EXPERIMENTAL HARVEST OF RED SEA URCHINS, Mesocentrotus franciscanus [A. Agassiz, 1863], AND TRENDS IN RED, GREEN (Strongylocentrotus droebachiensis; [Des Moulins, 1837]) AND PURPLE (S. purpuratus; [Stimpson, 1857]) SEA URCHIN POPULATIONS WITHIN THE TOFINO RESEARCH AREA (1994-2012)

Lyanne J. F. Curtis and Dan Leus

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
Nanaimo, British Columbia
V9T 6N7

2022

Canadian Manuscript Report of Fisheries and Aquatic Sciences 3244

Canadian Manuscript Report of Fisheries and Aquatic Sciences

Manuscript reports contain scientific and technical information that contributes to existing knowledge but which deals with national or regional problems. Distribution is restricted to institutions or individuals located in particular regions of Canada. However, no restriction is placed on subject matter, and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Manuscript reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Manuscript reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-900 in this series were issued as Manuscript Reports (Biological Series) of the Biological Board of Canada, and subsequent to 1937 when the name of the Board was changed by Act of Parliament, as Manuscript Reports (Biological Series) of the Fisheries Research Board of Canada. Numbers 1426 - 1550 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Manuscript Reports. The current series name was changed with report number 1551.

Rapport manuscrit canadien des sciences halieutiques et aquatiques

Les rapports manuscrits contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui traitent de problèmes nationaux ou régionaux. La distribution en est limitée aux organismes et aux personnes de régions particulières du Canada. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports manuscrits peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports manuscrits sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports manuscrits sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 900 de cette série ont été publiés à titre de Manuscrits (série biologique) de l'Office de biologie du Canada, et après le changement de la désignation de cet organisme par décret du Parlement, en 1937, ont été classés comme Manuscrits (série biologique) de l'Office des recherches sur les pêcheries du Canada. Les numéros 901 à 1425 ont été publiés à titre de Rapports manuscrits de l'Office des recherches sur les pêcheries du Canada. Les numéros 1426 à 1550 sont parus à titre de Rapports manuscrits du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 1551.

Canadian Manuscript Report of
Fisheries and Aquatic Sciences 3244

2022

EXPERIMENTAL HARVEST OF RED SEA URCHINS, *Mesocentrotus franciscanus* [A. Agassiz, 1863], AND TRENDS IN RED, GREEN (*Strongylocentrotus droebachiensis*; [Des Moulins, 1837]) AND PURPLE (*S. purpuratus*; [Stimpson, 1857]) SEA URCHIN POPULATIONS WITHIN THE TOFINO RESEARCH AREA (1994-2012)

By

Lyanne J. F. Curtis and Dan Leus

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
Nanaimo, British Columbia
V9T 6N7

Cat. No. Fs97-4/3244E-PDF ISBN 978-0-660-43618-0 ISSN 1488-5387

Correct citation for this publication:

Curtis, L. J. F. and Leus, D. 2022. Experimental harvest of Red Sea Urchins, *Mesocentrotus franciscanus* [A. Agassiz, 1863], and trends in Red, Green (*Strongylocentrotus droebachiensis;* [Des Moulins, 1837]) and Purple (*S. purpuratus;* [Stimpson, 1857]) Sea Urchin populations within the Tofino research area (1994-2012). Can. Manuscr. Rep. Fish. Aquat. Sci. 3244: xi + 57 p.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Curtis, L. J. F. and Leus, D. 2022. Experimental harvest of Red Sea Urchins, *Mesocentrotus franciscanus* [A. Agassiz, 1863], and trends in Red, Green (*Strongylocentrotus droebachiensis;* [Des Moulins, 1837]) and Purple (*S. purpuratus;* [Stimpson, 1857]) Sea Urchin populations within the Tofino research area (1994-2012). Can. Manuscr. Rep. Fish. Aquat. Sci. 3244: xi + 57 p.

In the early 1990s, a sea urchin research area was established near Tofino, BC, Canada, to conduct research on sea urchin populations. This report focuses on two studies between 1994 and 2012. The first study investigated the impacts of harvesting Red Sea Urchins (RSU; *Mesocentrotus franciscanus*) and the second study describes trends of RSU, Green Sea Urchin (GSU; *Strongylocentrotus droebachiensis*), and Purple Sea Urchin (PSU; *S. purpuratus*) populations over an eighteen year timespan. Experimental harvesting had minimal short (< 2 years) or long (5 year) term impacts on RSU. Within 2 years of harvest, significant decreases in mature and total RSU populations only occurred at a few sites. In contrast, immature RSU decreased significantly 5 years after harvesting at several sites, which may be associated with an El Niño event. Although variability was evident in all three species, populations remained relatively stable from 1994 through 2005 and then after 2005, urchin populations began to decline steadily until 2009 reaching near zero values of all indices until the end of the study period. The decline in sea urchin populations was likely associated with the establishment of a Sea Otter population near the research area in 2004.

RÉSUMÉ

Curtis, L. J. F. et Leus, D. 2022. Experimental harvest of Red Sea Urchins, *Mesocentrotus franciscanus* [A. Agassiz, 1863], and trends in Red, Green (*Strongylocentrotus droebachiensis;* [Des Moulins, 1837]) and Purple (*S. purpuratus;* [Stimpson, 1857]) Sea Urchin populations within the Tofino research area (1994-2012). Can. Manuscr. Rep. Fish. Aquat. Sci. 3244: xi + 57 p.

Au début des années 1990, une zone de recherche sur l'ourson a été établie près de Tofino, Colombie-Britannique, Canada, pour étudier les populations d'oursins. Le présent rapport se concentre sur deux études menées entre 1994 et 2012. La première étude portait sur les répercussions de la récolte de l'oursin rouge (*Mesocentrotus franciscanus*), et la deuxième décrivait les tendances des populations d'oursins rouges, des oursins verts (*Strongylocentrotus droebachiensis*) et des oursins violets (*S. purpuratus*) sur une période de 18 ans. La récolte aux fins d'expérience a eu des incidences minimales à court (< 2 ans) et à long (5 ans) terme sur les oursins rouges. Dans les deux années suivant la récolte, des diminutions importantes des populations matures et totales d'oursins rouges se sont produites seulement à quelques endroits. En revanche, les oursins rouges immatures ont diminué considérablement cinq ans après la récolte à plusieurs endroits, ce qui peut être associé au phénomène El Niño. Bien que la variabilité était évidente pour les trois espèces, les populations sont demeurées relativement stables de 1994 à 2005. Après 2005, les populations d'oursins ont commencé à diminuer progressivement jusqu'en 2009, pour atteindre des valeurs presque nulles sur tous les indices jusqu'à la fin de l'étude. La diminution des populations d'oursins était probablement liée à l'établissement d'une population de loutres de mer près de la zone de recherche en 2004.

INTRODUCTION

Red Sea Urchins (*Mesocentrotus franciscanus*; RSU; [A. Agassiz, 1863]) are distributed from the Aleutian Islands, Alaska to Baja California, Mexico (including the Gulf of California) (DFO 2018, Campbell and Harbo 1992) in North America. Along the Western Pacific, they are distributed from north of the Aleutian Islands to Hokkaido Island, Japan (DFO 2018, Campbell and Harbo 1992). RSU are broadcast spawners with separate sexes that generally spawn from May to June along the coast of British Columbia (BC) (Kramer & Nordin 1975). Fertilization is generally followed by a 6 – 9 week pelagic larval period, after which the larvae settle. The larval period can extend to longer periods of time, due to many factors like food availability (Rogers-Bennett and Okomato 2020). RSU are reproductively mature at approximately 50 mm Test Diameter (TD; Bernard & Miller 1973), which is roughly 3 – 5 years of age.

The commercial fishery for RSU in BC began in 1971 with a minimum harvest size limit of 100 mm TD (Campbell et al. 1999). In the 1990s, commercial harvesters and processors requested a reduction of the minimum size limit to meet market demands (Campbell et al. 1999). One of the most common management measures placed on the commercial harvest of aquatic organisms is size limit restrictions (Fenberg and Roy 2007). Often, minimum size limits are used to prevent recruitment overfishing and they are easily enforced (Perry et al. 1999). Minimum size limits can prevent recruitment overfishing by ensuring that individual animals spawn at least once before they reach a harvestable size (Perry et al. 1999). While such management practices are intended to mitigate some impacts of harvesting, the impact of lowering the minimum harvest limit for RSU in BC was unknown, and more research was deemed necessary.

As such during the 1990s, Fisheries and Oceans Canada (DFO), the Pacific Urchin Harvesters Association (PUHA), and coastal First Nations collaborated and established four experimental research areas in BC to conduct studies on sea urchins. One of these areas was in Clayoquot Sound, near Tofino (Pacific Fisheries Management Area 24; PFMA). Standardized SCUBA surveys and multiple studies began in the Tofino research area in 1994 and continued until 2012. While several studies occurred in the research area, the work presented here focused on two studies: (1) to assess the impacts of experimentally harvesting RSU up to five years after harvesting and, (2) to describe the population trends of RSU, Green Sea Urchins (*Strongylocentrotus droebachiensis;* GSU; [Des Moulins, 1837]), and Purple Sea Urchins (*S. purpuratus;* PSU; [Stimpson, 1857]) over an 18 year period (1994 – 2012). Publications arising from other studies in this research area include estimates of growth rates and natural mortality rates from tagging studies (Zhang et al. 2008), recruitment and juvenile-adult association analyses (Zhang et al. 2011), and weight-at-length allometric relationships (Campbell 1998, Lochead et al. 2015).

First, we investigated the impact of harvesting RSU using two different minimum size limits (≥ 100 mm TD and ≥ 85 mm TD) annually for a two year period from 1995 to 1996 on the density (number of urchins per m^2) and biomass (kg per m^2) of the total, immature (< 50 mm TD), and mature (≥ 50 mm TD) RSU population components. The total RSU population in these studies represents all sizes of urchin combined, i.e. total density (no. urchins per m^2) of RSU is estimated using the survey data of the total count of all sizes of RSU observed. This definition of total population (e.g., total RSU density and total RSU biomass) will be used and termed such henceforth. Potential changes in the density and biomass of these RSU size classes, and the size frequency distributions due to experimental harvesting were investigated up to five years after the last experimental harvesting event (1996). This approach allowed us to assess potential harvest impacts on the reproductive RSU population present during the time of harvest and the future reproductive population of RSU. Additionally, we described the spatial and temporal trends of sea urchin populations within the Tofino research area over an 18 year period.

Temporal and spatial trends in RSU total, mature, and immature density and biomass as well as the size frequency distributions are described for each study site and the entire study area (1994 – 2012). Similarly, trends in total density of GSU and PSU are also described for each study site and the entire study area. For RSU, these trends are discussed in the context of broader trends of the population along its distributional range and other potential ecological impacts such as Sea Otter (*Enhydra lutris*) predation.

METHODOLOGY

SITE LOCATIONS AND DESCRIPTIONS

This study took place near Tofino, BC, in Pacific Fishery Management Area (PFMA) 24-8, and this area has been closed to commercial urchin harvesting since the early 1994. Nine sites were selected in 1993 to test the effects of harvesting RSU using different minimum size limits (Table 1, Figure 1). Site selection features were the presence of RSU, similarity in slope, exposure, surge, and primary bottom substrate (Table 1). Sites consisted of rocky substrate (predominantly bedrock and/or boulders) from the surface to approximately 15m depth, where the substrate changed to sand which was thought to limit immigration to the sites from deeper depths. The sites were grouped into two different types: shore and pinnacle sites. These different site types were chosen based on their estimated differences in immigration potential. Pinnacles with sand encircling them were thought to potentially limit immigration and emigration, thereby allowing the impact of experimental harvesting to be more clearly detected. The exact area (m^2) of each site is unknown as there is no record of geographic information (i.e., GPS coordinates along site boundaries).

From 2001 through 2007, one of the planned control sites, 7, was not surveyed. Rather, study participants erroneously surveyed another location. This new location became site 70 and the total number of sites for the entire study area became 10. Unfortunately due to this unforeseen error, a second control site for the shore-type sites was lost and was not part of experimental harvest study (1995 – 2001). The data from sites 7 and 70 were presented and discussed during the second study, temporal and spatial trends of sea urchin populations in the Tofino sea urchin research area (1994 – 2012). Both sites, 7 and 70, were surveyed from 2008 through 2012.

DATA COLLECTION

SCUBA surveys were conducted from 1994 – 1998, in 2001, and from 2003 – 2012. Five transects per study site were randomly selected and surveyed during each survey as conditions allowed, except for 1994 and 1995 (n = 3 per site). At the beginning of the study, each site was divided into 100 approximately equal sections. Prior to each survey, five random numbers were generated from 1 to 100 to determine the starting point of each transect. Further details on transect starting locations and selection criteria were missing or not found when this report was written.

During each survey, transects were laid perpendicular to the shore from shallow water to approximately 15 m chart datum depth; transect length was dependent on slope. A float was attached to the deep end of the transect and a team of two divers surveyed each transect from deep to shallow. One diver measured urchins and the second diver recorded the measurements and additional data (depth, etc.). Using 1 m^2 quadrats, divers recorded the number of RSU, GSU, and PSU as well as habitat characteristics (described below) within every other quadrat along the transect (i.e., data were collected only within every 2nd quadrat). According to project contract documents, test diameter measurements in 1995 involved randomly collecting data within each transect (desired N = 450 - 500 urchins measured). The experimental harvest protocol documents suggest that the quadrat skipping pattern for test diameter measurements were based on the observed density within each site as follows:

(1) > 20 – 30 urchins per m^2, sample every 6th quadrat;
(2) 10 – 20 urchins per m^2, sample every 4th quadrat;
(3) ≤ 10 urchins per m^2, sample every 2nd quadrat;
(4) Scattered urchin distribution; sample either every 2nd, 4th, or 6th quadrat depending on time constraints.

These patterns did not change within a site during a survey year. Further documentation regarding the surveying pattern to collect urchin size data was not available or found during the time this report was written. From 1996 through 2012, size measurements were predominantly taken in every 2nd quadrat along the transect. For specific details regarding the pattern of urchin size data collection please see Appendix I (below). Counts and test diameters of GSUs and PSUs were not recorded in 1994 for unknown reasons.

Within each surveyed quadrat, the following habitat characteristics were recorded: depth, substrate type, algae species, and percent cover of different categories of algae. Depth (in feet) from divers' depth gauges was recorded within each quadrat, and after completion of the survey, depth was corrected to chart datum for each quadrat using tide height predictions from the Canadian Hydrographic Service (CHS) and converted to meters. Substrate within each quadrat was classified using the following codes: 0= wood/bark, 1 = smooth bedrock; 2 = bedrock with crevices; 3 = boulders (>30 cm); 4 = cobble (between 7.5 cm and 30 cm); 5 = gravel (between 1 cm and 7.5 cm); 6 = pea gravel (between 0.25 cm and 1 cm); 7 = sand; 8 = shell; 9 = mud; 10 = crushed shell, and 11 = whole shell (Code 8 was replaced with codes 10 and 11 in 2006; Davies et al. 2018; Waddell and Perry, 2012). The collection of substrate data changed over the course of the study period. Very little substrate data were collected in 1995, only the most dominant substrate was recorded in 1996 (one code value only), and from 1997 through 2012, the three most dominant substrates were recorded. For each surveyed quadrat, algae species, and percent cover were estimated and recorded for canopy (taller than 2 m), understorey (30 cm to 2 m) and turf (<30 cm). Percent cover was estimated and recorded for encrusting and drift algae as well. The exposure of each transect within a site was ranked using the following codes: 0 = extreme shelter; 1 = minimal sea movement; 2 = well sheltered; 3 = occasional current; 4 = moderate current; 5 = strong tidal flow; 6 = high tide surge only; 7 = ground swell normal; 8 = high exposure. These exposure rankings were recorded in 1994 and 1995 as well as 2001 through 2007.

POPULATION DENSITY AND BIOMASS ESTIMATION

Urchin density and biomass were estimated from survey data using the Red Urchin Analysis Program (RUAP; no depth restrictions were applied) (Lochead et al. 2015). One of the intended control sites, 7, was excluded from the analyses in the experimental harvest study because it was not surveyed consistently (see Site locations and descriptions above). Estimates derived for the harvest impact study came from 8 survey sites; five shore and three pinnacle sites (1995 – 2001; Table 1). One control site was available for each of the pinnacle and shore site types.

Sites 7 and 70 were not included in the analyses of the harvest impacts because they were not consistently surveyed between 1995 and 2001. Site 7 was surveyed from 1995 – 2001 and 2008 - 2012, while site 70 was surveyed from 2001 – 2012. For the analysis of long term population trends, estimates came from all 10 study sites in the research area (five shore, three pinnacle, as well as sites 7 and 70; 1994 – 2012 when available).

Transect is the sampling unit throughout this study. The plotted mean density and biomass estimates, and confidence bounds were calculated at various spatial (e.g., site, study area) and temporal scales (e.g., year, all years) by pooling transect estimates to the relevant scale and then computing the mean and confidence bounds for each RSU size category. For example, mean density at a study site in 1996 was estimated by combining all transect density estimates from that site in 1996. Pooling was also applied in the same manner across all sites in the study area, and across all years. The density (no. urchins per m^2) and biomass (kg per m^2) of urchins within each sampled transect was estimated using the RUAP program and an allometric relationship between urchin test diameter and weight.

Briefly, the RUAP program estimates density and biomass for each transect, and size category as well as the mean and confidence bounds around the mean of pooled data (e.g. mean density per site, entire research area, year or all years). The confidence bounds (95%) on density and biomass estimates were generated through bootstrapping unless otherwise stated. CI*t* is used to denote instances in which 95% confidence intervals were generated from t-tests.

Urchin weights are not measured during surveys, but are estimated from an established allometric relationship (Equation 1; Lochead et al. 2015).

Equation 1: $W_{T,q,r} = 0.0010169(\mathrm{TD}^{2.7787})$

where TD is the Test Diameter (mm) of each measured urchin and $W_{T,q,r}$, is the estimated weight (in grams) of an urchin *r* in quadrat *q* on transect *T*.

RUAP uses linear interpolation to fill in the non-surveyed quadrats, based on the assumption that density, depth and the proportion of urchins in each size category (immature RSU <50 mm TD and mature RSU $\geq$ 50 mm TD) change linearly between surveyed quadrats of the same transect. Therefore, RSU size, counts or both from surveyed quadrats and Equation 1, were used to estimate data from neighboring non-surveyed quadrats using linear interpolation of the number of individuals and the proportion of immature and mature urchins. Mean immature and mature RSU weights were calculated for each transect and applied to the non-measured RSUs in each size category. The counts/biomass from surveyed and non-surveyed quadrats were then summed and divided by the transect area to estimate density (urchins per m^2) and biomass (kg per m^2) for each transect (i.e. sampling unit).

HARVEST TREATMENTS AND DATA ANALYSES

The effect of harvesting was investigated using data from eight sites: five shore and three pinnacle sites (see Population Density and Biomass Estimation section, for the reason why sites 7 and 70 were omitted from the analyses). The harvest treatments consisted of three treatments that were applied to individual sites: (1) the removal of all RSU of $\geq$ 85 mm TD from the site, (2) the removal of all RSU of $\geq$100 mm TD from the site and, (3) no removal (control). The harvest treatments were randomly assigned to each of the study sites (Table 1). Each site type, shore or pinnacle, had one control each, and the replication of the harvesting treatments differed. Of the five shore sites, one was a control site, two were ≥ 85 mm TD harvest treatments and two were ≥100 mm TD harvest treatments (Table 1). Of the three pinnacle sites, one was a control, one was a ≥85 mm TD harvest treatment and one was a ≥100 mm TD harvest treatment (Table 1). Hereafter, the harvest treatment and the respective site will be referred to as the harvest treatment site(s), as treatments were not replicated within each site (Table 1). The harvest treatments were conducted in 1995 (Sept-Oct) and 1996 (April-May), with one exception. Due to logistical constraints, the ≥100 mm TD treatment at the shore type site "100_Shore_2" was not done in 1995.

The RSU harvesting was conducted by PUHA commercial urchin divers in the fall of 1995 and the spring of 1996, and every attempt was made to harvest all RSU at or above the size limit at each site during each harvest event. Each year a set quota (weight) was allocated by DFO Fisheries Management in order to complete this project. Unfortunately details surrounding the 1995 quota were not available. In 1996, the quota for the entire research area was ~20,000 kg. All harvested RSU were transported and offloaded to a processing facility where they were transferred into totes. These totes were then weighed to the nearest kg. Protocol documents suggest the totes were 4' by 4', but documentation after harvest regarding these details and the location of the processing plant were not found at the time this report was written.

The potential impacts of harvesting RSU using different minimum size limits on the density and biomass of total, immature (< 50 mm TD), and mature (≥ 50 mm TD) RSU were assessed through PERMANOVA analyses based on Euclidean distance based matrices (Anderson et al. 2008; Clarke and Gorley 2006) using a fixed effects model with year (1995, 1996, 1997, 1998 and 2001), harvest treatment site (i.e. applied harvest treatment per site: minimum size limits of ≥ 85 mm TD, ≥ 100 mm TD or control), and their interaction as effects (note, total (density or biomass) refers to the combined value of all sizes of RSU estimated from survey data). The data were separated and analyzed by site-type because of the difference in harvest treatment site replication. Within each site-type, separate analyses were conducted for the density and biomass of each size class, resulting in twelve individual PERMANOVA analyses. When an effect was statistically significant ($\alpha = 0.05$), pairwise comparisons were analyzed through subsequent PERMANOVAs. If the interaction between year and harvest treatment site was significant, pairwise comparisons of year within each harvest treatment site were conducted ($\alpha = 0.05$). The effect of harvest treatment site incorporated variability due to both site level and harvest treatment effects, which could not be separated due to the experimental design. However, when the interaction was significant ($\alpha = 0.05$), pairwise comparisons between harvest treatment site and year were done within a site, which allowed for a direct comparison of pre- and post-harvest RSU population estimates. Subsequent qualitative comparisons of trends among the control and harvest sites when the interaction was significant determined whether trends were likely due to harvest impacts or other effects. If the model produced few unique permutations, the associated *p*-values were determined through Monte-Carlo sampling (Anderson et al. 2008; Clarke and Gorley 2006).

The 2001 dataset (5-years post-harvest) was chosen as the upper limit to include in these PERMANOVA analyses based on the time required for immature RSU at the time of experimental harvest and shortly after harvest (< 2 years) to become part of the reproductive population of RSU. Most RSU become sexually mature around 50 mm TD, which may equate to 3 to 5 years of age in BC (Bernard and Miller 1973). Using these data, we may be able to assess whether experimental harvesting impacted the survival and recovery of immature RSU as well as the subsequent generation of reproductively mature RSU.

The potential impact of the harvest treatments on the size structure of the RSU population was also investigated at each harvest treatment site separately through kernel density probability distributions and size frequency distributions. Kernel density probability distributions were conducted through pair-wise comparisons between the pre-harvest survey (1995) and each of the following post-harvest surveys: 1-year post-harvest (1997), two years post-harvest (1998), and 5-years post-harvest (2001) (Langlois et al. 2012; Bowman and Azzalini 2010; Wand 2011; R Core Team 2019). We used the R code developed by Langlois et al. (2012) that compares the Kernel Density Estimates (KDE) using the Sheather-Jones method to estimate bandwidths (triweight) with the ‘dpik’ function in the package ‘KernSmooth’(Wand 2011 version 2.23). Two metrics were considered: (1) mean length of the distributions (location); and (2) the shape and location of the distributions. According to Langlois et. al. (2012), differences in location can indicate an overall bias towards either smaller or larger individuals, while differences in location and shape can indicate a particular bias towards a certain length class. In the plots of the KDE comparisons, the grey strip represents the null model of no difference between the paired comparison of distributions. This strip indicates the region on the size frequency that is likely responsible for any significant differences found ($\alpha = 0.05$). The strip is centred around the mean KDE and spreads across one standard error above and below the mean (Langlois et al. 2012; Bowman and Azzalini 2010). For brevity only the resulting *p*-values will be presented along with the 1995 versus 2001 plots.

