

POPULATION DYNAMICS AND SPATIAL DISTRIBUTION OF TWO COMMERCIALY
IMPORTANT SPECIES OF SEA CUCUMBER, *PARASTICHOPUS CALIFORNICUS* AND
PARASTICHOPUS LEUKOTHELE, IN DEEP CENTRAL CALIFORNIA WATERS

By

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Abstract

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Sea cucumbers are fished around the world. Along the west coast of the U.S., *Parastichopus californicus* is the primary species targeted in both trawl and SCUBA dive fisheries; *Parastichopus leukothele* is also likely collected in trawls. As most fishery stock assessments target shallow populations of sea cucumbers, deeper populations often go unmonitored. The purpose of this study was to identify the spatial distribution and dynamics of the continental shelf and slope (25-365m) populations of *P. californicus* and *P. leukothele* in central California (Monterey Bay to Big Sur). From September-November 2007, 174 dives were conducted using the occupied submersible *Delta* from 25 to 365m. Using the video transects recorded during these dives, individual sea cucumbers of these species were identified and sized, and habitat was classified by substrate type. In total, 864 *P. californicus* and 478 *P. leukothele*, ranging in size from 10-45cm and 5-35cm respectively, were identified on transects. *P. californicus* was found from 25-248m (average=77m) depths and had an overall density of 57 cucumbers/hectare. *P. leukothele* was found from 99-317m (average=211m) depths with an

overall density of 34 cucumbers/hectare. Both species varied significantly in density by depth, habitat type, and site. *P. californicus* was found in the highest densities at Portuguese Ledge and in depths from 50-100m; *P. leukothele* was densest at Soquel Canyon and from 200-250m. Both species were most abundant on hard substrates. In general, *P. californicus* was most strongly associated with the continental shelf environment while *P. leukothele* was more associated with the slope. Results from this study provide a fishery-independent analysis of understudied continental shelf and slope sea cucumber populations that may be helpful in the management of these species.

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INTRODUCTION

Marine organisms worldwide are undergoing increased commercial exploitation and habitat destruction, and the combination of these factors may be driving some species to extinction (Southward et al., 2005). Although finfish are primarily considered in issues related to fisheries, marine invertebrates also play an important role in world fisheries, as well as in the ecosystem; in fact, over 40% of the world fishery trade is comprised of invertebrates (Conand and Byrne, 1993). Some invertebrates involved in fisheries, such as scallop and shrimp, have been well studied and their fisheries are well managed; others, however, such as giant clams and sea urchins, are often heavily overfished, poorly managed, and understudied (Southward et al., 2005). Another example of the latter is the fishery for sea cucumbers.

Sea Cucumbers

Sea cucumbers (Class Holothuroidea) have been fished in the Indo-Pacific region for over a thousand years. Although there are over 1400 species of sea cucumbers worldwide, the fishery targets about 30 of these that have thick body walls and a shallow depth distribution, which will fetch a higher market price (Bruckner et al., 2003; Conand and Byrne, 1993). Traditionally, the sea cucumber fishery has been largely artisanal, with collectors gathering them in shallow waters by hand or in deeper waters with a handmade forked weight (Li, 2004). In more recent years, fishing methods have expanded to use snorkel, SCUBA, and trawls. Because they are relatively easy to ‘catch,’ women and children in developing countries often collect them for supplementary income. After harvesting, the collectors sell their catch to a local dealer, who boils and dries the organisms before selling them at an increased rate to a trader. The trader further processes the sea cucumbers into a final dried product, called *beche-de-mer* or *trepang*,

which consists of the dried body wall and longitudinal muscles; the viscera are sometimes eaten raw (Li, 2004). Although many countries now participate in the fishery as exporters, the primary importer of *beche-de-mer* is China (Conand and Byrne, 1993).

Beche-de-mer has a wide variety of uses in the Chinese culture and is now imported raw, dried, boiled, pickled, frozen, salted, or in brine (Clarke, 2004). Historically, Chinese people have consumed the processed sea cucumber and used it in traditional medicines. Some of the proposed medical benefits of sea cucumbers include supporting kidney and stomach health, increasing sexual drive, curing some cancers, and preventing constipation (Li, 2004). More recent medical research of sea cucumbers has revealed that the high levels of acidic amylase and saponins could be the root of their medicinal properties (Renbo and Yuan, 2004). Additionally, mucoitin found in sea cucumbers might slow signs of aging, suppress tumor growth, and enhance blood coagulation (Xiyin et al., 2004).

Unfortunately, effects of the increasingly high demand for sea cucumber are being detected at the population level. Due to their late sexual maturity, slow growth rate, and the relative ease with which they are caught, sea cucumbers are exceptionally susceptible to overexploitation (Bruckner et al., 2003). The most probable mechanism driving local depletions is likely the sea cucumber's method of reproduction; similar to many marine invertebrates, sea cucumbers are primarily broadcast spawners. The success of this reproductive method is density dependent and is subject to the 'Allee effect' (Lundquist and Botsford, 2004); when the density of individuals of a population becomes low, reproduction rates decline dramatically. The threshold density, or the density below which reproductive success is unlikely, for broadcast-spawning invertebrates ranges among species. For the sea urchin *Diadema antillarum*, Levitan (1991) found a population density of 20,000 individuals/hectare resulted in only a 7.3%

fertilization success. Shepherd and Brown (1993) determined a minimum viable population for red abalone to be 2,000 individuals/hectare. And while such research for sea cucumbers is rare, one study found that the minimum threshold density for a commercial species of sea cucumber (*Stichopus fuscus*) in Ecuador was 1,000 individuals/hectare and estimated a 50% reproductive success rate at 12,000 individuals/hectare (Shepherd et al., 2004). Such density-dependent reproductive success makes it extremely difficult or even impossible for many populations that have been heavily overfished to recover (Lundquist and Botsford, 2004).

Most commercial species of sea cucumbers are deposit feeders, and their elimination is harmful to the ecosystems in which they live (Conand and Byrne, 1993). When feeding, sea cucumbers ingest substrate and detritus, selectively digest the organic matter, and excrete the left-over material in 'beads' (Pouget, 2004). This process overturns and aerates the sediment, which provides a favorable substrate for other benthic organisms (Bruckner et al., 2003).

Although the full extent of their role as nutrient and sediment recyclers in the environment is not completely known, the removal of sea cucumbers has been shown to lead to a hardening of the sea floor (Bruckner et al., 2003). Furthermore, Uthicke et al. (2004) noted that the depletion of sea cucumbers would decrease reef productivity, which might eventually affect larger-scale fisheries as well. Because of the detrimental effects that would result from the loss of sea cucumbers, the fishery status and local population levels should be closely monitored.

Global market trends

Although sea cucumber has typically been served as a delicacy in China, the rapidly increasing standard of living in the country has led to an increase in demand for the product without a decrease in market value, thus increasing the fishery's appeal (Clarke, 2004). In

China, the once exclusively high-end restaurant product is now also sold at small food stands on the street. Demand is also on the rise in major U.S. cities with growing Asian populations such as San Francisco and Los Angeles (Conand and Byrne, 1993). The resulting market expansion and fishery pressure strongly contribute to a common trend in the fishery: a broadening shift in exploited species, leading to serial depletion (Conand and Byrne, 1993). A fast-expanding fishery often reaches peak harvests before rapidly experiencing a significant drop in production, and after a slight recovery, production levels steadily decline (FAO, 2000; Conand and Byrne, 1993). Sea cucumber fishers initially target species that fetch the highest values at the market, generally members of the Holothuroidea or Stichopodidae families (Bruckner et al., 2003). As local populations become too scarce, fishers begin to harvest the lower-value species intensely. And as all species become rare, the fishers expand their search radius to include more areas and depths and begin to exploit new populations (Bruckner et al., 2003). Such 'serial depletion' led to the over-exploitation and near extinction of the white abalone, another broadcast spawning marine invertebrate, in California (Hobday et al., 2001). For sea cucumbers, this pattern of collection primarily occurs in tropical fisheries consisting of multiple species, but as tropical species are increasingly exploited, the demand for temperate species is expanding (Conand and Byrne, 1993).

North American west coast fishery

One of the primary commercial temperate species is *Parastichopus californicus*, fished along the western coast of the United States and Canada. Sea cucumbers have historically been collected for subsistence purposes by Native American tribes in this region, since before the early 1800s (Mathews et al., 1990). Commercial harvests along the west coast began in 1971 in

Washington (Mathews et al., 1990) and then expanded to California in 1978 (CDFG, 2001), British Columbia in 1980 (Mathews et al., 1990), and Alaska in 1983 (Woodby et al., 2005). Oregon began an exploratory fishery in 1993 but deemed harvesting *P. californicus* unsustainable (Bruckner, 2004). These west coast fisheries sell to regional markets including New York, San Francisco, Los Angeles, and Vancouver, B.C., as well as to larger world markets (Mathews et al., 1990).

The harvest of *P. californicus* along the west coast has increased significantly since the fishery's introduction. In Southeast Alaska, the total landings soared from 15,440kg in 1986 to 652,480kg in 2001, with an estimated value of \$2,517,289 (Bruckner, 2004). Washington's harvest reached 529,000kg in 1995, but increasingly restrictive permit sales, location closures and harvest quotas have since reduced the landings (Bruckner, 2004); for the 2008-2009 season, the Washington Department of Fish & Wildlife (WDFW) set a total allowable catch (TAC) of 189,750kg (WDFW, 2008). Similarly, the fishery in British Columbia peaked at 1,900,000kg in 1988 before more restrictive management measures were established (CADFO, 1999); the TAC since 2003 has remained about 544,000kg (CADFO, 2010).

While the sea cucumber fisheries in Alaska, Washington, and British Columbia are solely SCUBA dive fisheries, California supports both a dive and a trawl fishery (Rogers-Bennett and Ono, 2001). The trawl fishery is a limited-entry fishery, requiring a permit to participate, and targets *P. californicus*, although it has been suggested that a relatively newly described species, *Parastichopus leukothele*, is also being collected in trawls (CDFG, 2008; Lambert, 1997). The dive fishery also requires a permit to harvest, and targets both *P. californicus* and a congener species found in southern California, *Parastichopus parvimensis*; until recently, though, sea cucumber landings were not separated by species (CDFG, 2010). Through 1996, 75% of the

total sea cucumber landings were from the trawl fishery, in which 38 permit holders participated (Rogers-Bennett and Ono, 2001; CDFG, 2008). However, between 1997 and 1999, the primary collection method shifted, the number of trawl permit holders declined, and 80% of the landings came from divers, as former abalone and urchin fishermen switched to sea cucumbers (Rogers-Bennett and Ono, 2001). Sea cucumber harvest totals for California, averaging less than 40,000kg per year before 1988, reached nearly 430,000kg in 2002; by 2006, however, landings had declined to 216,000kg (Figure i; Rogers-Bennett and Ono, 2008).

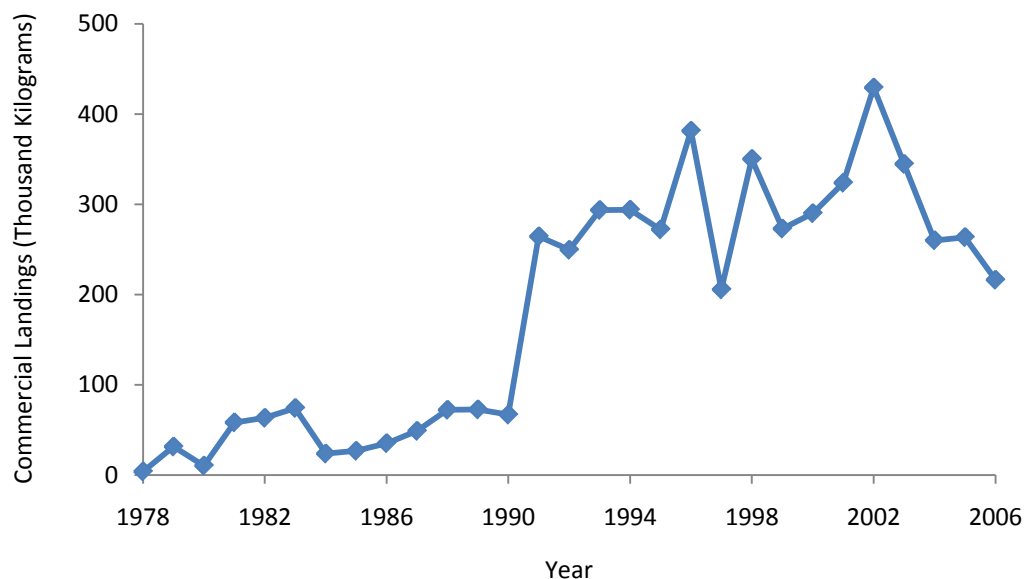


Figure i: Annual commercial landings of sea cucumbers (in thousand kilograms) for California from 1978-2006; data from Rogers-Bennett and Ono (2008).

Project and objectives

As with any fishery, knowing the density and distribution of sea cucumbers is important to developing suitable management measures. Fishery-independent stock assessment surveys are typically conducted with scuba, which limits the surveys to shallower (<25m) populations of sea cucumbers (Woodby et al., 2005). While various sources report different maximum depth

distributions for *P. californicus*, ranging from 90m to 249m, it is clear that these sea cucumbers live in depths far below scuba range (Gotshall, 1994; Lambert, 1997). Unfortunately, little is known about these deeper populations, of this species or of others, though researchers have speculated on their importance.

As spawning events have only been observed via scuba diving in shallow depths, *P. californicus* might migrate to shallow depths to spawn (Cameron and Fankboner, 1986; Lambert, 1997; Woodby *et al.*, 2000). However, it is unknown whether the deep populations are reproducing and self-replenishing. If they are, then perhaps larvae from deeper spawning populations of sea cucumbers might also be exported to shallow, heavily-fished areas. This theory is supported in part by some observations of juveniles settling in shallow areas and migrating to greater depths over time (Conand, 1993; Zhou and Shirley, 1996) and by one study that found no genetic differences between adjacent deep and shallow populations, indicating a significant amount of mixing (Uthicke and Purcell, 2004). Additional information on deeper populations of sea cucumbers is needed.

