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Urchin Gonad Response to Kelp Forest Restoration on the Palos Verdes Peninsula, California

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Abstract.—Along the Palos Verdes Peninsula in southern California, high densities of *Strongylocentrotus purpuratus* (purple sea urchin) have consumed almost all macroalgae on large expanses (61 ha) of rocky reef habitat, creating "urchin barrens." *Mesocentrotus franciscanus* (red sea urchin) harvesting comprises an important fishery in the region, as their gonads are sold as a high-value sushi product called "uni." However, with a lack of macroalgal food resources, urchins in barrens are smaller and exist in a starved state, meaning little, if any, gonad product is available to the fishery. To restore local kelp forests and increase gonad biomass available to the *M. franciscanus* fishery, beginning in October 2013, *S. purpuratus* were culled in barrens to a target density of 2 per m^2 across 5.2 ha of rocky reef on the Palos Verdes Peninsula. *Mesocentrotus franciscanus* were collected from urchin barren, restoration, and kelp reference sites from April to November 2014 to compare differences in gonad production among the three site types. Culling *S. purpuratus* resulted in the recovery of normal seasonal *M. franciscanus* gonad production throughout the 8-month study. *Mesocentrotus franciscanus* gonad weights at a given test diameter length in restoration sites were equivalent to, and sometimes exceeded, the gonad production of those from the kelp reference sites. The urchin test length distributions of collected *M. franciscanus* were consistently smaller at urchin barren sites than at kelp reference sites, while those in restoration sites generally fell in between.

Giant kelp (*Macrocystis pyrifera*) forests are among the most productive and diverse ecosystems in the world (Dayton 1985; Graham 2004). Kelps are autogenic engineers, providing physical structure for a high diversity of flora and fauna. In addition, they are a food source for a wide variety of taxa, contributing to the food web through direct grazing and as dissolved organic materials (Graham 2004; Duarte et al. 2022). Yet, the combined effects of overfishing, pollution, and increasing frequency of warm water events have led to the destructive grazing of kelp by sea urchins and the formation of "urchin barrens" that can last decades (Steneck et al. 2002; Cavanaugh et al. 2019; Rogers-Bennett and Catton 2019; Kawamata and Taino 2021) (Fig. 1). These barren reefs are largely devoid of macroalgae and covered instead by high proportions of bare rock and encrusting coralline algae

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Fig. 1. (A) High densities of *S. purpuratus* in an urchin barren state, (B) kelp forest state in southern California, (C) partially dissected *Mesocentrotus franciscanus* from a kelp forest site, and (D) extracted *M. franciscanus* urchin gonad (i.e., uni).

(Dayton 1985; Steneck et al. 2002; Cavanaugh et al. 2011; Rogers-Bennett and Catton 2019; Gizzi et al. 2021; Williams et al. 2021).

Feedback mechanisms on temperate rocky reefs increase the resilience of both healthy kelp forest and urchin barren states (Levin and Lubchenco 2008; Baskett and Salomon 2010; Filbee-Dexter and Scheibling 2014). The kelp forest state is maintained by positive feedback mechanisms that prevent high densities of urchins from forming and destructively grazing (Baskett and Salomon 2010; Filbee-Dexter and Scheibling 2014). In the presence of abundant predators, urchins exhibit cryptic behavior and lower densities are maintained (Nichols et al. 2015). However, overfishing of urchin predators can reduce top-down control of urchin abundance, leading to a phase shift where sea urchins have a greater impact on the ecosystem dynamics (Jackson et al. 2001; Steneck et al. 2002; Filbee-Dexter and Scheibling 2014; Melis et al. 2019). When urchin densities subsequently increase above a critical threshold, the transition from a kelp forest to an urchin barren occurs rapidly, resulting in destructive grazing and prevention of substratum growth (Baskett and Salomon 2010; Filbee-Dexter and Scheibling 2014; Karatayev and Baskett 2020; Kawamata and Taino 2021). Evidence from various studies show a phase shift threshold from an algal dominated system to barren formation occurs when urchin biomass exceeds 700 g/m^2, though exact numbers are highly dependent on region specific dynamics (Ling et al. 2015). An urchin barren state is then maintained by positive feedback mechanisms that promote sea urchin recruitment, settlement, and overgrazing, all of which inhibit kelp settlement (Filbee-Dexter and Scheibling 2014; Sangil and Hernández 2022).

Destructive sea urchin grazing is the leading cause of kelp deforestation in the world (Steneck et al. 2002) and has multi-trophic level impacts on species' use of kelp forest habitat resources (Graham 2004; Rogers-Bennett and Catton 2019). Urchin barrens occur globally in most regions where kelp forests exist (Steneck et al. 2002; Gagnon et al. 2004; Ling et al. 2015). In southern California, urchin barrens have been present on the Palos Verdes Peninsula since the 1950s (North 1963; Foster and Schiel 2010). Surveys conducted in the late 1960s had described a near total absence of adult giant kelp on the Palos Verdes Peninsula (Wilson et al. 1977; Foster and Schiel 2010) likely due to the combined influence of increased coastal development, sedimentation, urban runoff, pollution, and direct kelp removal from storms (North 1963; Dayton 1985; Steneck et al. 2002; Ford and Meux 2010; Foster and Schiel 2010). Following this large-scale kelp reduction, a transition to an urchin dominated system further prevented kelp recruitment (North 1963; Foster and Schiel 2010; Filbee-Dexter and Scheibling 2014). As of 2012, there were 61 ha of rocky reef persisting in an urchin barren state on the Palos Verdes Peninsula (Claisse et al. 2013).

Kelp forest loss and the resulting urchin barrens have systemic ecological implications, as well as significant economic impacts on sea urchin fisheries (Claisse et al. 2013; Rogers-Bennett and Catton 2019). Historically, the *Mesocentrotus franciscanus* (red sea urchin) fishery was consistently one of the largest fisheries in California by annual tonnage harvested (NMFS 2018). *Mesocentrotus franciscanus* are harvested for their gonads, as a high value sushi product called "uni" (Rogers-Bennett 2007; Teck et al. 2018). In urchin barrens, particularly when coexisting with high densities of *S. purpuratus*, *M. franciscanus* gonads are substantially underdeveloped (Harrold and Reed 1985; Kato and Schroeter 1985; Rogers-Bennett et al. 1995; Spindel et al. 2021), resulting in a decreased amount of gonad product available to the fishery (Claisse et al. 2013). For example, in northern California, the *M. franciscanus* fishery remained stable from 2000-2014, but recent extensive losses of kelp, combined with increases in *S. purpuratus* dominated urchin barrens, resulted in urchin gonad biomass declines that eventually led to the collapse of the *M. franciscanus* commercial fishery (Rogers-Bennett and Catton 2019; Angwin et al. 2022).

