Population dynamics of the sheep crab Loxorhynchus grandis (Majidae) Stimpson 1857 at La Jolla California

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Abstract.

An unexploited population of the sheep crab Loxorhynchus grandis (Majidae, Brachyura) was studied for three years in the nearshore region adjacent to the Scripps Institution of Oceanography. Over 1000 crabs were collected in monthly surveys at three sites in water of between 10 and 20 meters depth. Size, sex, reproductive condition, carapace condition, and leg damage were recorded before crabs were individually tagged and released. Four crab aggregations were observed at one of the sites (Sand Plain). The function of these aggregations seems to be for reproduction, as a lower percentage of brooding females, and a higher percentage of males was observed than when crabs were not aggregated. A total of 564 crabs was tagged at the Pier site and the overall recapture rate was 39%. At the Pier adult females were more abundant than males, were recaptured more often (46% vs. 20%), and were also more sedentary than males. The Jolly-Seber mark-recapture technique was used to estimate the regional L. grandis population size, which ranged between zero and 300 crabs. Juvenile crabs were only found at the Dike Rock site and exhibited a peak in abundance between January and May. Adults were found occasionally at Dike Rock, but were most abundant at the Pier. Peak crab abundance at the Pier was in July for two years, and in January for one year. Adult males had significantly more damage to the claws and first pair of walking legs, and likely lose them in aggressive interactions. Females had a high frequency of damage to the first pair, perhaps sustained in mating behavior, while juveniles had radially symmetric patterns of leg damage, suggesting they were more passive and did not react to threats of leg damage. The speed that these crabs can move (0.40 km hr^{-1}) was estimated by following tagged crabs for short periods of time. The results of this study also suggest that L. grandis has both alongshore and offshore separation of ontogenetic stages.

Keywords: carapace condition, leg loss, mark-recapture, ontogenetic migration, sex ratio, sheep crab.

1. Introduction

Majid crabs are often extremely mobile, can reach large sizes and occur in high densities (Hooper, 1986; Stevens et al., 1993a, b; Comeau et al., 1998). Large majids also support substantial commercial harvests in many regions (e.g. Somerton, 1981; Watanabe, 1992; Lovrich et al., 1995; Byrne and Cross, 1997). Despite their importance and potential influence in nearshore ecosystems and fisheries, little research in the field has been conducted on the population dynamics, reproductive cycles, habitat use, or behavior of unexploited populations. The sheep crab (Loxorhychus grandis, Family Majidae) is a regionally exploited crab (Culver and Kuris, 1992), and with all life stages represented within diving depths, represents a valuable opportunity for the study of the population dynamics and ecology of a large majid crab in the absence of intense commercial fishing.

L. grandis is the largest crab found off the Californian coast. The latitudinal range is from Cordell Bank (Marin County, CA) to Punta San Bartolome (Baja California) and the depth range is subtidal to depths of 130 meters (Morris et al., 1980), however, unpublished submersible observations extend the lower depth limit to 200 meters (E. W. Vetter, pers. comm.). Despite a plodding appearance, L. grandis is an agile crab, parachuting from pilings, or moving rapidly across the bottom when disturbed or foraging. They are dietary generalists, eating algae, mussels, other crabs and even smaller members of the same species (Hines, 1982; Hobday and Rumsey, unpublished data).

L. grandis, like many of the Majidae, is an extensive carapace decorator as a juvenile although this behavior ceases with maturity (Wicksten, 1979; 1983; 1993; Hines, 1982). While active decoration may cease at larger sizes, many epibionts occur on the carapace of larger crabs. Carapace condition in terms of epibiont size and density has been used as an indication of the time since the last molt for other crab species (Abello et al., 1990; Gili et al., 1993). The majid family has been widely reported to have both a male and a female terminal molt, i.e. no more molting occurs once sexual maturity is reached (Hartnoll, 1963, 1982; Hines, 1982; Conan and Comeau, 1986; Donaldson and Johnson, 1988; Gonzalez-Gurriaran et al., 1995).