The purpose of my study is to use the submersible transects conducted in the 2007 Central California Marine Protected Area Baseline Survey to describe the spatial distribution and population dynamics of the continental shelf and slope populations of *Parastichopus californicus* and *Parastichopus leukothele*, both of which bear some commercial importance. *P. leukothele* is likely targeted in the sea cucumber trawl fishery (Lambert, 1997), but no studies have investigated the species' habitat and depth distributions. And as previously mentioned, *P. californicus* is widely fished along the west coast of North America, but both the dive fishery and the fishery stock assessments target the shallow shelf populations (<25m), leaving the deeper shelf and slope populations fished in trawls unmonitored. I intend to examine the *P. californicus*

and *P. leukothele* populations' density, habitat, depth, size-frequency, and spatial distributions in order to identify the factors or combination of factors that might most influence the populations' density and size distributions. While these results will provide a fishery-independent assessment of the populations of central CA that could be used for the development of management plans, they may also provide information that can help address the many questions associated with deep populations of commercially-important sea cucumbers.

METHODS

From 13 September to 5 November 2007, 174 dives were conducted using the occupied submersible *Delta* as part of the baseline surveys for the newly-established central California Marine Protected Areas (MPAs) (Fig. 1; Starr et al., 2008). The baseline surveys were focused on five MPA sites: Soquel Canyon, Portuguese Ledge, Point Lobos, Point Sur, and Big Creek. Both Soquel Canyon and Portuguese Ledge are within Monterey Bay. Soquel Canyon, located in the north-central part of the Bay, is a 'tributary' submarine canyon to the Monterey Submarine Canyon (Fig. 1). Vertical rock and steep mud walls dominate the habitat of Soquel Canyon (Starr et al., 2008). Portuguese Ledge, a historically popular recreational fishing site in the south-central portion of the Bay, consists primarily of rock outcrops surrounded by mud and loose rubble substrates (Graiff et al., unpublished; Starr et al., 2008). South of the Monterey Peninsula and adjacent to Carmel Bay, Point Lobos encompasses a variety of habitats, including high-relief rock outcrops, cobble fields, mud flats and some sand patches (Starr et al., 2008). Further south, Point Sur (35km south of Monterey) and Big Creek (70km south of Monterey) are located on an exposed stretch of coastline and experience strong upwelling (Graiff et al.,

unpublished; Starr et al., 2008). Point Sur is dominated by rocky reefs interspersed with sand patches while Big Creek consists of rock walls, outcrops, and mud flats (Starr et al., 2008).

On each submersible dive of the survey, two to four visual strip transects were conducted at random locations within 10x10 minute microblocks both inside and outside of these five marine protected areas. Each transect was 2 meters wide and 10 minutes long while the sub was traveling at approximately 1 knot; a total of 344 transects were completed in depths from 24-365m. Each transect was recorded on video by an external Sony H-B video camera mounted on the starboard side of the submersible. All data for this analysis were collected from the video footage of these transects.

The video footage was first analyzed to characterize the habitat environments. This procedure (as described in Tissot et al., 2006), assigns a two-letter code to a swath, or 'patch,' of similar substrate lasting more than 10 seconds on the video. The letters correspond to the type of substrate found in the patch, including: bacterial mat (Q), mud (M), sand (S), gravel (G), pebble (P), cobble (C), boulder (B), flat bedrock (F), rock ridge (R), and pinnacles (T). The first letter of the two-letter code represents the substrate that accounts for $\geq 50\%$ of the patch and the second for $>20\%$ and $<50\%$. For example, 'RS' would code for a patch consisting of 50-80% rock ridge, with 20-50% consisting of sand.

Using this classification system, 23 total habitat types were identified. These types were simplified for analysis and compatibility with other studies into three main substrate categories: soft, mixed, and hard. The simplified naming was based on the previously assigned two-letter code. Mud, sand, and bacterial mat habitats were changed to 'soft'; cobble, boulder, pebble, gravel rock ridge, flat bedrock, and pinnacles were 'hard,' and any combination of 'soft' and 'hard' substrates was classified as 'mixed.' For example, the habitat type RS, consisting of rock

and sand substrates, would become ‘mixed,’ and BC, consisting of boulders and cobbles, would be ‘hard.’

To calculate the area of each habitat patch, the length in kilometers was determined with the starting and ending latitude and longitude of each patch with the following Great Circle Distance equation, $\text{length} = \text{ACOS}(\text{COS}(b) * \text{COS}(a) * \text{COS}(d) * \text{COS}(c) + \text{COS}(b) * \text{SIN}(a) * \text{COS}(d) * \text{SIN}(c) + (\text{SIN}(b) * \text{SIN}(d))) / 360 * 2 * \text{Pi} * 6378$, where a = Start Latitude, b = Start Longitude, c = End Latitude, and d = End Longitude (Drexel, 1995). The result was then multiplied by the 2m width of the transect.

The video footage of the transects, over 56 hours of tape, was then examined to collect sea cucumber-specific data for the species *P. californicus* and *P. leukothele*. The length of each individual was estimated to the nearest 5cm (due to screen resolution) using the two laser beams spaced 20cm apart and visible on the tape. The exact time when each individual sea cucumber was observed on transect was recorded by using a Horita time code reader; the time linked to the sub’s navigation in order to acquire latitude and longitude. This also provided a link to the sub’s CTD data so that the salinity and temperature at each observation point could be extracted. Using the latitude and longitude bearings, the position of each individual sea cucumber was plotted using ArcGIS 9.3 (ESRI, 2009). Data for cucumbers observed off transect were also completed for potential further analysis but were not used in density calculations. Comments or other observations regarding each cucumber’s behavior, orientation, and color were also recorded.

To examine differences in density of each species by site, depth, and habitat, a series of Kruskal-Wallis tests was conducted. A parametric ANOVA was not used for density analysis as the data did not meet the assumptions of normality or equal variances (Underwood, 1997). The

Kruskal-Wallis analysis of variance is a non-parametric test based on ranks (Chan and Walmsley, 1997; McDonald, 2009). To calculate the densities of each species, the number of individuals in each habitat patch was divided by the area (m^2) of the habitat patch. Due to the small magnitude of the resulting densities, the values were then multiplied by 10,000 to obtain the number of cucumbers per hectare.

As habitat varies by depth, and both depth and habitat vary by site, density was examined by each of these factors at each site, providing a more detailed look at the populations' distribution patterns. For this site-specific density analysis, the percent substrate composition by 50m depth zone was first characterized for each site. The density of each species by habitat and 50m depth zone was then calculated and graphed separately.

Lastly, in order to examine the size (averaged by habitat patch) of each species by site, depth, and habitat, a series of one-way ANOVAs was conducted. ANOVA requires data to meet the assumptions of normality and equal variances; data were transformed as necessary to meet these (Underwood, 1997). If, however, the assumption of normality could not be met but the variances were equal, the ANOVA results were still reported, as ANOVA is robust to departures from normality (Underwood, 1997). Significant results ($p < 0.05$) were followed with a Tukey post-hoc multiple range test (Underwood, 1997).

RESULTS

A total of 864 *P. californicus* and 478 *P. leukothele* were identified on transects during the video analysis (Table 1). *P. californicus* was present at each of the five study sites; *P. leukothele* was found at all sites except Point Sur, but 99% were found at Soquel Canyon and Big Creek (Table 1, Fig. 2a, b).

Density

P. californicus ranged in density by site from 29 cucumbers/hectare at Soquel Canyon to 134 cucumbers/hectare at Portuguese Ledge (Fig. 3a). *P. californicus* density was significantly higher at Portuguese Ledge compared to densities at all other sites (Kruskal-Wallis: $H=27.81$, $df=4$, $p<0.0001$). Similarly, the density of *P. leukothele* was significantly higher at Soquel Canyon (113 cucumbers/hectare) relative to other sites (Fig. 3b; $H=41.67$, $df=4$, $p<0.0001$).

P. californicus was observed throughout a wide range of depths (25m to 248m); however, 85% of individuals were found in shelf waters shallower than 100m, with an average depth of 77m. This species' density was greatest (163 cucumbers/hectare) at 50-100m depths, and the differences among densities by depth zones were significant (Fig. 4; $H=34.50$, $df=5$, $p<0.0001$). *P. leukothele*, on the other hand, was typically found in deeper waters at the edge of the shelf and on slope habitats; the average depth was 211m, although they ranged from 99m-317m. This species' density was significantly highest (87 cucumbers/hectare) from 200-250m (Fig. 4; $H=18.83$, $df=5$, $p=0.002$). Between 100-150m, both species overlapped in their depth distributions, with similar densities of about 40 cucumbers/hectare (Fig. 4).

Both species increased in density with increasing relief in habitat (as characterized by substrate type; Fig. 5). *P. californicus* had the lowest density, 0.7 cucumbers/hectare, in soft substrates and the highest density, 113 cucumbers/hectare, in hard substrates ($H=42.51$; $df=2$; $p<0.0001$). *P. leukothele* also had the highest density in hard substrates (46 cucumbers/hectare), but was found in higher densities on mixed and soft substrates (35.3 and 7.3 cucumbers/hectare, respectively) than *P. californicus*. *P. leukothele* density in hard substrates was significantly greater than the densities in the mixed and soft substrates ($H=11.6$, $df=2$, $p=0.003$, adjusted for ties).

Site-specific density analysis

The density of both species was also examined by depth and habitat at each site to give a site-specific density analysis. At Soquel Canyon, hard substrate comprised 87% of the transect areas from 50-100m and between 36-45% of the other depth zones (Fig. 6a). *P. californicus* was found almost entirely on hard substrates, and primarily from 50-100m, at the top of the canyon drop-off (sampling was not conducted <50m). Eighty-eight percent of all *P. leukothele* identified in the study were found at Soquel Canyon. This species had the highest density, 535 cucumbers/hectare, from 200-250m. In all depth zones, *P. leukothele* was primarily found on hard substrates, but was found increasingly more on mixed substrates as well with deeper depths.

Portuguese Ledge had the most varied habitat distributions of the five sites (Fig. 7a). Hard substrates dominated the 50-100m depth zone while no hard substrates were present from 100-150m, and the depths 200m and below had a mix of all three substrate types. No surveys, however, were conducted from 25-50m or from 150-200m. *P. californicus* was found on hard and mixed substrates primarily between 50-100m on the shelf (Fig. 7b, d). This depth zone at this site supported the highest density of *P. californicus* found across all sites and depths—497 cucumbers/hectare. Only two *P. leukothele* were found on transect at this site: one at 107m deep and one at 248m, both on mixed substrate on the continental shelf drop-off and slope (Fig. 7c, e).

Dives were conducted in each depth zone at Point Lobos, and with each deeper zone, the habitat composition gradually shifted from hard-substrate-dominated to mixed-substrate-dominated (Fig. 8a). Thirty-five percent of all *P. californicus* from the study were found at this site, and the majority of these were found on the shelf from 50-100m on hard substrates (Fig. 8b, c). One *P. leukothele* was found on transect at this site on hard slope substrate at 310m.

At Point Sur, 83% of the area surveyed between 25-100m was dominated by hard substrate, while dive sites from 150-200m consisted primarily (72%) of soft substrate (Fig. 9a). Only *P. californicus* were found at this site, with all but two being in the 25-50m depth range (Fig. 9b-c); however, the majority of dives conducted at Point Sur were shallower than 100m, making it unlikely that *P. leukothele* would be encountered.

Big Creek had the least hard-substrate-dominated habitat composition of the three sites, with an almost equal amount of hard and soft substrates in each depth category (Fig. 10a). *P. californicus* was primarily found on the shelf from 25-50m, and while hard substrate was not the most readily available substrate type, 91% of all *P. californicus* were found in this habitat (Fig. 10b, d). *P. leukothele*, on the other hand, was found further offshore with the highest density, 317 cucumbers/hectare, from 200-250m—the depth around which the continental shelf drops off at this site (Fig. 10c, e). In this depth range, this species was also found more on mixed substrates than hard or soft substrates.

Size

P. californicus ranged in size from 10-45cm, and averaged 22cm (5cm standard deviation; Fig. 11). *P. leukothele* was slightly smaller overall, ranging in size from 5-35cm, with an average of 20cm (5cm standard deviation; Fig. 11). In general by site, the average size of each species varied slightly; however, *P. californicus* was significantly larger at Soquel Canyon and Portuguese Ledge than the rest of the sites according to a one-way ANOVA on log-transformed data and a post-hoc Tukey test (Fig. 12; ANOVA: df=4, 315, $p<0.0001$). There was also a significant substrate by size relationship for both species. *P. californicus* were significantly smaller on average on hard substrates than on mixed substrates (ANOVA: df=2,

317, $p < 0.0001$), and *P. leukothele* were significantly larger on soft substrates than on hard or mixed substrates (Fig. 13; ANOVA: $df=2$, 167, $p < 0.0001$). Both species exhibited size variations with depth (Fig. 14). From 25-150m, *P. californicus* increased significantly in size with each deeper 50m depth zone (ANOVA: $df=4$, 315, $p < 0.0001$). And from 100-300m, *P. leukothele* decreased in size with each deeper 50m depth zone; *P. leukothele* from 100-150m were significantly larger than those from 250-300+m (ANOVA: $df=4$, 165, $p = 0.005$). While the raw data provide no linear correlation, this general pattern in size variation by depth may warrant further investigation in future studies.

DISCUSSION

Population-level information is key to the development of effective management plans for fisheries. However, resources and funding to undertake such surveys are often lacking, particularly for continental shelf and slope populations and for those less popular species, such as sea cucumbers. The purpose of this study was to examine the population dynamics of the continental shelf and slope *Parastichopus californicus* and *Parastichopus leukothele* populations in central California. The results of the species' density, depth, habitat, site, and size distributions are presented, and their implications to the fishery are discussed.