In an urchin barren state, urchin gonad biomass is reduced due to the lack of macroalgal food available (Bernard 1977; Rogers-Bennett 2007). Other urchin health metrics, including growth rates, test diameter size, density, and biomass, can also be negatively affected by reductions in food resources (Ebert 1967; Claisse et al. 2013; Teck et al. 2017). In addition to using their gonads for reproduction, urchins also use gonads to store nutrients as fats and carbohydrates within the tissue (Doezema and Phillips 1970), having the ability to resorb their gut and gonad complex for energy (Giese et al. 1966; Pearse et al. 1970; Kato and Schroeter 1985; Rogers-Bennett et al. 1995). With the almost complete absence of macroalgal food availability in barrens, urchins exist in a starved state (Kato and Schroeter 1985) through metabolic depression, which induces morphological changes (Smith and Garcia 2021; Spindel et al. 2021), permitting the urchins to survive by feeding on plankton and diatoms (Pearse et al. 1970; Kato and Schroeter 1985; Hernández et al. 2011). However, most populations of urchins in barrens have poor health, reduced gonads, and smaller test diameter sizes (Pearse et al. 1970; Ling and Johnson 2009; Claisse et al. 2013; Williams et al. 2021).

In kelp forests, urchin gonad development and spawning follow a seasonal pattern (Ebert et al. 1994; Hernández et al. 2011; Teck et al. 2018), although there is high variation even within the same species over relatively small spatial scales (Kato and Schroeter 1985). In California, increased seasonal gonad production typically occurs in late fall or early winter seasons as a direct result of higher drift kelp availability due to natural kelp forest growth and kelp recovery following winter and spring storms (Cavanaugh et al. 2011; Teck et al. 2018). Spawning typically occurs directly following a period of peak kelp abundance and gonad production when sea urchins are investing energy into developing gonads for reproduction (Ebert et al. 1994; Teck et al. 2018). While an increase in gonad production is an indicator or cue to spawn, there is evidence that gonad development also occurs independently for energy storage, suggesting there are other seasonal cues at play that induce spawning (Hernández et al. 2011). It is therefore necessary to consider both direct food availability and other seasonal influences on gonad production when considering management efforts to maintain both the commercial urchin fishery and the kelp forest state (Teck et al. 2017; 2018), as well as to inform restoration efforts (Claisse et al. 2013).

A variety of restoration techniques have been implemented to try to restore barrens to kelp forests, and most have involved removing the main driver (i.e., sea urchins) of kelp deforestation (Flukes et al. 2012; Eger et al. 2020; 2022; Layton et al. 2020). On the Palos Verdes Peninsula, kelp forest restoration efforts aimed at reducing barren-forming urchin densities have been ongoing since the early 2000s (Ford and Meux 2010; Williams et al. 2021). In this area, the vast majority of urchins in these barrens are *S. purpuratus* (Claisse et al. 2013). Beginning in 2013, commercial urchin harvesters were employed as part of a large-scale kelp restoration effort along the Palos Verdes Peninsula to reduce *S. purpuratus* density to 2 per m^2 through urchin culling. The commercially important *M. franciscanus* were not culled in an effort to increase production for the local commercial urchin fishery (Claisse et al. 2013).

The present study examines how *M. franciscanus* gonad biomass production responded to the effects of culling *S. purpuratus* in barrens to restore kelp forests along the Palos Verdes Peninsula in 2014, prior to a natural urchin mass mortality event at the end of that year (Williams et al. 2021). We compare changes in *M. franciscanus* gonad biomass over time collected from three site types: kelp forest reference sites, urchin barren sites, and restoration sites following urchin density reduction from active culling. Sea urchin nutrition and gonad production is positively influenced by increases in kelp availability (Pearse et al. 1970; Claisse et al. 2013; Teck et al. 2018). Further, kelp forests have the ability to rebound rapidly following disturbances (Cavanaugh et al. 2011; Williams et al. 2021), suggesting gonad production should also increase rapidly following restoration activities.

Materials and Methods

All project activities occurred on the Palos Verdes Peninsula, located in Los Angeles County, California (Fig. 2). Habitat areas within sites were initially classified as urchin barrens or kelp forests by a previous study (Claisse et al. 2013). The three site types in this study were designated as urchin barren, kelp reference, and restoration. Urchin barrens were identified as areas of rocky reef almost entirely devoid of macroalgae, characterized by high percent cover of bare substrate, encrusting coralline algae, and high densities of *S. purpuratus* (Claisse et al. 2013; Gizzi et al. 2021). Restoration activities occurred at Honeymoon Cove from 29 October 2013, to 7 April 2014, and at Underwater Arch from 10 September 2013, to 5 August 2014 (Table 1). Divers used rock hammers to reduce *S. purpuratus* densities in barrens to a target density of $< 2/m^2$. Divers left *M. franciscanus* in place as they were not overabundant and are economically valuable to the urchin fishery (Claisse et al. 2013). Given the large spatial scale of this restoration effort in the region (22.8 ha total target area), and the nature of the labor force (e.g., three commercial urchin