A qualitative assessment of the effects of experimental harvesting on the size frequency distribution of RSU within each harvest treatment site was also conducted by examining size frequency histograms. These histograms were created using the plyr (Wickham 2011), and the ggplot2 (Wickham 2016) packages in R (version 4.1.2; R core team 2022). Size bins were 2 mm in width. All other plots were produced using the ggplot2 package in R (Wickham 2016, R core team 2022).

RESULTS

SELECTIVE HARVEST

A total of 29,203 kg and 20,286 kg of RSU were harvested from all of the study sites in 1995 and 1996, respectively (Table 2; Appendix II below). An average of 5,804 (± 766; SE) and 3,340 (± 10; SE) kg of RSU were removed from each study site in 1995 and 1996, respectively. The biomass removed from the sites ranged from 465 to 8,959 kg, with an average of 8,218 kg (± 1633; SE) per site. On the second harvest (in 1996), the biomass of RSU removed per site ranged from 5 - 162% of the biomass removed during the first harvest (1995). Harvesters collected more RSU in the second harvest (1996) than the first (1995) at the 85_Pinnacle (162%) and 100_Shore_1 sites (146%). During the second harvest (1996), the biomass of RSU harvested at all the other treatment sites was under 20% of that harvested in 1995 (100_Shore_2 was not harvested in 1995). The total biomass removed from all ≥ 100 mm TD and ≥ 85 mm TD harvest events was 27,421 kg and 21,887 kg, respectively. In 1996, the entire allocated quota was harvested, but the 1995 quota is unknown. Further, the efficacy of urchin removals during each harvest event was not detailed (i.e., did the harvest remove all relevant sized RSU) in any documentation or data found to date.

RSU Density

Total RSU density

The effects of harvest treatment site, year, and their interaction on the total densities of RSU varied between shore and pinnacle sites (Table 3). The total density of RSU at the shore sites was significantly affected by harvest treatment site and year, while at pinnacle sites only year significantly affected total RSU density. Although harvest treatment sites significantly affected RSU total density at shore sites, a clear trend caused by this effect was not evident (Figure 2). With the highest densities, both Control_Shore and 100_Shore_1 were not significantly different from one another (Figure 2). Similarly, with the lowest densities among the sites, 100_Shore_2 and 85_Shore_1 were also not significantly different from each other. These two sets of paired sites were also significantly different from each other and 85_Shore_2.

The total density estimate of RSU in 1995 (pre-harvest) at shore sites was significantly greater than those found in 1996 and 2001 (Figure 3). While at pinnacles sites, total RSU density was significantly lower in 1996, 1998, and 2001 (5 years post-harvest) when compared to the 1995 estimate (pre-harvest) (Figure 3).

Mature RSU (≥ 50 mm TD) density

Similar to RSU total density, the effects of harvest treatment site, year, and their interaction on the mature RSU densities varied between site types (Table 3; Figure 4). At shore sites, harvest treatment site, year, and their interaction significantly affected mature RSU density. Two months after the second harvest (1996), mature RSU densities were significantly lower than pre-harvest estimates (1995) within 85_Shore_1 and 100_Shore_1sites. Five years after harvest (2001), mature RSU densities within shore sites were not significantly different than pre-harvest estimates (1995), except within 85_Shore_1. None of the experimental effects significantly affected mature RSU densities at pinnacle sites (Figure 4).

Immature RSU (< 50 mm TD) density

Harvest treatment site, year, and their interaction also affected immature RSU densities differently between the site types (Table 3; Figure 5). Immature RSU densities at shore sites were affected by harvest treatment site, year and their interaction. Immature RSU density estimates within Control_Shore, 85_Shore_1 and 100_Shore_1 decreased significantly in 2001 when compared to those from 1995, 1996, 1997, and 1998. Furthermore, within 100_Shore_2, immature RSU densities in 2001 were significantly lower than those estimated from 1995 through 1997. At the pinnacle sites, the only effect that significantly impacted immature density was year. The most striking trend among years at pinnacle sites was the significant decrease in immature RSU density in 2001 (mean ± 95% CI_t; 3.7 ± 1.2 urchins per m^2), compared to estimates from 1995 (9.8 ± 4.5 urchins per m^2; $p = 0.0001$) and 1996 (4.3 ± 1.5 urchins per m^2; $p < 0.001$)(data not presented, but see Figure 5 for general trend).

RSU Biomass

Total RSU biomass

The effects of harvest treatment site, year, and their interaction on total RSU biomass varied between site types (Table 4; Figure 6; Figure 7). At shore sites, total RSU biomass was significantly affected by harvest treatment site, year, and their interaction. Although the interaction of year and harvest treatment site significantly affected total RSU biomass, significant pairwise interactions were only found at 100_Shore_1 (Figure 6). Within that site, total biomass estimates from 1996 and 1998 were significantly lower than those found in 1995 and 2001 (Figure 6). At the pinnacle sites, total biomass was only affected by year (Figure 7). Total biomass at pinnacle sites in 1995 (pre-harvest) was significantly higher than those estimated in 1996 and 1998. Total RSU biomass estimates from 1995, 1997, and 2001 were also not significantly different from each other (Figure 7).

Mature RSU (≥ 50 mm TD) biomass

Similar to RSU total biomass, the effects of harvest treatment site, year, and their interaction varied between site types (Table 4; Figure 8). For shore sites, mature RSU biomass was significantly affected by harvest treatment site, year, and their interaction, while at pinnacle sites it was only affected by year. Although the interaction of harvest treatment site and year significantly affected mature RSU biomass, significant pairwise interactions were only found within 100_Shore_1(Figure 8). Within 100_Shore_1, mature RSU biomass estimates 2 months (1996) and 1 year (1997) after harvesting were significantly lower than pre-harvest (1995) and 5-year post-harvest (2001) estimates. At pinnacle sites, mature RSU biomass in 2001 was significantly greater than estimates from 1996, 1997, and 1998. Mature RSU biomass in 1996 also decreased significantly when compared to 1995 (pre-harvest)(data not presented, but see Figure 8 for general trends).

Immature RSU (< 50 mm TD) biomass

Harvest treatment site, year, and their interaction affected the immature RSU biomass at shore and pinnacle sites differently (Table 3; Table 4; Figure 9). Immature RSU biomass at shore sites was affected by harvest treatment sites, year, and their interaction, but for pinnacles sites year was the only significant effect. Within shore sites, immature RSU biomass estimates at all sites decreased significantly in 2001 when compared to those from 1995 and 1996 (exception: 100_Shore_2 in 1996). For pinnacle sites, the most striking trend among years was the significant decrease in immature RSU biomass in 1998 (mean ± 95% CI_t; 0.036 ± 0.014 kg per m^2) and 2001 (0.026 ± 0.008 kg per m^2), when compared to estimates from 1995 (0.14 ± 0.59 kg per m^2; $p_{1998} < 0.001; p_{2001} < 0.001$) and 1996 estimates (0.10 ± 0.031 kg per m^2; $p_{1998} < 0.001; p_{2001} < 0.001$)(data not presented but see Figure 9 for trend).

Size frequency distribution and kernel density estimate comparisons

Qualitative assessment of the size frequency distributions of RSU between 1994 and 2001 showed that two trends occurred after experimental harvesting was conducted (Figure 10 and Figure 11). First, the proportion of RSU greater than 100 mm TD at many experimental sites initially decreased after harvesting, but rebounded to levels similar to pre-harvest frequencies by 2001. This trend did not occur at any of the control sites. The second trend occurred in the proportion of immature RSU (under 50 mm TD). At many sites including the controls, the proportion of small RSU in 2001 was notably lower relative to previous years. When the Kernel Density Estimates (KDE) of RSU in 1995 were compared with those from subsequent surveys within each site, significant differences in the location (mean length of distribution) as well as the location and shape of the distributions were found between each comparison (Figure 12 and Figure 13; Table 5). This indicates that within each harvest treatment site, the probability distribution of certain sizes of RSU varied significantly when KDEs from 1995 were compared to those from 1997, 1998, and 2001 surveys. Both control sites began with bimodal probability density distributions that became unimodal in 1997 with a peak at ~60-75 mm TD. These distributions stayed consistently unimodal in 1998 and 2001, but the peak shifted to larger individuals (~80-90 mm TD), and the probability associated with the peak increased slightly over time. This trend was echoed at all of the sites with the exception of 100_Shore_2, where bimodal KDEs occurred in 1995 and 1998, but the size range of RSU at those peaks varied between years. In 1995, the peaks at 100_Shore_2 were at ~25 mm TD and ~110 mm TD, whereas 1998 peaks were at ~25 and ~ 88 mm TD. The probability of these peaks also changed with a decrease of 25 mm TD individuals in 1998 and increase of larger sized RSU in 1998.

RSU POPULATION TRENDS FROM 1994-2012: DENSITY, BIOMASS AND SIZE DISTRIBUTIONS

The highest total mean density of RSU recorded at the Tofino research area was observed during the first survey (1994) at the Control_Shore site (Figure 14). The total mean density at that site and time was 33.37 (95% CI , 12.75 to 42.90) RSU per m^2. During the experimental harvest study (1995 – 2001), the lowest observed density was 8.82 urchins per m^2 at site 85_Shore_1 (95% CI, 6.39 to 10.11) in August 1995. After the experimental harvesting (1998 - 2003), the Control_Shore and 85_Shore_1 sites again showed the highest and lowest observed densities for the period with 31.11 (95% CI, 26.65 to 37.09) and 2.52 urchins per m^2 (95% CI, 2.08 - 2.89), respectively. All sites showed a steady decline in total RSU density after 2004 and, by 2009, RSU densities had dropped to nearly 0 urchins per m^2 (Figure 14). Similar trends occurred with immature RSU densities (< 50 mm TD, Figure 16), while for the mature densities this trend largely began in 2008. At all sites, RSU densities, were 0 RSU per m^2 from 2009 to 2012. This trend was also echoed when the data from the entire research area were pooled (Figure 17).

Generally, similar patterns occurred with RSU biomass. The highest total mean biomass of RSU recorded at the Tofino research area was observed during the first harvest year (1995) at the 100_Shore_1 (Figure 18). The total mean biomass at that time was 8.9 kg per m^2 (95% CI; 7.9 to 10 kg). During the experimental harvest study (1995 – 2001), the lowest observed biomass was 1.2 kg per m^2 at site 100_Shore_2 (95% CI; 0.8 to 1.9) in 1996, 2 months after the second harvest event. After the experimental harvesting between 1998 and 2005, the Control_Shore and 100_Shore_1 sites showed the lowest and highest observed total biomass for the period with 1 (95% CI, 0.8 -1.5), and 8 kg per m^2 in 2003 and 2005 (2003: 95% CI, 4.4 – 11.3; 2005: 95% CI, 6.3-9.9), respectively. After 2004, steady declines in total biomass also occurred at all the research sites. This declining trend occurred for mature and immature RSU as well and by 2009 total, mature, and immature RSU biomass declined to ~ 0 kg per m^2 at all sites and remained near zero until 2012 (Figure 19 and Figure 20).

Prior to 2006, the size frequency distribution at many sites was largely bimodal, one peak at < 50 mm TD and the other at > 85 – 100 mm TD (Figure 21 and Figure 22). Size frequency distributions remained stable and the majority of the size bins (2 mm each) were below 3% of the total population structure until 2006. After 2006, the size frequency distributions became narrower, indicating the range of sizes encountered on surveys was decreasing, and few individuals were present to be measured during surveys. The variation in density and biomass declines among the sites suggest there may be a spatial pattern involved in the decline of RSU within the Tofino research area.

In 2004, the first raft of male Sea Otters was spotted around the northern area of Vargas Island and the La Croix islands (PFMA 24-6; Linda Nichol, Marine Mammal Biologist, Fisheries and Oceans, Canada, 2020, pers. comm.). Once male Sea Otter rafts are observed, Sea Otters are considered established in the area (Linda Nichol, Marine Mammal Biologist, Fisheries and Oceans, Canada, 2020, pers. comm.). The establishment of Sea Otters in 2004 is denoted on the density and biomass graphs of RSU and other marine invertebrates (Figure 14 through Figure 20 and, Figure 24).

GSU AND PSU DENSITY TRENDS FROM 1994-2012

During the entire study period (1994 – 2012), the mean density of GSU seldom exceeded 1 GSU per m^2 (Figure 23). Exceptions to this did occur at Control_Shore and 100_Shore_1 prior to 2004 (Figure 23). The highest observed density of 1.23 GSU per m^2 (95% CI, 0.82 to 1.74) occurred at 100_Shore_1 in 1997. High densities in 1997 were also found at Control_Shore with 1.08 GSU per m^2 (95% CI, 0.56 to 1.51). Similar to temporal trends in the RSU population, total densities of GSU also declined to near zero (< 0.05 GSU per m^2) by 2009, and remained near zero until 2012 (exception: Control_Shore in 2011). PSU abundance followed similar patterns as GSU, but with relatively low densities (<1 PSU per m^2) at all sites in all years, except site 100_Shore_1 (Figure 24). All sites dropped to 0.00 PSU per m^2 (95% CI, 0.00 to 0.00) from 2009 onwards (Figure 24).

The overall (all sites combined) GSU density was relatively constant until 2006 after which the GSU population in the research area began to steadily decline until 2010 (Figure 17). In 2011 and 2012, the GSU population increased slightly, but never to levels estimated pre-2006. Overall PSU densities were variable in the research area over time with a high in 1996 of 0.66 PSU per m^2 (95% CI, 0.36 to 1.19) and a low of 0.00 PSU per m^2 from 2009 through 2012.

DISCUSSION

This multi-year study investigated the impacts of selective harvesting on the density, biomass, and size frequency distributions of RSU populations. It also reported the trends in RSU, GSU, and PSU populations over an 18 year period at the RSU research area near Tofino, British Columbia. For many benthic invertebrates, density and biomass are important indicators of the sustainability of the population and the fishery. For example, successful fertilization of gametes can be density-dependent and subject to environmental factors like oceanic pH (Rogers-Bennett and Okamoto 2020 and the references therein). To date, few studies have examined the impacts of selectively harvesting RSU populations, particularly over the course of many years (but see Carter and VanBlaricom 2002; Carter et al. 2007). Similarly, few long-term, annual monitoring studies of benthic marine invertebrates have been conducted along the coast of BC (but see Curtis *in prep.* and Hand et al. 2009). This study also encompasses a rare dataset along the northern distribution of RSU that includes both pre- and post-Sea Otter occupation in the study area.

HARVEST IMPACTS ON RSU POPULATIONS

Regardless of the minimum size limit, experimentally harvesting RSU over a two-year period had no long term impact on the densities and biomass of total and mature RSU within the study area (i.e., 5 years post-harvesting; 2001). Shorter term impacts of harvest treatment site on RSU density were observed for mature individuals at two sites (85_Shore_1 and 100_Shore_1), but were not reflected in the total RSU category (i.e., no significant impact). In contrast, mature and total RSU biomass were both affected by the harvest treatment site effect, with short term impacts at 100_Shore_1. These short-term harvest impacts at 100_Shore_1 and 85_Shore_1 may be explained by intraspecific competition or differing levels of RSU population reservoirs among the sites (Britton-Simmons et al. 2009; Narveaz et al. 2020; Rogers-Bennett and Okamoto 2020). Recent studies on GSU have shown that both interference and exploitative competition occurs within the species, but that the strength and impact of each type of competition varies with GSU size (Narvaez et al. 2020). In this study, the harvest of larger RSU (≥ 100 mm TD) may not have reduced the competition (exploitative) among mature RSU (> 50 mm TD) at those sites over the short-term (Narvaez et al. 2020). The removal of larger RSU may not have released enough physical space for other RSU to migrate back into the area when compared other harvest treatment sites (i.e., 85_Shore_2 and 100_Shore_2). Alternatively, RSU populations also exist in sub-tidal (> 20 m) and deep benthic (> 30 m) areas (Britton-Simmons et al. 2009; Rogers-Bennett and Okamoto 2020; Carson et al. 2018), and the affected treatment sites may not have had abundant enough populations near them to replenish RSU to pre-harvest levels over the short-term. Declines in total density after selective, experimental harvesting of RSU were also found in the San Juan Islands, Washington (Carter and VanBlaricom 2002). This is the first experimental study to examine the impacts of harvesting RSU using differing size limits (i.e., ≥ 85 and 100 mm TD) on RSU populations.

Carter and VanBlaricon (2002) found that when larger RSU were harvested (102 -140 mm TD) in the San Juan Islands, significant declines in total RSU densities occurred; however, the impact of this decline was much more severe than in the current study. Eighteen months after experimental harvesting, RSU populations were on average 37.7% of their original densities (Carter and VanBlaricom 2002). By comparison, we found that on average total RSU densities were 88% and 87% of their original densities (1995), one and two years after harvesting RSU > 100 mm TD, respectively, and not significantly different than the original densities within each site (1995, shore-type sites only). Similar declines due to experimental harvesting of RSU were also reflected in another Washington study, but total densities were not presented and therefore not directly comparable (Carter et al. 2007). The difference in harvest impacts between this study and the others may be explained by greater RSU densities and the difference in size frequencies found in British Columbia at the time. RSU densities in both of the Washington studies were less than 2 RSU per m^2 (Carter and VanBlaricon 2002; Carter 2007) and were considered high, whereas RSU densities in this harvest study were ≥ 5.8 RSU per m^2 with a median density of 8.9 RSU per m^2 (1994 - 2003). The size frequency distributions at control sites in Washington indicated that the RSU population had a unimodal distribution with most individuals greater than 85 mm TD. Whereas in this study, the pre-harvest and control site size frequency distributions were largely bimodal, and in comparison to the Washington study, BC populations had higher frequencies of smaller size classes (i. e. < 85 mm TD). Immature RSU (< 50 mm TD) were also far more abundant in BC (in this study) than in Washington in 1997 and 1998 (Carter and VanBlaricon 2002).

When mean immature densities (<50 mm TD) from experimental harvesting sites in Washington were compared to those from this study (> 100 mm TD harvest at shore-type sites), we found they were over 5,000 and 800 times greater in our study areas in 1997 and 1998, respectively (Carter and VanBlaricon 2002). Regardless, Carter and VanBlaricon (2002) also found that selectively harvesting RSU (102 – 140 mm TD) had no effect on the density of RSU juveniles within 2 years of harvesting. This trend did not continue as we found a significant decrease in immature RSU density and biomass in the later survey years of this study (1998 and 2001). However, experimental harvesting was likely not the only contributing factor as significant declines in immature RSU density and biomass occurred at sites that were not harvested.

When pre-harvest (1995) and subsequent survey estimates (1996, 1997, 1998) of immature densities and biomass at Control_Shore were compared to estimates five years after harvesting (2001), a significant decline was found for both indicators (exception: 1998 biomass). Similar results were observed for immature RSU density and biomass within other harvest treatment sites. At three of the harvested shore sites, 85_Shore_1, 100_Shore_1, and 100_Shore_2, immature RSU density significantly declined when pre-harvest and other survey estimates were compared to 5 year post-harvest estimates (exception: 100_Shore_2 in 1998; Figure 5). Immature RSU biomass from pre-harvest (1995) and some post-harvest estimates were also significantly greater than those found in 2001 at 85_Shore_1, 85_Shore_2, and 100_Shore_1 (Figure 9). The same trend was seen with the significant effect of year at pinnacle sites. When the pinnacle site data within each year were pooled, immature RSU density and biomass were also found to be significantly lower in 2001 when compared to estimates from 1995 and 1996. Further, total RSU density at both site-types (i.e. shore and pinnacle) 5-years post-harvest (2001) declined significantly when compared to pre-harvest estimates (1995). These results indicate that experimental harvesting was not the only factor that affected immature RSU density and biomass in this study. These site level variations in immature RSU could be explained by intraspecific interactions, food availability, and oceanographic conditions (Tegner and Dayton 1991; Rogers-Bennett et al. 1995; Edwards and Estes 2006; Parnell et al. 2017; Rogers-Bennett and Catton 2019; Beas-Luna et al. 2020).

Immature RSU are known to hide under the spine canopy of mature RSU, which protects them from predation and strong current (Tegner and Dayton 1981; Rogers-Bennett et al. 1995; Nishizaki and Ackerman 2007, Zhang et al. 2011). The experimental removal of large RSU may have affected immature RSU survival after settlement or interacted with larger oceanographic processes like El Niño. In 1997, a strong El Niño event occurred in the north Pacific (Freeland and Thomson 1999). Such strong oceanographic events are known to result in high sea surface temperature anomalies, increased storm activity, and declines in kelp abundance and nutritional quality (Tegner and Dayton 1991; Edwards and Estes 2006; Rogers-Bennett and Catton 2019; Beas-Luna et al. 2020; Lowman et al. 2021). Studies on the Purple Sea Urchin, *Strongylocentrous purpuratus* (PSU), suggest that El Niño events may impact fecundity and larval settlement (Ebert et al. 2012; Okamoto et al. 2020) as gonad weight during El Niño events were lower than either La Niña or non El Niño years. However, this trend was not consistent along the species range as variability among sites along the coast of California and British Columbia were found (Ebert et al. 2012; Okamoto et al. 2020). There is little direct evidence of the effect of El Niño on RSU and kelp populations within BC (but see Milligan et al. 1999). While Watson and Estes (2011) suggest that the 1997 El Niño event had little long term impact on subtidal *Macrocystis* kelp beds along the west coast of Vancouver Island, surveys were not conducted in 1997 and may not reflect decreases in food availability for RSU during that event. While we cannot state with certainty that the declines in immature RSU in the years after harvest were caused by the 1997 El Niño event, it may have had some impact on the reproductive potential of mature RSU. Subsequently, this may have impacted successful reproduction, settlement and survival of immature RSU in 1997, a year class that would be predominantly < 50 mm TD in 1998 and 2001 (Bernard and Miller 1973). Conversely, declines in total and mature

RSU densities and biomass did not occur in the later years of the harvest study (i.e., 2001, 5-years post-harvest).

Comparable experimental studies that assess the longer term impacts of harvesting RSU are lacking, but see Curtis (*in prep.*). However, studies that compare RSU population dynamics between Marine Protected Areas (MPAs) and fished areas, shed some light on the long term impact of RSU harvesting (Shears et al. 2012; Tuya et al. 2000; Teck et al. 2017; Malakhoff and Miller 2021). Studies in the Channel Islands, California suggest that total RSU density did not differ between selectively fished areas and MPAs (established for at least 4 years), but that reproductive biomass and potential were significantly greater within MPAs (Shears et al. 2012; Malakhoff and Miller 2021). Similarly, in the San Juan Islands, Washington, greater abundances of medium and large sized RSU were found within well-established MPAs (established 8 years; Tuya et al. 2000) when compared to newly established MPAs (1-year; Tuya et al. 2000). The results of the current study did not echo those of MPA studies as experimental harvesting did not lead to declines in total or mature RSU biomass and density at most sites 5 years after harvesting (exception: 85_Shore_1, mature density). Similar to the short term harvest impacts on RSU density and biomass, a plausible explanation for these differences may lie in the much higher densities and biomass of RSU in the current study area when compared to studies from California and Washington (Tuya et al. 2000; Shears et al. 2012; Malakhoff and Miller 2021). These differences may have led to greater immigration potential in the Tofino sea urchin research area than in studies conducted in Washington and California.

At pinnacle sites, harvest treatment site did not significantly affect the density and biomass of any of the RSU size classes assessed. During the planning and design of this study, it was assumed that RSU migration was limited by sand, but published observations to support this assertion do not exist. On the contrary, there is evidence that RSU are found on sand and will travel across it (Laur et al. 1986; Carson et al. 2018; DFO 2022a). Therefore the potential contribution of RSU migrating to the pinnacles from surrounding areas is unclear. There are several possible reasons why harvesting RSU had no effect on RSU populations at pinnacle sites. One possible explanation for more rapid recovery at pinnacle sites than at shore sites is physical differences between the sites. Due to the nature of pinnacles, they inherently have less area as water depth decreases. Therefore, the total number of RSU immigrating into the harvest area may be the same, but the resulting density at pinnacle sites would be higher. Other explanations may include natural variation in RSU populations among sites (Sloan et al. 1987; Morgan et al. 2000; Britton-Simmons et al. 2009) and the efficacy of harvesting (see Study Uncertainties section). Variability in size frequency and kernel density probability distributions of RSU was also evident among the harvest treatment sites.

