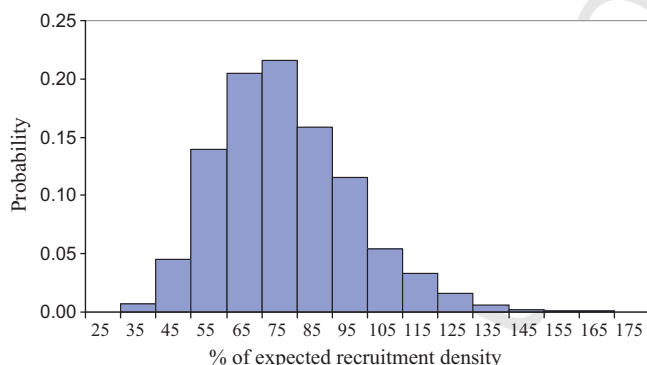

Fig. 8. Probability distribution for estimated changes in recruitment densities due to the intensive harvesting in Haida Gwaii. The y-axis indicates the probability of recruitment density change in terms of percentage of expected recruitment density if the harvesting had not been conducted.

4. Discussion

The current study described, for the first time, the probability of red urchin juvenile–adult associations in relation to size (TD), juvenile and adult densities. The study showed the amount of temporal and spatial variation in recruitment in different locations. This study also provided evidence that intensive harvesting of large red urchins would likely cause a negative effect on the subsequent recruitment to the red urchin population.

Since Tegner and Dayton (1977) found that small red urchins are often sheltered under the spines of larger individuals, many others have also reported on this juvenile–adult association (Duggins, 1981; Breen et al., 1985; Sloan et al., 1987; Rogers-Bennett et al., 1995; Carter and VanBlaricom, 2002; Nishizaki and Ackerman, 2007). Juvenile sheltering is a complex post-settlement behaviour, which seems to balance the risk of predation and the cost of intercohort competition (Nishizaki and Ackerman, 2005). Sheltering under large individuals could contribute to increased survival rates for juveniles due to protection from predators and from destructive exposure to strong water current (Nishizaki and Ackerman, 2007). The presence of an adult red urchin was found to greatly reduce the average water velocity, thereby creating a hydrodynamic refuge for juveniles (Nishizaki and Ackerman, 2007). Sheltering behaviour may, however, also have a negative impact due to increased competition for food causing a nutritional disadvantage for the juvenile (Nishizaki and Ackerman, 2004).

We showed that the probability for juveniles to be found sheltered under the spines of adults decreased with increasing juvenile TD, as reported by Tegner and Dayton (1977). The current study also revealed that the probability for juveniles receiving protection from adults increased with increasing adult densities, but had no statistical correlation with juvenile densities. A higher adult density would increase opportunities for juveniles to come across adult spine canopies, leading to a higher number of protected juveniles. Given an adult density, the proportion of juveniles seeking protection from adults may be relatively stable irrespective of juvenile densities. In addition, our study also presented size-specific probabilities for large red urchins providing shelters to smaller ones. This shelter-providing probability increased with TD of adults, probably because an increase in room under spines and test would provide a higher sheltering opportunity. We also showed that juvenile densities had a consistently positive effect, but that adult densities had variable effects on this shelter-providing probability in the different areas. When juvenile density increases, the number of juveniles receiving protection from adults would likely also increase, leading to more adults providing shelters at a given adult density. The impact of adult densities on the shelter-providing probability seems to be more complex than the impact of juvenile density. When adult density increases, the number of juveniles being protected by adults would expectedly increase at a given juvenile density. An increase in adult density also means an increase in the number of adults. The difference between the relative increases in the number of adults providing shelters and in the number of adults would determine the effect of adult density increase on the shelter-providing probability. If the former increase is higher than the latter, the shelter-providing probability would increase, as is the case in PI; if the former increase is lower than the latter, the

shelter-providing probability would decrease, as is the case in TO; if the former increase is similar to the latter one, the shelter-providing probability would remain about same, as is the case in HG.

Although the general patterns of the juvenile–adult association appeared to be similar in different areas, values of the estimated model parameters generally were significantly different for different areas, indicating that the magnitude of impact of TD, adult and juvenile densities were different. The variable magnitude of impact in different areas may have been caused by different levels of predation, different red urchin densities and/or structural/substrate complexities which could influence hydrodynamic flow (Nowell and Jumars, 1984; Ackerman and Okubo, 1993). Pace (1975) showed that water motion could impose a metabolic demand that exceeds the capacity of aerobic metabolism in adult red urchins. Considering that the mainstream water velocities are reduced by over 60% under the adult spine canopy, hydrodynamic refugia around adults may reduce the energetic requirements needed to maintain similar metabolic processes for juveniles (Nishizaki and Ackerman, 2007).