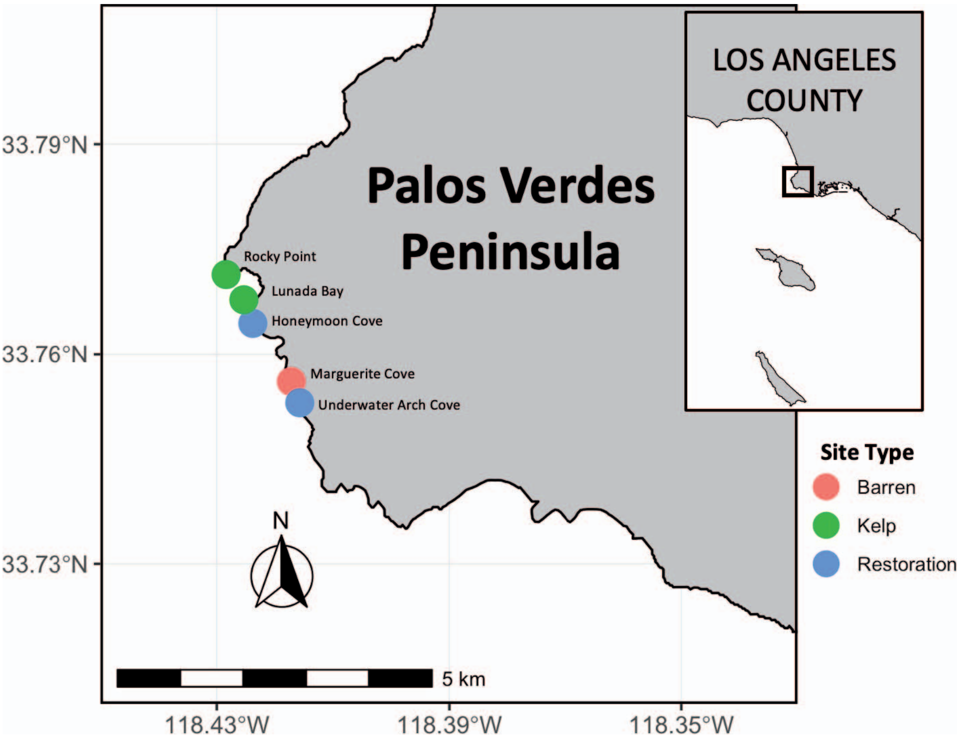

Fig. 2. Urchin survey and collection sites on the Palos Verdes Peninsula, California. Site types are designated by color. Some areas within the restoration sites were used as urchin barren collection sites prior to restoration activities beginning in those areas (Sub-site IDs in Table 1).

diver teams, The Bay Foundation non-profit employees, volunteers), restoration of sites was initially intended to occur sequentially. However, practical considerations resulted in restoration efforts occurring concurrently at some reefs, and divers would often return to sites after a period of weeks to months to monitor and cull additional *S. purpuratus* urchins found in small high-density patches until the entire site was considered 'restored' with a target density of $< 2/\text{m}^2$ (restoration end dates listed in Table 1). It is also important to note that *S. purpuratus* densities within most of the restoration areas were typically reduced to the target density months prior to the restoration end date.

In 2013, prior to the start of restoration activities at a given area (Sub-site ID, Table 1), pre-restoration monitoring was conducted at urchin barren sites to be restored per California Department of Fish and Wildlife (CDFW) standards in accordance with the terms of the Scientific Collecting Permit issued to the Bay Foundation (TBF; S-183390001-19133-001). Urchin barren sites were divided into 30 m x 30 m blocks, each comprised of 15 parallel and adjacent (30 m x 2 m) transects. TBF biologists counted *S. purpuratus* along five of the fifteen 30 m x 2 m transects per block to estimate pre-restoration density of *S. purpuratus* of the block (range $57.2 – 21.2/\text{m}^2$; Table 1).

Post-restoration monitoring was conducted once the team doing the restoration reported to TBF that *S. purpuratus* densities within the block had been reduced to the target density of $< 2/\text{m}^2$. All 15 transects within each 30 m x 30 m block were then surveyed by TBF staff to ensure that no pockets of high-density *S. purpuratus* remained at the site, and if this was

Table 1. *Mesocentrotus franciscanus* collection and restoration activities (i.e., culling *S. purpuratus)*. Sub-site ID and associated latitude and longitude give the specific areas for each collection within the overall site location (Site Name): Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), Rocky Point (RP). Restoration Start is the first day restoration actions began, and Restoration End is the last day restoration actions occurred in a specific Sub-site ID. Pre and Post refers to the *S. purpuratus* density before and after culling in a specific Sub-site ID. n is the number of *M. franciscanus* collected from each location on each collection date.

Collection Date	Site Type	Site Name	Latitude	Longitude	Sub-site ID	Restoration Start	Pre (No./m^2)	Restoration End	Post (No./m^2)	n
29 Apr 2014	Barren	HMC	33.7648	-118.4232	HMC_B1_B	-	-	-	-	47
	Kelp	LB	33.7690	-118.4255	LB_K1_K	-	-	-	-	30
	Rest.	HMC	33.7637	-118.4234	HMC_T1_R	29 Oct 2013	54.4	26 Feb 2014	1.6	49
	Rest.	UAC	33.7521	-118.4157	UAC_J1_R	25 Oct 2013	48.9	11 Apr 2014	2.3	48
28 May 2014	Barren	UAC	33.7539	-118.4156	UAC_B2_B	-	-	-	-	26
	Kelp	LB	33.7691	-118.4246	LB_K2_K	-	-	-	-	37
	Rest.	HMC	33.7637	-118.4234	HMC_T1_R	29 Oct 2013	54.4	26 Feb 2014	1.6	52
	Rest.	HMC	33.7648	-118.4247	HMC_R1_R	01 Nov 2013	42.6	21 Mar 2014	1.6	51
	Rest.	UAC	33.7521	-118.4157	UAC_J1_R	25 Oct 2013	48.9	11 Apr 2014	2.3	50
	Rest.	UAC	33.7541	-118.4163	UAC_3_R	10 Sep 2013	57.2	11 Dec 2013	3.1	62
26 June 2014	Barren	UAC	33.7536	-118.4150	UAC_B3_B	-	-	-	-	36
	Kelp	LB	33.7664	-118.4257	LB_K3_K	-	-	-	-	33
	Rest.	HMC	33.7637	-118.4234	HMC_T1_R	29 Oct 2013	54.4	26 Feb 2014	1.6	38
	Rest.	UAC	33.7521	-118.4157	UAC_J1_R	25 Oct 2013	48.9	11 Apr 2014	2.3	39
22 July 2014	Barren	UAC	33.7525	-118.4148	UAC_B4_B	-	-	-	-	29
	Kelp	LB	33.7680	-118.4256	LB_K4_K	-	-	-	-	50
	Rest.	HMC	33.7650	-118.4250	HMC_R1_R	01 Nov 2013	42.6	21 Mar 2014	1.6	43
	Rest.	UAC	33.7521	-118.4157	UAC_J1_R	25 Oct 2013	48.9	11 Apr 2014	2.3	53
30 Oct 2014	Barren	MC	33.7556	-118.4174	MC_B5_B	-	-	-	-	58
	Kelp	RP	33.7714	-118.4284	RP_K5_K	-	-	-	-	42
	Rest.	HMC	33.7643	-118.4234	HMC_T2_R	11 Mar 2014	21.2	07 Apr 2014	1.9	47
	Rest.	UAC	33.7539	-118.4158	UAC_W1_R	11 Dec 2013	34.6	05 Aug 2014	1.5	60
18 Nov 2014	Barren	MC	33.7560	-118.4166	MC_B6_B	-	-	-	-	55
	Kelp	LB	33.7662	-118.4254	LB_K6_K	-	-	-	-	54
	Rest.	HMC	33.7640	-118.4234	HMC_T1_R	29 Oct 2013	54.4	26 Feb 2014	1.6	55
	Rest.	UAC	33.7522	-118.4154	UAC_J1_R	25 Oct 2013	48.9	11 Apr 2014	2.3	54

the case, then that was recorded as the restoration end date. Post-restoration *S. purpuratus* densities ranged from 3.1 to 1.5/m^2 across blocks (Table 1).