The size distribution of RSU (kernel density probability distributions) within each of the harvest treatment sites changed significantly when pre-harvest probabilities (1995) were compared with each of the subsequent survey years (1996 – 1998, 2001) (Figure 12 and Figure 13; Table 5). Most sites showed largely bimodal distributions with the peak TD shifting slightly for each mode from 1995 through 1998 (Figure 10 and Figure 11). The shift in the peak TD for each peak was not consistent among years or sites, and may have led to the significant differences seen between most years and the pre-harvest kernel density probability distributions (1995) within each site. At all sites (including the control sites), the kernel density probability distribution of RSU <50 mm TD decreased between 1995 and 2001; indicating that harvesting was not the only factor contributing to that change over time. Variability in size distributions fine (0 – 10s km) and small spatial scales (10 – 100 km) as well as at temporal scales has been well documented in RSU populations throughout much of their range (Sloan et al. 1987; Ebert et al. 1999; Morgan et al. 2000; Botsford 2001; Britton-Simmons et al. 2009). The exact cause of this variability is unknown, but is theorized to include habitat and environmental factors unrelated to experimental harvesting (Sloan et al. 1987; Morgan et al. 2000; Britton-Simmons et al. 2009). Such factors may include variability in predator and kelp abundance (Jenkinson et al. 2020), climatic conditions (Shears et al. 2012; Teck et al. 2017; Jenkinson et al. 2020), large oceanic processes like ENSO (Botsford 2001) as well as wave and current exposure (Parnell et al. 2017).

TEMPORAL TRENDS OF SEA URCHIN POPULATIONS FROM 1994 THROUGH 2012

While sea urchin populations varied among the sites and years surveyed, they remained relatively consistent from 1994 through 2005, after which all urchin populations began to decline (Figure 17). After the decline, RSU and PSU populations remained at near zero urchins per m^2 while GSU populations increased slightly in 2011 (surveys from 2009 to 2012). The population crash of RSU represented a drop from an average of 27.2 RSU per m^2 prior to 2005 to an average of 0 RSU per m^2 in 2009. Rapid declines in RSU populations during the same time period did not occur in other areas of BC (e. g. Haida Gwaii; density and biomass; DFO unpublished data), Mexico (density; Medellín-Ortiz et al. 2020), Washington (density; Carson et al. 2016), California (biomass; Malakhoff et al., 2021), nor Southeast Alaska (total commercial fishery landings; ADF&G 2021). The population crash of GSU represented a drop of an average of 0.36 urchins per m^2 to 0 urchins per m^2 in 2009, and the crash of PSU represented a drop of an average 0.65 urchins per m^2 to 0 urchins per m^2 in 2009. Similar to RSU populations, a similar crash in the GSU population did not occur in other areas of BC (DFO 2021), but this pattern was not clear for PSU populations as few studies with high densities occurred during the same time period (but see Rogers-Bennett and Catton 2019 for a consistent, low density trend).

The lack of similar declines in RSU, GSU, and PSU along their distributional ranges implies that something other than large oceanographic processes affected urchin populations within the study area. Based on the sighting of male Sea Otters near the research area in 2004 (Nichol et al. 2005; Linda Nichol, Marine Mammal Biologist, Fisheries and Oceans, Canada, 2020, pers. comm.), it is likely that these declines were associated with the expansion of Sea Otter distribution and their establishment in southern Clayoquot Sound, BC.

The rapid depletion of RSU associated with Sea Otter recolonization observed in this study is consistent with observations and predictions from Laur et al. (1988), Laidre and Jameson (2006), Honka (2014), Stevenson et al. (2016), Burt et al. (2018), and Shelton et al. (2018; RSU and GSU combined). Similar studies that focus on the interaction of GSU and Sea Otters are not as numerous, but in parts of Alaska, Sea Otters caused a decline in GSU populations (Kodiak archipelago; Kvitek et al. 1992) or did not have an effect at all (Prince William Sound; Dean et al. 2000, Bodkin and Dean 2000); therefore, the discussion will focus primarily on the RSU and Sea Otter interaction.

Sea Otters were re-introduced from Southeast Alaska to the west coast of Vancouver Island between 1969 and 1972, and a self-sustaining population subsequently established along the coast of BC (Bigg and MacAskie 1978). By 2008, Sea Otter numbers in BC grew to about 4,700 with populations along most of the west coast of Vancouver Island and portions of the central coast (Nichol et al. 2009). Sea Otters were considered established in our study area as of 2004. Similar to model predictions by Honka (2014) and Stevenson et al. (2016), drastic reductions in RSU occurred within the first six years of Sea Otter occupation within our study area. Modelling by Stevenson et al. (2016) and data presented by Honka (2014) also suggested that large RSU decrease in abundance with increasing Sea Otter predation and that large RSU (> 90 mm TD) are the predominant part of the Sea Otter diet in the first year of occupation. This decline in biomass was also observed in the current study as the frequency of large RSU (> 100 mm TD; Figure 21 and Figure 22) decreased one year before declines were noticeable in the mature size class (density and biomass; ≥ 50 mm TD; Figure 15; Figure 19). After the first year of Sea Otter occupation, the frequency of larger RSU (> 100 mm TD) as well as total and mature density and biomass declined at some harvest treatments sites but not at others.

Both the decline in total biomass (<1 kg per m^2) and the frequencies of larger RSU (≥ 100 mm TD) occurred in 2006 at the La Croix Group sites, but occurred later at the sites in Father Charles Channel. Declines occurred one year later at two sites in Father Charles Channel (100_Shore_2 and 70) and two years later at other sites in Father Charles Channel (Control_Shore, 85_Shore_1 and 100_Shore). Declines in total density (<1 RSU per m^2) followed a similar spatial pattern, albeit somewhat delayed. In 2007, RSU densities declined to less than one individual per square meter at LaCroix Group sites (Control_Pinnacle, 85_Pinnacle, 100_Pinnacle and 85_Shore_2) and one year later at some of the sites in Father Charles Channel (100_Shore_2, 85_Shore_1, 70). Two years later (2009), this decline occurred at the remaining sites (Control_Shore and 100_Shore_1). The fact that biomass was observed decreasing before density may be due to Sea Otters first targeting the largest, and therefore the heaviest, as is suggested by the changes in size frequency distributions between 2004 and 2007.

One plausible explanation of this pattern is that Sea Otters avoided the Father Charles Channel during their initial establishment in the research area. The Father Charles channel has greater current speed and boat traffic than the La Croix Group. Both current speed and boat traffic are known to influence Sea Otter behavior (Kvitek et al. 1992; Anthony 1995). According to Kvitek et al. (1992), high current speed may discourage Sea Otters from foraging at a site when sites with lower current speed are available. Current speeds within the centre of Father Charles channel are known to be 1 – 1.5 ms^{-1}, but were likely much higher at the study sites, and fall within the range that likely affects Sea Otter behavior (DFO 2022b; Kvitek et al. 1992). There also appears to be a difference in boat traffic between the Father Charles channel and the La Croix Group, with a greater density of boats travelling past the northern tip of Wickaninnish Island and into Father Charles channel (MarineTraffic 2022). Boat strikes are also a known cause of Sea Otter death in California and Alaska (Estes et al. 2003; Ballachey and Bodkin 2015). Without accompanying Sea Otter data, determining with certainty whether current speed, boat traffic or both influenced Sea Otter foraging of RSU in the study area is not possible. Another cause of the spatial pattern of RSU depletion may have been prey quality.

A recent study conducted at fine spatial scales (0 – 10 km), showed that Sea Otters in California do not actively select Purple Sea Urchins in barrens where roe quality is lower than neighboring areas with kelp beds (Smith et al. 2021). Kelp and biological sampling data (including RSU roe data) were collected in the Tofino research area (biological sampling 1995 – 1998), but have not been analyzed. While beyond the scope of the current study, an analysis of these roe and kelp data may provide a test of the hypothesis that variation in roe quality among sites affects Sea Otter foraging behaviour. Interestingly, Sea Otter predation after their arrival in the study area had long term impacts on RSU abundance while the experimental harvesting of RSU had no long term (> 5 years) impacts on RSU populations within the Tofino research area.

IMPACTS OF SEA OTTER PREDATION AND EXPERIMENTAL HARVESTING

While quantitative comparisons between the impacts of Sea Otter predation and the experimental harvesting on RSU populations were not part of this study, there are some noteworthy differences that can be assessed qualitatively. The most striking observation was the difference in recovery of RSU after the two parts of this study. During the harvest study, most sites returned to the same levels of density and biomass of total and mature RSU within two years after harvesting. This did not occur after Sea Otter occupation as none of the RSU population indicators returned to their pre-Sea Otter occupation, pre- or post-experimental harvesting levels (i. e. 1995 – 1997 estimates). All of these RSU population indicators actually dropped to near zero after Sea Otters were established and remained so until the last survey was conducted. The differing long term impacts between experimental harvesting and Sea Otter occupation was also seen between the two different site types. While there were no statistically significant impacts of experimental harvesting on RSU populations at pinnacle sites, a rapid downward trend in all RSU population indicators occurred within two years (2006) of Sea Otter occupation at these sites. Unlike experimental harvesting, RSU populations at both pinnacle and shore sites did not recover after Sea Otter occupation. This was likely due to the difference in harvest pressure between RSU experimental harvesting and Sea Otter predation.

The experimental harvesting of RSU occurred over 11 days in 1995 and 11 days in 1996, while Sea Otter foraging was likely continuous. Over time, the continuous consumption of RSU by Sea Otters likely exceeded any potential recovery of RSU populations in the area through mechanisms like immigration and recruitment. Sea Otters have high prey consumption rates due to their relatively large body size, high metabolism, and lack of body fat to insulate them from environmental conditions (Riedman and Estes 1990). These high consumption rates have been documented along the central coast of BC (Honka 2014). Honka (2014) suggested that consumption rates of RSU in the first year of occupation could be as high as 20 – 50 urchins per hour and that it may decline to 14 urchins per hour (maximum) after two years of occupation. The subsequent depletion of RSU and other urchin species in this study is not surprising given this consumption rate in BC (Honka 2014), similar RSU depletion trends observed along the Pacific coast when Sea Otters reoccupied areas (Laur et al. 1998; Laidre and Jameson 2006; Watson and Estes 2011; Honka 2014; Burt et al. 2018), as well as RSU depletion trends in studies that mimicked Sea Otter predation (Carter et al. 2007). The comparison between Sea Otter predation and selective harvesting of RSU under the same constraints of the experimental harvest study (i.e., applied on a small spatial scale to abundant RSU populations $\geq$ 5 RSU per m^2 (mean) and annually harvest over two years) suggests that selective harvesting had limited impacts on RSU populations. Further, there was no evidence that using an 85 mm TD size limit hampered RSU population recovery compared to using the 100 mm TD size limit under the same experimental constraints.

STUDY UNCERTAINTIES

During the RSU harvest impact study, RSU were collected from the Tofino research area as part of multiple scientific studies. Most notably the determination of growth and natural mortality rates in RSU (hereafter referred to as mark-recapture; Zhang et al. 2008), recruitment patterns, and the association between juveniles and adults (Zhang et al. 2011), as well as the relationship between test diameter and biomass (Campbell 1998; Lochead et al. 2015; hereafter referred to as biological sampling). These studies removed RSU from all experimental sites including the control sites (i. e. Control_Pinnacle, Control_Shore). The RSU collection for

Zhang et al. (2008), Campbell (1998), and Lochead et al. (2015) occurred at the same time as the harvest impact study (1995 – 1997), but in a different area within each site than survey transects (see Data Collection). Survey transects were also completed before the biological sampling and mark-recapture collection. For biological sampling collections, divers targeted roughly 60 RSU per site, but the total collection of RSU was 549, 382, unknown, and 585 RSU in 1995, 1996, 1997, and 1998, respectively. During mark-recapture collections roughly 1,000 RSU were collected from all sites except Control_Shore and Control_Pinnacle in 1997 (total no. urchins removed = 6,759). In 1998, almost 1,000 RSU were removed from the Control_Pinnacle and 85_Shore_1 sites (total no. urchins removed = 938).

Given the small number of RSU removed from each site during each biological sampling event (n ~ 55) relative to the high RSU abundances present at the time, the impact of those removals on the harvest study was likely minimal. Further, the RSU biological sampling removals were spread across all the sizes of urchin present (10 − 110 mm TD), and also occurred after the survey transects. The mark-recapture removals were also spread across the size distribution of RSU present at each site. While the number of RSU removed during the mark-recapture study seems large, relative to the high abundances in the area at the time and the large amount of RSU harvested during experimental harvesting (approximately 50,000 kg in total), these mark-recapture removals likely did not impact experimental results. Documentation, field notes, and metadata regarding this study did not exist or were not found when this manuscript was written, the information provided here was found in a protocol document. Although we cannot say with certainty that these other studies did not impact the experimental harvest study, based on our knowledge of the sites, the methodologies used, and the very abundant RSU populations at the time of harvest we believe these RSU removals had little impact on the experimental harvest study.

As mentioned in the methodology section, the efficacy of the experimental harvesting was unknown at the time this manuscript was written. Our understanding of harvest efficacy is also further complicated by the study design. Post-harvest surveys were not conducted immediately after harvesting in 1995 or 1996. However, given the known seasonal movements of urchins (Konar 2001; Carter and VanBlaricom 2002), the methodology and results of similar echinoderm studies, (Robles et al. 2009; Carter VanBlaricom 2002; Elahi and Sebens 2013), and some of the study results herein, it is likely that harvesting was effective and that immigration of RSU into the sites occurred between the 1996 harvest and first post-harvest survey (2 months after harvest). While the goal of the present study did not involve investigating the long term removal of RSU, echinoderm removal studies provide insight into the rate at which echinoderms immigrate back into sites after removals. In echinoderm removal studies, the time interval between removal events ranged from every 2 weeks (Carter and VanBlarimo 2002; Elahi and Sebens 2013) to a month (Robles et al. 2009) in order to ensure densities remained near zero. Based on these frequent removal events, Carter and VanBlaricom (2002) determined that the monthly immigration rate of RSU into removal sites was 17.2 RSU per month. RSU densities in this study were far greater than those of Carter and VanBlaricom (2002), which may indicate that the immigration rate of RSU after harvest was much higher in the Tofino Research area.

While we are uncertain to what extent immigration after the 1996 harvest may have impacted this study, it is certain that the harvesting events were large scale, removing ~50,000 kg of RSU from a relatively small research area (i.e. all sites within a 1.5 km radius). These harvests may equate to as many as 168,652 RSU removed over the course of the study (approx. total no. RSU harvested = [85mm TD harvest/W_{TD85}] + [100 mm TD harvest/W_{TD100}] = [21,887 kg/0.223

kg per urchin] + [27,421 kg/0.367 kg per urchin], where W_{TD85} = weight of a 85 mm TD RSU and W_{TD100} = weight of a 100 mm TD; Equation 1; Table 2). Some of the study results also suggest that harvesting successfully depleted RSU. For example, total RSU density at both site types in 1996 was significantly lower than pre-harvest surveys (1995; Figure 3), pre-harvest estimates of mature RSU density and biomass at 100_Shore_1 in 1995 were significantly greater than 1996 estimates (Figure 4 and Figure 8) and, pre-harvest estimates of total and mature biomass at pinnacle sites were significantly greater than 1996 estimates. Given the potential immigration between harvesting and surveying in 1996, and the significant decrease in some RSU population indicators between 1995 and 1996, it is evident that experimental harvesting effectively removed a substantial portion of the RSU population and that other factors such as immigration and recruitment likely led to recovery of RSU populations.

ACKNOWLEDGEMENTS

The authors would like to thank the Pacific Urchin Harvesters Association and their many divers for participating in the surveys and providing financial support, and the many DFO staff that helped collect data over the years. We would like to acknowledge, posthumously, Alan Campbell’s lead on the project. Many thanks to Hannah Stewart, Brenda Waddell and Lynn Yamanaka for their initial review of the manuscript, as well as to Dominique Bureau and Christine Hansen for their review of the final version. Grant Garner thank you for your great map making skills. Thank you Janet Lochead for reviewing and providing kind and thoughtful support during the development of the manuscript.

REFERENCES

ADF&G (Alaska Department of Fish and Game). https://www.adfg.alaska.gov/index.cfm?adfg=commercialbyareasoutheast.dive_harvest_urchin [accessed May 3, 2021].

Anderson, M. J., Gorley, R. N. and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd.

Anthony, J. A. M. 1995. Habitat utilization By Sea Otters (*Enhydra lutris*) In Port Valdez, Prince William Sound, Alaska. Retrieved from http://hdl.handle.net/11122/8519.

Ballachey, B. E., and J. L., Bodkin. 2015. Chapter 4 - Challenges to Sea Otter Recovery and Conservation. In S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom (Eds.), *Sea Otter Conservation* (pp. 63-96). Boston: Academic Press.

Beas-Luna, R., F. Micheli, C. B. Woodson, M. Carr, D. Malone, J. Torre, C. Boch, J. E. Caselle, M. Edwards, J. Freiwald, S. L. Hamilton, A. Hernandez, B. Konar, K. J. Kroeker, J. Lorda, G. Montaño-Moctezuma, and G. Torres-Moye. 2020. Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes. Glob. Change Biol. 26:6457-6473.

Bernard, F.R. and D.C. Miller. 1973. Preliminary investigation of the red sea urchin (*Strongylocentrotus franciscanus,* Agassiz) resources of British Columbia. Fish. Res. Board Can. Tech. Rep. 400. 37 p.

Bigg, M. A., and I. B. MacAskie.1978. Sea Otters reestablished in British Columbia. J. Mammal. 59(4), 874-876.

Bodkin, J. L. and T. A., Dean. 2002. Patterns and processes of population change in Sea Otters, Exxon Valdez oil spill restoration project annual report (Restoration Project 99423), U. S. Geological Survey, Anchorage, Alaska.

Botsford, L. W., Smith, B. D., and Quinn, J. F. 1994. Bimodality in Size Distributions: The Red Sea Urchin *Strongylocentrotus franciscanus* as an Example. Ecol. App., 4(1), 42-50. Retrieved from http://www.jstor.org/stable/1942113. doi:10.2307/1942113.

Bowman, A. W. and A., Azzalini. 2010. Applied smoothing techniques for data analysis: the kernel approach with S-Plus illustrations. Oxford, Oxford University Press.

Britton-Simmons, K. H., G. Foley, and D. Okamoto. 2009. Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. Aquat. Biol. 5:233-243.

Burt, J. M., M. T. Tinker, D. K. Okamoto, K. W. Demes, K. Holmes, and A. K. Salomon. 2018. Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. Proc. Royal Soc. B. 285:20180553.

Campbell, A. and R. M. Harbo. 1992. The sea urchin fisheries in British Columbia, Canada. p. 191-199. In: T. Yanagisawa, I. Yasumasu, C. Oguro, N. Suzuki and T. Motokawa [eds.]. Biology of Echinodermata. A.A. Balkema, Rotterdam.

Campbell, A. 1998. Catch, effort and quota estimates for the red sea urchin fishery in British Columbia. pp. 83-109. In: R. I. Waddell, G. B. Gillespie, and L. C. Walthers [eds.]. Invertebrate working papers reviewed by the Pacific Stock Assessment Review Committee (PSARC) in 1995. Part 2. Echinoderms. Can. Tech. Rep. Fish. Aquat. Sci. 2215.

Campbell, A., J. Boutillier, and J. Rogers. 1999. Discussion on a precautionary approach for management of the red sea urchin fishery in British Columbia. Can. Stock Assess. Sec. Res. Doc. 99/094.

Campbell, A., D., Tzotzos, Hajas, W.C., and L. L., Barton. 2001. Quota options for the Red Sea Urchin fishery in British Columbia for Fishing Season 2002/2003. Can . Sci. Advis. Sec.

Carson, H. S., M. Ulrich, D. Lowry, R. E. Pacunski, and R. Sizemore. 2016. Status of the California sea cucumber (*Parastichopus californicus*) and red sea urchin (*Mesocentrotus franciscanus*) commercial dive fisheries in the San Juan Islands, Washington State, USA. Fish. Res. 179:179-190.

Carter, S. K., and G. R. VanBlaricom. 2002. Effects of experimental harvest on red sea urchins (*Strongylocentrotus franciscanus*) in northern Washington. Fish. Bull. 100.

Carter, S. K., G. R. VanBlaricom, and B. L. Allen. 2007. Testing the generality of the trophic cascade paradigm for Sea Otters: a case study with kelp forests in northern Washington, USA. Hydrobiologia 579:233-249.

Clarke, K. R. and R. N., Gorley, 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Curtis, L. J. F. *in prep*. Experimental harvest of Red Sea Urchins, *Mesocentrotus franciscanus*, and trends in Red, Green (*Strongylocentrotus droebachiensis*) and Purple (*S. purpuratus*) Sea Urchin populations within the K̲'uuna Gwaay (Louise Island) research area (1996–2013). Can. Tech. Rep. Fish. Aquat. Sci.

Davies, S.C., D. Bureau, J. Lessard, S. Taylor, G.E. Gillespie. 2018. Benthic habitat mapping surveys of eastern Haida Gwaii and the North Coast of British Columbia, 2013-2015. Can. Tech. Rep. Fish. Aquat. Sci. 3278: vi + 24 p.

Dean, T. A., J. L. Bodkin, S. C. Jewett, D. H. Monson and D. Jung. 2000. Changes in sea urchins and kelp following a reduction in sea otter density as a result of the Exxon Valdez oil spill. Mar. Ecol. Prog. Ser., 199, 281-291. Retrieved from https://www.int-res.com/abstracts/meps/v199/p281-291/.

DFO. 2017. Pacific Region Integrated Fisheries Management Plan, Red Sea Urchin, August 1, 2017 to July 31, 2018.

DFO. 2009. A fishery decision-making framework incorporating the precautionary approach. (Accessed May 18, 2021).

DFO. 2018. Pacific Region 2018-19 Red Sea Urchin Integrated Fisheries Management Plan. (Accessed May 3, 2021).

DFO. 2021. Stock status update and harvest options for the Green Sea Urchin (*Strongylocentrotus droebachiensis*) fishery in British Columbia, 2021-2024. Can. Sci. Advis. Sec. Sci. Resp., 2021/036.

DFO. 2022a. Data archived in the Red Sea Urchin biological database, maintained by the Shellfish Data Unit at the Pacific Biological Station. [accessed November 2021].

DFO. 2022b. Canadian Hydrographic Service. V-3685-CA-570088/Chart 3685. https://www.charts.gc.ca/charts-cartes/chart-index-carte-eng.html. [accessed: May 2022].

Ebert, T. A., J. C. Hernández, and M. P. Russell. 2012. Ocean conditions and bottom-up modifications of gonad development in the sea urchin *Strongylocentrotus purpuratus* over space and time. Mar. Ecol. Prog. Ser. 467:147-166.

Edwards, M. S., and J. A. Estes. 2006. Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. Mar. Ecol. Prog. Ser. 320:79-87.

Elahi, R., and Sebens, K. P. 2013. Experimental Removal and Recovery of Subtidal Grazers Highlights the importance of functional redundancy and temporal context. *PLoS ONE, 8*(11), e78969. Retrieved from https://doi.org/10.1371/journal.pone.0078969. doi:10.1371/journal.pone.0078969.

Estes, J., B. B. Hatfield, K. Ralls and J. Ames. 2003. Causes of mortality in California Sea Otters during periods of population growth and deceline. Mar. Mamm. Sci. , 19(1), 198-216.

Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1748-7692.2003.tb01102.x. doi:https://doi.org/10.1111/j.1748-7692.2003.tb01102.x

Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molec. Ecol. 17:209-220.

Freeland, H., and R. Thomson. 1999. The El Niño signal along the west coast of Canada -- temperature, salinity and velocity. Proceedings of the 1998 Science Board Symposium on the impacts of the 1997/98 El Niño event on the North Pacific Ocean and its marginal seas:55-58.