P. leukothele

Little research has been conducted on *P. leukothele*; in fact, to my knowledge, this is the first ecological study on this species. Lambert (1986) originally collected 62 specimens in order to describe the species, with the majority being from British Columbia. These ranged in depth from 24-285m, with an average depth of 134m, and in size from 7-38cm, with an average of

16.2cm (Lambert, 1986). The *P. leukothele* observed in the current study were found to be slightly deeper; 478 individuals were observed from 99-317m, with an average depth of 211m. The size ranges of the two studies were more comparable, as those from this study ranged from 5-35cm; however, the average size was slightly larger, at 20cm.

While Lambert (1986) did not report the habitats from which each individual was collected, he stated that most were collected from soft-sediment trawls on the continental shelf, while some were observed on SCUBA or submersible dives on rocky substrates. In the current study, *P. leukothele* was found most frequently on hard and mixed (combination of hard and soft) substrates; however, it was also found on softer substrates as well in deeper waters—more so than *P. californicus*.

Lambert (1986) noted the necessity for additional studies on these two species in order to better document their habitat and depth ranges. He observed that in British Columbia, the species appeared to overlap in depth from 24-116m with no obvious difference in habitat association (Lambert, 1986). In the current study, both species also were observed to occupy similar habitats and overlapped in depth distribution from 99-248m, although most overlap was from 100-150m. The difference in depths occupied between CA and BC could be a result of latitudinal gradients in depth distribution in response to temperature; if there is an optimum temperature for a species, populations might be shallower in northern latitudes' colder waters and deeper further south (Smale et al., 2010).

P. californicus

P. californicus was found in the greatest densities from 25-100m. In the three northernmost sites (Soquel Canyon, Portuguese Ledge, and Point Lobos), this species was most abundant

from 50-100m, while in the remaining two sites (Point Sur and Big Creek) it was most abundant from 25-50m. In each depth zone at every site, *P. californicus* was found in the highest densities on hard substrates, most commonly rock walls. This pattern was found even where, in terms of surveyed habitat, hard substrates were not the most readily available type, as was the case at Big Creek, suggesting that this species has a strong association with this substrate.

While *P. californicus* has been the subject of much more research than *P. leukothele*, there are still relatively few population studies with which to compare these deep-water results. Two studies, however, also used the *Delta* submersible to study deep water populations of *P. californicus* in Alaska (Zhou and Shirley, 1996; Woodby et al., 2000). Zhou and Shirley (1996) were the first to examine sea cucumber distribution and habitat association beyond 15m depth. In 29 successful dives between 2 and 198m in Barlow Cove, they observed 132 *P. californicus*. Woodby et al. (2000) conducted a similar study near Sitka and observed 487 *P. californicus* on 20 submersible dives and 10 SCUBA dives between 0 and 118m. While the methods of all three studies varied, the results from the current study are more aligned with those of Zhou and Shirley (1996). Both found *P. californicus* to be densest on hard solid substrates and had an overall density of around 50 cucumbers/hectare. Woodby et al. (2000) found the species in very high densities (up to 4000 cucumbers/hectare); they were most dense in very shallow depths (<10m) and on hard loose substrates. Although these shallow depths were not included in the current study, it is possible that there would be extremely low densities of *P. californicus* in these depths in central California due to latitudinal gradients in their distributions. While this species can be found intertidally in places in Alaska, it is found subtidally at Monterey, CA (Woodby et al., 2000). Temperature may not be the only influence, though, as in southern CA, *P. californicus*

seems to be displaced by *P. parvimensis*, another commercial congener, in waters shallower than 30m (Woodby et al., 2000; Yingst, 1982).

Size distribution

The density distribution patterns by substrate type could contribute to size differences among populations due to differences in nutrients or ontogenetic patterns. Yingst (1982) observed that a congener, *P. parvimensis*, in southern CA was smaller and more abundant on hard substrates than on soft substrates. *P. parvimensis* individuals feeding on the detritus of rock substrates ingested three times more organic matter per gram of sediment than those feeding on the detritus of soft substrates (Yingst, 1982). However, individuals on soft substrates consumed a greater quantity of sediment and ultimately ingested almost eight times the organics, leading them to be larger in size (Yingst, 1982). This size-substrate pattern was observed for *P. leukothele*, which were largest and least dense on soft sediments, and smallest and most dense on hard substrates. This pattern could also be explained through ontogenetic changes. For example, the smaller juveniles might live and grow on the rock on which they settle as larvae; then as larger adults, they may migrate between the rock wall segments. Commonly the individuals observed on softer substrates were actually on mud channels between hard rock walls, and these individuals were also frequently larger in size. These size-substrate patterns were not observed in *P. californicus*, but only 15 of the 864 individuals were found on soft substrates.

Detritus nutrient content may also contribute to the size and depth patterns observed in the current study. Though not linearly significant, *P. californicus* tended to increase in size with increasing depth while *P. leukothele* decreased in size, and both species were largest in the 100-150m depth range. This depth range commonly includes the continental shelf drop-off and could

be optimal in terms of percent organic matter, as organic matter accumulates from the surface and is also brought up from upwelling.

Habitat & depth distributions

Both *P. californicus* and *P. leukothele* were found most frequently on hard substrates. Much of the hard substrate habitat observed in the surveys was of high relief and was frequently covered with other invertebrates or encrusting organisms; such habitat likely provides camouflage and protection for the cucumbers from visual predators. Hard substrates may also provide the cucumbers more secure footing as their tube feet can better grip the surface, particularly in high velocity currents (Woodby et al., 2000). Zhou & Shirley (1996) suggested that *P. californicus* depth distribution was based on hard substrate availability rather than depth. *P. californicus* commonly inhabited shallower depths than *P. leukothele*, but the depth distributions of both species do not appear to be based solely on the availability of hard substrate.

Additional influences on depth distribution could include temperature and salinity patterns, as temperature decreases with depth and salinity increases with depth. At Point Lobos, for example, over 50% of the available habitat surveyed was hard substrate between 100-150m, but no *P. californicus* was found below 100m depth. However, there was a 1.5°C drop in average temperature between the 50-100m and the 100-150m depth zones (Appendix A). Likewise at Point Sur, no sea cucumber was found deeper than 50m despite there being 60-80% hard substrate available from 50-150m, but there was a 1 °C drop in average temperature to the next deepest depth zone. Although *P. californicus* was found in average temperatures from 8.5°C to 11.8 °C (Appendix B), these steep thermoclines also marked the area of the continental shelf break at these sites.

The species' distributions may not be clearly explained by just one or two factors; therefore, it is important to consider the combination of factors that contribute towards describing the broader environments in which each species were found. *P. californicus* was found mostly on the continental shelf whereas *P. leukothele* was found mostly on the slope. The shallower depths of the shelf tend to have rockier substrate, warmer temperatures, and lower salinities than the deeper waters of the slope (Appendices A, D). The average temperature of *P. californicus* observation points was 10.6 °C (Appendix B), and the average salinity was 33.9ppt (Appendix E). The slope habitats, typically below 200m, were comprised of steep mud slopes and mud-covered rock walls. The average temperature of *P. leukothele* observation points was 8.6 °C (Appendix C) and the average salinity was 34.1ppt (Appendix F). The prevalence of these environments, among other environmental factors, likely contributes to the variation in population distributions among sites.

Oceanographic influences on distribution

The sites included in this study contain different coastal features that may begin to provide more explanation for the varying adult population distributions, particularly given that *P. californicus* was found primarily on the continental shelf and *P. californicus* on the slope primarily in submarine canyons. Big Creek, the southernmost site, is located on a wave-exposed portion of the coast (with no major headlands or embayments) with multiple narrow submarine canyons and a relatively short shelf (~2km to shelf break), and is therefore subjected to strong upwelling (Starr et al., 2008). About 15km north, Point Sur is also exposed but lies on a much broader shelf (8-11km to shelf break). The Point Lobos study site includes a variety of coastal features that affect circulation, including a small embayment (Carmel Bay) with the Monterey

Peninsula headland to the north and a submarine canyon (Carmel Canyon) within; however, no *P. leukothele* were found along the rim of this submarine canyon. On the northern side of the peninsula, Portuguese Ledge is protected on a shallow shelf in Monterey Bay from the strong coastal upwelling currents (Breaker and Broenkow, 1994). And while Soquel Canyon is also within Monterey Bay, the site sits at the top of a deep submarine canyon, which yields lower water temperatures, higher salinities, and different current patterns than the rest of the Bay (Appendices A, D; Breaker and Broenkow, 1994). Current strength is a factor known to influence sea cucumber distributions. Silva et al. (1986) found that *P. californicus* will avoid areas with currents greater than 4km/h, and McEuen (1988) established that fertilization is most successful in currents with slow, steady velocities.

The various aforementioned coastal features lead to differing circulation patterns, which also directly influence larval transport. In terms of considering larval flow as an influence in subsequent adult populations, it is important to determine at which depth spawning occurs. Two recent studies in larval dispersal along the CA coast found that larvae released below 20m (Petersen et al., 2010) had high rates of retention on the shelf, whereas shallower releases had higher rates of exportation due to upwelling (Petersen et al., 2010; Morgan and Fisher, 2010). Additionally, eggs of *P. californicus* are neutrally to slightly negatively buoyant, so their distribution is highly influenced by the currents at depth rather than on the surface (McEuen, 1988). In the present study, adult populations at Point Sur and Big Creek were typically shallower and less dense than other sites, which could be partly due to a lower larval retention as a result of upwelling effects. Within Monterey Bay, waters above 25m flow northward while deeper waters flow southward (Breaker and Broenkow, 1994); this may contribute to the higher

density of sea cucumbers at Portuguese Ledge, as the larvae flow towards the site and may be retained along the protected shelf.

Spawning observations and implications

Due to the differences in larval flow in deeper versus shallow waters, knowing the depth at which *P. californicus* spawn should clearly be an important consideration in the management of this species. While it has been unknown whether deeper *P. californicus* migrate to shallow waters to spawn (Cameron and Fankboner, 1986; Lambert, 1997; Woodby *et al.*, 2000) or whether they spawn in the deeper waters, the video footage from the 2007 and 2008 dives of the central CA marine protected areas captured populations of both species spawning at deeper shelf depths (50-150m). When spawning, sea cucumbers lift their anterior ends off the substrate, commonly at a 90° angle, as they release their gametes into the water column; this behavior is visible on the video footage. The most notable spawning event observed from the 2007 dives occurred at Soquel Canyon on 31 October at 10:45am and 150m depth, and included 9 *P. leukothele* between 15 and 30cm long. Each individual in supposed spawning posture was either on the top of boulders or the edge of a rock wall. During the dives in 2008, 14 *P. californicus* were observed in spawning posture on 19 September on a dive in Point Sur beginning at 4:30pm; the individuals were between 20 and 25cm long and were all on the tops of boulders between 54 and 58m deep.

As sea cucumbers are broadcast spawners and subject to population Allee effects, population densities are important to consider. For the sea cucumber species *Stichopus fuscus* in Ecuador, the density below which reproductive success crashed was 1,000 individuals/hectare (Shepherd *et al.*, 2004). For other broadcast spawning marine invertebrates, this density level

has been reported at levels greater than 2,000 individuals/hectare (Levitan, 1991; Shepherd and Brown, 1993). In the present study, the largest density for a study site was 134 individuals/hectare for *P. californicus* and 113 individuals/hectare for *P. leukothele*. On a smaller scale, the largest density within one depth zone at a site was 497 individuals/hectare for *P. californicus* and 535 individuals/hectare for *P. leukothele*.

These densities are much lower than any reported threshold density and thus initially indicate that the studied populations may not be viable; however, the distribution of both species appeared to be highly clustered. In low population sizes, some broadcast spawning marine invertebrates form spawning aggregations as part of their reproductive strategy (Gascoigne and Lipcius, 2004); it is possible that sea cucumbers do so as well (McEuen, 1988). Such aggregations and clustered distributional patterns may be lost or diluted when calculating densities for a large area. When re-examining the aforementioned spawning event observed in the 2007 dives on a smaller scale, 85 sea cucumbers (20 *P. californicus*, 65 *P. leukothele*) were observed in just 3 minutes, equating to a density estimate of 2,300 cucumbers/hectare. Therefore, the studied populations may indeed be viable, but densities of broadcast spawning marine invertebrates should perhaps be examined at both large and small spatial scales to better understand the population distribution.

The density of the adult population may affect recruitment potentially in terms other than insufficient fertilization. Neuman et al. (2010) found that recruitment of black abalone (*Haliotis cracherodii*) in southern California declined to zero when the average adult population density lowered to 3400 individuals/hectare; however, factors influencing sea cucumber larval recruitment are not fully known. While sea cucumber spawning was observed in the deeper shelf waters, the lack of smaller individuals reported suggests that juveniles do not settle in the

continental shelf and slope habitats. However, cryptic juveniles 5cm or smaller were nearly impossible to spot from the submersible videos, but still-photos taken from a digital camera within the sub did capture a few juveniles of this size. One was observed in Point Sur at 40m depth, one in Point Lobos at 50m, and three in Point Lobos at 83m. All were present on hard rock walls encrusted with other organisms, and the juveniles were well camouflaged. While species identifications of the juveniles were not possible, these observations of them support the idea that larvae do settle on the continental shelf.

Management implications

The commercial sea cucumbers in California are primarily fished by SCUBA divers in waters shallower than 25m. While there are ample dive sites in the study areas, the fishery appears to be most active in southern California (Santa Barbara to San Diego), based on the landings-by-port data (CDFG, 2010). Therefore, the populations surveyed in this study are likely an unexploited population and could therefore serve as a useful reference with which to compare more heavily fished areas to the south. Due to larval transport, however, these populations are not necessarily independent of each other and should rather be viewed as a metapopulation. Fishing pressure from the dive and trawl fisheries, although not occurring in the areas themselves, might still affect the studied populations.