To examine differences in gonad production between site types over time, TBF staff and volunteers collected a total of 1,198 *M. franciscanus* $>$ 40 mm test diameter from urchin barrens, restoration sites, and kelp reference sites on six sampling dates (29 April, 28 May, 26 June, 22 July, 30 October, and 18 November) throughout 2014. On each collection date, urchins were collected from one urchin barren, one kelp reference, and two restoration sites (Fig. 2, Table 1). Divers attempted to collect at least 30 *M. franciscanus* along a 30 m x 2 m transect using pry bars. They were placed into game bags, brought to the boat, and placed in dry coolers. They were then transported live to Loyola Marymount University's Seaver Science Center for dissection. Urchin tests were measured to the nearest mm using calipers and urchin weight was measured to the nearest hundredth of a gram. Gonads (Fig. 1) were then removed and weighed to nearest hundredth of gram. All analyses and figures for this study were produced in R (R Core Development Team 2021).

The modeling approach used in this analysis followed Claisse et al. (2013). An allometry model was used to quantify the relationship between mean gonad weight and test diameter length: $G = \alpha(L - 40)^{\beta}$ (Eq. 1) (Ebert et al. 2011), where G is gonad weight (g), L is test diameter length (mm), 40 mm is the test diameter length at which *M. franciscanus* is able to first produce a gonad and reproduce (Tegner and Dayton 1981; Kato and Schroeter 1985; Tegner 1989), and both α and β are equation constants. Mean gonad weight at test diameter length was fitted to the data using the 'mle2' package in R by minimizing the negative log-likelihood and assuming that G follows a lognormal distribution with mean

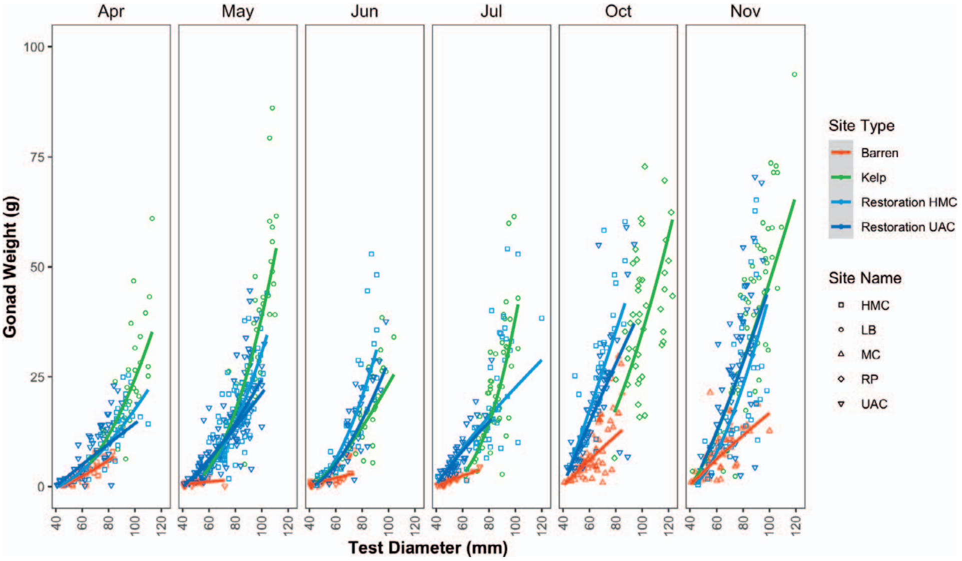

Fig. 3. The relationship between mean gonad weight (g) and test diameter size (mm) of *M. franciscanus* collected from April-November 2014 by the site type (color) and site name (shape): Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), and Rocky Point (RP). Parameter estimates for each curve are reported in Appendix Table A1 and A2. One point in the November panel from Restoration HMC (gonad weight 121.52 g at 91 mm test diameter) is not shown so to better visualize the y-axis range of most data.

determined by Eq. 1 and the standard deviation of the logarithm (sdlog) (Bolker 2008; Claisse et al. 2013).

In order to account for differences in *M. franciscanus* size structure among urchin barrens, kelp reference, and restoration sites, a bootstrapping approach was used to estimate the 95% confidence intervals to compare differences in mean gonad weight at test diameter length from each site following Haddon (2011) and Claisse et al. (2013). The 95% confidence intervals were then used to assess differences between site types on each collection date, with non-overlapping 95% confidence intervals considered "significant". In addition to the full model, we also specifically compared 95% CIs for mean gonad weight at test diameter lengths 84 mm and 68 mm. The size of 84 mm was chosen as it is the minimum size limit of *M. franciscanus* in the California urchin fishery, while 68 mm was chosen as being more representative of the size structure within urchin barrens, since most urchins in these sites were $<$ 84 mm.

Results

Mesocentrotus franciscanus urchin gonad weight at a given test diameter in restoration sites was higher than in urchin barrens and similar to kelp reference sites throughout most of the year following the completion of restoration activities (Fig. 3). By May 2014, gonad production in the sampled restoration sites had "recovered," i.e., mean gonad weight at a given test size was similar to that from kelp sites (Fig. 3), and significantly higher than mean gonad weights at barren sites (Fig. 4, Appendix Table A1, Appendix Fig. A2). A seasonal temporal pattern in this relationship was also present for each site type with gonad weight