Hand, C.M., Hajas, W., Duprey, N., Lochead, J., Deault, J. and Caldwell, J. 2008. An evaluation of fishery and research data collected during the phase 1 Sea Cucumber fishery in British Columbia, 1998 to 2007. Can. Sci. Advis. Sec. Res. Doc. 065, Fisheries and Oceans Canada, Nanaimo, BC, Canada.

Honka, L. D. 2014. Quantifying the drivers and mechanisms of sea otter (*Enhydra lutris*) foraging behavior on the central coast of British Columbia, Canada. M. Sc. Thesis. Simon Fraser University.

Jenkinson, R. S., K. A. Hovel, R. P. Dunn, and M. S. Edwards. 2020. Biogeographical variation in the distribution, abundance, and interactions among key species on rocky reefs of the northeast Pacific. Mar. Ecol. Prog. Ser. 648:51-65.

Konar, B. 2001. Seasonal changes in subarctic sea urchin populations from different habitats. Polar Biology, 24(10), 754-763. Retrieved from https://doi.org/10.1007/s003000100280. doi:10.1007/s003000100280.

Kramer, D. E. and D. M. A. Nordin. 1975. Physical data from a study of size, weight and gonad quality for the red sea urchin (*Strongylocentrotus franciscanus* (Agassiz) over a one-year period. Fish. Res. Board Can. MS Rep. 1372: 91pp.

Kvitek, R. G., J. S. Oliver, A. R. DeGange & B. S. Anderson. 1992. Changes in Alaskan Soft-Bottom Prey communities along a gradient in Sea Otter predation. Ecology, *73*(2), 413-428. doi:https://doi.org/10.2307/1940749.

Laidre, K., and R. Jameson. 2006. Foraging patterns and prey selection in an increasing and expanding Sea Otter population. J. Mamm. 87(4):799–807.

Langlois, T. J., B. R. Fitzpatrick, D. V. Fairclough, C. B. Wakefield, S. A. Hesp, D. L. McLean, E. S. Harvey, and J. J. Meeuwig. 2012. Similarities between line fishing and baited stereo-video estimations of length-frequency: novel application of kernel density estimates. PLoS ONE 7:e45973.

Laur, D.R., A.W. Ebeling, D.A. Coon. 1988. Effects of Sea Otter foraging on subtidal reef communities off central California. In: VanBlaricom G.R., Estes J.A. (eds) The community ecology of Sea Otters. Ecological Studies (Analysis and Synthesis), vol. 65. Springer, Berlin, Heidelberg.

Lochead, J., Hajas, W., and Leus, D. 2015. Calculation of mean abundance in the Red Urchin Analysis Program and Green Urchin Analysis Program. Can. Manuscr. Rep. Fish. Aquat. Sci. 3065: vi + 41 p.

Lowman, H. E., K. A. Emery, J. E. Dugan, and R. J. Miller. Nutritional quality of giant kelp declines due to warming ocean temperatures. Oikos 00:1-14.

Malakhoff, K. D., and R. J. Miller. 2021. After 15 years, no evidence for trophic cascades in marine protected areas. Proc. Biol. Sci. 288: 20203061.

MarineTraffic. 2022. Density maps. https://www.marinetraffic.com/en/ais/home/centerx:-125.9/centery:49.1/zoom:11 [accessed April 2022].

Medellín-Ortiz, A., G. Montaño-Moctezuma, C. Alvarez-Flores, and E. Santamaria-del-Angel. 2020. Retelling the History of the Red Sea Urchin Fishery in Mexico. Frontiers in Marine Science 7.

Milligan, K., C. Levings, and R. DeWreede. 1999. Data Compilation and Preliminary Time Series Analysis of Abundance of a Dominant Intertidal Kelp Species in Relation to the 1997/1998 El Niño Event.

Morgan, L. E., L. W. Botsford, S. R. Wing, and B. D. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, *Strongylocentrotus franciscanus*, in northern California. Can. J. Fish. Aquat. Sci. 57:980-992.

Narvaez, C. A., B. Sainte-Marie and L. E. Johnson. 2020. Intraspecific competition in size-structured populations: ontogenetic shift in the importance of interference competition in a key marine herbivore. Mar. Ecol. Prog. Ser. 649, 97-110. Retrieved from https://www.int-res.com/abstracts/meps/v649/p97-110/.

Nichol, L. M., J.C. Watson, G. E. Ellis and J. K. B. Ford. 2005. An assessment of abundance and growth of the Sea Otter (*Enhydra lutris*) population in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/094. ii + 22pp.

Nichol, L.M., M.D. Boogaards, R. Abernethy. 2009. Recent trends in the abundance and distribution of Sea Otters (*Enhydra lutris*) in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/016. iv + 16 p.

Nishizaki, M. T. and J. D. Ackerman. 2007. Juvenile–adult associations in sea urchins (*Strongylocentrotus franciscanus* and *S. droebachiensis*): protection from predation and hydrodynamics in *S. franciscanus*. Mar. Biol. 151:135–145.

Okamoto, D. K., S. C. Schroeter and D. C. Reed. 2020. Effects of ocean climate onspatiotemporal variation in sea urchin settlement and recruitment. Limnol. Oceangr. 65:2076-2091.

Parnell, P. E., J. T. Fumo, C. E. Lennert-Cody, S. C. Schroeter, and P. K. Dayton. 2017. Sea Urchin behavior in a southern California kelp forest: food, fear, behavioral niches, and scaling up individual behavior. J. Shellfish Res. 36:529-543, 515.

Perry, R. I., C. J. Walters, and J. A. Boutillier. 1999. A framework for providing scientific advice for the management of new and developing invertebrate fisheries. Rev. Fish Biol. Fisher. 9:125-150.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria. Retrieved from https://www.R-project.org/.

Riedman, M. L., and J. A. Estes. 1990. The Sea Otter (*Enhydra lutris*): Behaviour, ecology and natural history. US Fish and Wildl. Serv. Biol. Rep. 90(14).6 p.

Robles, C. D., R. A. Desharnais, C. Garza, M. J. Donahue and C. A. Martinez. 2009. Complex equilibria in the maintenance of boundaries: experiments with mussel beds. Ecology, *90*(4), 985-995. doi:https://doi.org/10.1890/08-0919.1.

Rogers-Bennett, L., W. A. Bennett, H. C. Fastenau, and C. M. Dewees. 1995. Spatial variation in Red Sea Urchin reproduction and morphology: implications for harvest refugia. Ecol. Appl. 5:1171-1180.

Rogers-Bennett, L., and C. A. Catton. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci. Rep. 9:15050.

Rogers-Bennett, L., and D. Okamoto. 2020. Chapter 32 - *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*. Pages 593-608 *in* J. M. Lawrence, editor. Developments in Aquaculture and Fisheries Science. Elsevier.

Shears, N. T., D. J. Kushner, S. L. Katz, and S. D. Gaines. 2012. Reconciling conflict between the direct and indirect effects of marine reserve protection. Environ. Conserv. 39:225-236.

Shelton, A. O., C. J. Harvey, J. F. Samhouri, K. S. Andrews, B. E. Feist, K. E. Frick, N. Tolimieri, G. D. Williams, L. D. Antrim, and H. D. Berry. 2018. From the predictable to the unexpected: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion. Oecologia 188:1105-1119.

Sloan, N. A., C. P. Lauridsen, and R. M. Harbo. 1987. Recruitment characteristics of the commercially harvested red sea urchin *Strongylocentrotus franciscanus* in Southern British Columbia, Canada. Fish. Res. 5:55-69.

Smith, J. G., J. Tomoleoni, M. Staedler, S. Lyon, J. Fujii, and M. T. Tinker. 2021. Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. P. Natl. Acad. Sci. 118:e2012493118.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. Ecol. Evol. 6:1041-1053.

Teck, S. J., J. Lorda, N. T. Shears, T. W. Bell, J. Cornejo-Donoso, J. E. Caselle, S. L. Hamilton, and S. D. Gaines. 2017. Disentangling the effects of fishing and environmental forcing on demographic variation in an exploited species. Biol. Conserv. 209:488-498.

Tegner, M. J., and P. K. Dayton. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus and S. purpuratus*) in a kelp forest. Mar. Ecol. Prog. Ser. 5:255-268.

Tegner, M. J., and P. K. Dayton. 1991. Sea urchins, El Niños, and the long term stability of Southern California kelp forest communities. Mar. Ecol. Prog. Ser. 77:49-63.

Tuya, F. C., M. L. Soboil, and J. Kido. 2000. An assessment of the effectiveness of marine protected areas in the San Juan Islands, Washington, USA. ICES J. Mar. Sci. 57:1218-1226.

Waddell, B.J., and Perry, R.I. 2012. Survey results of green sea urchin (*Strongylocentrotus droebachiensis*) populations in Queen Charlotte Strait, British Columbia, October 2008 and November 2010. Can. Tech. Rep. Fish. Aquat. Sci. 3000: ix + 73 p.

Wand, M. 2011. KernSmooth: functions for kernel smoothing for Wand and Jones (1995; version 2.23) in R. p. v. 3.5.0, editor., Available: http://CRANR-projectorg/ package=KernSmooth..

Watson, J., and J. A. Estes. 2011. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecol. Monogr. 81:215-239.

Wickham, H. 2011. The split-apply-combine strategy for data analysis. J. Stat. Soft., 40(1), 1–29. https://www.jstatsoft.org/v40/i01/.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Zhang, Z., A. Campbell, D. Bureau. 2008. Growth and natural mortality rates of red sea urchin (*Strongylocentrotus franciscanus*) in British Columbia. J. Shellfish Res. 27: 1291–1299.

Zhang, Z., A. Campbell, D. Leus and D. Bureau. 2011. Recruitment patterns and juvenile–adult associations of red sea urchins in three areas of British Columbia. Fish. Res. 109: 276–284.

Table 1. Tofino area (PFMA 24-8) research sites by type, (a), shore,(b), pinnacle, and (c), other sites with assigned harvest treatment, characteristics and naming used throughout the document (Harvest treatment site; italics; Unk = unknown).

(a) Shore-type sites

Harvest treatment	**Control - no harvest**	**≥ 85 mm TD**		**≥ 100 mm TD**	
Harvest treatment site	*Control_Shore*	*85_Shore_1*	*85_Shore_2*	*100_Shore_1*	*100_Shore_2*
Database site name	3	2	10	5	8
Slope (degrees)	30	50	20	30	40
Side Boundary	n	n	n	n	n
Substrate (Primary/ Secondary)	Bedrock/ boulder	Bedrock/ boulder	Bedrock/ boulder	Bedrock/ cobble	Bedrock

(b) Pinnacle-type sites

Harvest treatment	**Control - no harvest**	**≥ 85 mm TD**	**≥ 100 mm TD**
Harvest treatment site	*Control_Pinnacle*	*85_Pinnacle*	*100_Pinnacle*
Database site name	12	11	4
Slope (degrees)	10	50	40
Bottom Boundary	y	y	y
Side Boundary	y	y	y
Substrate (Primary/ Secondary)	Bedrock	Bedrock/ boulder	Bedrock/ sand

(c) Other sites

Harvest treatment	**No harvest**	**No harvest**
Harvest treatment site	*NA*	*NA*
Database site name	7	70
Slope (degrees)	40	Ukn
Side Boundary	n	Ukn
Bottom boundary	n	Ukn
Substrate (Primary/ Secondary)	Bedrock/Sand	Bedrock

Table 2. The weight (kg) of Red Sea Urchin harvested and removed from harvest treatment sites in 1995 and 1996 at the Tofino sea urchin research area.

Site	1995	1996	Total
85_Shore_1	5,990	1,149	7,139
85_Shore_2	4,910	847	5,757
85_Pinnacle	3,429	5,562	8,991
≥ 85 mm TD Total harvest			*21,887*
100_Pinnacle	8,552	464	9,016
100_Shore_1	6,141	8,960	15,101
100_Shore_2	-	3,304	3,304
≥ 100 mm TD Total harvest			*27,421*
Grand Total	29,022	20,286	49,308

Table 3. PERMANOVA analyses results on the effects of Harvest Treatment Site (HTS), year, and their interaction on the total, mature (≥ 50 mm TD), immature (< 50 mm TD) densities of Red Sea Urchins (no. of RSU per m^2). Each row represents an independent analysis. Text in bold represent significant effects (α = 0.05).

Site type	RSU Density	Source	df	SS	MS	Pseudo-F	*p* (perm)	Unique perms.
Shore	Total	**HTS**	**4**	**10840**	**2710.1**	**78.6**	**0.0001**	**9955**
		Year	**4**	**498.2**	**124.5**	**3.6**	**<0.001**	**9945**
		HTSxYear	16	586.1	36.6	1.1	>0.05	9930
		Residual	90	3102.9	34.5			
		Total	114	15230				
Pinnacle	Total	HTS	2	331.5	165.8	1.9	>0.05	9952
		Year	**4**	**1105.6**	**276.4**	**3.2**	**<0.05**	**9944**
		HTSxYear	8	629.3	78.7	0.9	>0.05	9930
		Residual	54	4686.3	86.8			
		Total	68	6696.5				
Shore	Mature	**HTS**	**4**	**5467.5**	**1366.9**	**66.6**	**<0.0001**	**9939**
		Year	**4**	**202.8**	**50.7**	**2.5**	**<0.05**	**9953**
		HTSxYear	**16**	**579.8**	**36.2**	**1.8**	**<0.05**	**9922**
		Residual	90	1848.5	20.5			
		Total	114	8229.3				
Pinnacle	Mature	HST	2	82.4	41.2	1.2	>0.05	9955
		Year	4	254.6	63.6	1.8	>0.05	9945
		HSTxYear	8	292.1	36.5	1.0	>0.05	9935
		Residual	54	1928.2	35.7			
		Total	68	2546.3				
Shore	Immature	**HST**	**4**	**1062.4**	**265.6**	**65.0**	**0.0001**	**9945**
		Year	**4**	**367.5**	**91.9**	**22.5**	**0.0001**	**9943**
		HTSxYear	**16**	**209.8**	**13.1**	**3.2**	**<0.001**	**9928**
		Residual	90	367.6	4.1			
		Total	114	1993.8				
Pinnacle	Immature	HTS	2	100.6	50.3	2.7	>0.05	9966
		Year	**4**	**492.7**	**123.2**	**6.6**	**<0.001**	**9947**
		HTSxYear	8	103.3	12.9	0.7	>0.05	9933
		Residual	54	1015.1	18.8			
		Total	68	1707.2				

Table 4. PERMANOVA analyses results on the effects of Harvest Treatment Site (HTS), year, and their interaction on the total, mature (≥ 50 mm TD), immature (< 50 mm TD) biomass of Red Sea Urchins (kg RSU per m^2). Each row represents an independent analysis. Text in bold represent significant effects ($\alpha = 0.05$).

Site type	RSU Biomass	Source	df	SS	MS	Pseudo-F	*p* (perm)	Unique perms.
Shore	Total	**HTS**	**4**	**459.5**	**114.9**	**69.0**	**0.0001**	**9954**
		Year	**4**	**63.5**	**15.9**	**9.5**	**0.0001**	**9950**
		HTSxYear	**16**	**86.3**	**5.4**	**3.2**	**<0.001**	**9922**
		Residual	90	149.7	1.7			
		Total	114	754.7				
Pinnacle	Total	HTS	2	14.4	7.2	2.1	>0.05	9949
		Year	**4**	**57.0**	**14.3**	**4.1**	**<0.01**	**9952**
		HTSxYear	8	51.0	6.4	1.8	>0.05	9943
		Residual	54	186.8	3.5			
		Total	68	306.6				
Shore	Mature	**HTS**	**4**	**430.0**	**107.5**	**65.9**	**0.0001**	**9944**
		Year	**4**	**64.2**	**16.0**	**9.8**	**0.0001**	**9954**
		HTSxYear	**16**	**88.3**	**5.5**	**3.4**	**0.0001**	**9917**
		Residual	90	146.8	1.6			
		Total	114	726.7				
Pinnacle	Mature	HTS	2	13.0	6.5	1.9	>0.05	9951
		Year	**4**	**53.5**	**13.4**	**3.8**	**<0.01**	**9961**
		HTSxYear	8	48.2	6.0	1.7	0.10	9949
		Residual	54	190.1	3.5			
		Total	68	303.2				
Shore	Immature	**HTS**	**4**	**0.35**	**0.0087**	**55.4**	**0.0001**	**9942**
		Year	**4**	**0.11**	**0.0027**	**17.1**	**0.0001**	**9948**
		HTSxYear	**16**	**0.0071**	**0.00045**	**2.8**	**<0.0001**	**9904**
		Residual	90	0.14	0.00016			
		Total	114	0.68				
Pinnacle	Immature	HTS	2	0.0046	0.0023	2.8	>0.05	9948
		Year	**4**	**0.15**	**0.0036**	**4.3**	**<0.01**	**9947**
		HTSxYear	8	0.0046	0.00058	0.69	>0.05	9918
		Residual	54	0.45	0.00084			
		Total	68	0.69				

Table 5. The *p*-values associated with the kernel density estimate comparisons of RSU size distributions during the pre-harvest survey (1995) and the post-harvest surveys (1997, 1998 and 2001) within each harvest treatment site. Location refers to the mean length of the distributions.

Harvest treatment site	**1995 vs 1997** Location & shape	Location only	**1995 vs 1998** Location & shape	Shape only	**1995 vs 2001** Location & shape	Shape only
Control_Shore	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
100_Shore_1	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
100_Shore_2	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
85_Shore_1	<0.0001	<0.05	<0.0001	<0.0001	<0.0001	<0.0001
85_Shore_2	<0.0001	<0.01	<0.0001	<0.0001	<0.0001	<0.0001
Control_Pinnacle	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
100_Pinnacle	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
85_Pinnacle	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

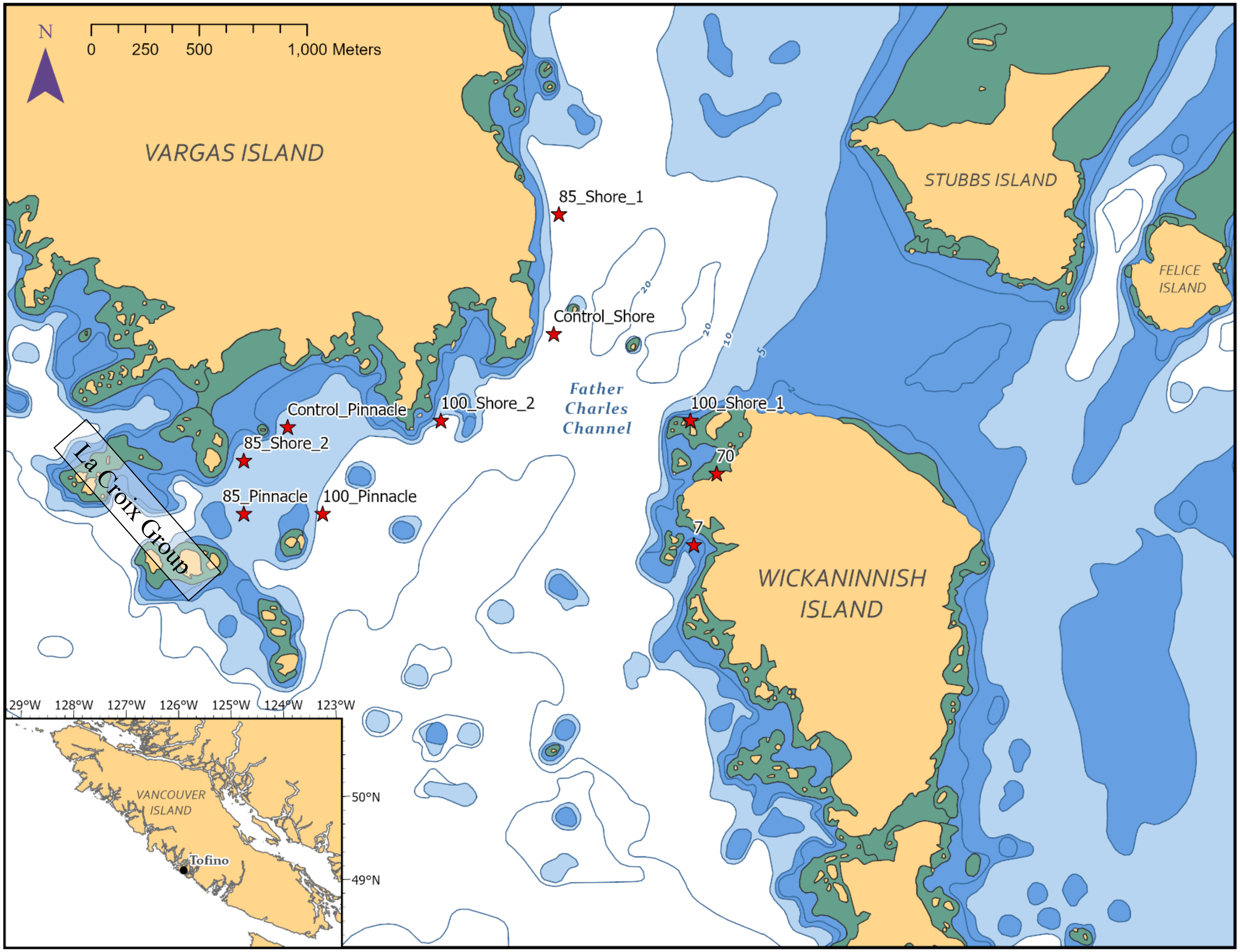


Figure 1. The Tofino sea urchin research area with the individual research site locations (red stars; see Table 1 for site and code descriptions; bathymetry units are meters). The inset of Vancouver Island shows the approximate location of the area (black circle).

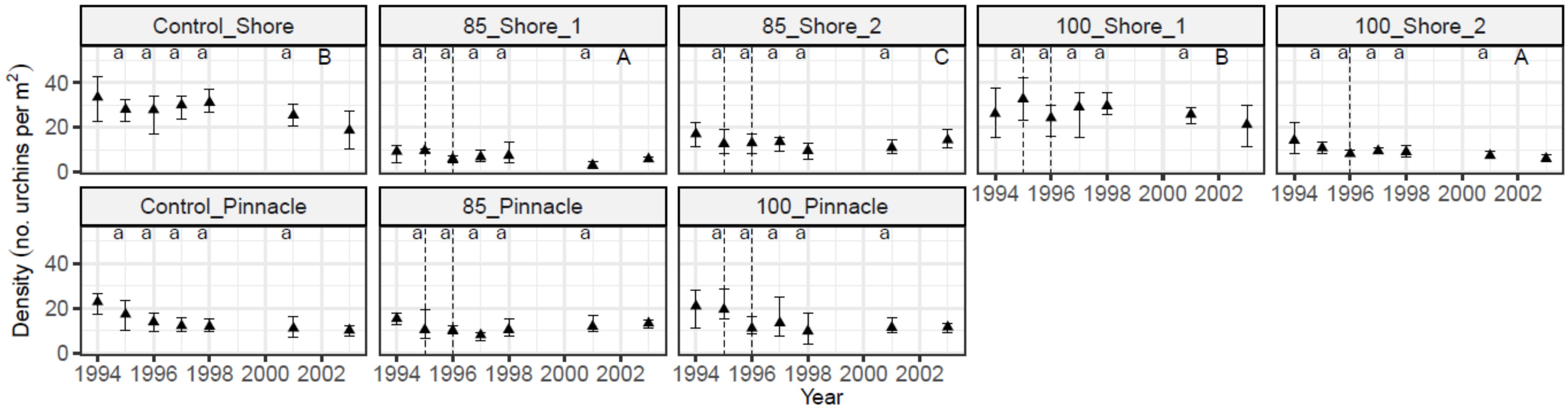


Figure 2. The mean total density of Red Sea Urchins (urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Lower case letters represent pairwise comparisons within each site (PERMANOVA) and years with different letters are significantly different from one another ($\alpha = 0.05$). Upper case letters represent pairwise differences among the harvest treatment sites (main effect, combined data) and those with different letters are significantly different from another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest. The years 1994 and 2003 were not statistically analyzed. Dashed lines represent the years when harvesting occurred, see Table 1 for harvest treatment site descriptions.