While large majid crab species are harvested commercially in Alaska and elsewhere (e.g. Comeau and Conan, 1992), there was little commercial interest in L. grandis prior to 1984. A substantial claw and live market in the Santa Barbara region was established in the 1980’s (Culver, 1991; Culver and Kuris, 1992). In 1984 between 30,000 and 40,000 pounds were landed. The harvest peaked in 1988 with landings of over 100,000 pounds of live crabs and 385,000 pounds of claws (both Cancer sp. and L. grandis claws are included in this total) (Culver and Kuris, 1992). Both males and females L. grandis were taken for the live market, but only male claws were harvested for the claw market. This crab is virtually unexploited in the region studied here (La Jolla); harvest is limited to infrequent captures by recreational divers, and bycatch in commercial lobster traps. Recreational harvesting is limited due to the unappetizing appearance of adults, while individuals captured in commercial traps are usually released (R. McConnaughey, pers. comm.).

This species has several unexplained and interesting behaviors. For example, large aggregations numbering hundreds of L. grandis have been observed (Hanauer, 1988), but the purpose of these aggregations is unclear. Aggregations are comprised of animals of both sexes, and some mating behavior has been observed (Hanauer, 1988).

Other Majidae may aggregate in large numbers for mating (DeGoursey and Auster, 1992; Stevens et al., 1993a, b) and molting (DeGoursey and Stewart, 1985).

Fluctuations in local L. grandis population size, habitat use, and behavior in the various stages of maturity have not been described in the field. In this paper we report the results of a three year mark-recapture study of a population adjacent to the Scripps Institution of Oceanography, La Jolla, California. We monitored the composition of aggregations, patterns of juvenile and adult abundance, carapace condition, leg loss, and reproductive cycles. Specific goals included determining the explanation and significance of the dense adult aggregations, monitoring the spatial and temporal variation in habitat use and reproductive behavior, and estimating the local population size.

2. Methods.

2.1. Collection sites

Loxorhynchus grandis were collected between December 1995 and November 1998 using SCUBA at three sites adjacent to the Scripps Institution of Oceanography (**Figure 1)**. The first site was a 1.5 m diameter railway-wheel mooring base located at a depth of 20 m one kilometer southwest of the Pier. Crab aggregations were occasionally observed here earlier in 1995, and it was these observations that led to this study. When an aggregation was found, all crabs in the aggregation were collected. Crabs were also collected, even when there was no large aggregation. The mooring base became completely buried by sand in December 1996, and sampling was discontinued as the site could no longer be reliably located, and no longer attracted any crabs. When visibility was poor (< 2 m) at any site collection was abandoned for that day.

The second site (Dike Rock), approximately one kilometer to the north of the Pier, is located on a gently sloping sandy bottom at the head of the Scripps Canyon (**Figure 1)**. Macroalgal detritus is scattered over much of the sandy bottom (see Vetter, 1995). The dive boat was anchored in the region of the site, according to onshore landmarks, at a depth of approximately 15 m. From the anchor, four 60 m long bottom transects were conducted: two transects in opposite along-shore directions; one transect onshore; and one transect in the offshore direction. The area surveyed was between 10 and 20 m depth. Two divers swam each transect side by side, approximately 2-5 m apart, depending on visibility, the length of a 60 m survey tape. Divers observed a non-overlapping swath between 2-5 meters wide. Thus the area surveyed by both divers at Dike Rock each month was between approximately 960 m^2 and 2400 m^2. All L. grandis within the survey area were collected.

The last site (Pier) consisted of the 26 most seaward pilings supporting the Scripps Pier (**Figure 1)**. The water was between six to ten meters deep at the base of the pilings. These one meter diameter pilings are heavily covered with fouling organisms, especially Mytilus spp, and are separated from each other by two to ten meters. Two divers collected all L. grandis on these pilings and the sand beneath the pilings at monthly intervals.

2.2. Measurements and tagging.

All crabs seen at the three sites were placed in canvas dive bags and returned to the dive boat for recording. In the first year collected crabs of all sizes were tagged with zip ties in various unique leg combinations which allowed individuals to be identified. For the following years tagging was with two identical pre-numbered zip ties attached to the rear legs (numbers 4 and 5 in **Figure 2**). Double tagging with the numbered tags also allowed tag loss to be evaluated, and was much easier to read than the combination method. Only morphologically mature crabs were number-tagged in the second and third year, as results from the first year showed that recaptures of juvenile crabs were minimal. Crabs with the original tag scheme were re-tagged if they were recaptured after the first year.