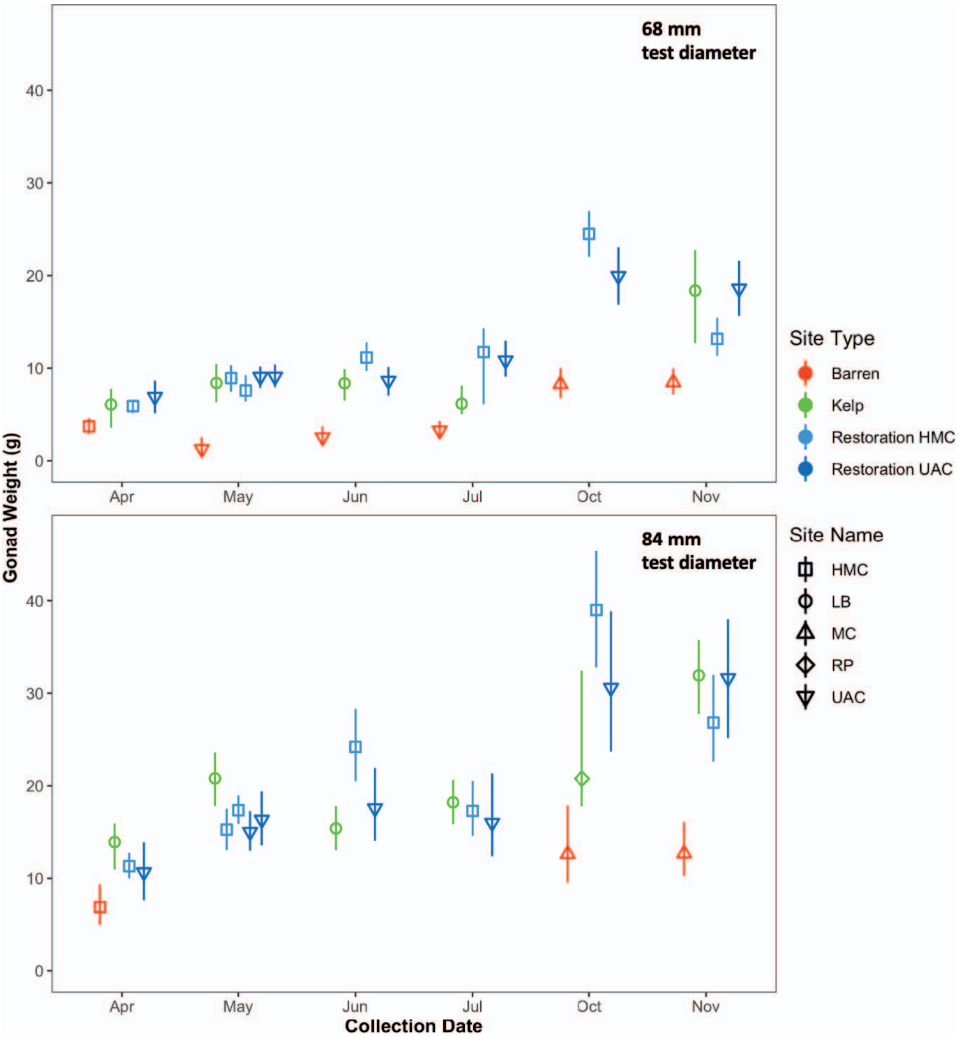

Fig. 4. *Mesocentrotus franciscanus* mean gonad weight (g) with 95% bootstrap confidence interval error bars at 68 mm (top) and 84 mm (bottom) test diameter collected from April-November 2014 by the site type (color) and site name (shape): Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), and Rocky Point (RP). The size of 84 mm was chosen as it is the minimum size limit of *M. franciscanus* in the California urchin fishery, while 68 mm was chosen as being more representative of the size structure within urchin barrens, since most urchins in these sites were < 84 mm. *Mesocentrotus franciscanus* collected from Rocky Point (kelp reference site) in October 2014 were not included in top panel because all urchin test diameters exceeded 68 mm. *Mesocentrotus franciscanus* collected from Underwater Arch Cove barren sites May-July were not included in the lower panel because all urchin test diameters were less than 84 mm. Mean gonad weights at test diameter length with 95% CIs are reported in Appendix Table A1.

at a given length generally increasing across the April to November sampling period (Fig. 3, Appendix Fig. A1). In April 2014, *M. franciscanus* gonads from restoration sites had an average of 72.5% and 60% larger weight at test diameters 68 mm and 84 mm than those from urchin barrens, respectively. During the peak season (October-November) the average

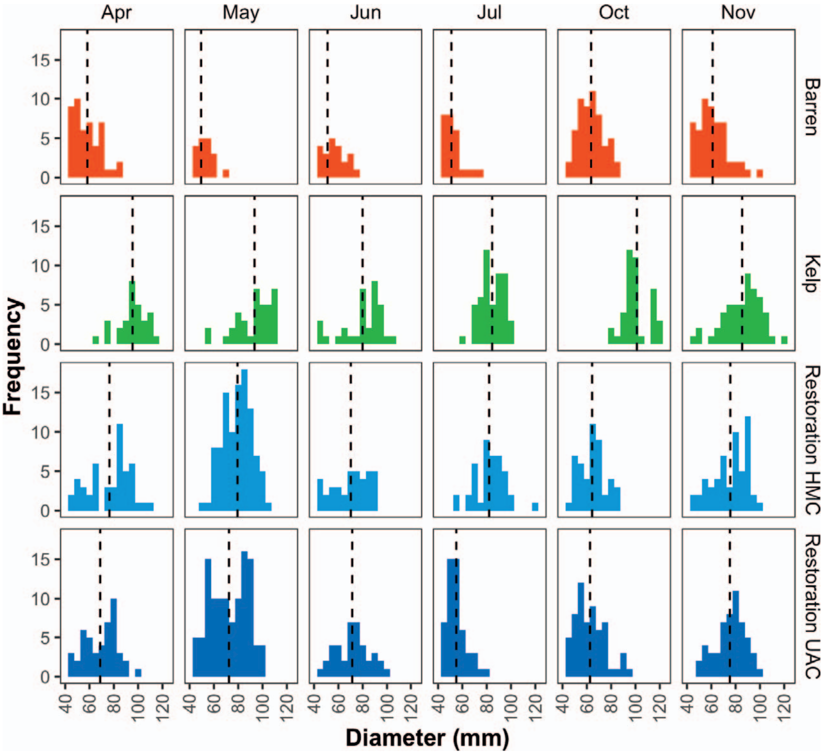

Fig. 5. *Mesocentrotus franciscanus* test diameter (mm) size distribution (5 mm size classes) for urchins collected across April to November 2014 from urchin barrens (red), kelp reference sites (green), and the two restoration sites (blue): Honeymoon Cove (HMC) and Underwater Arch Cove (UAC). Mean lengths are indicated by a vertical dashed line. All *M. franciscanus* less than 40 mm test diameter were removed from analysis, which is the size at which they can first produce a gonad and reproduce (Tegner and Dayton 1981; Kato and Schroeter 1985; Tegner 1989).

gonad weight at 68 mm and 84 mm test diameter at restoration sites increased to 128% and 154% greater than those from urchin barrens, respectively (Fig. 4, Appendix Table A1).

Generally, *M. franciscanus* collected at urchin barren sites had smaller test diameters and those collected at kelp reference sites had larger test diameters, with those from restoration sites falling in between (Fig. 5, Appendix Table A3). In all six data collection months between April-November 2014, *M. franciscanus* collected at kelp reference sites had greater mean test diameter than those collected at urchin barrens and restoration sites. In five of the six data collection months, *M. franciscanus* collected at restoration sites had higher mean test diameters than those collected at urchin barrens.