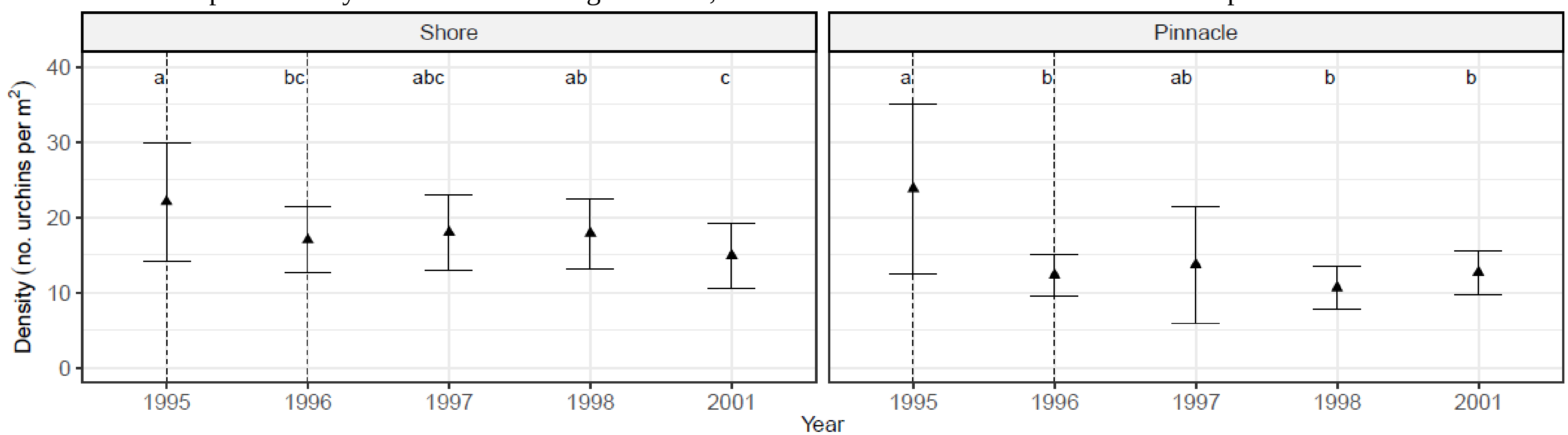


Figure 3. The mean total RSU density (RSU per m^2) with 95% confidence intervals (*t*-distribution) across time (Year) at shore and pinnacles type sites. Pairwise comparisons are within each site type (PERMANOVA) and years with different letters are significantly different from one another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest.

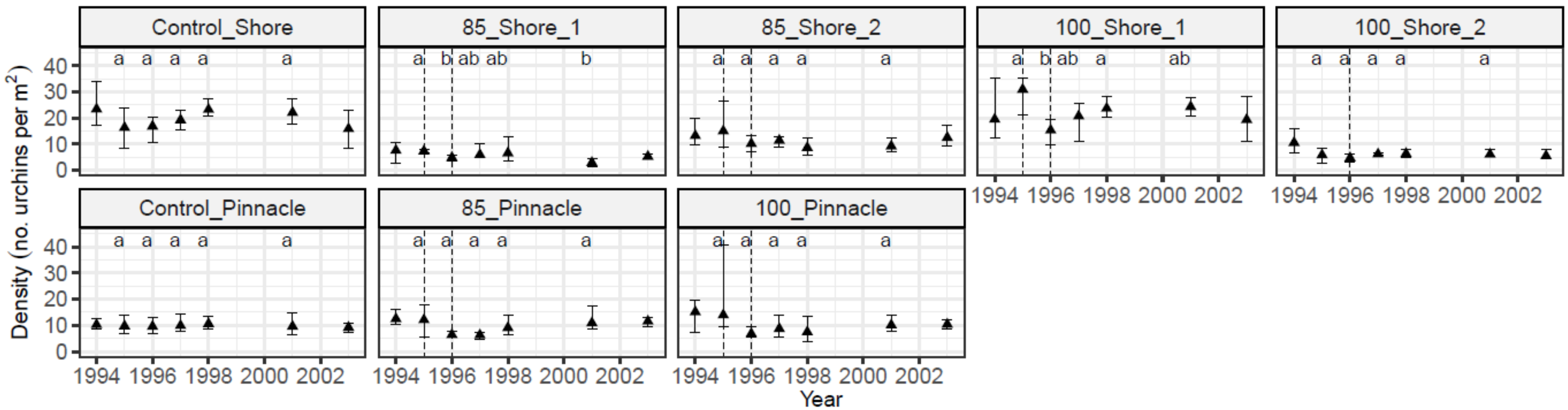


Figure 4. The mean density of mature (≥ 50 mm TD) Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Pairwise comparisons are within each site (PERMANOVA) and years with different letters are significantly different from one another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest. The years 1994 and 2003 were not statistically analyzed. Dashed lines represent the years when experimental harvesting occurred, see Table 1 for harvest treatment site descriptions.

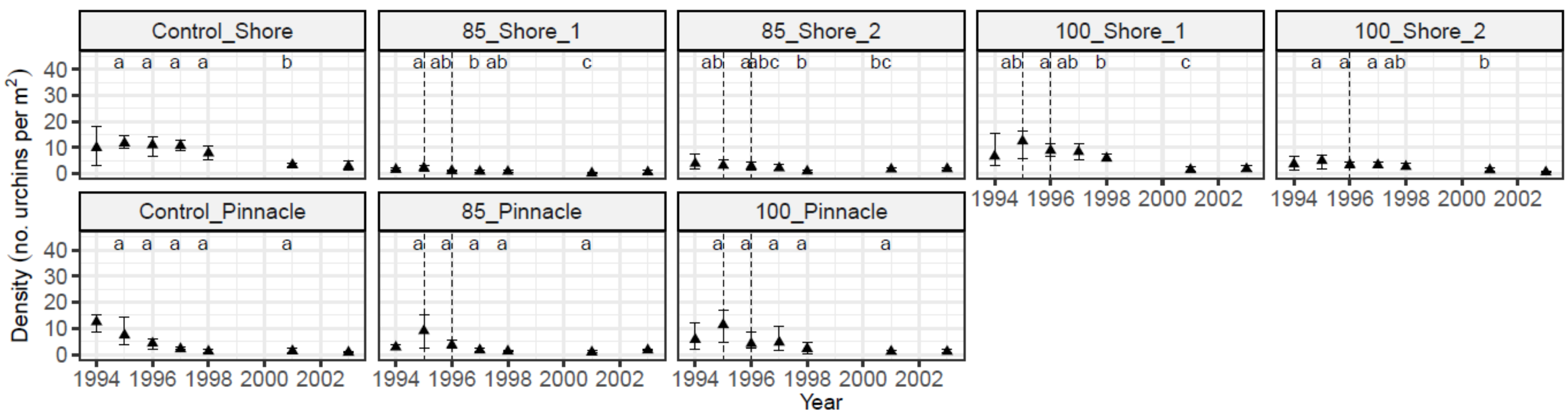


Figure 5. The mean density of immature (< 50 mm TD) Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Pairwise comparisons are within each site (PERMANOVA) and years with different letters are significantly different from one another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest. The years 1994 and 2003 were not statistically analyzed. Dashed lines represent the years when experimental harvesting occurred, see Table 1 for harvest treatment site descriptions.

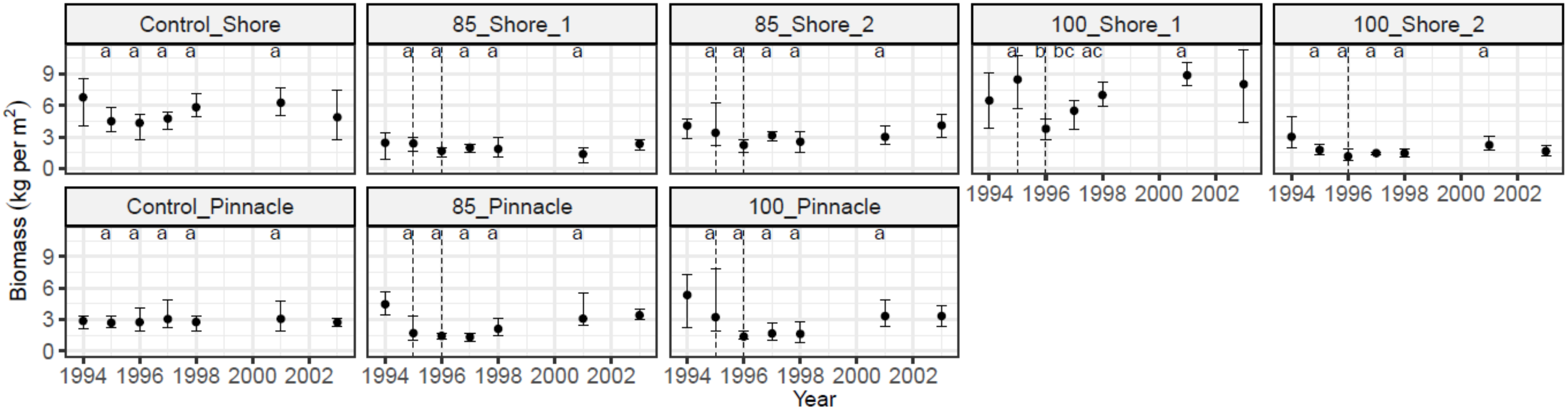


Figure 6. The mean total biomass of Red Sea Urchins (kg per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Pairwise comparisons are within each site (PERMANOVA) and years with different letters are significantly different from one another (α = 0.05). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The years 1994 and 2003 were not statistically analyzed. The 1996 survey was 2 months post-harvest. Dashed lines represent the years when harvesting occurred, see Table 1 for harvest treatment site descriptions.

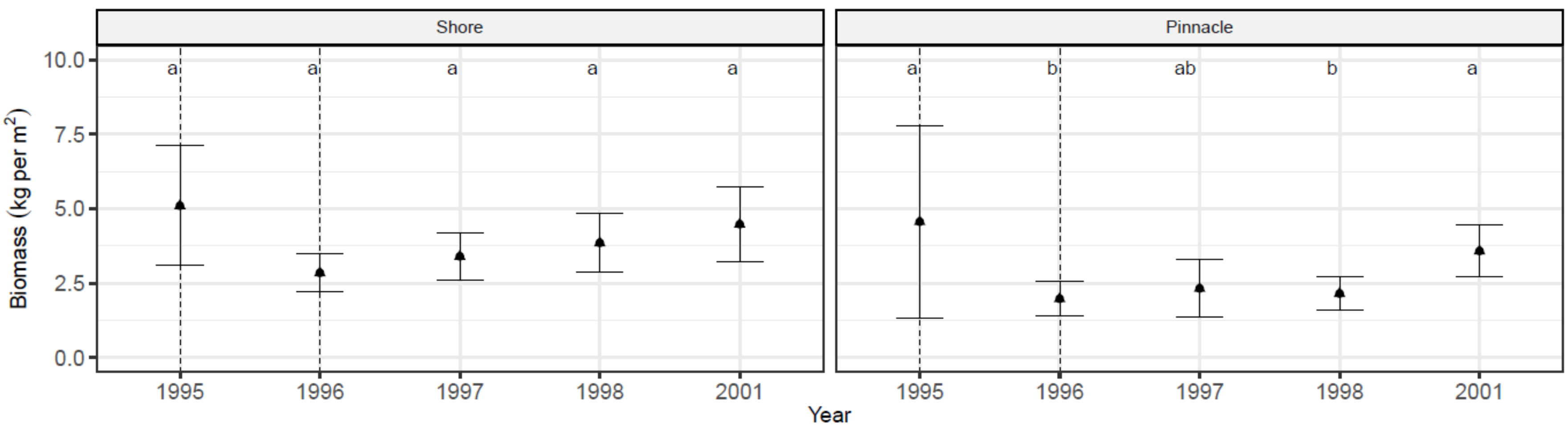


Figure 7. The mean total biomass of Red Sea Urchins (kg per m^2) with 95% confidence intervals (*t*-distribution) across time (Year) at Shore and Pinnacles type sites. Pairwise comparisons are within each site type (PERMANOVA) and years with different letters are significantly different from one another (α = 0.05. Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest.

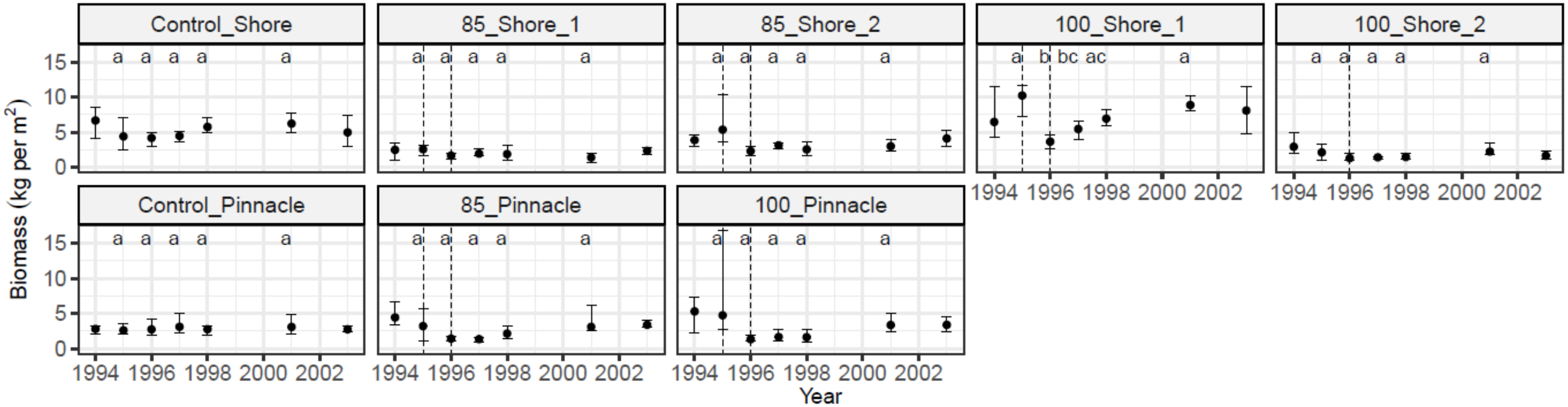


Figure 8. The mean biomass of mature (≥ 50 mm TD) Red Sea Urchins (kg per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Pairwise comparisons are within each site (PERMANOVA) and years with different letters are significantly different rom one another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest. The years 1994 and 2003 were not statistically analyzed. Dashed lines represent the years when harvesting occurred, see Table 1 for harvest treatment site descriptions.

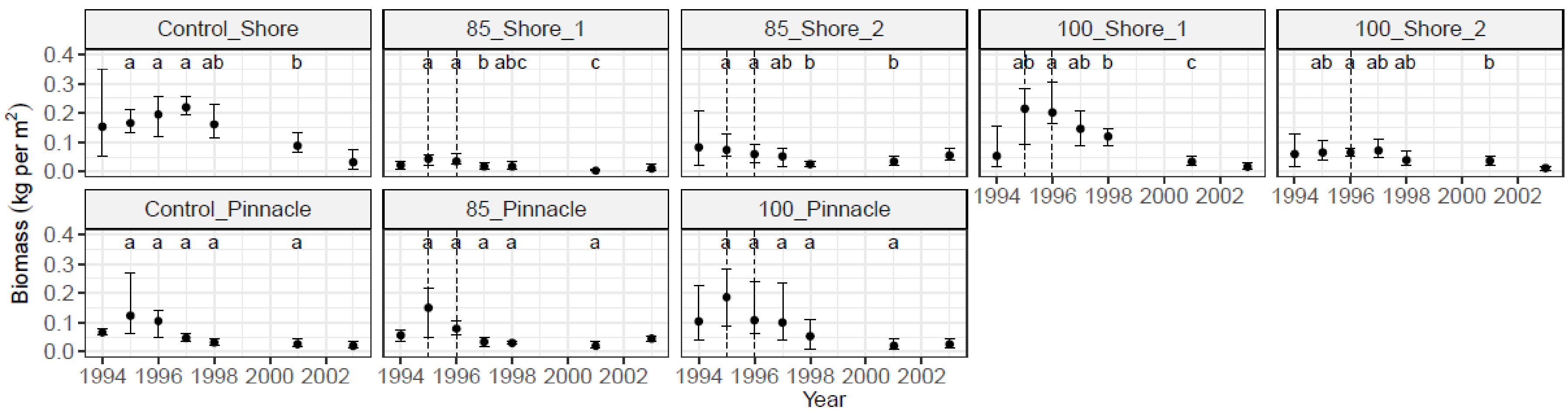


Figure 9. The mean biomass of immature (< 50 mm TD) Red Sea Urchins (kg per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the harvest treatment sites. Pairwise comparisons are within each site (PERMANOVA) and years with different letters are significantly different from one another ($\alpha = 0.05$). Separate, independent analyses were conducted between site type, i.e. shore and pinnacle type sites. The 1996 survey was 2 months post-harvest. The years 1994 and 2003 were not statistically analyzed. Dashed lines represent the years when experimental harvesting occurred, see Table 1 for harvest treatment site descriptions.

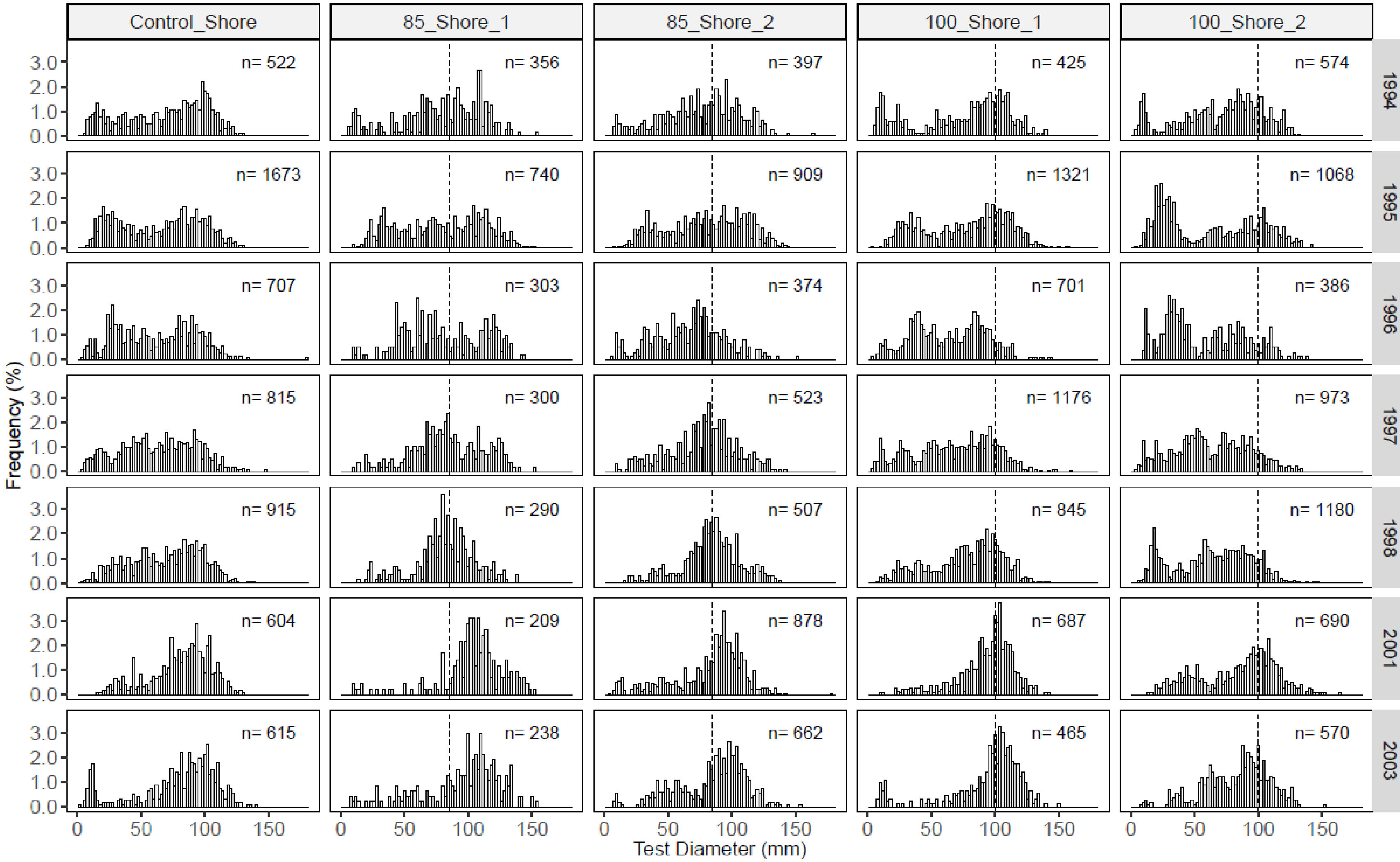


Figure 10. The size frequency distributions (percentage; 2 mm bin width) of the Red Sea Urchin populations at shore sites within the Tofino Research area from 1994 through 2003. The dot-dash lines represent the minimum size limit of each experimental harvest treatment; n equals the total number of urchins measured, see Table 1 for harvest treatment site descriptions. Harvesting occurred at non-control sites in 1995 (pre-harvest) and 1996 (survey 2 months post-harvest).