Aboard the boat, each crab was examined for an existing tag, and if present the combination or number was recorded. A number of measurements were made to the nearest 0.1 mm with calipers on both recaptured and new crabs. For the analyses presented here, only body size, measured as carapace width (CW) at the widest point, is reported. Sex was determined from abdominal allometry. The presence of eggs was recorded (brooding/not brooding) and if the female was brooding, the color of the eggs was noted, which indicates the stage of development; orange (fresh), red (intermediate), brown (eyed and soon to be released)). Rhizocephalan parasites were also noted if they occurred in the abdominal cavity of either sex. Carapace decorating was recorded, and for individuals not decorating, a carapace condition (CC) in terms of freshness and degree of epibiont cover and size was subjectively scored by one author (SR) on a relative scale from 1-4. CC 1 included carapaces that were covered with a brown epicuticle with sharp spines, and had no epibionts. CC 2 included those crabs with a blue-green exocuticle and worn spines, and limited epibiont growth. CC 3 was assigned to crabs with a blue-green exoskeleton and a heavy cover of small sized epibionts, while CC 4 was reserved for crabs with well-worn carapaces that bore a heavy cover of large epibionts. Missing, regenerating, or broken legs were recorded as “damaged” using a leg-numbering scheme that allowed the leg that was damaged to be noted (**Figure 2).**

At the Pier, crabs were returned to the water by divers and replaced on the pilings. Approximately 20% of crabs, mostly males, refused to remain on the pilings, and parachuted to the sand where they remained or dispersed. At the Dike Rock and Sand Plain sites, animals were dropped over the side of the boat after processing. Care was taken to “de-gas” animals before release, so they would not float.

Recapture rate, sex ratio and leg loss patterns, and female reproductive and carapace condition cycles were variously analyzed by sex, size and location. Adult crabs were identified by abdominal allometry in the case of females, and claw morphology for males. All crabs larger than 10 cm CW were morphometrically mature, and this size was used to separate adult and juvenile crabs for some analyses, even though a small number of crabs below this size were morphometrically mature. Chi-square (χ^2, with Yeats Correction when df = 1), t-test and regression analyses were used to test the significance of these patterns.

2.3. Population Size.

The regional population size was calculated for L. grandis living in the vicinity of the Pier using the Jolly-Seber mark-recapture method (Krebs, 1989; Seber, 1986). This method was preferred over the more commonly used Peterson Method, which is used for sequential pairs of samples and has a tendency to overestimate population size (Krebs, 1989). The Jolly-Seber method of estimating population size is appropriate for open populations which are sampled multiple times, and allows for immigration, emigration, births and deaths. The assumptions of this method are based on random sampling, and it is important that (i) marked and unmarked animals have equal probability of being captured, (ii) tagged individuals have the same probability of survival between sample dates, (iii) individuals do not lose tags or have tags missed during sampling, and (iv) sampling time is negligible with regard to the interval between sampling. Assumptions (i) (iii) and (iv) are met, however assumption (ii) may not be, as older animals may have a lower probability of survival than younger animals. It was not possible to test this assumption, as the age of crabs was unknown. It was hoped to use carapace condition as a proxy for age, however, it varies with habitat (see Results).

For this analysis, crabs were counted as new when they were collected at the Pier for the first time, even if they were tagged elsewhere (a few animals arrived at the Pier after being tagged in aggregations on the Sand Plain site). Recaptures were those crabs previously collected at the Pier. This method provides an estimate of the regional population size that the Pier “samples”.

2.4. Movements.

On two days adult crabs collected from the Sand Plain were released and then observed moving across the sand to determine movement speeds. On the first day estimates of maximum walking speed were obtained, using six adult crabs once each. One diver timed the trial, while the other diver swam closely behind the crab with a measuring tape. When the crab paused for more than a few seconds, deviated markedly from a straight line, or had walked approximately 60 meters, the trial was terminated. On the second date, a single adult male was released and observed from a distance as it walked across a sandy bottom. This trial was expected to provide more natural estimates of walking speed, and was repeated four times with the same crab. Speed was calculated as the walking time divided by the displacement distance from the release point.

3. Results

3.1 Sand Plain and Aggregations.

Four aggregations were observed on the Sand Plain site between December 1995 and November 1996 **(Table 1)**. Crabs were piled on top of each other around the base of the railway-wheel anchor. Each aggregation was 1-2 meters in diameter, and averaged 24 animals in size. All crabs were morphometrically mature adults and all had hard carapaces, indicating that none had molted recently (see also CC results below). Piles were comprised largely of females (average 84%), but all contained at least one male. Between 13 and 33% of the females sampled were brooding eggs, however, the egg color was not recorded.