Discussion and Conclusions

Reducing *S. purpuratus* density in urchin barrens on nearshore rocky reefs along the Palos Verdes Peninsula to the target density of $2/m^2$ through active culling resulted in the recovery of normal seasonal *M. franciscanus* gonad production throughout the 8 mos sampled following completion of restoration activities. Gonad weight at a given length from urchin in restoration sites matched, and sometimes exceeded, the gonad production of urchin in kelp reference sites. For *M. franciscanus* collected throughout 2014, test diameter, gonad weight relative to test diameter, and gonad weight at a given test diameter in restoration sites were higher than in urchin barrens and similar to those in kelp reference sites. Even though a seasonal effect of increased gonad production was apparent at all site types throughout the year, in restoration sites, *M. franciscanus* gonad weight of legal-size urchins (84 mm test diameter) were 154% higher than in urchin barrens during October and November when the largest gonads weights were observed. Claisse et al. (2013) estimated the potential effects of restoration on gonad biomass by reporting differences between urchin barrens and kelp reference sites indicating restoration could potentially increase gonad biomass available to the commercial urchin fishery. The present study expands on those findings by also assessing urchins in restoration sites relative to urchin barrens and kelp reference sites using the same methods. These results build upon a concurrent study on the Palos Verdes Peninsula, which concluded that declines in urchin density initiated a quick recovery of kelp dominated state in approximately 6 mos (Williams et al. 2021), a timeline consistent with the results of other urchin reduction kelp restoration studies (Sangil and Hernández 2022).

A seasonal pattern was evident in *M. franciscanus* as gonad weight relative to test diameter size increased from the earlier to later months in 2014 across all three site types. This pattern has been observed elsewhere in southern California, as sea urchin spawning normally occurs in the winter and early spring after an annual peak in gonad size is reached in the late fall, although there is some variability among geographic areas (Kato and Schroeter 1985; Ebert et al. 1994; Teck et al. 2018). These seasonal increases in gonad development coincide with natural patterns of kelp growth and recovery following winter and spring storms (Cavanaugh et al. 2011; Teck et al. 2018). Spawning then occurs right after peak gonad production when kelp becomes less abundant (Teck et al. 2018). Therefore, increases in gonad weight relative to test diameter size at all three site types in our study was likely due to natural growth of kelp in the summer and fall months. In restoration sites, gonad weight relative to test diameter increased in accordance with this seasonal pattern but at an even greater magnitude than kelp reference sites and urchin barren sites, indicative of the additional effect of restoration on gonad production. Interestingly, urchin barrens also exhibited a low level of seasonal increase on gonad production, even though these sites maintained an almost complete lack of macroalgae (Williams et al. 2021). This is expected considering natural increases in macroalgae abundance over this period (Cavanaugh et al. 2011; Teck et al. 2018) would result in increased drift algae availability across all site types, in turn, increasing gonad production even at barren sites (Rogers-Bennett et al. 1995; Britton-Simmons et al. 2012).

Claisse et al. (2013) determined that although *M. franciscanus* densities were far greater in urchin barrens than in kelp forests, the lack of gonad production in urchins from barrens resulted in gonad biomass in kelp reference sites greatly exceeding the overall biomass from urchin barrens. However, collections from their study were made in April-May 2011, prior to the peak season of gonad development (Claisse et al. 2013; Teck et al. 2018). When comparing mean gonad weight at 84 mm test diameter, the minimum size limit for the fishery, between urchin barrens and restored sites, we found the difference increased from 60% greater in April to 154% greater during the peak season (October-November). This suggests that the estimates made by Claisse et al. (2013) that restoration could potentially result in an approximately 900% increase in *M. franciscanus* gonad biomass available to the fishery were likely conservative, and the fishery benefits of restoration may be substantially higher.

The test size distributions of collected *M. franciscanus* were significantly smaller at urchin barren sites than at kelp reference sites, while those in restoration sites generally fell in between [$p < 0.001$; mean test diameter (95% CI); Kelp 90 mm (84 – 96), Barren 56 mm (50 – 62), Restoration HMC 75 mm (69 – 81), Restoration UAC 68 mm (62 – 74); Fig. 5]. These results are consistent with Claisse et al. (2013) who found urchins collected in kelp reference sites had mean test diameters that were approximately 50% larger than those in urchin barrens. Similarly, Williams et al. (2021) found that average test lengths of *S. purpuratus* were also lower urchin barrens but increased following recovery to kelp forest conditions.

Resource management strategies that maintain urchin predator abundance, such as marine protected areas, are beneficial to maintaining stable kelp forests (Kawamata and Taino 2021), however, additional adaptive management actions are likely necessary beyond establishing marine reserves if urchin barrens are extensive (Levin and Lubchenco 2008; Baskett and Salomon 2010; Bonaviri et al. 2011; Claisse et al. 2013; Gizzi et al. 2021; Miller et al. 2022). While marine reserves can increase urchin predator populations such as the California spiny lobster (*Panulirus interruptus*) and California Sheephead (*Bodianus pulcher*) (Teck et al. 2017), this recovery can take more than fifteen years after implementation of protection and fishing ceases (Malakhoff and Miller 2021). Further, Eurich et al. (2014) experimentally demonstrated that California spiny lobster would actively select *S. purpuratus* from kelp forests over those from barrens, likely due to their diminished nutritional capacity with a lack of gonad tissue. Accordingly, the recovery of gonad biomass production observed in our study after culling *S. purpuratus* should accelerate the return of these important trophic pathways, ultimately increasing the resilience of restored kelp forests. Quantifying gonad production in sea urchins is an important measure of ecological function in kelp forest ecosystems and should be used to inform adaptive management of restoration projects.

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Appendix Table A1. Model parameter estimates of *M. franciscanus* mean gonad weight at test diameter 84 mm and 68 mm with 95% bootstrap CIs in parentheses for urchins collected April-November 2014 from urchin barrens, kelp reference, and restoration sites (Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), Rocky Point (RP)). *M. franciscanus* collected from Underwater Arch Cove barren sites May-July were removed from this analysis because all urchin test diameters were less than 84 mm. *Mesocentrotus franciscanus* collected from the Rocky Point kelp reference site in October were removed from this analysis because all urchin test diameters exceeded 68 mm.