Other commercial trawl fisheries may also affect sea cucumber populations. In a trawling bycatch survey outside of Santa Barbara, sea cucumbers were found to be one of the top 6 invertebrate species caught as bycatch (CDFG, 2008). Although bottom trawling was closed to waters within 3 nautical miles of the California coastline in 1953, trawling effort intensities were fairly high along the border of this zone outside of Point Sur, Portuguese Ledge, and the northern

portion of Monterey Bay, which was closed to trawling in 2006 (Graiff et al., unpublished; CDFG, 2008). This historically high fishing pressure in these regions may have influenced the populations of sea cucumbers overtime through habitat destruction and bycatch mortality. Sea cucumber bycatch in halibut trawls is common enough that almost 65% of halibut trawlers in southern California have obtained permits to target sea cucumbers as well (CDFG, 2008).

The southern California sea cucumber trawl fishery targets *P. californicus*; however, Lambert (1997) theorized that *P. leukothele* might actually be collected in the trawl fishery. The majority of the specimens in his 1986 study were collected from trawls on soft sediment substrates on the continental shelf. Additionally, in the current study, more *P. leukothele* were observed on the softer, trawable substrates than *P. californicus*; *P. californicus* was found almost exclusively on hard rock substrates. Additional support for the theory that *P. leukothele* is exploited but not reported stems from the fact that landings are typically reported using common names, and the common name used for *P. californicus* in the fishery is the ‘Giant Red Cucumber.’ This name implies that the sea cucumber is red in color, but more commonly *P. californicus* is brown while *P. leukothele* is red. Under this naming system, any specimens of *P. leukothele* could easily be misidentified as a ‘Giant Red Cucumber.’

A lack of species-specific landings data was one of many factors that contributed to the over-exploitation, serial depletion, and near extinction of the white abalone (*Haliotis sorenseni*) in California; two other factors included the lack of catch spatial analysis and fishery-independent data (Hobday et al., 2001). According to Hobday et al. (2001), sea cucumbers and other commercial broadcast-spawning marine invertebrates run the risk of repeating the unfortunate decline of the abalone if the fisheries continue to be improperly managed and unmonitored. In addition, *P. californicus* in particular shares other traits with *H. sorenseni* that

may make it especially vulnerable to the same over-exploitation, such as a slow growth rate and relatively late sexual maturity; both do not reach sexual maturity until 4-6 years of age (Hobday et al., 2001; Cameron and Fankboner, 1989).

California's Department of Fish and Game prioritized sea cucumbers as one of the top ten species groups in need of a fishery management plan (CDFG, 2001). Proper management is essential to protecting populations from overfishing; however, such management cannot be designed or implemented without accurate landings data and sufficient population studies. It is recommended that the catches from sea cucumber trawls be closely examined to ensure proper identification, and that additional research be conducted on populations of *P. leukothele*, especially if they are found to be collected in the fishery. Catch data should also be examined spatially to avoid serial depletion (Hobday et al., 2001). In addition to the fishery-dependent monitoring, fishery-independent population surveys should also be continued, as stock declines are not always detected in catch data (Shroeter et al., 2001).

Spatial management measures, such as marine protected areas (MPAs), have already shown to benefit to sea cucumber populations. In the Solomon Islands, the commercial species *Holothuria fuscogilva* almost doubled in abundance at one marine conservation area after four years of closure (Lincoln-Smith et al., 2006). Along the Australia's Great Barrier Reef, *Holothuria nobilis* populations were four times denser on average in protected areas than in unprotected areas (Uthicke and Benzie, 2000). In southern California's Channel Islands, *Parastichopus parvimensis* populations inside no-take reserves were higher than those fished populations outside of the reserves (Schroeter et al., 2001). The submersible dives on which the present study is based were completed both inside and outside of the central California MPAs to gather fishery-independent baseline data. Therefore, when the MPAs are re-surveyed in the

future, the data from the present study can be used to determine the effectiveness of the reserves in enhancing sea cucumber populations. Such enhancement could be the result of direct fishing pressure relief or relief from any adverse effects, such as bycatch, inflicted on sea cucumber populations by other fisheries.

In conclusion, the baseline survey project for the central California MPAs provided a unique opportunity to study the commercial species *P. californicus* in its deeper distributional range, as well as to provide the first population-level study of *P. leukothele*, which may also bear commercial importance. The results presented here on the species' density, depth, habitat, site, and size distributions provide important and previously unknown population-level dynamics and could lead to better management of the sea cucumber fisheries in California and elsewhere.

REFERENCES

- Breaker LC and Broenkow WW (1994) The circulation of Monterey Bay and related processes. *Oceanography and Marine Biology: an Annual Review* 32:1-64.
- Bruckner A (2004) Sea cucumber population status, fisheries and trade in the United States. *Convention on International Trade in Endangered Species of Wild Fauna and Flora, Doc.* 6.13.
- Bruckner AW, Johnson KA, and Field JD (2003) Conservation strategies for sea cucumbers: can a CITES Appendix II listing promote sustainable international trade? *SPC Beche-de-mer Information Bulletin* 18:24-33.
- California Department of Fish and Game (CDFG) (2001) Chapter 3: Prioritization of Fisheries, pp. 3.1-3.10 *in: The master plan: a guide for the development of fishery management plans as directed by the Marine Life Management Act of 1998.*
- CDFG (2008) Review of California halibut trawl fishery in the California halibut trawl grounds. *Marine Region State Fisheries Evaluation Project*, 44pp.
- CDFG (2010) Final California commercial landings for 2009. *State of California Resources Agency*. <<http://www.dfg.ca.gov/marine/landings09.asp>>
- California State University Seafloor Mapping Lab (CSUSML) (2007) <<http://seafloor.csumb.edu>>
- Cameron JL and Fankboner PV (1986) Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). I. Reproductive periodicity and spawning behavior. *Canadian Journal of Zoology* 64:168-175.
- Cameron JL and Fankboner PV (1989) Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). II. Observations on the ecology of development, recruitment, and the juvenile life stage. *Journal of Experimental Marine Biology and Ecology* 127:43-67.
- Canadian Department of Fisheries and Oceans (CADFO) (1999) Giant Red Sea Cucumber. *DFO Science Stock Status Report C6-10.*
- CADFO (2010) Sea cucumber by dive: October 1, 2010-September 30, 2011. *Draft Pacific Region Integrated Fisheries Management Plan.*

- Chan Y and Walmsley RP (1997) Learning and understanding the Kruskal-Wallis one-way analysis-of-variance-by-ranks test for differences among three or more independent groups. *Physical Therapy* 77:1755-1762.
- Clarke S (2004) Understanding pressures on fishery resources through trade statistics: a pilot study of four products in the Chinese dried seafood market. *Fish and Fisheries* 5:53-74.
- Conand C (1993) Ecology and reproductive biology of *Stichopus variegatus*, an Indo-Pacific coral reef sea cucumber (Echinodermata: Holothuroidea). *Bulletin of Marine Science* 52:970-981.
- Conand C and Byrne M (1993) A review of recent developments in the world sea cucumber fisheries. *Marine Fisheries Review* 55:13p.
- Drexel University (1995) Math forum: distance on a sphere. <http://www.mathforum.com>
- ESRI (2009) ArcGIS 9.3 computer software.
- FAO (2000) Fishery Statistics: Capture production, 90(1):352.
- Gascoigne J and Lipcius RN (2004) Allee effects in marine systems. *Marine Ecology Progress Series* 269:49-59.
- Gotshall DW (1994) Guide to Marine Invertebrates: Alaska to Baja California. Sea Challengers Publishing: Monterey, CA, 105pp.
- Graiff KW, Tissot BN, and Yoklavich MM (unpublished) The abundance and distribution of megafaunal marine invertebrates in relation to fishing intensity off central California.
- Hobday AJ, Tegner MJ, and Haaker PL (2001) Over-exploitation of a broadcast spawning marine invertebrate: Decline of the white abalone. *Reviews in Fish Biology and Fisheries* 10:493-514.
- Lambert P (1986) Northeast Pacific holothurians of the genus *Parastichopus* with a description of a new species, *Parastichopus leukothele* (Echinodermata). *Canadian Journal of Zoology* 64: 2266-2272.
- Lambert P (1997) Sea Cucumbers of British Columbia, Southeast Alaska, and Puget Sound. UBC Press: Vancouver, 166pp.

- Levitan D (1991) Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181:261-268.
- Li X (2004) Fishery and resource management of tropical sea cucumbers in the islands of the South China Sea. In: *Advances in sea cucumber aquaculture and management*. FAO Fisheries Technical Paper 463:261-265.
- Lincoln-Smith MP, Pitt KA, Bell JD, and Mapstone BD (2006) Using impact assessment methods to determine the effects of a marine reserve on abundances and sizes of valuable tropical invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 63:1251-1266.
- Lundquist CJ and Botsford LW (2004) Model projections of the fishery implications of the Allee effect in broadcast spawners. *Ecological Applications* 14:929-941.
- Mathews V, Kookesh M, and Bosworth R (1990) Subsistence harvest and use of sea cucumber in southeast Alaska. Division of Substance, Alaska Department of Fish and Game, Technical Paper No. 190.
- McEuen FS (1988) Spawning behaviors of northeast Pacific sea cucumbers (Holothuroidea: Echinodermata). *Marine Biology* 98:565-585.
- McDonald JH (2009) *Handbook of Biological Statistics*. Sparky House Publishing: Baltimore, Maryland, 319 pp.
- Morgan SG and Fisher JL (2010) Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Marine Ecology Progress Series* 404:109-126.
- Neuman M, Tissot B, and VanBlaricom G (2010) Overall status and threats assessment of black abalone (*Haliotis cracherodii* Leach, 1814) populations in California. *Journal of Shellfish Research* 29:577-586.
- Petersen CH, Drake PT, Edwards CA, and Ralston S (2010) A numerical study of inferred rockfish (*Sebastes* spp.) larval dispersal along the central California coast. *Fisheries Oceanography* 19:21-41.
- Pouget A (2004) Relationship between sea cucumber (echinoderm) nutrition and reef sediment microbenthos in Reunion Island (Indian Ocean). In: *Abstracts and publications of beche-de-mer*. SPC Beche-de-mer Information Bulletin 21:38.

- Renbo W and Yuan C (2004) Breeding and culture of the sea cucumber, *Apostichopus japonicus*, Lian. In: Advances in sea cucumber aquaculture and management. FAO Fisheries Technical Paper 463:277-286.
- Rogers-Bennett L and Ono DS (2001) Sea cucumbers. California Department of Fish and Game. California's Living Marine Resources: A Status Report, pp. 131-134.
- Rogers-Bennett L and Ono DS (2008) Sea cucumbers. In: Barsky, K, *ed.* California Department of Fish and Game Status of the Fisheries Report: An update through 2008, ch. 5, pp. 1-10.
- Schroeter SC, Reed DC, Kushner DJ, Estes JA, and Ono DS (2001) The use of marine reserves in evaluating the dive fishery for the warty sea cucumber (*Parastichopus parvimensis*) in California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 58:1773-1781.
- Shepherd SA and Brown LD (1993) What is an abalone stock: implications for the role of refugia in conservation. Canadian Journal of Fisheries and Aquatic Sciences 50:2001-2009.
- Shepherd SA, Martinez P, Toral-Granda MV, and Edgar GJ (2004) The Galapagos sea cucumber fishery: management improves as stocks decline. Environmental Conservation 31:102-110.
- Silva JD, Cameron JL, and Fankboner PV (1986) Movement and orientation patterns in the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Holothuroidea: Aspidochirotida). Marine Behavior and Physiology 12:133-147.
- Smale DA, Kendrick GA, Waddington KI, Van Niel KP, Meeuwig JJ, and Harvey ES (2010) Benthic assemblage composition on subtidal reefs along a latitudinal gradient in Western Australia. Estuarine, Coastal and Shelf Science 86:83-92.
- Southward AJ, Young CM, and Fuiman LE (2005) Restocking Initiatives. In: Restocking and Stock Enhancement of Marine Invertebrate Fisheries. Advances in Marine Biology 49:9-41.
- Starr R, Yoklavich M, and Tissot BN (2008) Monitoring MPAs in deep water off central California: 2007 IMPACT submersible Baseline Survey. California Sea Grant College Program Publication No. T-067, 21pp.

- Tissot BN, Yoklavich MM, Love MS, York K, and Amend M (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. *Fishery Bulletin* 104:167-181.
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. University Press: Cambridge, 504pp.
- Uthicke S and Benzie JAH (2000) Effect of beche-de-mer fishing on densities and size structure of *Holothura nobilis* (Echinodermata: Holothuroidea) populations on the Great Barrier Reef. *Coral Reefs* 19:271-276.
- Uthicke S and Purcell S (2004) Preservation of genetic diversity in restocking of the sea cucumber *Holothuria scabra* investigated by allozyme electrophoresis. *Canadian Journal of Fisheries and Aquatic Sciences* 61:519-528.
- Washington Department of Fish and Wildlife (WDFW) (2008) Commercial Cucumber Regulations. <http://wdfw.wa.gov/fish/shelfish/divereg/cucumber.shtml>
- Woodby D, Smiley S, and Larson R (2000) Depth and habitat distribution of *Parastichopus californicus* near Sitka, Alaska. *Alaska Fishery Research Bulletin* 7:22-32.
- Woodby D, Carlile D, Siddeek S, Funk F, Clark JH, and Hulbert L (2005) Sea cucumber fisheries. In: *Commercial Fisheries of Alaska*. Alaska Department of Fish and Game Special Publication No. 05-09, pp.34-36.
- Xiyin L (2004) Studies on hatchery techniques of the sea cucumber, *Apostichopus japonicus*. In: *Advances in sea cucumber aquaculture and management*. FAO Fisheries Technical Paper 463:287-295.
- Yingst JY (1982) Factors influencing rates of sediment ingestion by *Parastichopus parvimensis* (Clark), an epibenthic deposit-feeding holothurians. *Estuarine, Coastal and Shelf Science* 14:119-134.
- Zhou S and Shirley TC (1996) Habitat and depth distribution of the red sea cucumber *Parastichopus californicus* in a southeast Alaska bay. *Alaska Fishery Research Bulletin* 3:123-131.