On occasions when aggregations were not found, some crabs were still collected. These animals are included in some of the analyses described below. About December 1996, the wheel was buried by sand and sampling was discontinued at this site. Sporadic visits in the next two years to the vicinity of the site did not detect any sign of the wheel, or aggregations.

3.2. Dike Rock.

A total of 518 L. grandis was collected at the Dike Rock site, over 33 sampling dates between February 1996 and December 1998 (**Figure 3)**. Of this total, 94.2% were less than 10 cm in CW, while 5.8% were larger, and classified as adults in subsequent analyses. The adult crabs were collected through the study period. Juveniles at the Dike Rock were usually single, although occasionally several crabs were collected in a depression, or adjacent to an isolated boulder. The smallest crabs were about 1 cm CW. Smaller crabs of other species were seen by divers during collections, thus this size likely represents the smallest L. grandis that occurred at the site. There was a distinct cycle in the abundance, and a less distinct cycle in size, of the juvenile animals (**Figure 3).** Juveniles were most abundant between January and May, depending on the year of the study. The average size of juveniles during peak abundance was about 7 cm in March 1996, and 2 cm in both May 1997 and January 1998. The average size of juvenile crabs at this site increased as the abundance declined, indicating growth of the recruit cohort. Juvenile crabs with soft carapaces were occasionally collected, especially when large numbers were found, indicating that they had recently molted.

3.3. Pier.

The Pier was sampled at monthly intervals 31 times between March 1996 and November 1998 (**Table 2)**. In contrast to the Sand Plain, adult crabs at the Pier were never aggregated in piles. Crabs occurred from the piling base to within one meter of the surface as well as on the sand beneath the pilings. Multiple crabs were often found on pilings, but were not interacting. On some occasions, when replacing crabs about an hour after collection, one or two crabs that were either initially missed or had arrived since the first collection were observed. On most occasions no additional crabs were seen, indicating that all crabs at the site were collected. Any additional crabs were collected and sampled, then released.

A total of 939 crabs was collected at the Pier (some animals were collected on more than one occasion), and the average Pier population size was 30.29 ± 24.91 crabs per month. On average, 51.5% of collected crabs had been tagged previously, and an average of 38.75% had also been collected the previous month (**Table 2)**. Peaks in abundance occurred in July 1996, July/August 1997, and January 1998 (**Figure 4A, Table 2)**.

All crabs seen at the Pier were morphologically mature. The largest (smallest) male collected was 17.99 cm (8.43 cm) CW, while the largest (smallest) female was 15.54 cm (9.38 cm) CW. The average size of male (12.54 ± 2.02, n=174) and female crabs (12.32 ± 1.07 n=765) collected at the Pier was not significantly different (t-test with unequal variances, $t_{197} = 1.40$, p=0.162). The average size of male and female crabs collected did not change with sampling date (**Figure 4B).**

Dead crabs, both tagged and untagged, were occasionally observed at the Pier throughout the study period (n ~ 10-20). They were often heavily encrusted with epibionts. Dead females usually still had a brood of eggs. Cause of death was not determined.

3.4. Sex ratio.

The average percentage of morphologically mature males in aggregations sampled at the Sand Plain was 26% (range 4-17%) (**Table 1)**. Crabs collected at the Pier and at Dike Rock were pooled and divided into one cm size classes by sex. Each crab was only included the first time it was collected. A total of 1077 crabs was measured, however only 811 crabs were sexed at these sites (539 females, 272 males). Additional smaller animals (n = 266) were collected but could not be sexed due to uncertainty about abdomen shape. Our ability to sex crabs smaller than about 5 cm CW increased over the period of the study. The sex ratio (% males) by size class fluctuated around 50% up to 10 cm CW, although males were significantly more abundant between 3 and 5 cm CW ($p<0.05$) **(Figure 5).** Between 10 and 15 cm CW, females were significantly more abundant ($p<0.05$-0.005), while above 15 cm, males were most frequent ($p<0.05$-0.01) **(Figure 5).**

When the sex ratio for all crabs collected (again each crab was included only once) was examined separately at each site, a slightly different pattern emerged (**Table 3).** At both the Pier and Dike Rock the percentage of males below 10 cm CW was 54 % for animals smaller than 4.20 cm CW (chosen because some crabs smaller than this were not able to be sexed early in the study), and 53 % for crabs between 4.20 cm and 10 cm CW. At sizes above 10 cm CW the Pier was dominated by females (only 23.7 % of crabs collected were male), however, at Dike Rock the sex ratio was more equitable, with 46.6 % of collected crabs being males.