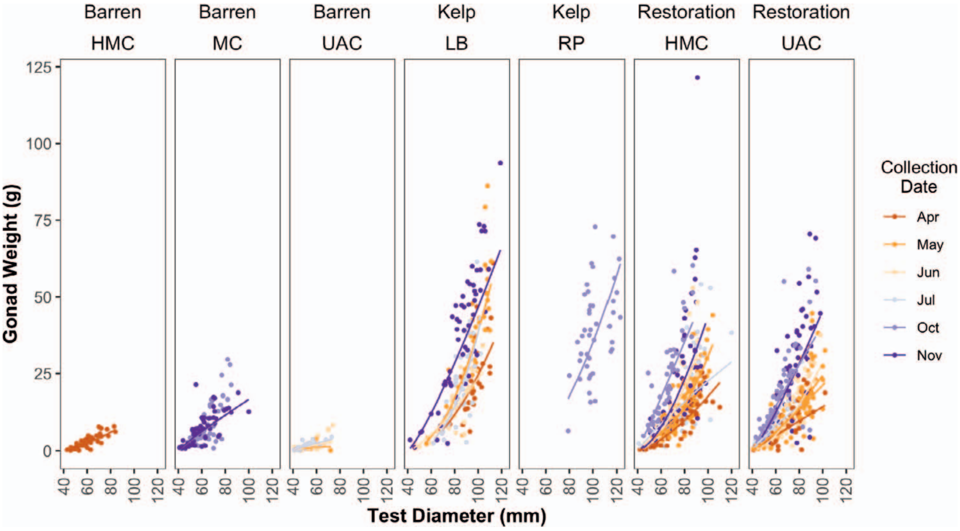
Collection Date	Site Type	Site Name	Site ID	84 mm Test Diameter		68 mm Test Diameter	
				Mean Weight (g)	95% CI	Mean Weight (g)	95% CI
29 Apr 2014	Barren	HMC	HMC_B1_B	6.9	(5–9.3)	3.7	(2.9–4.6)
	Kelp	LB	LB_K1_K	13.9	(11–15.9)	6.1	(3.6–7.8)
	Rest.	HMC	HMC_T1_R	11.3	(10–12.7)	5.9	(5.1–6.6)
	Rest.	UAC	UAC_J1_R	10.7	(7.6–13.9)	6.9	(5.2–8.6)
28 May 2014	Barren	UAC	UAC_B2_B	-	-	1.3	(0.6–2.6)
	Kelp	LB	LB_K2_K	20.8	(17.8–23.6)	8.4	(6.3–10.5)
	Rest.	HMC	HMC_T1_R	15.3	(13.1–17.5)	8.9	(7.5–10.3)
	Rest.	UAC	UAC_J1_R	15.0	(13–17.3)	9.1	(7.9–10.2)
	Rest.	UAC	UAC_2_R	16.3	(13.6–19.4)	9.1	(8–10.4)
	Rest.	HMC	HMC_R1_R	17.4	(15.9–19)	7.6	(6.4–9.2)
26 June 2014	Barren	UAC	UAC_B3_B	-	-	2.5	(1.7–3.7)
	Kelp	LB	LB_K3_K	15.4	(13.1–17.8)	8.4	(6.5–9.9)
	Rest.	HMC	HMC_T1_R	24.2	(20.5–28.3)	11.2	(9.7–12.8)
	Rest.	UAC	UAC_J1_R	17.6	(14.1–21.9)	8.7	(7.1–10.1)
22 July 2014	Barren	UAC	UAC_B4_B	-	-	3.3	(2.6–4.3)
	Kelp	LB	LB_K4_K	18.2	(15.8–20.6)	6.2	(5–8.1)
	Rest.	UAC	UAC_J1_R	16.0	(12.4–21.3)	10.8	(9.1–13)
	Rest.	HMC	HMC_R1_R	17.3	(14.6–20.5)	11.7	(6.1–14.3)
30 Oct 2014	Barren	MC	MC_B5_B	12.6	(9.6–17.8)	8.3	(6.8–10)
	Kelp	RP	RP_K5_K	20.8	(17.8–32.4)	-	-
	Rest.	HMC	HMC_T2_R	39.0	(32.8–45.4)	24.5	(22–26.9)
	Rest.	UAC	UAC_W1_R	30.6	(23.7–38.9)	20.0	(16.9–23)
18 Nov 2014	Barren	MC	MC_B6_B	12.7	(10.2–16.1)	8.5	(7.2–10)
	Kelp	LB	LB_K6_K	31.9	(27.8–35.8)	18.4	(12.7–22.7)
	Rest.	HMC	HMC_T1_R	26.8	(22.6–32)	13.2	(11.3–15.4)
	Rest.	UAC	UAC_J1_R	31.6	(25.1–38)	18.6	(15.6–21.6)

Appendix Table A2. Model parameter estimates of *M. franciscanus* mean gonad weight at test diameter for urchins collected April-November 2014 from urchin barrens, kelp reference, and restoration sites (Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), Rocky Point (RP)).