Table 1: Number of observed individuals and overall densities (number of cucumbers/hectare) of each species found on 10-minute transects, conducted from the *Delta* submersible, at each site in central CA.

Site	Transects	<i>P. californicus</i>		<i>P. leukothele</i>	
	n	n	Density	n	Density
Soquel Canyon	90	110	29	421	113
Portuguese Ledge	55	282	134	2	1
Point Lobos	92	301	81	1	0
Point Sur	50	68	31	0	0
Big Creek	57	103	54	54	28
<i>Total</i>		<i>864</i>	<i>63</i>	<i>478</i>	<i>35</i>

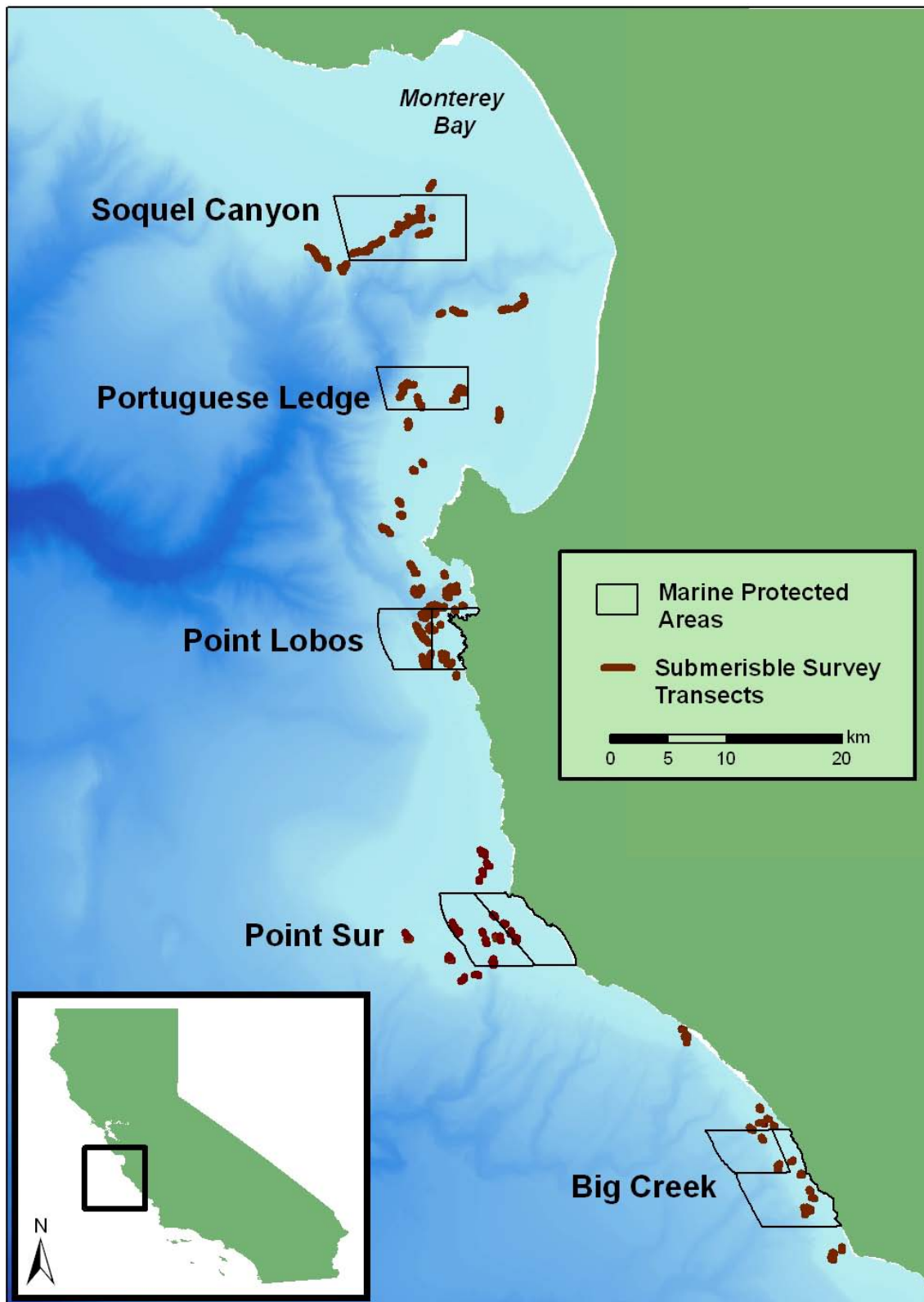
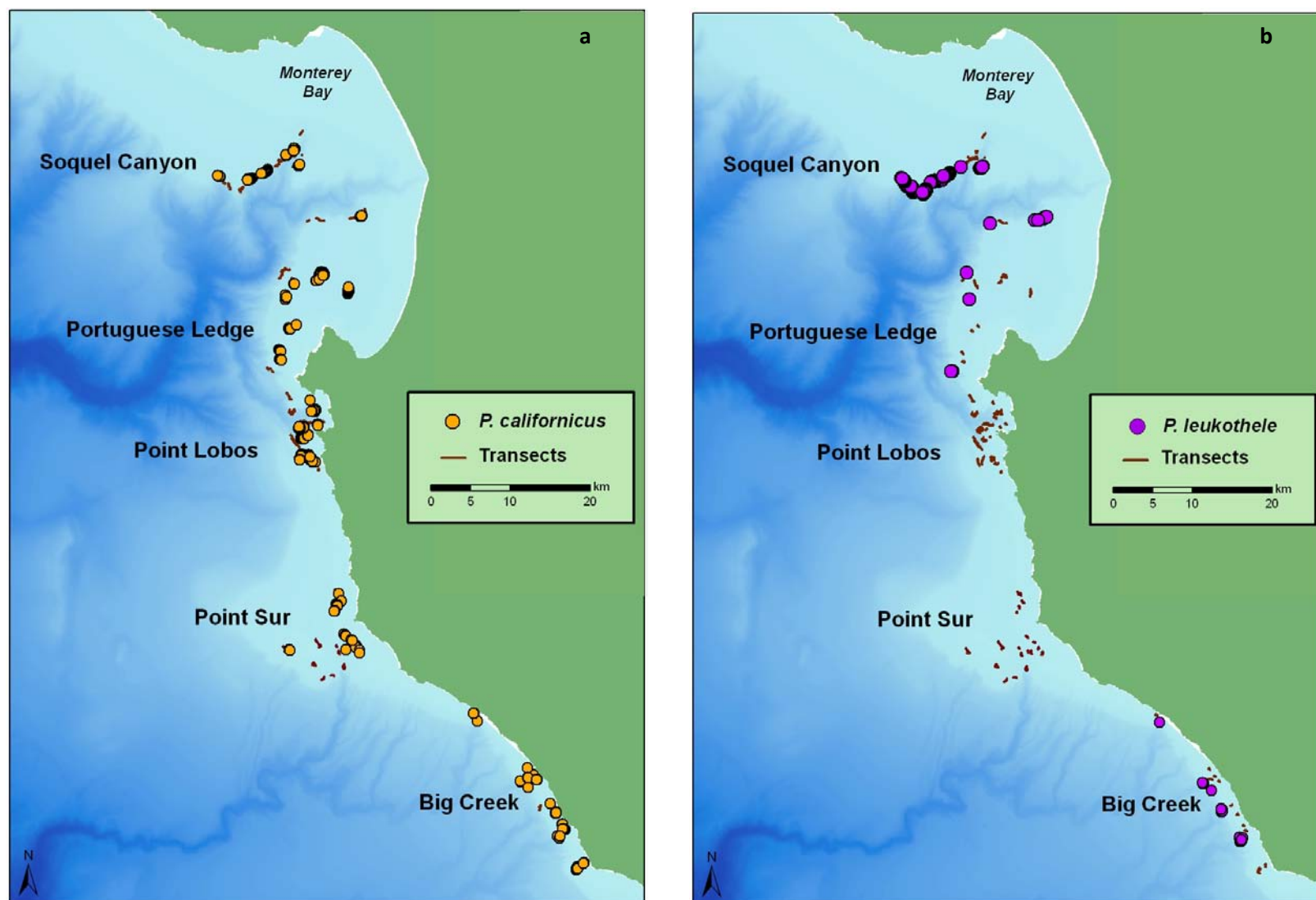
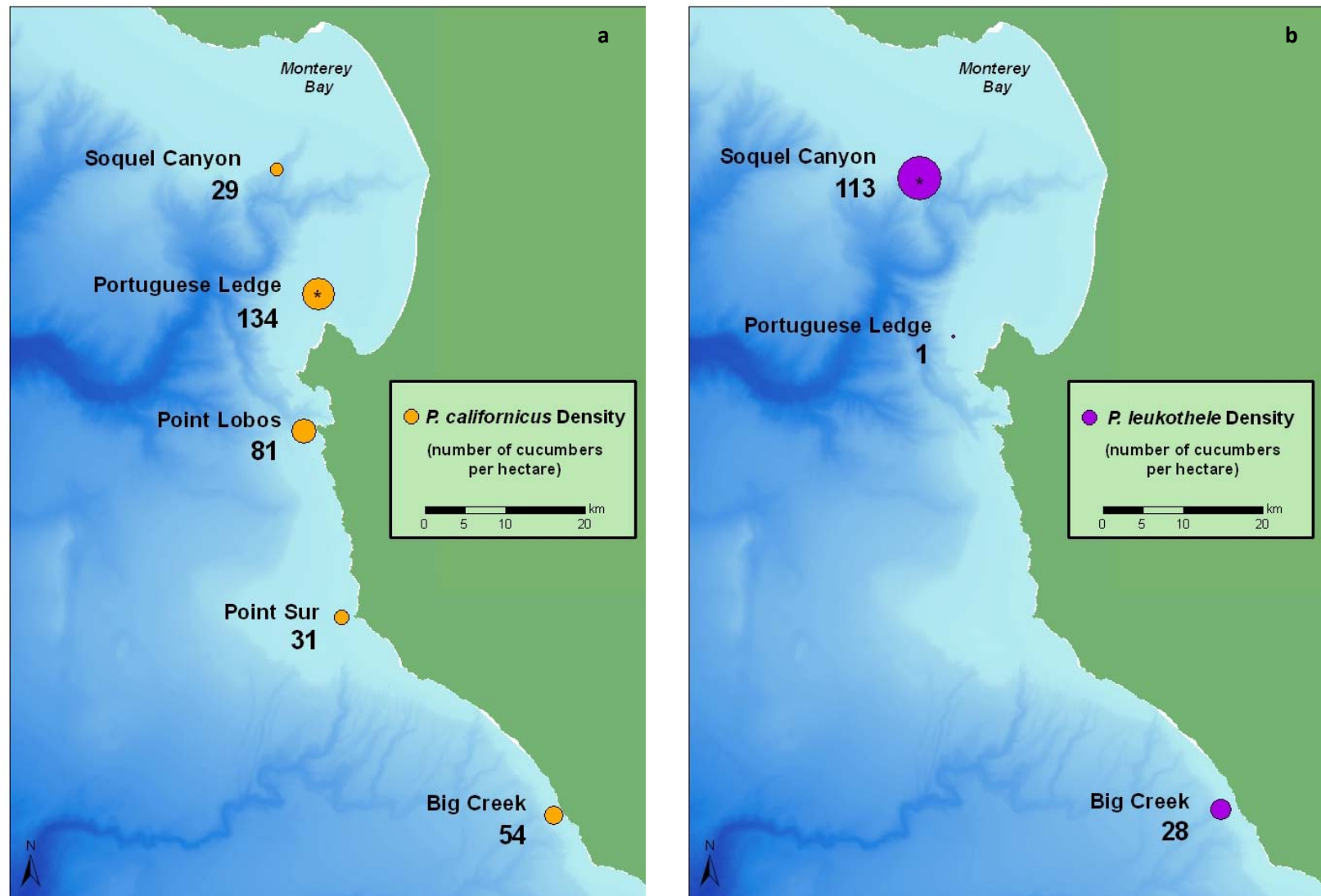


Figure 1: Map of central California Marine Protected Area study sites and 2007 submersible dive transects (n=344). Bathymetry from CSUSML (2007); map produced with ArcGIS 9.3 (ESRI, 2009).



Figures 2a,b: Overall distributions of *P. californicus* (a; n=864) and *P. leukothele* (b; n=478) in the central CA study sites. Colored circles represent individual observations on 10-minute video transects; red lines indicate submersible dive paths taken during transects (n=344). Bathymetry from CSUSML (2007); map produced with ArcGIS 9.3 (ESRI, 2009).



Figures 3a,b: Proportional densities of both *P. californicus* (a) and *P. leukothele* (b) found at each site. * indicates the sites at which each species was found in the highest densities (Kruskal-Wallis, $df=4$, $p<0.0001$ for both species). Bathymetry from CSUSML (2007); map produced with ArcGIS 9.3 (ESRI, 2009).