The percentage of males at the Pier collected in each months sampling ranged from 0-30%, averaging 14.9% male **(Table 2)**. This ratio was for the monthly samples, and included recaptured crabs. Male crabs were absent from the Pier more often than females (**Figure 4A**).

3.5. Pier recapture rates.

A total of 564 different L. grandis was tagged at the Pier between March 1995 and November, 1998, of which 39% were recaptured at least once (**Table 4)**. Females were recaptured more often than males (46% v's 20%). Crabs were recaptured between 0 and 7 times, with a higher proportion of females than males being recaptured (**Table 4).**

The most consecutive months a crab was seen at the Pier was 8 months. (**Figure 6A).** The average number of consecutive months that a crab was seen at the Pier was 1.49 months. Males remained at the Pier for significantly shorter periods than females (2-tailed unequal variances t-test on log(x+0.1) transformed data, $t_{296}=4.196$, $p<0.0001$), average residence time was 1.28 months compared to 1.55 months.

The maximum time between captures was nine months, which was recorded for two females **(Figure 6B).** The longest period between male captures was two months. The average number of months between captures for both sexes was 1.77 months, and was significantly higher ($t_{11}=2.38$, $p<0.037$), for females (1.81 months) than for males (1.14 months).

Finally, the maximum lifetime in the study was thirteen months for a female crab, while the longest male lifetime was seven months **(Figure 6C).** The average lifetime in the study (including animals captured only once) was 2.08 months. Females had a significantly longer average study lifetime (2.31 months) than males (1.40 months) (t_{384} = 7.15, p<0.0001).

3.6. Tag loss.

L. grandis held in the lab for other studies retained readable tags for over two years. In the field, the longest time between tagging and recovery of a tagged crab was 13 months (**Figure 6)**, indicating that tags lasted at least this long in the field. Of 510 crabs double-tagged with the numbered tags on legs 4 & 5, only two were recaptured with only a single tag, and the tag loss was due to loss of one of the tagged legs, and not to tag failure. Only three untagged crabs were captured with both legs 4 & 5 missing, and so the maximum potential loss of both tags due to leg loss is 0.6% (3/510). Thus the chance of a crab losing both tags (the two rear legs) and being recaptured and counted as a new animal if recaptured is negligible.

Tags will be also be lost if the crab molts, however at the Pier all the crabs tagged were morphometrically mature and are not believed to molt again. If this is true, tag loss on adults due to molting should not be a factor. Recoveries of juveniles tagged at Dike Rock (n=4) were negligible, and in this case molting is likely to lead to tag loss. No molt exuviae with tags were recovered at this site, and it is probable that juvenile tagged crabs moved out of the study area between surveys.

3.7. Population size estimate.

The Jolly-Seber mark-recapture method was used to estimate the total L. grandis population size in the vicinity of the Pier between March 1995 and October 1998 (the final month of sampling, November 1998, does not allow an population estimate using the Jolly-Seber method). The average adult population size was estimated at 60.8 crabs, with a maximum estimate of 258, while the minimum was zero (**Figure 7).** Confidence limits (95%) around the estimates ranged from 699 crabs to zero. The area that the population estimate applies to is unknown, and a "density" of crabs in this region cannot be calculated.

As for the real Pier abundance, there were seasonal peaks in the estimated local abundance. In the first two years of the study the population peaked in July-September period, at the time the temperature was also highest, however in the final year, the peak population estimate was in January-March, prior to the temperature increase (**Figure 7)**.

3.8. Leg loss.

A total of 1195 individual crabs was examined for leg loss, regeneration and breakage, collectively called "damage" (**Table 5)**. L. grandis did not autotomize legs during handling. Of 688 adults examined, 259 (37.65%) had damaged or were missing at least one appendage. The most frequent damage was a missing appendage, followed by regenerating and broken limbs. Adult males had a higher frequency of leg damage than adult females. Juvenile animals had much less damage, only 12.4% showed missing, regenerating or broken legs. Crabs with up to six legs damaged were collected, although the majority of damaged crabs (65%) had only one leg affected (**Table 5).**