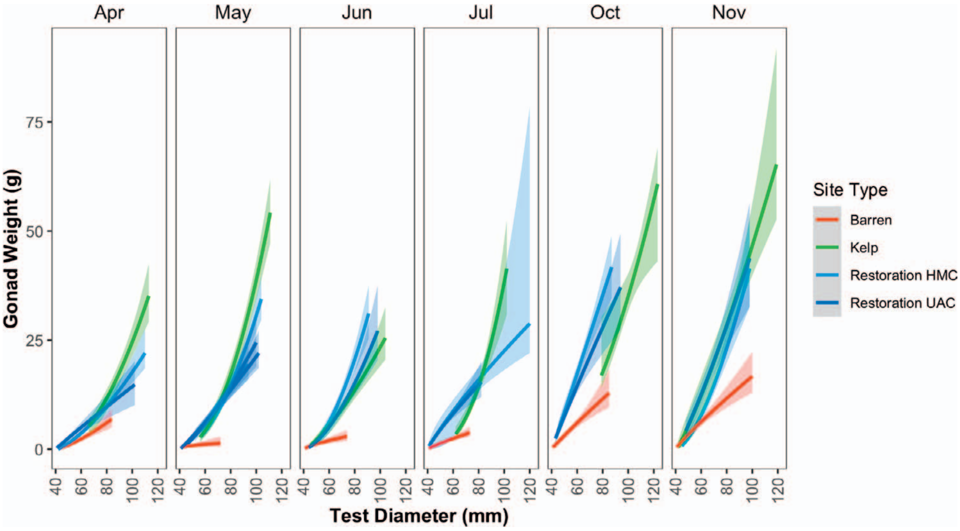
Collection Date	Site Type	Site Name	Site ID	α	β	sdlog
29 Apr 2014	Barren	HMC	HMC_B1_B	0.0400	1.36	0.67
	Kelp	LB	LB_K1_K	0.0136	1.83	0.37
	Rest.	HMC	HMC_T1_R	0.0495	1.44	0.41
	Rest.	UAC	UAC_J1_R	0.2823	0.96	0.86
28 May 2014	Barren	UAC	UAC_B2_B	0.3416	0.40	0.89
	Kelp	LB	LB_K2_K	0.0106	2.00	0.36
	Rest.	HMC	HMC_T1_R	0.1722	1.19	0.47
	Rest.	UAC	UAC_J1_R	0.2211	1.11	0.48
	Rest.	UAC	UAC_2_R	0.1202	1.30	0.53
	Rest.	HMC	HMC_R1_R	0.0170	1.83	0.34
26 June 2014	Barren	UAC	UAC_B3_B	0.2110	0.75	0.84
	Kelp	LB	LB_K3_K	0.0940	1.35	0.45
	Rest.	HMC	HMC_T1_R	0.0369	1.71	0.48
	Rest.	UAC	UAC_J1_R	0.0467	1.57	0.55
22 July 2014	Barren	UAC	UAC_B4_B	0.1876	0.86	0.60
	Kelp	LB	LB_K4_K	0.0021	2.40	0.47
	Rest.	UAC	UAC_J1_R	0.6185	0.86	0.36
	Rest.	HMC	HMC_R1_R	0.6817	0.85	0.60
30 Oct 2014	Barren	MC	MC_B5_B	0.3675	0.93	0.61
	Kelp	RP	RP_K5_K	0.0344	1.69	0.41
	Rest.	HMC	HMC_T2_R	0.7961	1.03	0.36
	Rest.	UAC	UAC_W1_R	0.8570	0.94	0.42
18 Nov 2014	Barren	MC	MC_B6_B	0.4363	0.89	0.56
	Kelp	LB	LB_K6_K	0.3130	1.22	0.53
	Rest.	HMC	HMC_T1_R	0.0692	1.58	0.54
	Rest.	UAC	UAC_J1_R	0.3722	1.17	0.60

Appendix Table A3. *Mesocentrotus franciscanus* collection metadata and descriptive summary statistics for each urchin collections April-November 2014 (Honeymoon Cove (HMC), Lunada Bay (LB), Underwater Arch Cove (UAC), Marguerite Cove (MC), Rocky Point (RP)).

Collection Date	Site Type	Site Name	Sub-site ID	n	Test Diameter (mm)					Gonad Weight (g)				
					Min	Med	Mean	Max	SD	Min	Med	Mean	Max	SD
29 Apr 2014	Barren	HMC	HMC_B1_B	47	43	56	58	84	11	0.00	1.84	2.58	7.92	2.23
	Kelp	LB	LB_K1_K	30	66	97	95	113	11	6.30	22.03	23.53	61.01	12.76
	Rest.	HMC	HMC_T1_R	49	42	83	76	110	17	0.41	10.48	10.20	25.36	7.27
	Rest.	UAC	UAC_J1_R	48	41	72	69	102	15	0.15	9.24	8.90	22.98	6.31
28 May 2014	Barren	UAC	UAC_B2_B	26	41	49	49	72	8	0.00	0.88	1.01	4.15	0.89
	Kelp	LB	LB_K2_K	37	56	96	93	111	15	2.29	35.70	34.78	86.16	19.94
	Rest.	HMC	HMC_T1_R	52	52	75	75	94	9	1.79	12.60	12.98	25.97	6.39
	Rest.	HMC	HMC_R1_R	51	57	87	84	104	12	1.88	17.72	18.82	44.02	10.19
	Rest.	UAC	UAC_J1_R	50	41	75	73	102	17	0.71	11.11	12.88	38.12	10.03
	Rest.	UAC	UAC_2_R	62	45	71	72	100	15	0.67	9.99	12.48	44.64	9.73
26 June 2014	Barren	UAC	UAC_B3_B	36	41	47	51	74	11	0.00	1.00	1.60	8.36	2.06
	Kelp	LB	LB_K3_K	33	45	83	80	104	16	0.71	15.48	15.65	38.47	10.42
	Rest.	HMC	HMC_T1_R	38	45	72	70	91	15	0.19	12.19	15.85	52.91	13.66
	Rest.	UAC	UAC_J1_R	39	44	72	71	98	13	0.64	9.61	12.71	37.60	9.55
22 July 2014	Barren	UAC	UAC_B4_B	29	41	50	51	73	8	0.13	1.54	1.61	4.47	1.15
	Kelp	LB	LB_K4_K	50	62	85	85	102	9	2.45	20.20	21.86	61.44	13.24
	Rest.	HMC	HMC_R1_R	43	41	83	82	120	14	1.36	15.37	19.91	54.10	13.59
	Rest.	UAC	UAC_J1_R	53	42	54	55	82	9	0.95	5.26	6.81	28.85	5.18
30 Oct 2014	Barren	MC	MC_B5_B	58	41	64	63	85	11	0.86	5.68	8.51	29.62	6.87
	Kelp	RP	RP_K5_K	42	79	98	101	123	11	6.48	38.34	39.14	72.82	14.88
	Rest.	HMC	HMC_T2_R	47	45	65	64	87	11	4.83	20.03	22.87	60.27	14.11
	Rest.	UAC	UAC_W1_R	60	43	61	63	94	12	3.48	12.96	17.85	59.04	13.14
18 Nov 2014	Barren	MC	MC_B6_B	55	41	60	61	100	13	0.80	6.70	7.37	21.37	5.13
	Kelp	LB	LB_K6_K	54	42	88	85	119	16	1.08	40.04	37.66	93.68	21.19
	Rest.	HMC	HMC_T1_R	55	45	79	76	98	14	0.44	18.76	23.67	121.52	20.73
	Rest.	UAC	UAC_J1_R	54	48	78	75	98	12	2.54	27.57	28.18	70.50	16.19



Appendix Fig. A1. The relationship between gonad weight (g) and test diameter size (mm) of *M. franciscanus* collected from April-November 2014 for urchin barrens, kelp reference sites, and restoration sites. Collection date is designated by color.



Appendix Fig. A2. The relationship between gonad weight (g) and test diameter size (mm) of *M. franciscanus* collected from April-November 2014, distributed by the site type (urchin barren: red; kelp reference: green; Honeymoon Cove restoration: light blue; Underwater Arch Cove restoration (dark blue). 95% bootstrapped confidence intervals are displayed for each curve corresponding to the site type. Parameter statistics for estimating curves are in Appendix Table 1.