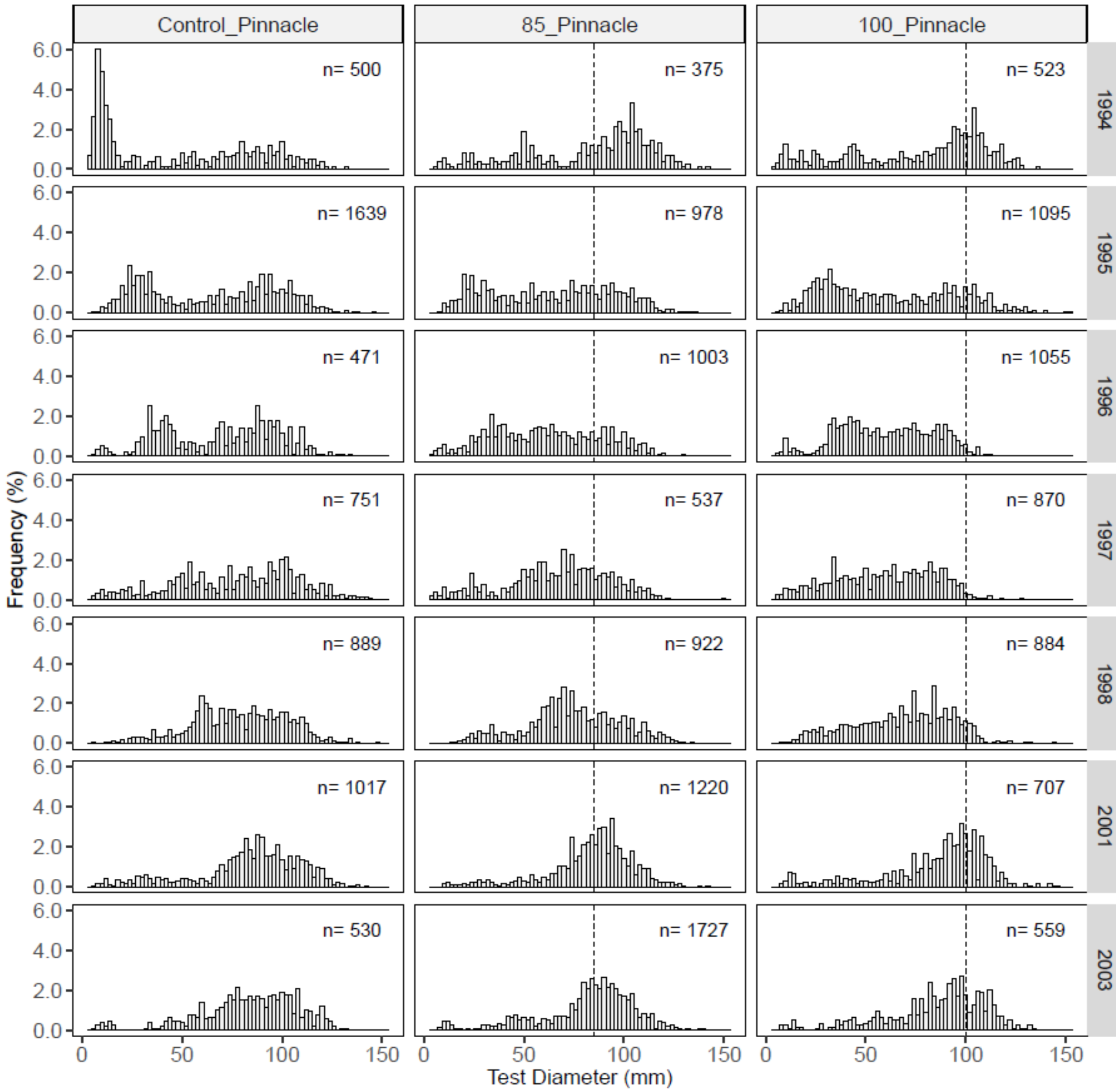
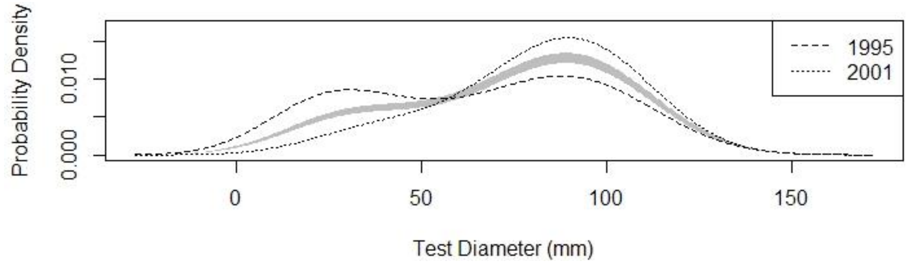
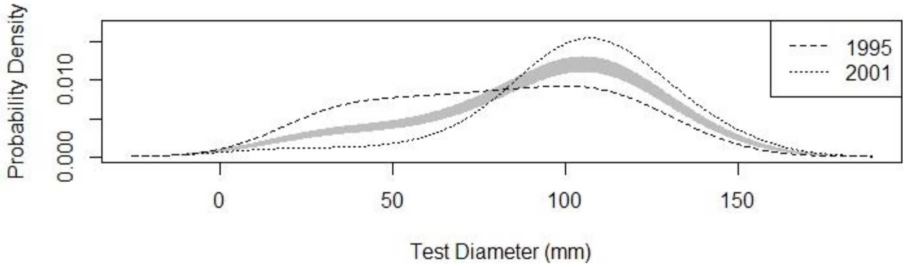


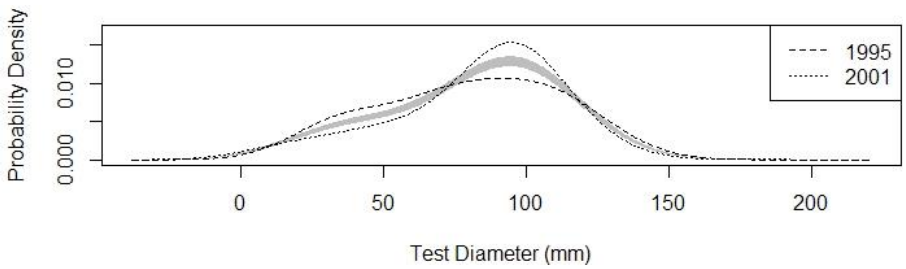
Figure 11. The size frequency distributions (percentage; 2 mm bin width) of the Red Sea Urchin populations at pinnacle sites within the Tofino Research area from 1994 through 2003. The dot-dash lines represent the minimum size limit of each experimental harvest treatment; n equals the total number of urchins measured, see Table 1 for harvest treatment site descriptions. Harvesting occurred at non-control sites in 1995 (pre-harvest) and 1996 (survey 2 post-harvest).



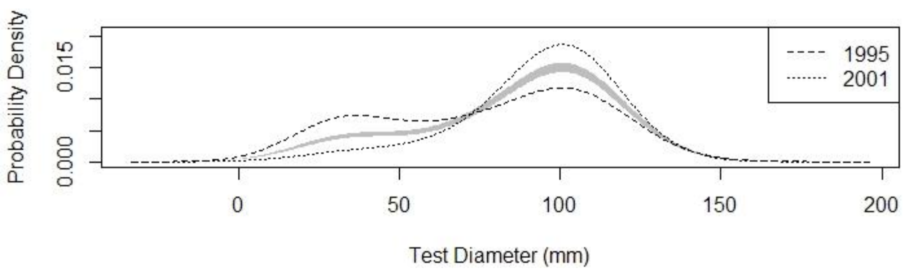
(a) Control_Shore



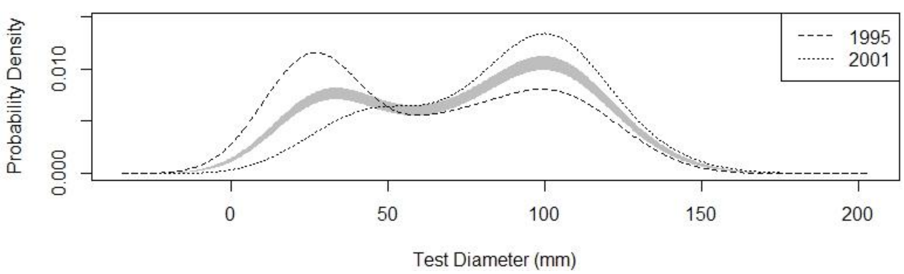
(b) 85_Shore_1



(c) 85_Shore_2

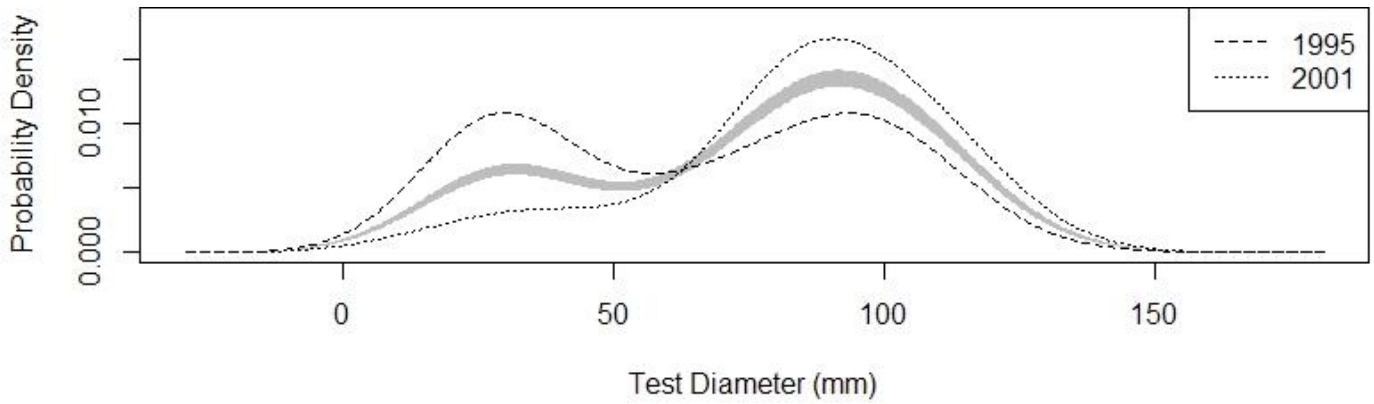


(d) 100_Shore_1

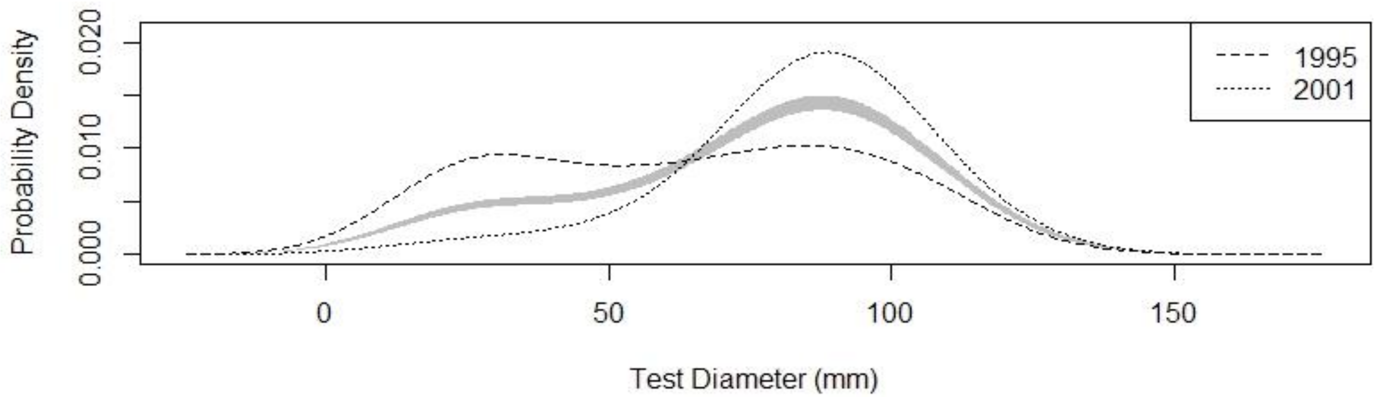


(e) 100_Shore_2

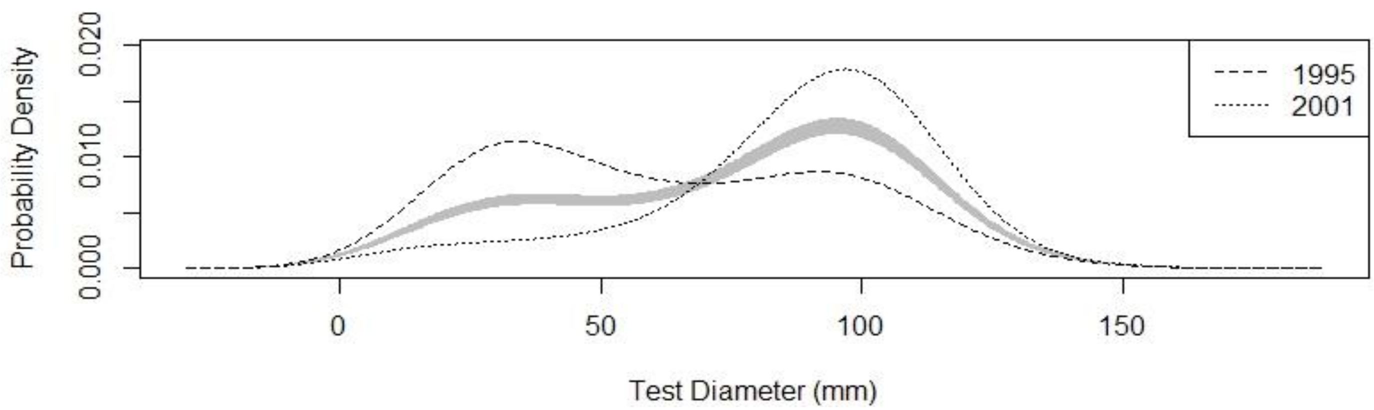
Figure 12. The comparisons of the kernel probability density estimates of RSU test diameter within (a-e) shore harvest treatment sites between pre-harvest (1995) and five years post-harvest surveys (2001). Shaded areas represent the null model of no significant difference between comparisons; all comparisons $p < 0.001$; $\alpha = 0.05$, see Table 1 for harvest treatment site descriptions.



(a) Control_Pinnacle



(b) 85_Pinnacle



(c) 100_Pinnacle

Figure 13. The comparisons of the kernel probability density estimates of RSU test diameter within (a-c) pinnacle harvest treatment sites between pre-harvest (1995) and five years post-harvest surveys (2001). Shaded areas represent the null model of no significant difference between comparisons; all comparisons $p < 0.001$; $\alpha = 0.05$, see Table 1 for harvest treatment site descriptions.

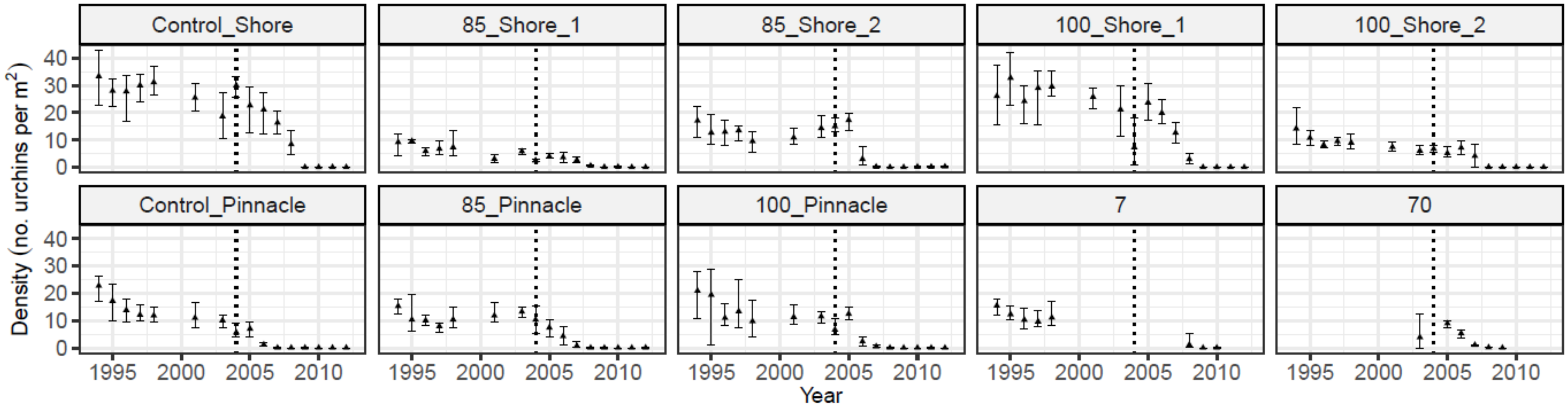


Figure 14. The mean total density of Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

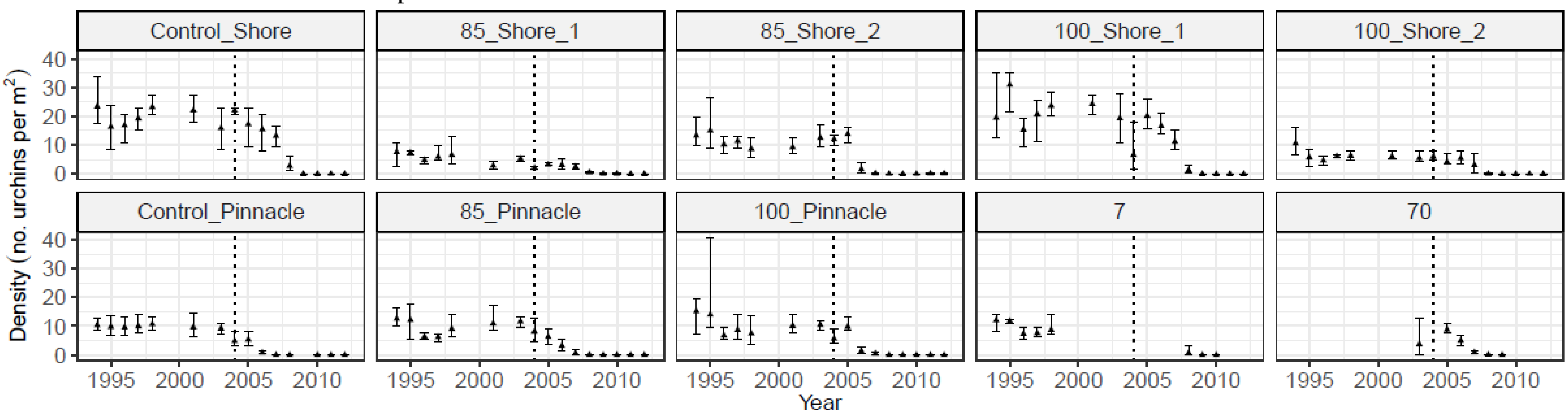


Figure 15. The mean mature density (≥ 50 mm TD) of Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

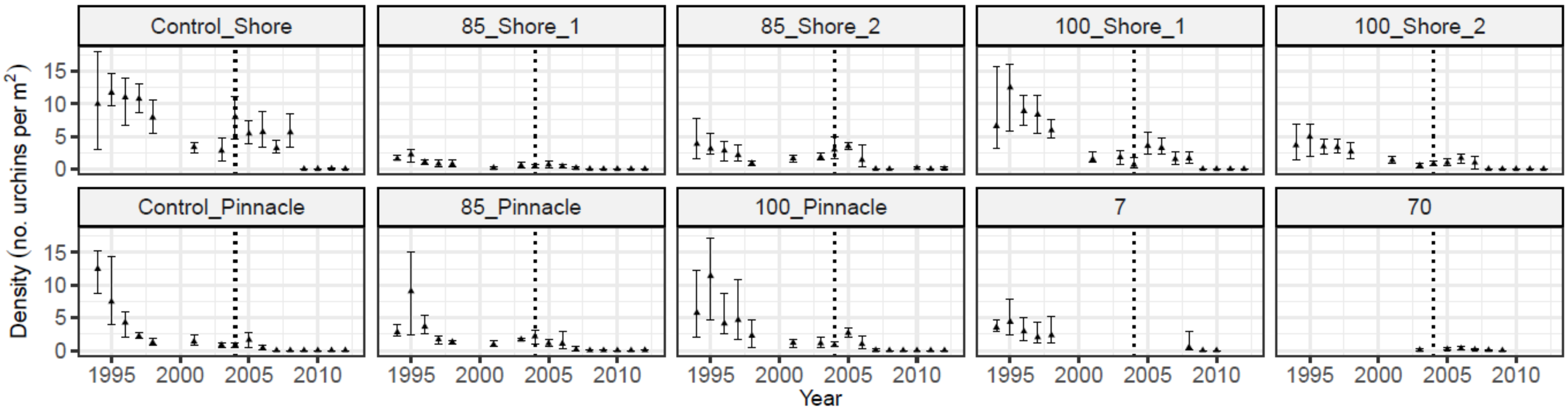


Figure 16. The mean density of immature (< 50 mm TD) of Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

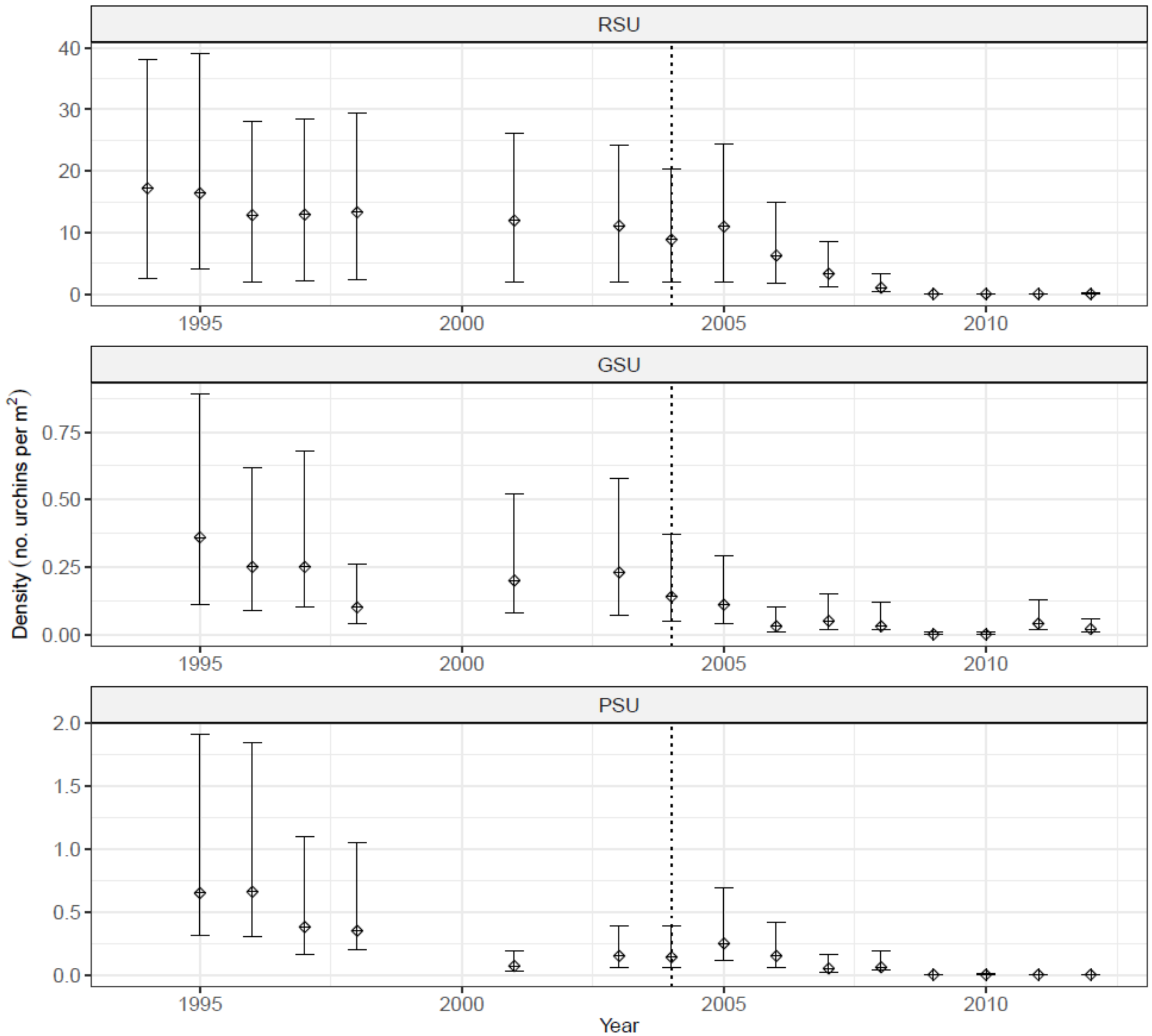


Figure 17. The mean density with 95% confidence intervals (bootstrap) of Red Sea Urchins (RSU), Green Sea Urchins (GSU) and Purple Sea Urchins (PSU) pooled for the entire Tofino research area, from 1995 through 2012. The dotted line represents the first observation of a male Sea Otter raft present near the research area.