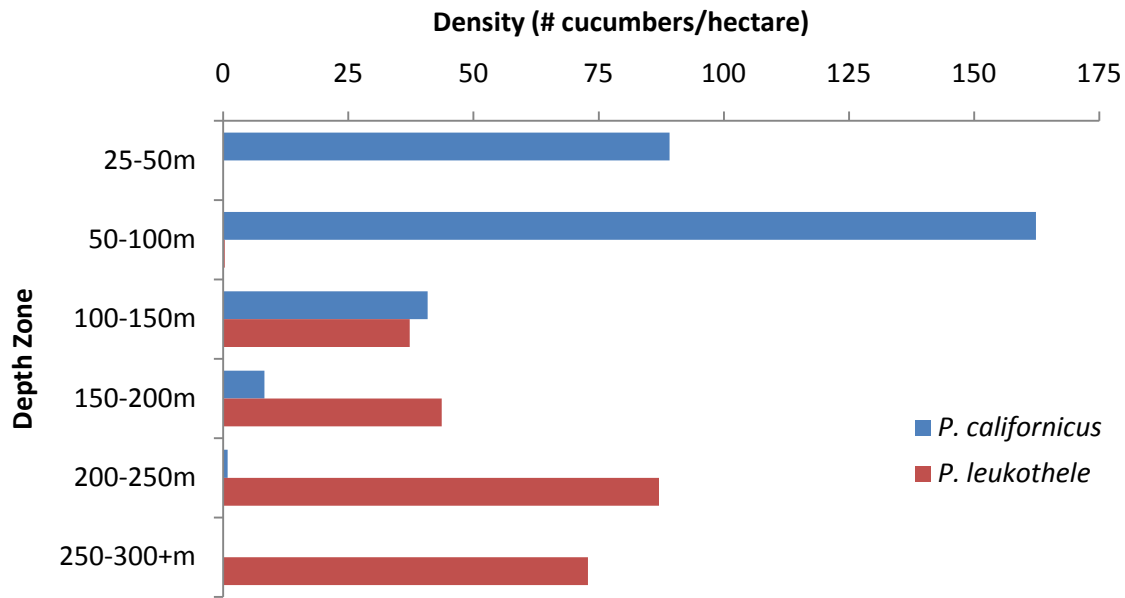


Figure 4: Density distribution of *P. californicus* (n=864) and *P. leukothele* (n=478) by 50m depth zone. *P. californicus* was significantly denser in the 50-100m zone compared to all other zones (Kruskal-Wallis, df=5, $p<0.0001$). *P. leukothele* was significantly denser in the 200-250m zone compared to all other zones (Kruskal-Wallis, df=5, $p=0.002$).

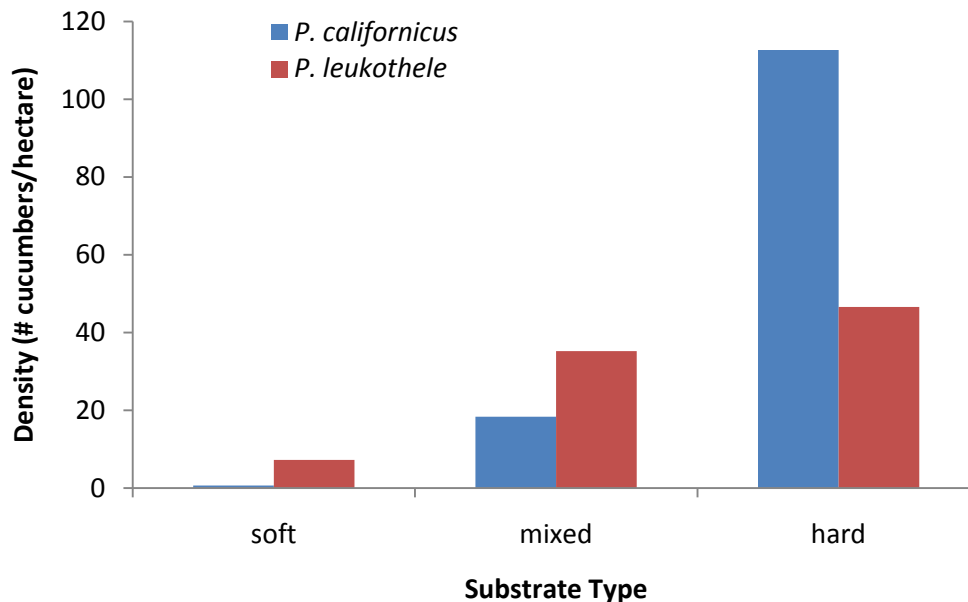
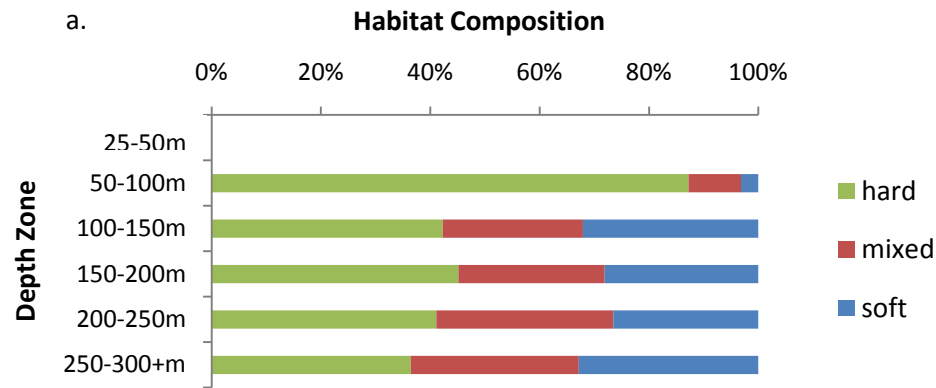
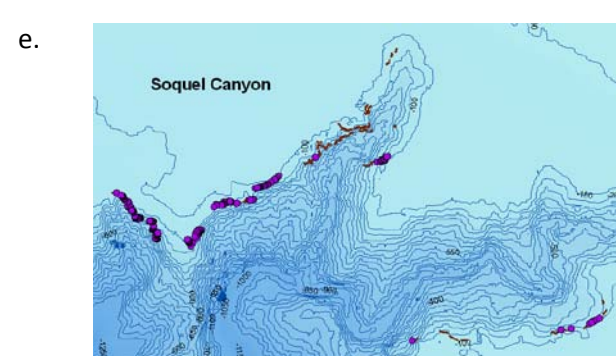
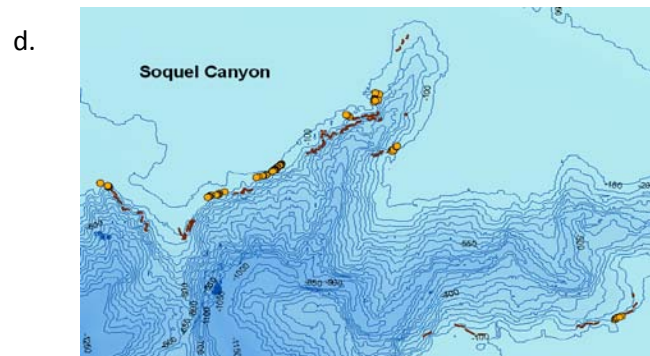
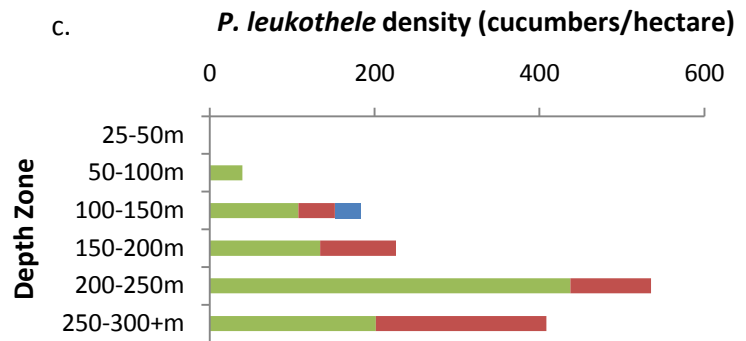
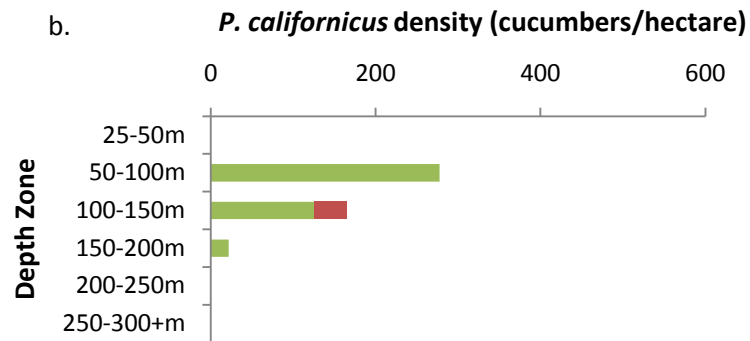
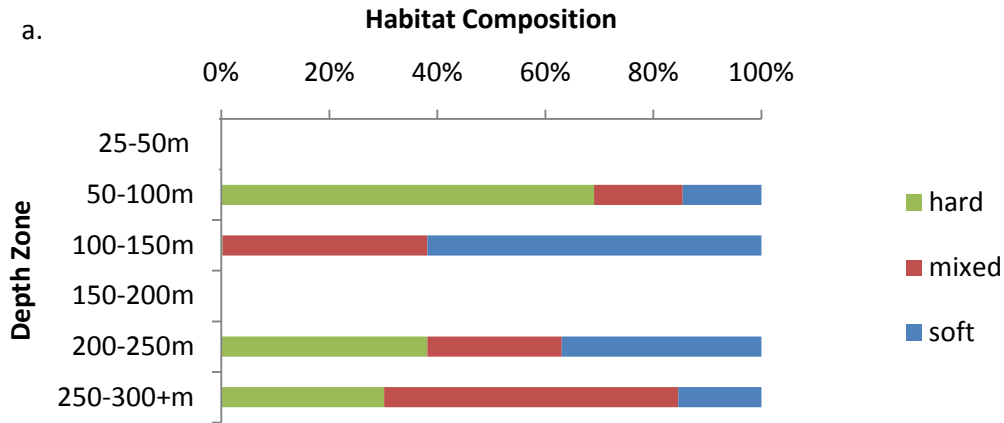


Figure 5: Density distribution of *P. californicus* (n=864) and *P. leukothele* (n=478) by substrate type. Both species were significantly densest in the hard substrates (Kruskal-Wallis, df=2: *P. californicus* $p<0.0001$, *P. leukothele* $p=0.003$).

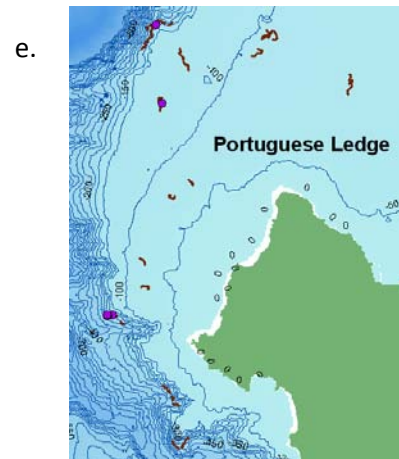
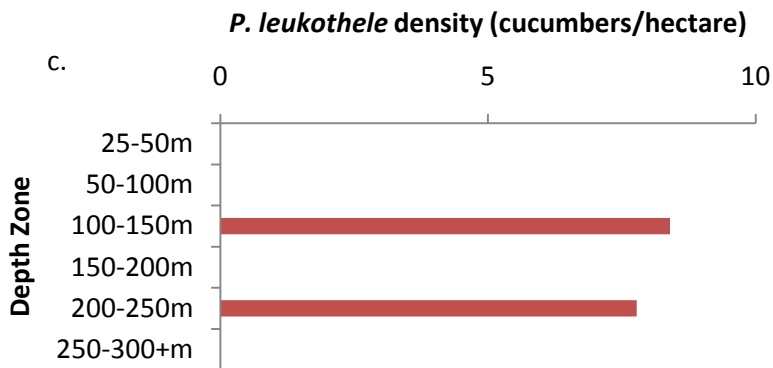
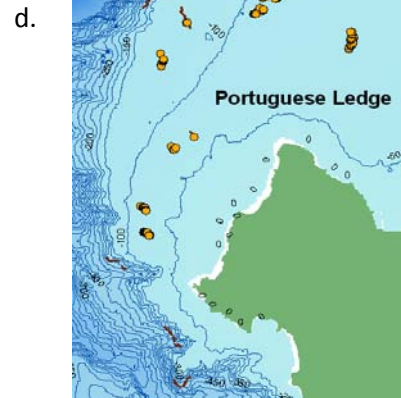
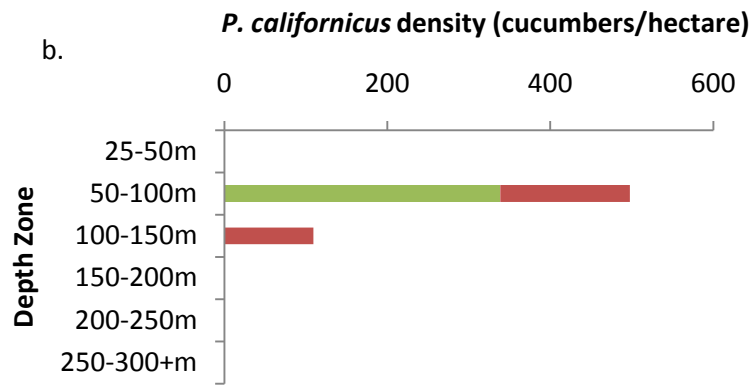