Not all appendages were equally likely to be damaged, however, damage was symmetrical about the longitudinal axis of the crab. Thus leg pairs were created for analysis of leg damage patterns (see **Figure 2).** A total of 490 legs were affected on the 1195 individuals, and the pattern of leg damage differed between adults (defined as CW > 10 cm) and juveniles (CW < 10 cm), and between the sexes (**Figure 8)**. The frequency of leg pair damage was not significantly different among pairs for juveniles ($\chi^2 = 5.16$, 4 df, χ^2 critical=9.488), but was significant for males ($\chi^2 = 11.28$, 4 df, $p<0.025$), and females ($\chi^2 = 18.92$, 4 df, $p<0.001$). Males had more damaged appendages from the forward two pairs (C1 & C2, 1 & 8), while females had more damaged legs from the second pair than expected, about 30% of all damaged female legs were from the 1 & 8 leg pair (**Figure 8).**

3.9. Female reproductive condition.

A total of 765 observations of brooding state was made on mature females collected from the Pier over 31 sampling months. An average of 24.6 females per month was examined (see **Figure 4** for sample sizes). An observation was made each time a female was collected, even if she had been previously tagged and examined. Females were observed to be carrying eggs at all times of the year (**Figure 9)**. Overall, 93% (range 66-100%) of females examined from the Pier were brooding eggs, with an average of 17.4% carrying brown eggs in any month.

There was no obvious cycle to the presence of eggs or brooding stage, although spawning events in January, 1997, September-December 1997, and August-November 1998 might be inferred from the drop in the percentage of females with eggs (**Figure 9)**. The length of time females carried eggs was not determined.

3.10. Carapace condition.

Crabs smaller than 8 cm CW collected at Dike Rock always had carapaces decorated with algae and other detritus. Crabs with soft carapaces (recently molted) were sometimes found when large numbers were collected. Decorated carapaces were not found on crabs greater than 8 cm CW, and these animals were assigned a carapace code.

Adult L. grandis collected at the Pier had all four carapace conditions (CC) throughout the year (**Figure 10).** CC 2 was the most common, while CC 4 was the least frequent. Crabs with CC 4 may have had reduced survival, or been at the end of their lifespan, as the heavy epibiont load of barnacles and mussels sometimes appeared to inhibit their movements. Peaks in the frequency of CC 1 indicates crabs that had recently molted, however, they were not soft when collected at the Pier. These peaks occurred in June, 1996, April, 1997, and December 1997/January 1998. These peaks were not always associated with increases in abundance at the Pier, which would suggest that the abundance peaks were due to the arrival of recently molted crabs from juvenile habitat such as Dike Rock.

The four CC were not found at all sites for crabs larger than 10 cm CW (**Figure 11).** The frequency of CC was similar between the sexes at each site, but differed between sites. The crabs collected at Dike Rock were typically CC 1, a condition which was rarely encountered at the Pier. The highest frequency of CC 4 was found amongst adult females at the Pier.

The four CC were associated with all sizes of crabs larger than 10 cm CW (**Figure 10, 11**). There was a slight, but significant increase in CC with CW for both males ($F_{1,116}$ = 4.471, p=0.037) and females ($F_{1,373}$ = 6.619, p=0.010) at the Pier, but it explained little of the variation in CC with size (R^2 < 0.04 for both sexes).

3.11. Rhizocephalan Parasites.

No crabs with visible externa of rhizocephalan parasites were collected at any of the sites.

3.12. Movement.

Adult L. grandis that were released and followed closely underwater gave estimates of maximum walking speed of between 0.47 and 0.80 km hr^{-1} (average 0.62 ± 0.15 km hr^{-1}, n=6)**.** These estimates should be considered burst speeds. A single male provided an estimate of "typical" walking speed of 0.40 ± 0.03 km hr^{-1} (range 0.36- 0.43 km hr^{-1}, n=4).

Anecdotal evidence of distances traveled by individual crabs is provided by sightings of tagged crabs by divers not associated with this project. For example, one male tagged and released at the Pier was observed at the head of Scripps Canyon one day later, a distance of approximately one kilometer. One tagged male (dead) was recovered at the La Jolla kelp forest, approximately two kilometers from the Pier, some two months after tagging.