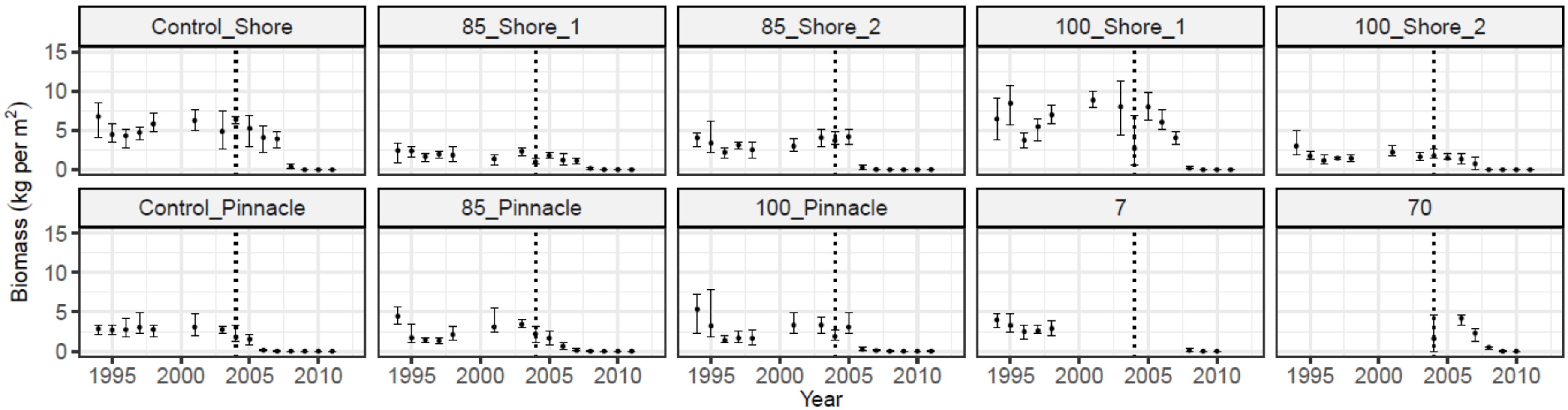


Figure 18. The mean total biomass of Red Sea Urchins (kg per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

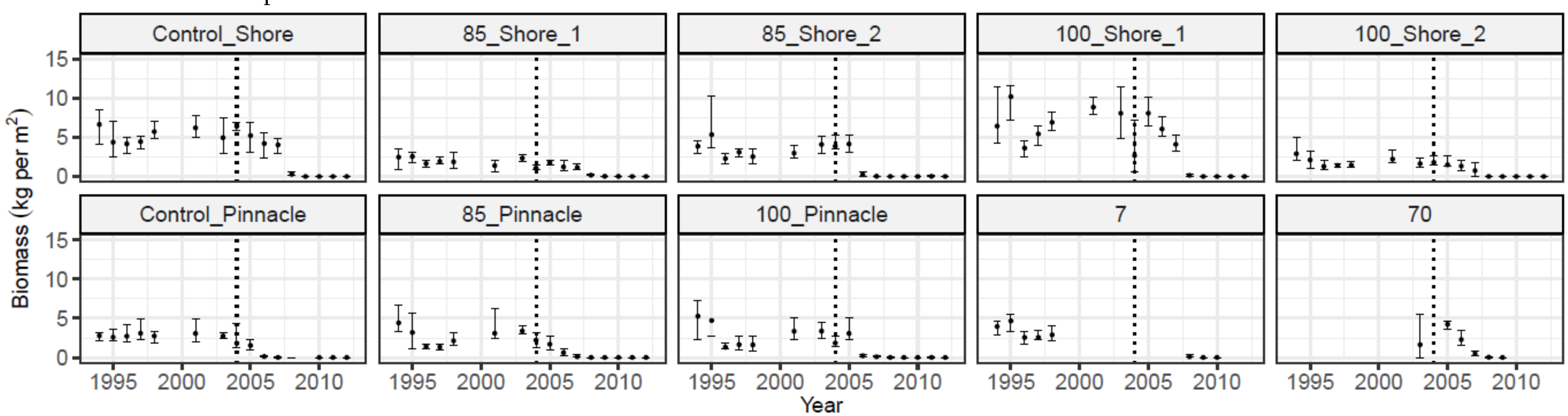


Figure 19. The mean biomass of mature (≥ 50 mm TD) Red Sea Urchins (no. urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

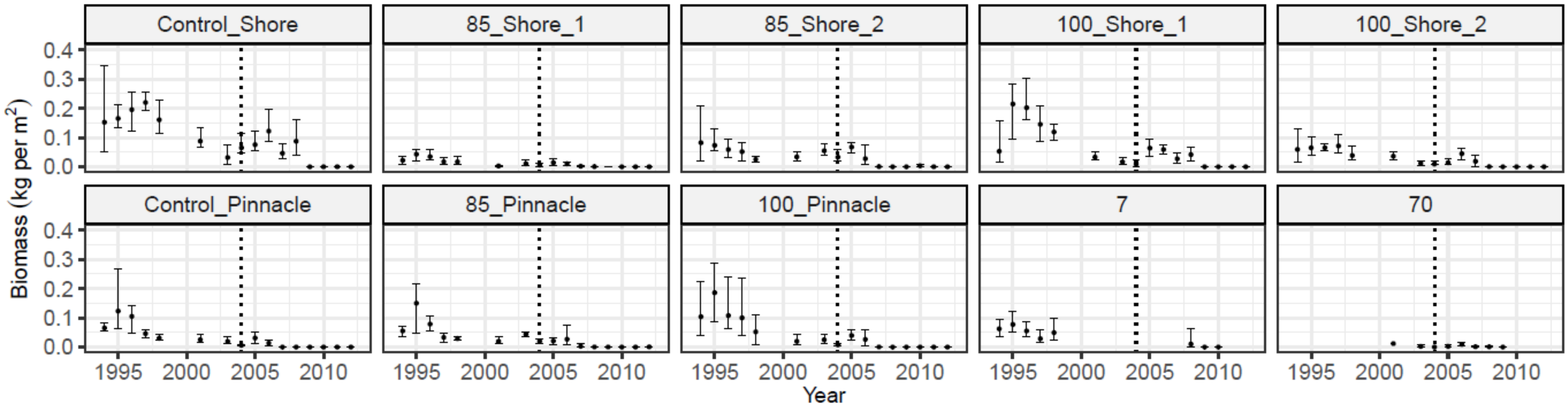


Figure 20. The mean biomass of immature (< 50 mm TD) of Red Sea Urchins (kg per m^2) with 95% confidence intervals (bootstrap) across time (Year) at the experimental research sites in the Tofino research area. The dotted line represents the first observation of a male Sea Otter raft near the research area, see Table 1 for harvest treatment site descriptions.

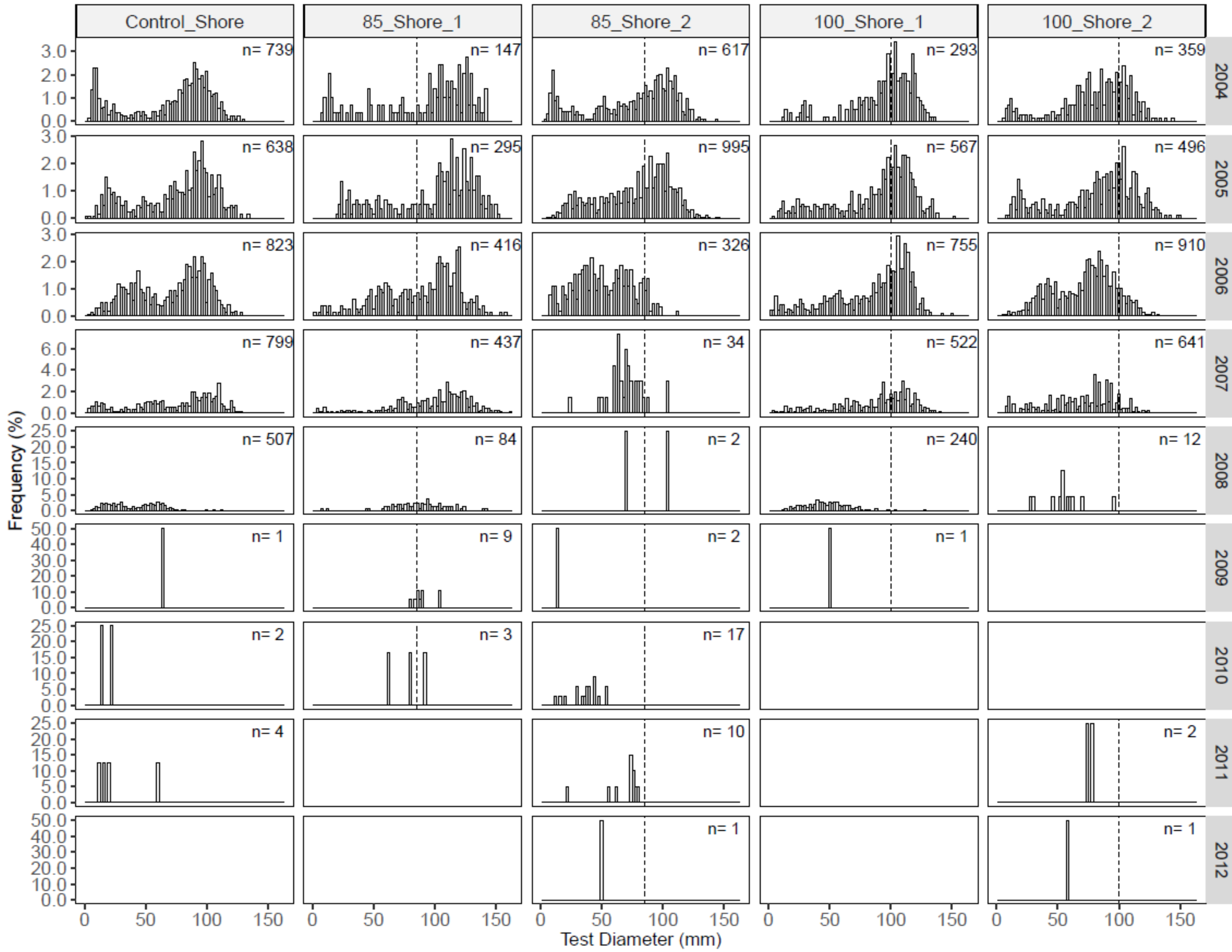


Figure 21. The size frequency distributions (percentage; 2 mm bin width) of the Red Sea Urchin populations at shore sites within the Tofino Research area from 2004 through 2012. The dot-dash lines represent the minimum size limit of each experimental harvest treatment; n equals the total number of urchins measured. Note: the y-axes range is not consistent throughout and that the empty cells for sites 7 and 70 are due to lack of surveying, not zero urchins found, see Table 1 for harvest treatment site descriptions.

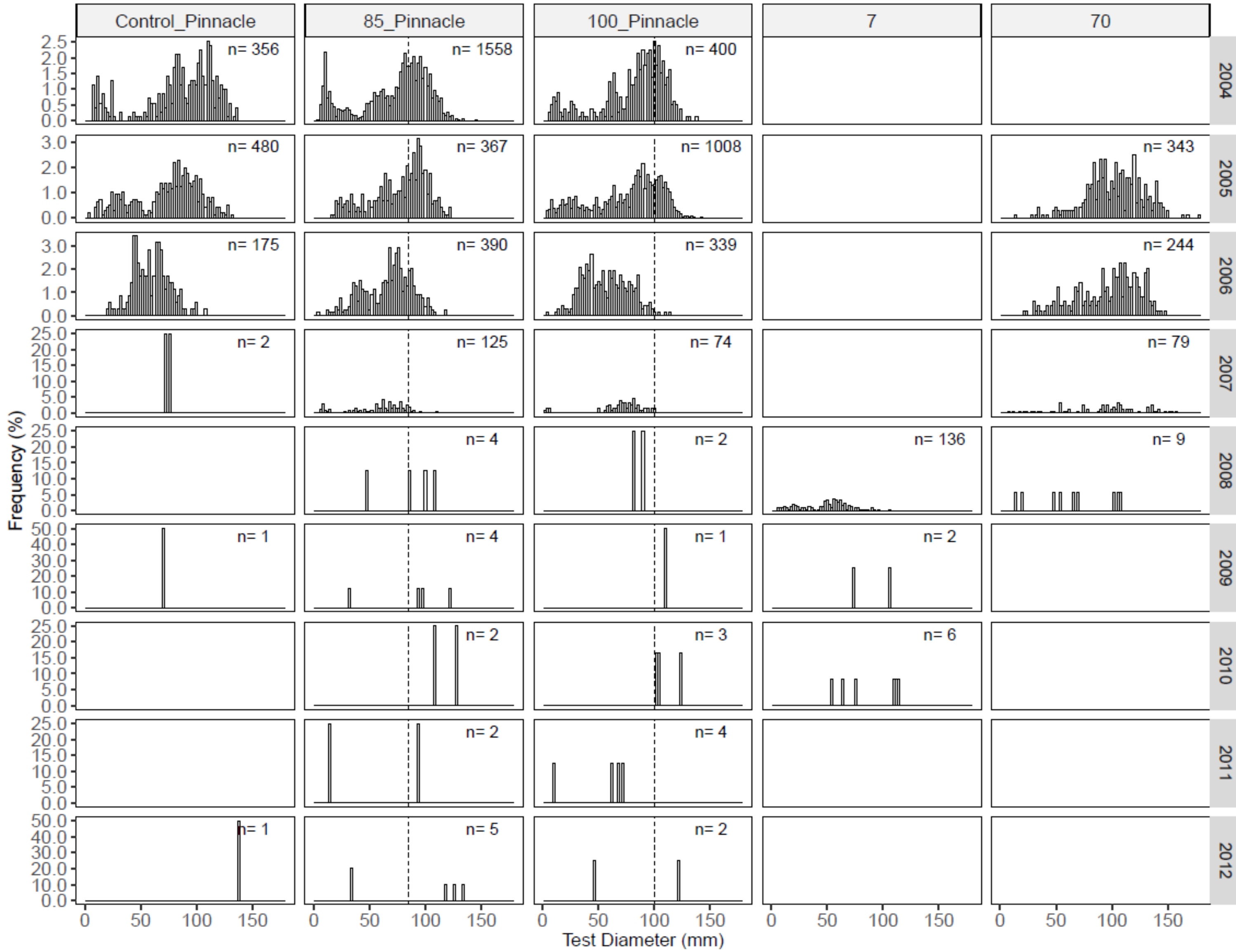


Figure 22. The size frequency distributions (percentage; 2 mm bin width) of the Red Sea Urchin populations at pinnacle sites as well as sites 70 and 7 within the Tofino Research area from 2004 through 2012. The dot-dash lines represent the minimum size limit of each experimental harvest treatment; n equals the total number of urchins measured. Note: the y-axes range is not consistent throughout and that the empty cells for sites 7 and 70 are due to lack of surveying, not zero urchins found, see Table 1 for harvest treatment site descriptions.

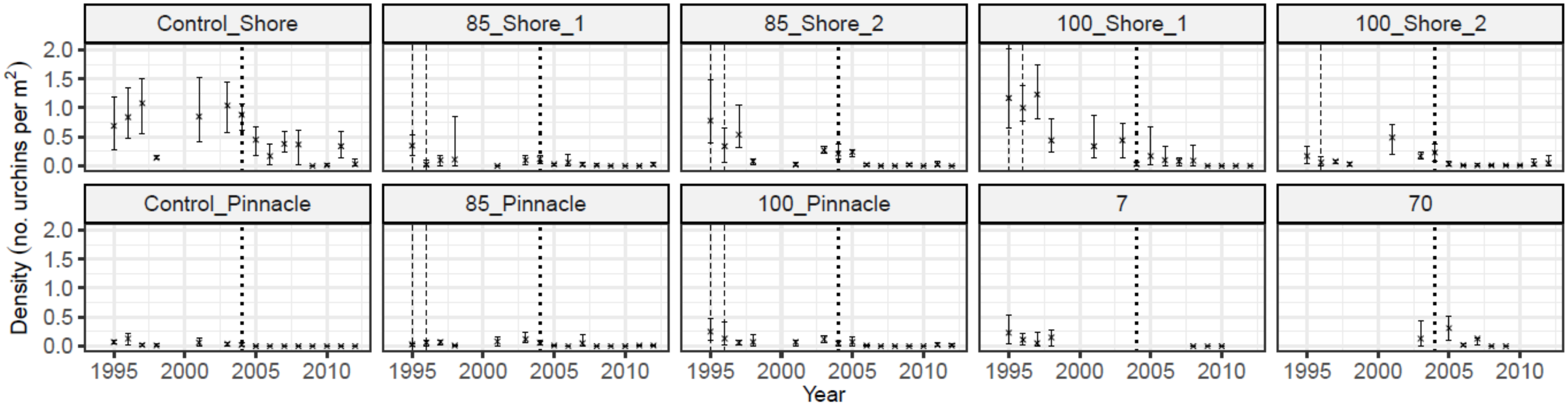


Figure 23. The total mean density of Green Sea Urchins (urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the experimental research sites. The dashed lines represent years when experimental harvesting of Red Sea Urchins occurred and the dotted line represents the first observation of a male Sea Otter raft near the Tofino research area, see Table 1 for harvest treatment site descriptions.

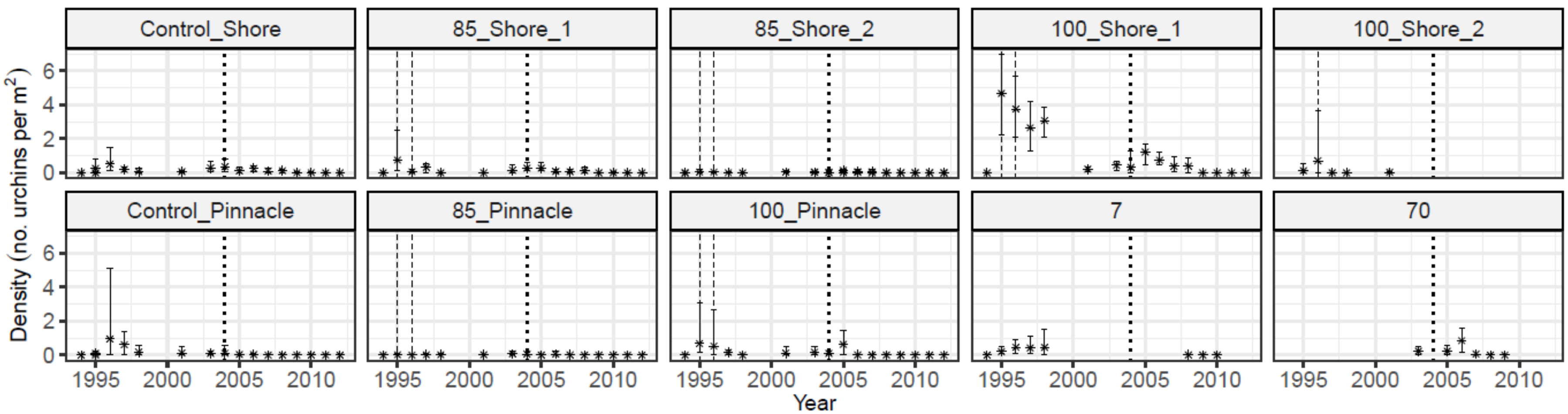


Figure 24. The total mean density of Purple Red Sea Urchins (urchins per m^2) with 95% confidence intervals (bootstrap) across time (Year) at each of the experimental research sites. The dashed lines represent years when experimental harvesting of Red Sea Urchins occurred and the dotted line represents the first observation of a male Sea Otter raft near the Tofino research area, see Table 1 for harvest treatment site descriptions

APPENDIX I: THE PATTERN OF SIZE MEASUREMENT DATA COLLECTION FROM 1995 THROUGH 2012 AT THE TOFINO SEA URCHIN RESEARCH AREA.

"Random" indicates a number of urchin were randomly selected to measure over the entire transect. The notations "2nd" and "4th" refer to the quadrat along transect where urchin measurements were taken (e.g. "2nd" implies that urchin size data were collected within every second quadrat within a transect); "NA" indicates that a survey at that site was not conducted.

	Site									
Year	*Control_Shore*	*85_Shore_1*	*85_Shore_2*	*100_Shore_1*	*100_Shore_2*	*Control_Pinnacle*	*85_Pinnacle*	*100_Pinnacle*	*7*	*70*
1995	Random	Random	Random	Random	Random	Random	Random	Random	Random	NA
1996	4th	2nd	4th	4th	2nd	4th	2nd	2nd	2nd	NA
1997	4th	4th	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA
1998	4th	2nd	2nd	4th	2nd	2nd	2nd	2nd	2nd	NA
2001	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	2nd
2003	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	2nd
2004	2nd	4th	4th	4th	4th	4th	2nd	4th	NA	NA
2005	4th	2nd	2nd	4th	2nd	2nd	4th	2nd	NA	2nd
2006	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	2nd
2007	4th	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	2nd
2008	4th	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd
2009	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd
2010	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA
2011	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	NA
2012	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	NA	NA

APPENDIX II: THE HARVEST OFFLOAD WEIGHT (KG) AND OTHER METADATA COLLECTED AT THE PROCESSING PLANT DURING THE EXPERIMENTAL HARVEST STUDY.*

hrv_dd	hrv_mm	YY	offload_dd	offload_mm	BagID	DEPCOD	rsuwt_kg	AREA	SAREA	SITE
22	9	1995	22	9		1	1338	24	8	2
23	9	1995	23	9		1	1638	24	8	2
29	9	1995	29	9		1	1041	24	8	2
23	9	1995	23	9		2	749	24	8	2
21	9	1995	21	9		2	1224	24	8	2
20	9	1995	20	9		2	2672	24	8	4
21	9	1995	21	9		2	366	24	8	4
22	9	1995	22	9		2	195	24	8	4
29	9	1995	29	9		2	641	24	8	4
30	9	1995	30	9		2	137	24	8	4
30	9	1995	30	9		1	2313	24	8	4
1	10	1995	1	10		1	1291	24	8	4
29	9	1995	29	9		1	937	24	8	4
4	10	1995	4	10		1	2815	24	8	5
4	10	1995	4	10		1	2628	24	8	5
12	10	1995	12	10		1	698	24	8	5
21	9	1995	21	9		3	181	24	8	9
12	10	1995	12	10		1	2205	24	8	10
11	10	1995	11	10		2	2705	24	8	10
2	10	1995	2	10		1	1727	24	8	11
1	10	1995	1	10		1	1702	24	8	11
3	5	1996	3	5	3	1	300	24	8	2
3	5	1996	3	5	4	1	238	24	8	2
3	5	1996	3	5	1	1	362	24	8	2
3	5	1996	3	5	2	1	249	24	8	2
1	5	1996	1	5	5	1	293	24	8	4
1	5	1996	1	5	6	1	171	24	8	4
1	5	1996	1	5	7	1	279	24	8	5
1	5	1996	1	5	8	1	126	24	8	5
2	5	1996	2	5	14	2	260	24	8	5
2	5	1996	2	5	12	2	239	24	8	5
2	5	1996	2	5	10	2	259	24	8	5
2	5	1996	2	5	11	2	237	24	8	5
2	5	1996	2	5	8	2	249	24	8	5
2	5	1996	2	5	9	2	254	24	8	5
2	5	1996	2	5	16	2	280	24	8	5
3	5	1996	3	5	15	2	183	24	8	5
3	5	1996	3	5	10+8	2	276	24	8	5
3	5	1996	3	5	8	2	253	24	8	5
3	5	1996	3	5	7	2	246	24	8	5
3	5	1996	3	5	5	2	214	24	8	5
3	5	1996	3	5	6	2	186	24	8	5
9	5	1996	9	5	1	1	220	24	8	5
9	5	1996	9	5	2	1	186	24	8	5
30	4	1996	30	4	4	1	235	24	8	5
6	5	1996	6	5	14+12	1	260	24	8	5
6	5	1996	6	5	11	1	203	24	8	5
6	5	1996	6	5	9	1	250	24	8	5
6	5	1996	6	5	10	1	238	24	8	5
6	5	1996	6	5	7+8	1	251	24	8	5
7	5	1996	7	5	5	1	225	24	8	5
7	5	1996	7	5	6	1	270	24	8	5
7	5	1996	7	5	3	1	192	24	8	5
7	5	1996	7	5	1	1	242	24	8	5

hrv_dd	hrv_mm	YY	offload_dd	offload_mm	BagID	DEPCOD	rsuwt_kg	AREA	SAREA	SITE
7	5	1996	7	5	4	1	234	24	8	5
7	5	1996	7	5	2	1	236	24	8	5
8	5	1996	8	5	10	2	217	24	8	5
8	5	1996	8	5	8	2	241	24	8	5
8	5	1996	8	5	9	2	234	24	8	5
8	5	1996	8	5	6	2	223	24	8	5
8	5	1996	8	5	7	2	259	24	8	5
8	5	1996	8	5	5	2	180	24	8	5
8	5	1996	8	5	5+4	2	214	24	8	5
8	5	1996	8	5	1	2	196	24	8	5
8	5	1996	8	5	3	2	192	24	8	5
8	5	1996	8	5	2	2	223	24	8	5
4	5	1996	4	5	19	2	225	24	8	8
4	5	1996	4	5	14+18	2	234	24	8	8
4	5	1996	4	5	17	2	264	24	8	8
4	5	1996	4	5	16	2	257	24	8	8
4	5	1996	4	5	15	2	235	24	8	8
4	5	1996	4	5	12+13	1	275	24	8	8
4	5	1996	4	5	10	1	277	24	8	8
4	5	1996	4	5	11	1	310	24	8	8
9	5	1996	9	5	8	2	272	24	8	8
9	5	1996	9	5	7+3	2	231	24	8	8
9	5	1996	9	5	6	2	254	24	8	8
9	5	1996	9	5	5	2	225	24	8	8
9	5	1996	9	5	4	2	244	24	8	8
30	4	1996	30	4		2	281	24	8	10
30	4	1996	30	4		2	87	24	8	10
30	4	1996	30	4		1	235	24	8	10
30	4	1996	30	4		1	244	24	8	10
6	5	1996	6	5	19	1	222	24	8	11
6	5	1996	6	5	17	1	270	24	8	11
6	5	1996	6	5	18	1	227	24	8	11
6	5	1996	6	5	16	1	227	24	8	11
6	5	1996	6	5	15	1	230	24	8	11
7	5	1996	7	5	10	1	217	24	8	11
7	5	1996	7	5	11	1	226	24	8	11
7	5	1996	7	5	9	1	242	24	8	11
9	5	1996	9	5	10	1	229	24	8	11
9	5	1996	9	5	9	1	238	24	8	11
9	5	1996	9	5	7	1	184	24	8	11
9	5	1996	9	5	8	1	225	24	8	11
9	5	1996	9	5	5	1	211	24	8	11
9	5	1996	9	5	6	1	225	24	8	11
9	5	1996	9	5	3+4	1	186	24	8	11
9	5	1996	9	5	1	1	236	24	8	11
9	5	1996	9	5	2	1	210	24	8	11
9	5	1996	9	5	2	1	179	24	8	11
9	5	1996	9	5	5	1	230	24	8	11
9	5	1996	9	5	6	1	268	24	8	11
10	5	1996	10	5	3	1	249	24	8	11
10	5	1996	10	5	4	1	237	24	8	11
10	5	1996	10	5	1	1	242	24	8	11
10	5	1996	10	5	2	1	206	24	8	11
10	5	1996	10	5	2	1	146	24	8	11

* See Table 1 for site names used in this report, site here refers to site numbers in the DFO database.