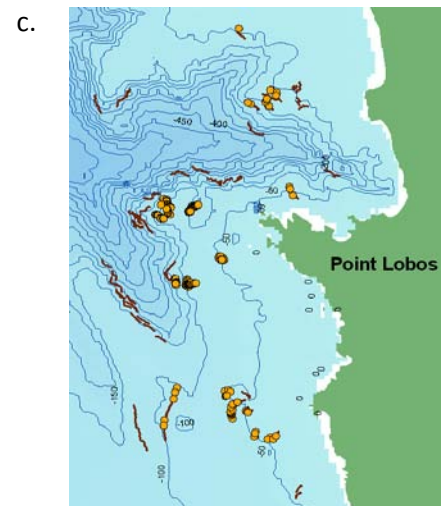
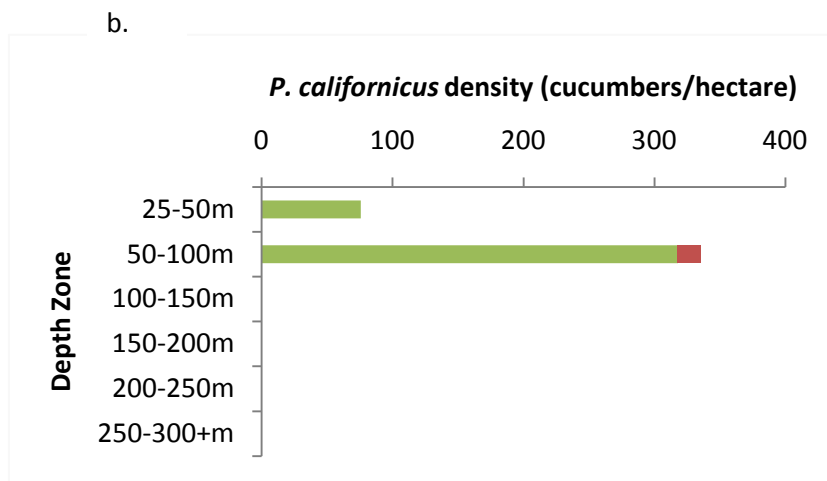
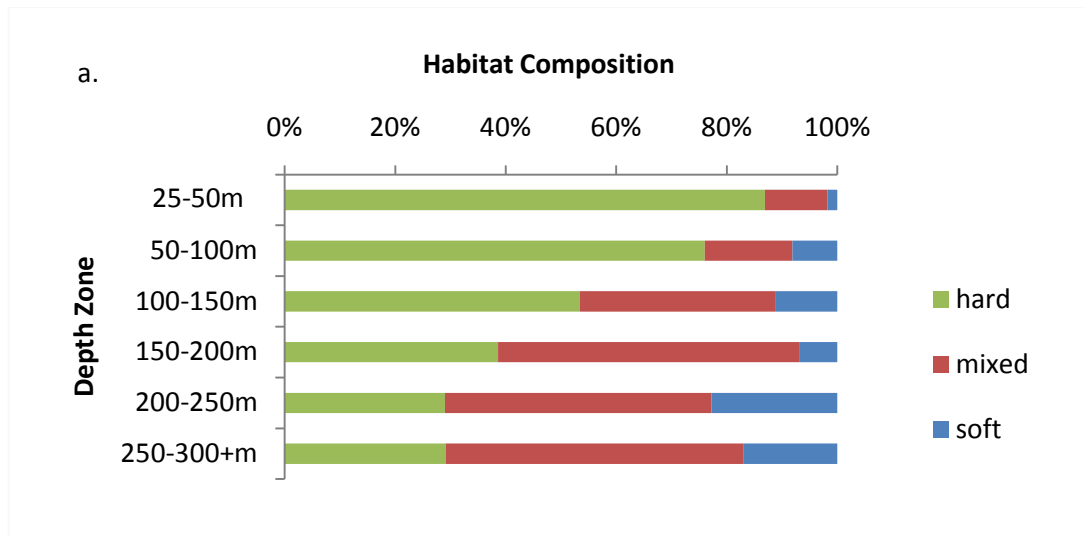
Figures 6a-e: Site-specific analysis for Soquel Canyon. 6a shows percent habitat composition by depth zone. 6b, c show the density of *P. californicus* (b; n=110) and *P. leukothele* (c; n=421) by depth zone and habitat type. 6d, e show the actual observations of *P. californicus* (d) and *P. leukothele* (e) at the site (colored dots= individual cucumbers, red lines= transects). The legend in 6a applies to 6b and 6c as well.



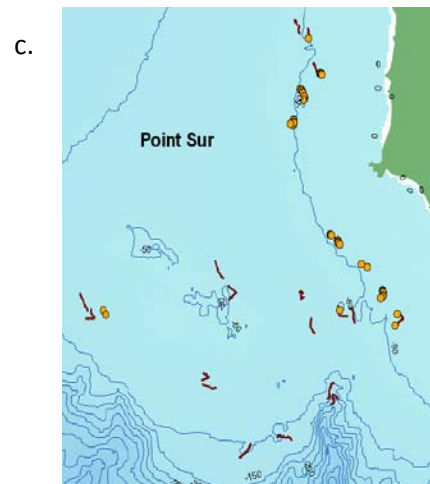
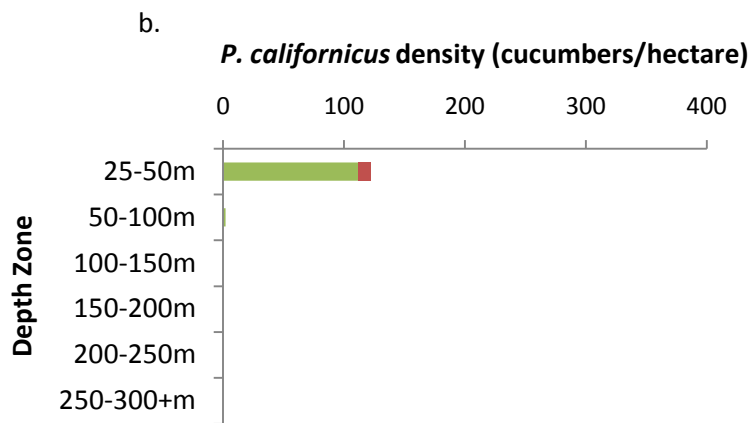
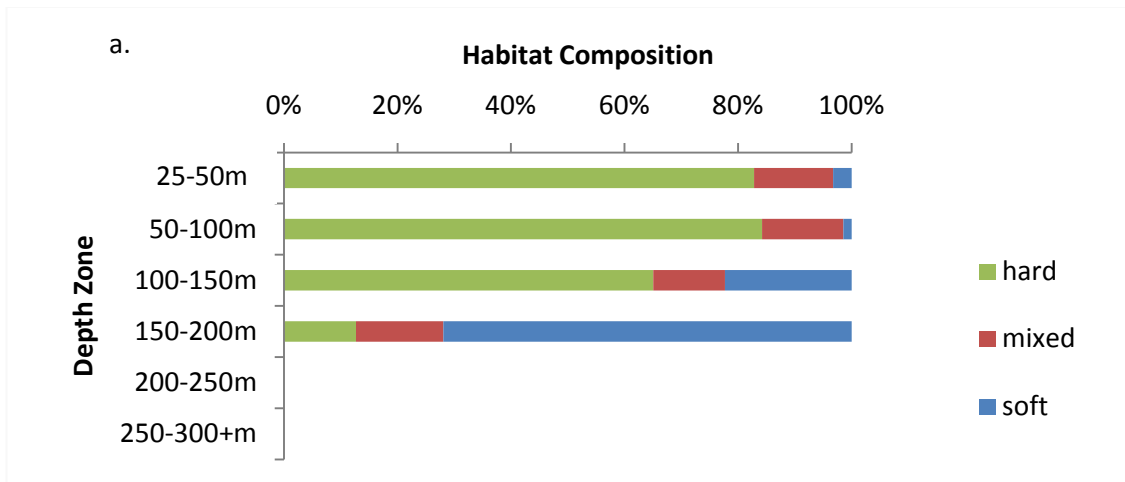


Figures 7a-e: Site-specific analysis for Portuguese Ledge. 7a shows percent habitat composition by depth zone. 7b, c show the density of *P. californicus* (b; n=282) and *P. leukothele* (c; n=2) by depth zone and habitat type. 7d, e show the actual observations of *P. californicus* (d) and *P. leukothele* (e) at the site (colored dots= individual cucumbers, red lines= transects). The legend in 7a applies to 7b and 7c as well.

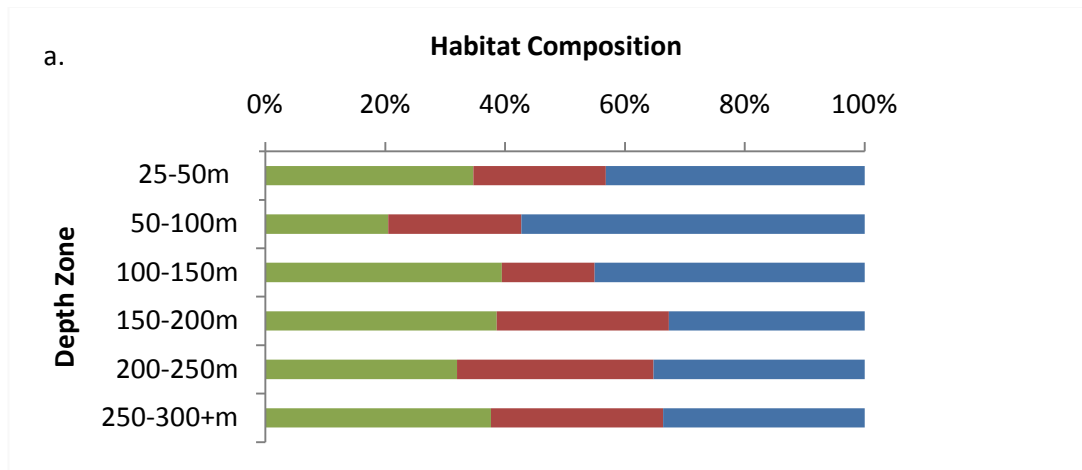




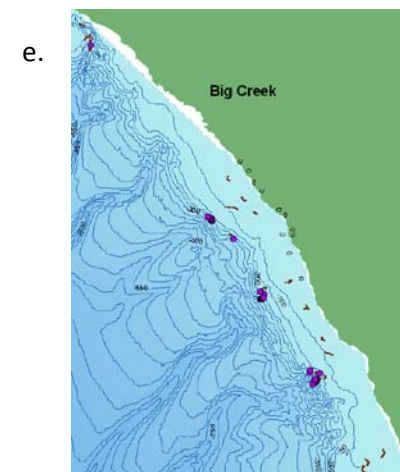
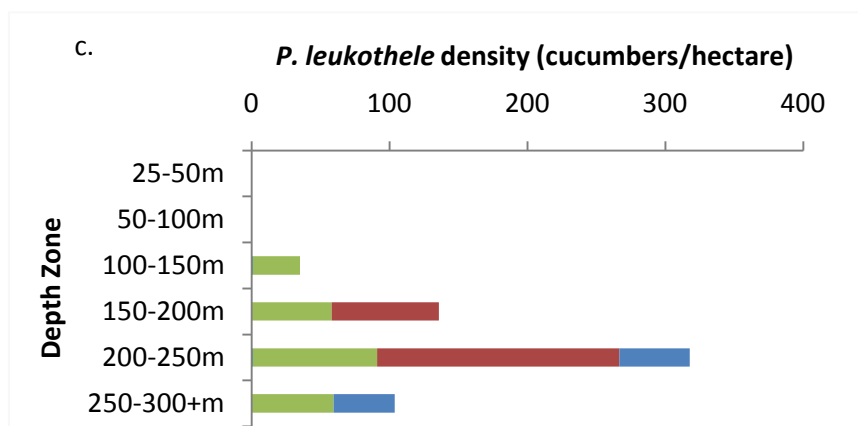
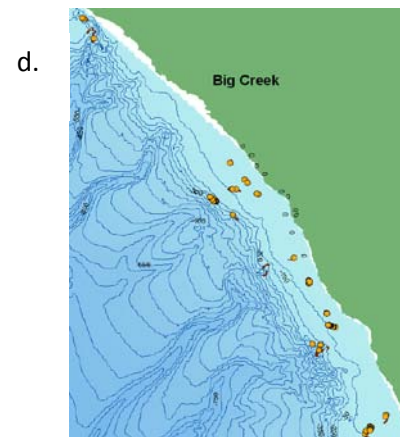
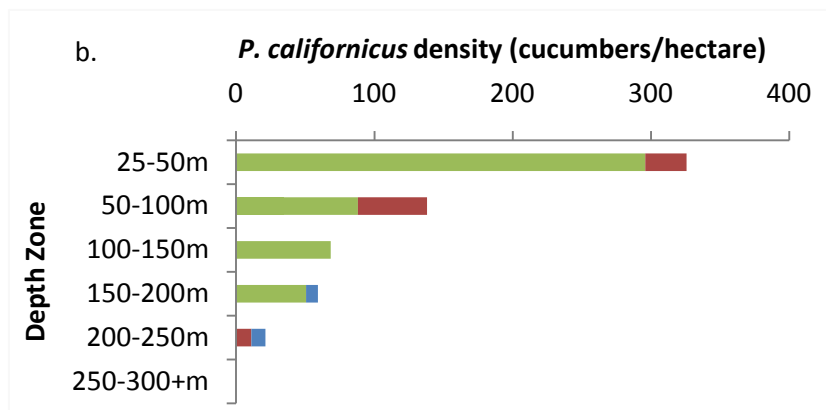
Figures 8a-c: Site-specific analysis for Point Lobos. 8a shows percent habitat composition by depth zone. 8b shows the density of *P. californicus* (n=301) by depth zone and habitat type. 8c shows the actual observations of *P. californicus* at the site (colored dots= individual cucumbers, red lines= transects). The legend in 8a applies to 8b as well.



Figures 9a-c: Site-specific analysis for Point Sur. 9a shows percent habitat composition by depth zone. 9b shows the density of *P. californicus* (n=68) by depth zone and habitat type. 9c shows the actual observations of *P. californicus* at the site (colored dots= individual cucumbers, red lines=transects). The legend in 9a applies to 9b as well.



Figures 10a-e: Site-specific analysis for Big Creek. 10a shows percent habitat composition by depth zone. 10b, c show the density of *P. californicus* (b; n=103) and *P. leukothele* (c; n=54) by depth zone and habitat type. 10d, e show the actual observations of *P. californicus* (d) and *P. leukothele* (e) at the site (colored dots= individual cucumbers, red lines=transects). The legend in 10a applies to 10b and 10c as well.