Recruitment is a key biological parameter regulating population production. Despite a large number of studies on the recruitment mechanisms for marine invertebrates, there is still a lack of understanding of the causes of spatial variability in recruitment over the ranges of a metapopulation connected by larval dispersal (Botsford et al., 1994). In general, recruitment for a marine metapopulation is influenced by three factors: amount of larval supply, success of larval settlement and post-settlement survival (Cameron and Schroeter, 1980). Studies on recruitment for marine invertebrates have often focused on larval supply and settlement (Gaines and Roughgarden, 1985), however post-settlement survival could be as important a factor in regulating recruitment for red urchins due to high post-settlement mortality rates (Nishizaki and Ackerman, 2004).

In this study, we were unable to separately study the impact of larval supply and post-settlement survival on recruitment, as there were no data allowing the estimation of larval settlement densities or early juvenile mortality rate. However, we specifically modelled the effect of adult densities on the estimated recruitment, as adult red urchins provide an important habitat to shelter juveniles and promote their survival rates. Tegner and Dayton (1977) showed that the number of small juveniles (0–20 mm TD) was significantly lower in experimental plots where adult red urchins (95–130 mm TD) were removed a few months earlier, when compared to the number of small juveniles in a control site. Sloan et al. (1987) suggested that the juvenile–adult association may be an important factor in red urchin recruitment success. Indeed, we found that higher adult densities would, in general, cause higher recruitment, given the same amount of larval settlement. However, when the adult density is higher than some threshold level, such as about 10 per m^2 in PI, the recruitment would start to decrease, possibly because of increased competition for food resources. The threshold density appears to vary between areas, however within the observed range of adult densities, there were no negative impacts of adult density on recruitment in HG.

Sloan et al. (1987) speculated that harvesting could have a negative impact on recruitment due to reduced adult spine canopy refugia, but they could not find any evidence to support their speculation. Carter and VanBlaricom (2002), using different experimental harvest rates, found that recolonization by red urchins varied seasonally through immigration of adults, but also that low recolonization occurred at heavily harvested sites. We found that intensive removal of adult red urchins had, indeed, a negative effect on the subsequent recruitment. Using a generalized linear model, our study showed that the intensive harvesting in HG likely resulted in reductions in the amount of subsequent annual recruitment, and that the overall mean annual reduction was most likely about 25%

for the next five surveyed years. Removal of large red urchins by sea otters also caused a severe reduction in small individuals in TO. Sea otters started to prey on red urchins in 2006 in TO, and subsequently the population size rapidly declined. Surveys in the most recent years found virtually no large or small red urchins in TO. The disappearance of small red urchins is unlikely due to predation since immature red urchins have no gonads, upon which the sea otters feed. The disappearance of juveniles is more likely a result of increased vulnerability due to the lack of adult spine canopy and resulting predation, and to strong destructive wave and or current exposure.

Recruitment of juvenile red urchins has been reported as occurring as infrequent pulses or not to occurring every year (Pearse and Hines, 1987; Sloan et al., 1987). More regular annual recruitment of juvenile red urchins has also been described (Tegner and Dayton, 1981; Ebert, 1983). We found that recruitment took place annually to each area in our study, although there were temporal variations in recruitment level in each of the three studied areas. Recruitment success also varied between areas and between sites within an area in the same years, agreeing with the finding of Ebert et al. (1994) that there was substantial variability in the number of settlers both from site-to-site within years and from year-to-year within sites.

Sea urchins are an ecological "keystone species", having a profound impact on the composition and productivity of shallow water benthic communities (Estes et al., 1989; Levitan, 1992; Rogers-Bennett and Pearse, 2001). Red urchins are also a commercially valuable species. The commercial dive fishery in BC began in the 1970s and is managed under a regime including a minimum size limit of 90 mm TD and harvest quotas (Campbell et al., 2003). To achieve conservation goals and sustainable harvesting, the Department of Fisheries and Oceans, Canada, adopts the precautionary approach to fisheries management decisions, which commonly entails establishing two biological reference points, a limit reference point and an upper stock reference point (DFO, 2006). The two reference points delineate stocks into three status zones: healthy (above the upper stock reference point), cautious (between upper stock and limit reference points) and critical (below the limit reference point). The harvest rate is adjusted according to the stock status to ensure a low risk of serious or irreversible harm to the stock. The red urchin fishery in BC currently has no established limit reference points.

Our study provided quantitative information about red urchin juvenile–adult associations and recruitment in BC. Together with our previous study on red urchin growth and mortality (Zhang et al., 2008), simulation models could be constructed to evaluate variations in the productivity of the red urchin population under alternative harvesting strategies. For model inputs, the amount of recruitment (age 3 red urchin) may be generated from observed variations in the past, and then modified according to the adult density. Some recruits would die from natural causes before reaching the minimum legal size for the fishery. Legal-sized red urchins would sustain an imposed fishing mortality in addition to natural mortality. The remaining abundance of adults would affect the amount of subsequent recruitment. Various harvesting rates and minimum size limits at different population densities may be used in the simulation model to evaluate consequences to the red urchin population in terms of changes in density and size structure. Biological reference points may thereby be formulated and appropriate exploitation rates demonstrated for the different stock status zones.

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