4. Discussion.

4.1. Aggregations.

Four L. grandis aggregations were sampled during the period of this study. They occurred between the months of October and December (late Fall, early Winter), but were only observed in the first year of the study. The feature (metal railway car wheel) with which the aggregation was associated was buried by sand in the second and third years. In addition to providing some elevation above the "featureless sand bottom", the wheel was also a potential food source, as mussels growing on the mooring line above the anchor fell to the anchor base from time to time. Culver (1991) reported that L. grandis aggregations in the Santa Barbara region occurred in the spring and summer, while Hanauer (1988) reported one in April near Redondo Beach, Los Angeles. The sporadic occurrence of large aggregations has been noted for L. grandis and for other majid species (DeGoursey and Stewart, 1985; Hanauer, 1988; Stevens et al., 1993a, b). The aggregations sampled here were also smaller in size than has been observed for this species elsewhere (Hanauer, 1988, Culver, 1996). The sex ratio was biased towards females (consistent with previous reports), the majority of which were not brooding (inconsistent with previous reports). No soft crabs were observed in aggregations in this study, thus the hypothesis that L. grandis forms molting aggregations was not supported. Compared to the populations sampled monthly at the Pier, the aggregations observed on the sand plain contained a lower percentage of brooding females and a greater percentage of males. In another observation of hundreds of aggregated L. grandis in approximately 30 feet of water the sex ratio was highly skewed towards the females, however, these crabs were all brooding (Hanauer, 1988). Many of the males had grasped females, and assumed mating positions. This behavior was not observed in the aggregations in this study, although a few single pairs at the Pier were observed while mating.

It is unknown whether females begin to aggregate prior to spawning, or if they disperse from aggregations before laying the new clutch. The presence of some brooding females in the aggregations observed suggests one of these patterns occurs, but unfortunately, the color of the eggs was not recorded early in this study, and no aggregations were observed in the later period. Nonetheless, non-brooding females may be aggregating to attract males. It is unknown what the signal is, but aggregation may increase the concentration of some chemical signal (Hooper, 1986). All the evidence suggests that the function of the aggregations observed here is to attract males for mating, as has been reported for other majid species (e.g. Hooper, 1986; DeGoursey and Auster, 1992).

The time of aggregation observations coincided with a drop in the abundance of crabs at the Pier (**Figure 4A)**, suggesting that aggregations on the sand plain may have been comprised of local crabs. Conversely, the aggregations could represent the first stage in an onshore migration that leads to higher abundance at the Pier. Clearly, additional investigation into this relationship is needed before conclusions are drawn.

4.2. Reproduction, recruitment, abundance and recapture patterns.

In this study females were found to brood eggs all year with no strong spawning signal detected, although a slight peak in spawning may have occurred between August-January, depending on the year. Culver (1991) also observed year round brooding, but suggested that a seasonal spawning peak occurred in late spring and through the summer, with peak numbers of larvae in July and August. In 1992 settlement of Loxorhynchus spp. was observed in May and June at Bodega Head in northern California (Wing et al., 1995). This information suggests that, while poorly understood, the timing of settlement is varied spatially and temporally.

Recruitment (as shown by the peaks in juvenile abundance at Dike Rock) is seasonal, and may result from episodic spawning events. Females brooding brown (eyed) eggs, however, were seen at all times of the year, but the length of time that eggs are in this condition before release is unknown. The total brood time is also unknown. If larvae are released all year, seasonal recruitment of juveniles may reflect variable transport of larvae to the nursery area (e.g. Wing et al., 1995). Differences in the signals might also be due to variability in post-settlement mortality. Year round reproduction amongst majid crabs is not unusual. It has been reported for most tropical species, while in temperate waters, breeding may be continuous or seasonal (Hartnoll, 1965). Investigation of the causes of variation in recruitment of this species is necessary to explain the observed pattern.

Peaks in abundance of both adults at the Pier and juveniles at Dike Rock were found in this study. Juvenile abundance was highest between March and May in all years, and represents a recruitment peak. The smallest crabs collected were 1 cm CW. These peaks occurred approximately three to six months after possible female spawning events but the average size of crabs during peak juvenile abundance varied between years (**Figure 3)**. The time from spawning to megalopal settlement, and for subsequent growth to the juvenile sizes found at Dike Rock is unknown. Juveniles were only detected at the

Dike Rock site, which is a detritus covered sandy bottom. A rocky intertidal platform is found inshore of the Dike Rock site, and may be the location of larval settlement. Subsequent offshore migration of crabs to the Dike Rock study area may have occurred. At the two other sites sandy bottoms occurred but no juveniles were collected. Spatial segregation of developmental stages and reproductive stages has been observed in other majid crabs (Gonzalez-Gurriaran and Freire 1994, and references within; Lovrich et al., 1995).