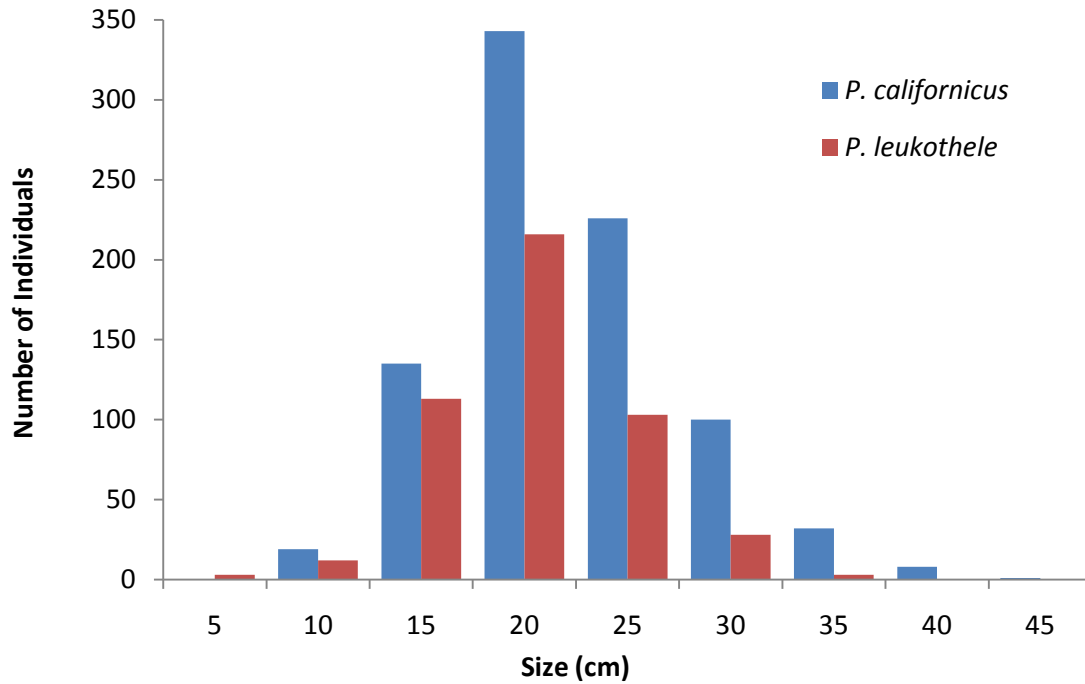


Figure 11: Overall size distribution for *P. californicus* (n=864) and *P. leukothele* (n=478). Individuals were sized to the nearest 5cm during video analysis of *Delta* submersible dives in central CA.

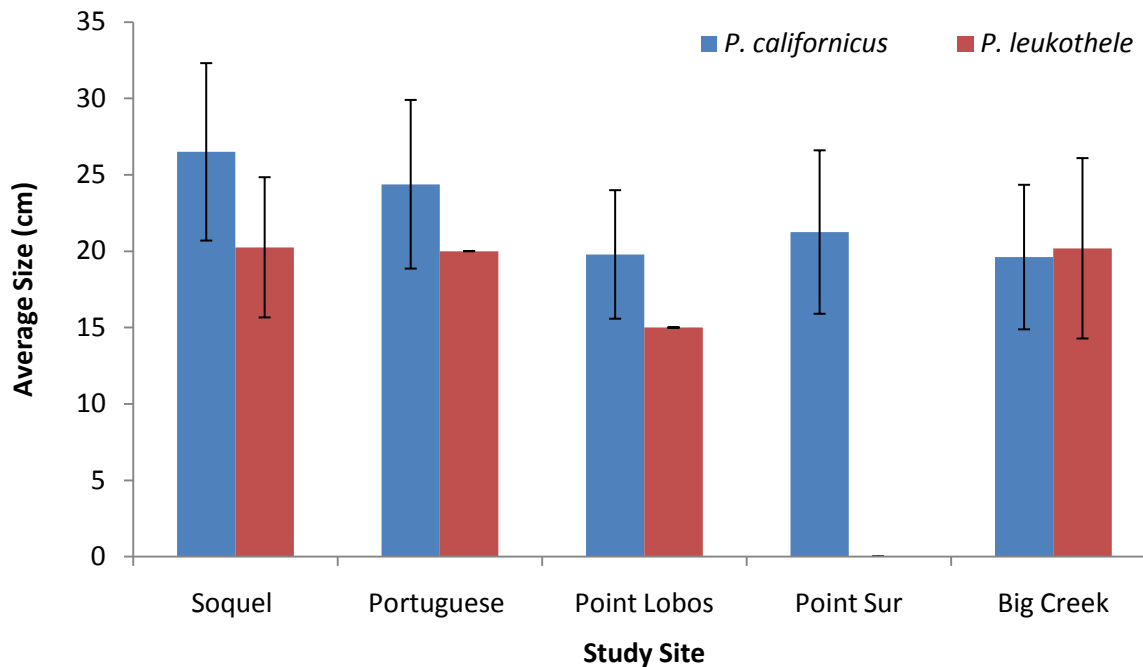


Figure 12: Average size of *P. californicus* (n=864) and *P. leukothele* (n=478) at each study site in central CA. Error bars are standard deviation. *P. californicus* was significantly larger in Soquel Canyon and Portuguese Ledge than in the other sites (ANOVA, df=4, 315, $p < 0.0001$).

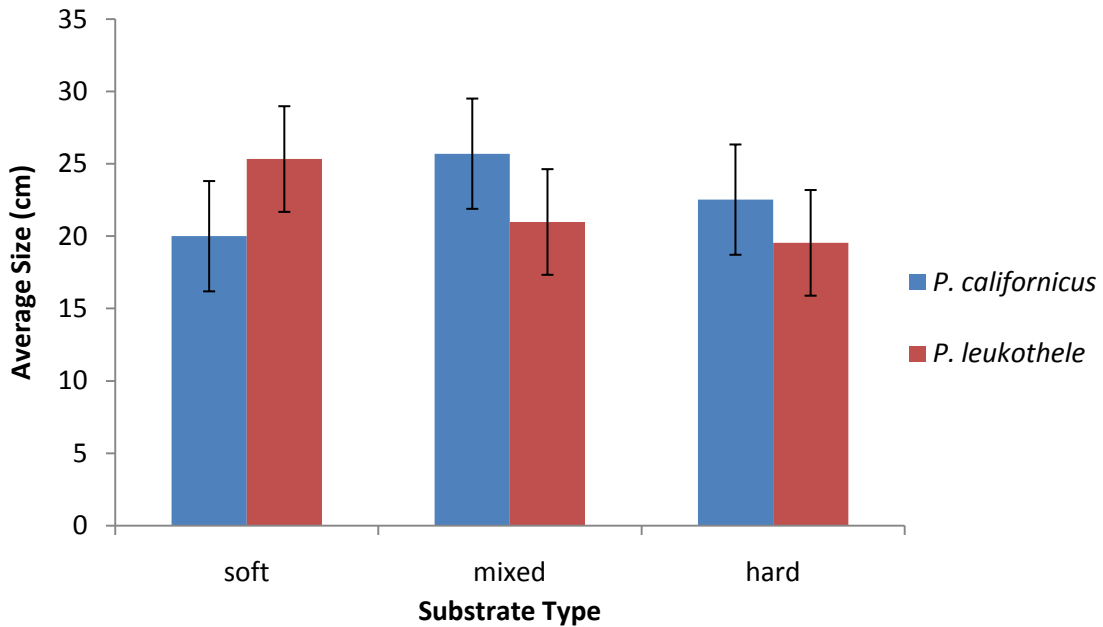


Figure 13: Average size of *P. californicus* (n=864) and *P. leukothele* (n=478) in each of the three substrate types. Error bars are standard deviation. *P. californicus* was significantly larger in mixed substrates than soft or hard (ANOVA, df=2, 317, $p<0.0001$); *P. leukothele* was significantly largest in soft substrates than in mixed or hard (ANOVA, df=2, 167, $p=0.003$).

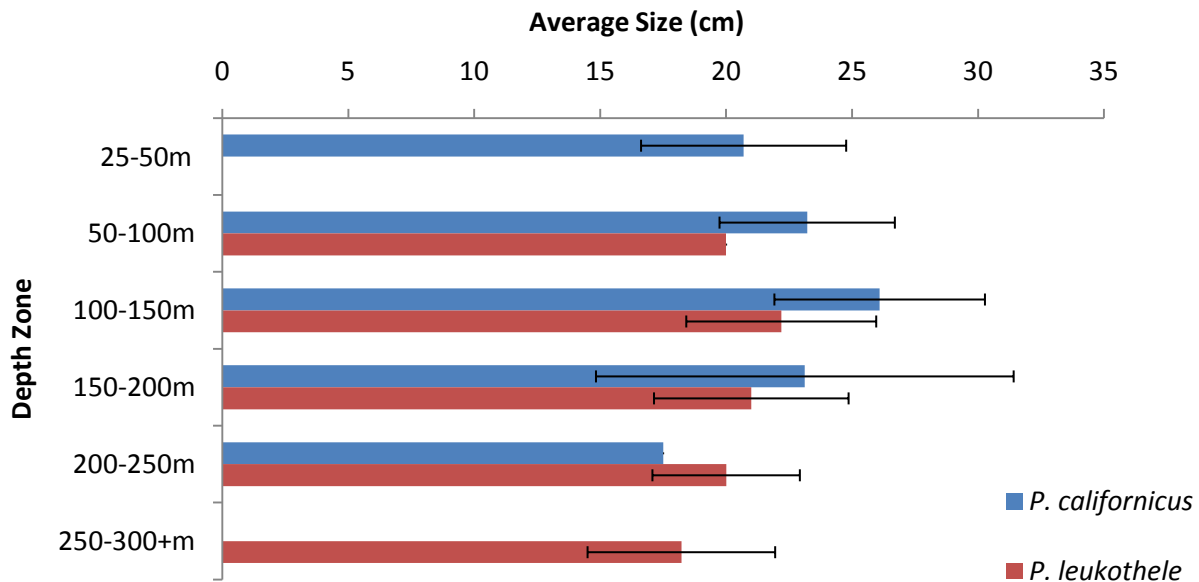


Figure 14: Average size of *P. californicus* (n=864) and *P. leukothele* (n=478) by 50m depth zone. Error bars are standard deviation.

APPENDIX A: Average temperatures ($^{\circ}$ C) of all dives by depth zone at each site. Temperature readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	11.4	11.8	11.6	<i>11.6</i>
50-100m	9.1	10.2	11.0	10.8	10.7	<i>10.4</i>
100-150m	9.2	9.9	9.5	10.0	9.7	<i>9.6</i>
150-200m	8.9	*	9.4	9.7	9.1	<i>9.3</i>
200-250m	8.0	8.5	8.7	*	8.6	<i>8.5</i>
250-300+m	7.7	7.8	8.1	*	8.2	<i>8.0</i>
Total	<i>8.6</i>	<i>9.3</i>	<i>10.1</i>	<i>11.1</i>	<i>10.2</i>	<i>9.9</i>

APPENDIX B: Average temperatures ($^{\circ}$ C) of *P. californicus* observation points by depth zone at each site. Temperature readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	11.5	11.8	11.5	<i>11.6</i>
50-100m	9.0	10.2	10.6	*	9.9	<i>9.9</i>
100-150m	9.1	9.8	*	*	9.7	<i>9.5</i>
150-200m	9.4	*	*	*	9.3	<i>9.4</i>
200-250m	*	*	*	*	8.5	<i>8.5</i>
250-300+m	*	*	*	*	*	<i>*</i>
Total	<i>9.2</i>	<i>10.2</i>	<i>10.7</i>	<i>11.8</i>	<i>11.0</i>	<i>10.6</i>

APPENDIX C: Average temperatures ($^{\circ}$ C) of *P. leukothele* observation points by depth zone at each site. Temperature readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	*	*	*	<i>*</i>
50-100m	8.8	*	*	*	*	<i>8.8</i>
100-150m	9.2	9.7	*	*	9.6	<i>9.5</i>
150-200m	9.2	*	*	*	9.2	<i>9.2</i>
200-250m	8.1	8.4	*	*	8.7	<i>8.4</i>
250-300+m	7.2	*	8.0	*	8.5	<i>7.9</i>
Total	<i>8.5</i>	<i>9.1</i>	<i>8.0</i>	<i>*</i>	<i>8.9</i>	<i>8.6</i>

APPENDIX D: Average salinities (ppt) of all dives by depth zone at each site. Salinity readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	33.7	33.7	33.8	33.7
50-100m	34.0	33.8	33.8	33.7	33.9	33.8
100-150m	34.0	33.8	33.9	33.8	34.0	33.9
150-200m	34.1	*	34.0	33.9	34.1	34.0
200-250m	34.1	34.1	34.1	*	34.1	34.1
250-300+m	34.2	34.2	34.2	*	34.2	34.2
Total	34.1	34.0	33.9	33.8	33.9	33.9

APPENDIX E: Average salinities (ppt) of *P. californicus* observation points by depth zone at each site. Salinity readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	33.7	33.7	33.8	33.8
50-100m	34.1	33.8	33.9	*	33.9	33.9
100-150m	34.0	33.9	*	*	34.0	34.0
150-200m	34.0	*	*	*	34.0	34.0
200-250m	*	*	*	*	34.2	34.2
250-300+m	*	*	*	*	*	*
Total	34.0	33.8	33.8	33.7	33.8	33.9

APPENDIX F: Average salinities (ppt) of *P. leukothele* observation points by depth zone at each site. Salinity readings were collected by the submersible's CTD each second. * indicates 'no data.'

Depth Zone	Site					Total
	Soquel Canyon	Portuguese Ledge	Point Lobos	Point Sur	Big Creek	
25-50m	*	*	*	*	*	*
50-100m	34.1	*	*	*	*	34.1
100-150m	34.0	33.9	*	*	34.0	34.0
150-200m	34.0	*	*	*	34.0	34.0
200-250m	34.1	34.1	*	*	34.1	34.1
250-300+m	34.2	*	34.2	*	34.2	34.2
Total	34.1	34.0	34.2	*	34.1	34.1