APPENDIX III: MEAN TOTAL DENSITY OF RSU BY SITE

The mean density (urchins per m^2) of Red Sea Urchins with lower and upper 95% confidence intervals (LCI, UCI; bootstrap) at experimental sites located in PFMA 24 (a), shore-type sites and (b), pinnacle-type sites, see Table 1 for harvest treatment site descriptions.

(a)

		Site				
Year	**Month**	**Control_Shore**	**85_Shore_1**	**85_Shore_2**	**100_Shore_1**	**100_Shore_2**
1994	July	33.4 (22.8, 42.9)	9.2 (4.3, 12.0)	17.1 (11.1, 22.2)	26.1 (15.4, 37.5)	14.2 (8.3, 21.9)
1995	May	27.9 (21.3, 34.2)				
1995	August	25 (19.3, 29.8)	8.8 (6.4, 10.1)	12.7 (8.4, 19.3)	32.7 (22.9, 41.9)	9.2 (8.2, 11.5)
1996	June	27.8 (16.8, 33.7)	5.9 (4.4, 7.1)	13 (7.7, 17.1)	24.2 (16.1, 29.5)	8.1 (7.2, 9.9)
1997	June	30 (23.1, 33.8)	6.8 (4.6, 9.4)	13.5 (9.5, 15.3)	29.1 (15.5, 35.3)	9.5 (8.1, 10.8)
1998	June	31.1 (26.7, 37.1)	7.3 (4.2, 12.8)	9.5 (5.6, 13.1)	29.6 (25.9, 35.6)	9 (6.3, 12)
2001	June	25.4 (21, 30.7)	3.1 (1.4, 4.5)	10.9 (8.3, 14.4)	25.8 (21.6, 29.0)	7.4 (6.0, 9.2)
2003	June	18.7 (10.5, 26.7)	5.8 (4.4, 6.6)	14.3 (10.8, 18.8)	21.2 (11.4, 29.8)	6.1 (4.6, 7.9)
2004	June	30 (25.6, 33.0)		14.9 (12.8, 17.9)		
2004	July		2.5 (2.1, 2.9)		7.3 (1.5, 18.2)	6.8 (5.5, 8.1)
2005	June	22.6 (13.6, 29.4)	4 (3.4, 5.0)	17.3 (13.3, 19.6)	23.7 (17.4, 30.5)	5.2 (3.8, 7.5)
2006	June	21.1 (12.3, 27.4)	3.6 (2.5, 8.0)	3 (0.7, 7.1)	19.9 (16.1, 24.8)	7.2 (4.5, 9.6)
2007	June	16.4 (12.1, 20.9)	2.7 (1.8, 3.7)	0.2 (0.1, 0.3)	12.6 (8.8, 16.3)	4.1 (0.2, 8.6)
2008	June	8.4 (4.6, 13.6)	0.6 (0.3, 0.9)	0 (0.0, 1.0)	3 (1.2, 5.1)	0.1 (0.9, 0.2)
2009	June	0.0 (0,0, 0.0)	0.1 (0.0, 0.2)	0 (0.0, 1,0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.1)	0.1 (0.0, 0.3)	0.2 (0.0, 0.4)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2011	June	0.1 (0.0, 0.1)	0.0 (0.0, 0.0)	0.2 (0.0, 0.4)	0.0 (0.0, 0.0)	0.0 (0.0, 1.0)
2012	May	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.2 (0.0, 0.6)	0.0 (0.0, 0.0)	0.0 (0.0,0.1)

(b)

Year	Month	Control_Pinnacle	85_Pinnacle	Site 100-Pinnacle	7	70
1994	July	22.7 (17.2, 26.3)	15.3 (12.6, 17.7)	20.9 (10.9, 27.9)	15.5 (11.9, 17.6)	
1995	May	10.6 (7.9, 12.8)				
1995	August	15.0 (11.2, 20.5)	10.3 (6.2, 19.4)	19.4 (14.9, 28.7)	12.3 (10.2, 15.5)	
1996	June	13.8 (9.4,18.1)	10.1 (8.2,12)	10.9 (8.4, 16.3)	10.3 (6.9, 14.3)	
1997	June	12.1 (9.7, 15.8)	8 (5.5, 9.1)	13.4 (7.3, 25.1)	9.6 (7.8, 13.5)	
1998	June	11.8 (9.5, 14.9)	10.4 (7.5, 15.1)	9.7 (4.1, 17.6)	11.1 (8.2, 17.2)	
2001	June	11.0 (7.2, 16.4)	11.8 (9.7, 18.1)	11.3 (8.7, 14.7)		
2003	June	10.1 (7.5,12.1)	13.2 (11, 14.7)	11.5 (9.1, 13.2)		3.9 (0, 10.7)
2004	June		10.3 (5.3, 15.2)	6.6 (4.9, 10.2)		
2004	July	5.6 (4.1, 8.7)				
2005	June	7.0 (3.9, 9.5)	7.4 (4.1, 10.5)	12.4 (10.4, 14.8)		9.0 (7.3, 10.1)
2006	June	1.2 (0.7, 2.0)	4.2 (1.1, 7.6)	2.3 (0.6, 4.0)		5.3 (3.5, 6.4)
2007	June	0.0 (0.0, 0.0)	0.7 (0.1, 2.6)	0.5 (0.2, 1.1)		1.1 (0.6, 1.1)
2008	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	1.1 (0.2,5.4)	0.1 (0.0, 0.3)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	
2011	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0 ,0.1)		
2012	May	0.0 (0.0, 0.0)	0.1 (0.0, 0.1)	0.0 (0.0, 0.0)		

APPENDIX IV: MEAN TOTAL BIOMASS OF RSU BY SITE

The mean biomass (kg per m^2) of Red Sea Urchins with upper and lower 95% confidence intervals (LCI, UCI; bootstrap) at experimental sites located in PFMA 24 (a), shore-type sites and (b), pinnacle-type sites, see Table 1 for harvest treatment site descriptions.

(a)

		Site				
Year	**Month**	**Control Shore**	**85 Shore 1**	**85 Shore 2**	**100 Shore 1**	**100 Shore 2**
1994	July	6.8 (4.1, 8.6)	2.5 (0.9, 3.5)	4.1 (2.9, 4.7)	6.5 (3.9, 9.1)	3.0 (2.0, 5.0)
1995	May	4.9 (2.9, 6.8)				
1995	August	4.5 (3.5, 5.8)	2.4 (1.7, 3.0)	3.4 (2.2, 6.2)	8.5 (5.7, 10.7)	1.8 (1.3, 2.3)
1996	June	4.3 (2.8, 5.1)	1.7 (1.1, 2.0)	2.2 (1.5, 2.8)	3.8 (2.8, 4.7)	1.2 (0.8, 1.9)
1997	June	4.8 (3.8, 5.4)	2 (1.5, 2.3)	3.2 (2.6, 3.5)	5.5 (3.7, 6.5)	1.5 (1.3, 1.6)
1998	June	5.8 (4.9, 7.2)	1.9 (1.1, 2.9)	2.6 (1.5, 3.5)	7 (5.9, 8.2)	1.5 (1.1, 1.9)
2001	June	6.3 (5.7, 7.0)	1.4 (0.6, 2.0)	3.0 (2.3, 4.0)	8.9 (7.9, 10.0)	2.2 (1.7, 3.1)
2003	June	4.9 (2.7,7.5)	2.3 (1.8,2.8)	4.1 (3.0, 5.1)	8.0 (4.4, 11.3)	1.7 (1.2, 2.2)
2004	June	6.4 (5.9, 6.8)		3.7 (3.3, 4.8)		
2004	July		1.0 (0.8, 1.5)		2.7 (0.6, 6.9)	1.8 (1.4, 2.6)
2005	June	5.3 (2.9, 6.9)	1.8 (1.5, 2.2)	4.2 (3.2, 5.2)	8.0 (6.3, 9.9)	1.5 (1.3, 2.1)
2006	June	4.1 (2.3, 5.6)	1.2 (0.6, 2.0)	0.3 (0.1, 0.6)	6.1 (5.2, 7.6)	1.4 (0.7, 2.1)
2007	June	3.9 (2.8, 4.8)	1.2 (0.8, 1.5)	0.0 (0.0, 0.1)	4.1 (3.2, 4.9)	0.8 (0.0 ,1.7)
2008	June	0.4 (0.2, 0.7)	0.2 (0.1, 0.3)	0.0 (0.0, 0.0)	0.2 (0.1, 0.4)	0.0 (0.0, 0.0)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2011	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2012	May	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)

(b)

		Site				
		Control Pinnacle	**85 Pinnacle**	**100 Pinnacle**	**7**	**70**
1994	July	2.9 (2.1, 3.3)	4.5 (3.5, 5.7)	5.3 (2.3, 7.3)	4.0 (3.0, 4.8)	
1995	May	2.0 (1.2, 2.4)				
1995	August	2.7 (2.2, 3.3)	1.7 (1.1, 3.4)	3.2 (1.9, 7.8)	3.3 (2.4, 4.8)	
1996	June	2.8 (1.9, 4.1)	1.5 (1.1, 1.7)	1.4 (1.1, 1.9)	2.5 (1.6, 3.3)	
1997	June	3.1 (2.2, 4.9)	1.3 (0.9, 1.6)	1.7 (1.1, 2.6)	2.6 (2.3, 3.3)	
1998	June	2.8 (1.9, 3.3)	2.1 (1.4, 3.1)	1.6 (0.9, 2.7)	2.9 (2.3, 9.0)	
2001	June	3.1 (1.9, 4.7)	3.1 (2.5, 5.6)	3.3 (2.3, 4.9)		
2003	June	2.7 (2.3, 3.1)	3.4 (3.0, 4.0)	3.3 (2.3, 4.3)		1.6 (0.0, 4.6)
2004	June		2.2 (1.1,3.2)	1.9 (1.3,2.7)		
2004	July	1.8 (1.2, 3.3)				
2005	June	1.5 (0.9, 2.2)	1.7 (0.8, 2.6)	3.1 (2.4, 5.0)		4.2 (3.3, 4.6)
2006	June	0.1 (0.1, 0.2)	0.6 (0.2, 1.1)	0.2 (0.1, 0.5)		2.3 (1.3, 2.9)
2007	June	0.0 (0.0, 0.0)	0.1 (0.0, 0.3)	0.1 (0.0, 0.2)		0.5 (0.2, 0.5)
2008	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.1 (0.0, 0.3)	0.0 (0.0, 0.1)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	
2011	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)		
2012	May	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)		

APPENDIX V: MEAN TOTAL DENSITY OF GSU BY SITE

The mean density (urchins per m^2) of Green Sea Urchins with upper and lower 95% confidence intervals (LCI, UCI; bootstrap) at experimental sites located in PFMA 24 at (a), shore-type sites and (b), pinnacle-type sites, see Table 1 for harvest treatment site descriptions.

(a)

		Site				
Year	**Month**	**Control Shore**	**85 Shore 1**	**85 Shore 2**	**100 Shore 1**	**100 Shore 2**
1995	August	0.7 (0.3, 1.2)	0.4 (0.2, 0.5)	0.8 (0.4, 1.5)	1.2 (0.7, 2.0)	0.2 (0.1, 0.3)
1996	June	0.8 (0.5, 1.3)	0.0 (0.0, 0.1)	0.3 (0.1, 0.7)	1.0 (0.8, 1.4)	0.1 (0.0, 0.2)
1997	June	1.1 (0.6, 1.5)	0.1 (0.0, 0.2)	0.5 (0.3,1.1)	1.2 (0.8, 1.7)	0.1 (0.0, 0.1)
1998	June	0.1 (0.1, 0.2)	0.1 (0.0, 0.9)	0.08 (0.02, 0.1)	0.4 (0.2, 0.8)	0.03 (0.01, 0.06)
2001	June	0.9 (0.4, 1.5)	0.0 (0.0, 0.0)	0.02 (0.0, 0.6)	0.3 (0.1, 0.9)	0.5 (0.2, 0.7)
2003	June	1.0 (0.6, 1.5)	0.1 (0.03, 0.2)	0.3 (0.2, 0.3)	0.4 (0.1, 0.7)	0.2 (0.1, 0.2)
2004	June	0.9 (0.6, 1.1)		0.2 (0.1, 0.4)		
2004	July		0.1 (0.04, 0.2)		0.03 (0.0, 0.06)	0.2 (0.08, 0.4)
2005	June	0.5 (0.2, 0.7)	0.03 (0.0, 0.05)	0.2 (0.2, 0.3)	0.2 (0.02, 0.7)	0.03 (0.0, 0.08)
2006	June	0.2 (0.03, 0.4)	0.06 (0.0, 0.2)	0.02 (0.0, 0.04)	0.1 (0.0, 0.3)	0.01 (0.0, 0.03)
2007	June	0.4 (0.2,0.6)	0.02 (0.0, 0.07)	0.0 (0.0, 0.0)	0.1 (0.01, 0.1)	0.01 (0.0,0.04)
2008	June	0.4 (0.03, 0.6)	0.01 (0.0, 0.04)	0.0 (0.0, 0.0)	0.1 (0.0, 0.4)	0.01 (0.0, 0.02)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.02 (0.0, 0.04)	0.0 (0.0, 0.0)	0.01 (0.0, 0.03)
2010	June	0.01 (0.0, 0.05)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.01 (0.0, 0.03)
2011	June	0.34 (0.13,0.59)	0.0 (0.0, 0.0)	0.02 (0.0, 0.1)	0.0 (0.0, 0.0)	0.03 (0.0, 0.11)
2012	May	0.03 (0.0, 0.12)	0.02 (0.0, 0.1)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.1 (0.0, 0.2)

(b)

Year	Month	Site: Control Pinnacle	85 Pinnacle	100 Pinnacle	7	70
1995	August	0.1 (0.04, 0.1)	0.03 (0.01, 0.05)	0.3 (0.1, 0.5)	0.2 (0.04, 0.5)	
1996	June	0.1 (0.03, 0.2)	0.06 (0.01, 0.1)	0.1 (0.02, 0.4)	0.1 (0.03, 0.2)	
1997	June	0.02 (0.0, 0.05)	0.07 (0.02, 0.1)	0.06 (0.02, 0.1)	0.05 (0.0, 0.2)	
1998	June	0.01 (0.0, 0.05)	0.01 (0.0, 0.03)	0.07 (0.0, 0.2)	0.2 (0.01, 0.3)	
2001	June	0.1 (0.01, 0.1)	0.1 (0.01, 0.2)	0.1 (0.0, 0.1)		
2003	June	0.04 (0.0, 0.1)	0.1 (0.1, 0.2)	0.1 (0.06, 0.2)		0.1 (0.0, 0.4)
2004	June		0.06 (0.02, 0.08)	0.05 (0.01,0.08)		
2004	July	0.02 (0.0, 0.07)				
2005	June	0.0 (0.0, 0.0)	0.01 (0.0, 0.03)	0.07 (0.0, 0.15)		0.3 (0.1, 0.5)
2006	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.01 (0.0, 0.03)		0.02 (0,0.04)
2007	June	0.0 (0.0, 0.0)	0.05 (0.0, 0.2)	0.0 (0.0, 0.0)		0.1 (0.03, 0.1)
2008	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	
2011	June	0.0 (0.0, 0.0)	0.01 (0,0.03)	0.02 (0,0.07)		
2012	May	0.0 (0.0, 0.0)	0.01 (0,0.03)	0.01 (0,0.04)		

APPENDIX VI: MEAN TOTAL DENSITY OF PSU BY SITE

The mean density (urchins per m^2) of Purple Sea Urchins with upper and lower 95% confidence intervals (LCI, UCI; bootstrap) at experimental sites located in PFMA 24 (a), shore-type sites and (b), pinnacle-type sites, see Table 1 for harvest treatment site descriptions.

(a)

		Site				
Year	**Month**	**Control Shore**	**85 Shore 1**	**85 Shore 2**	**100 Shore 1**	**100 Shore 2**
1995	August	0.3 (0.1, 0.8)	0.8 (0.1, 2.5)	0.04 (0.0, 0.2)	4.7 (2.2, 7.0)	0.1 (0.0, 0.5)
1996	June	0.5 (0.1, 1.5)	0.1 (0.0, 0.2)	0.04 (0.0, 0.1)	3.8 (2.1, 5.7)	0.7 (0.0, 3.7)
1997	June	0.2 (0.1, 0.3)	0.3 (0.0, 0.5)	0.01 (0.0, 0.05)	2.7 (1.3, 4.2)	0.01 (0.0 , 0.03)
1998	June	0.1 (0.0, 0.3)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	3.1 (2.1, 3.9)	0.0 (0.0, 0.0)
2001	June	0.1 (0.02, 0.1)	0.0 (0.0, 0.0)	0.04 (0.0, 0.1)	0.2 (0.1, 0.3)	0.03 (0.0, 0.1)
2003	June	0.3 (0.1, 0.7)	0.2 (0.0, 0.5)	0.04 (0.0, 0.1)	0.4 (0.2, 0.7)	0.03 (0.0, 0.1)
2004	June	0.4 (0.1, 0.8)		0.01 (0.0, 0.05)		
2004	July		0.3 (0.1, 0.6)		0.2 (0.03, 1.3)	0.03 (0.0, 0.1)
2005	June	0.1 (0.02, 0.3)	0.3 (0.1, 0.6)	0.1 (0.1, 0.2)	1.2 (0.5, 1.7)	0.02 (0.0, 0.07)
2006	June	0.3 (0.08, 0.4)	0.08 (0.02, 0.2)	0.03 (0.0, 0.1)	0.7 (0.5, 1.2)	0.1 (0.0, 0.2)
2007	June	0.1 (0.0, 0.2)	0.1 (0.0, 0.2)	0.0 (0.0, 0.0)	0.38 (0.1, 1.0)	0.06 (0.0, 0.2)
2008	June	0.1 (0.0, 0.2)	0.1 (0.0, 0.3)	0.0 (0.0, 0.0)	0.4 (0.0, 0.9)	0.01 (0.0, 0.02)
2009	June	0.01 (0,0.04)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.01 (0,0.04)	0.01 (0,0.04)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2011	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2012	May	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)

(b)

Year	Month	Site				
		Control Pinnacle	**85 Pinnacle**	**100 Pinnacle**	**7**	**70**
1994	July	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	
1995	May	0.0 (0.0, 0.0)				
1995	August	0.1 (0.0 ,0.3)	0.02 (0,0.07)	0.7 (0.2, 3.1)	0.2 (0.1, 0.5)	
1996	June	1.0 (0.0, 5.1)	0.0 (0.0, 0.0)	0.53 (0.0, 2.7)	0.5 (0.1, 1.0)	
1997	June	0.6 (0.0, 1.4)	0.0 (0.0, 0.1)	0.2 (0.1, 0.3)	0.4 (0.1, 1.1)	
1998	June	0.2 (0.02, 0.5)	0.02 (0.0, 0.1)	0.0 (0.0, 0.0)	0.5 (0.0, 1.5)	
2001	June	0.1 (0.0, 0.5)	0.02 (0.0, 0.1)	0.1 (0.0, 0.5)		
2003	June	0.1 (0.0, 0.2)	0.1 (0.0, 0.2)	0.2 (0.0, 0.5)		0.23(0.0, 0.5)
2004	June		0.1 (0.0, 0.2)	0.1 (0.0, 0.2)		
2004	July	0.1 (0.0,0.6)				
2005	June	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0.6 (0.0, 1.5)		0.2 (0.0, 0.5)
2006	June	0.0 (0.0, 0.1)	0.1 (0.0 ,0.2)	0.0 (0.0, 0.0)		0.9 (0.2, 1.6)
2007	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)		0.1 (0.0, 0.1)
2008	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.01 (0,0.05)	0.0 (0.0, 0.0)
2009	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	
2011	June	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)		
2012	May	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)		

APPENDIX VII: MEAN TOTAL DENSITY OF RSU, GSU AND PSU FOR THE ENTIRE RESEARCH AREA

The pooled, mean density (urchins per m^2) of Red Sea Urchins (RSU), Green Sea Urchins (GSU) and Purple Sea Urchins (PSU) with upper and lower 95% confidence intervals (LCI, UCI; bootstrap) within the Tofino research area in PFMA 24-8, see Table 1 for harvest treatment site descriptions.

Year	Month	RSU	GSU	PSU
1994	July	17.2 (14.7, 21.0)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
1995	May	16.4 (12.3, 22.6)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
1995	August	15.2 (12.8, 18.2)	0.4 (0.3, 0.5)	0.7 (0.3, 1.3)
1995	August	0.0		
1996	April	0.0		
1996	June	12.8 (11.0, 15.2)	0.3 (0.2, 0.4)	0.7 (0.4, 1.2)
1996	June	0.0		
1997	June	0.0		
1997	June	0.0		
1997	July	0.0		
1998	June	0.0		
1998	June	0.0	0.0	0.0
1999	April	0.0		
2001	June	11.94 (10.0, 14.3)	0.2 (0.1, 0.3)	0.1 (0.0, 0.1)
2003	June	11.1 (9.2, 13.2)	0.2 (0.2, 0.3)	0.2 (0.1, 0.2)
2004	June	8.8 (6.9, 11.4)	0.1 (0.1, 0.2)	0.1 (0.1, 0.3)
2004	July	0.0		
2005	June	10.9 (9.0, 13.4)	0.1 (0.1, 0.2)	0.3 (0.1, 0.4)
2006	June	6.3 (4.6, 8.7)	0.00 (0.0, 0.1)	0.2 (0.1, 0.3)
2007	June	3.3 (2.0, 5.2)	0.1 (0.0, 0.10)	0.1 (0.0, 0.1)
2008	June	1.0 (0.5, 2.2)	0.0 (0.0, 0.1)	0.1 (0.0, 0.1)
2009	June	0.0 (0.0, 0.0)	0.0 (0.00, 0.0)	0 (0.0, 0.0)
2010	June	0.0 (0.0, 0.1)	0.0 (0.0, 0.0)	0 (0.0, 0.0)
2011	June	0.0 (0.0, 0.1)	0.0 (0.0, 0.1)	0 (0.0, 0.0)
2012	May	0.03 (0.0, 0.1)	0.0 (0.0, 0.0)	0 (0.00, 0.00)