Abundance of adults at the Pier peaked later in the year, in July 1996 and 1997, and January 1998. The July peaks coincided with the warming of nearshore waters, but the January 1998 peak coincided with the coolest monthly temperatures. Temperature is also correlated with wave height, and day length, which would show a similar match with abundance in the first two years, but not in the third. The cue or signal for an onshore migration of adults remains unknown.

The seasonal peak in abundance at the Pier seems to be the result of an onshore migration of mature animals, rather than an alongshore migration from juvenile (e.g. Dike Rock) to adult (Pier) habitat by maturing crabs. No peak in frequency of recently molted carapaces was detected at Dike Rock during the increase in Pier abundance, which would support a hypothesis that adult abundance was due to immigration from nearby juvenile populations. Instead it is likely that, as for other majid species, juvenile L. grandis settle in shallow water, perhaps attracted to a detritus covered bottom such as at Dike Rock, move to deeper water as they mature, before later joining an onshore migration of deep-living adults (Taylor et al., 1985). This movement of juvenile L. grandis to deeper water was anecdotally supported by Culver (1991). Further evidence for deep living crabs was submersible observations of very large male L. grandis (CW>20 cm) at depths of 200 m 1-2 kilometers further offshore from the Pier in 1998 (S. M. Rumsey and E. W. Vetter, unpublished data). Similar seasonal and ontogenetic migrations have been reported in other majid crabs, and have been linked to water temperature and reproduction (Taylor et al., 1985; Lovrich et al., 1995).

At the Pier, there was a 35% chance of recapturing a crab in consecutive months. Females were more likely to be recaptured than males, remained at the Pier longer and returned to that site after considerable absences, and were in the study area for longer than males. This suggests that females are more sedentary than males, and if they do roam, move shorter distances than males. Adult females of other majid species are also more sedentary than males (Lovrich et al., 1995).

The region of the Pier is estimated to support an average population of 60 crabs, however this fluctuated through the year. Reasonably tight 95% confidence limits suggests that these population estimates are sound. The estimated abundance in the region of the Pier was similar to the population cycle on the Pier.

The Pier average population size of 30 crabs thus represents half of the local estimated population. More extensive tagging surveys are required to determine the extent of this local area, and the role of emigration and immigration. It is likely that a larger pool of animals offshore supplies new crabs each year, and these are detected in the onshore migrations that led to peaks in Pier abundance. Loss of a single tag due to leg loss was very rare (2 out of 1020 tags), the loss of both tags (legs) should be even less frequent. Thus, estimates of population size based on the mark-recapture information are not biased by recapture of animals that have lost tags.

Disturbance due to collection and tagging of crabs may have reduced the population size at the Pier. For example, crabs were observed leaving the Pier region after release. The magnitude of the disturbance effect is hard to determine. An estimated 10% of crabs replaced on the pilings by divers after collection refused to remain on the pilings, and moved away across the bottom. Thus the residence times and population sizes are probably underestimates of the situation in the absence of interference by collectors.

The total lifetime of L. grandis is unknown. An estimate of about three years can be made by combining the maximum lifetime in the study as an adult (13 months) with the time to reach adult size (2 years, Hobday, unpublished data). This estimate is expected to increase as tagged crabs are recaptured in future years.

4.3. Leg Loss.

The pattern of limb loss can be used to infer competitive and predatorial interactions, in the absence of direct observations. Overall leg damage frequency in this study was high, with 26% of L. grandis possessing some leg damage. Leg damage in other majid crabs has rarely been documented, however in three large anomuran species, leg loss ranged from 5-35% (Byrne and Cross, 1997).

In this study adult L. grandis had higher frequencies of leg loss than juveniles. This is in contrast to the pattern observed in Carcinus maenas where 14.7% of the adults and 25.6% of juveniles had missing or regenerating limbs (Abello et al., 1995).The pattern observed here may be due to a higher rate of antagonistic contact or predator attack as adults, a reduction in molt frequency and hence limb replacement, or to complete cessation of molting in the case of mature crabs. L. grandis did not automize legs during handling, indeed the crabs were extremely robust. This suggests that leg damage occurs only during very aggressive interactions, or during molting, when crabs are extremely vulnerable. Lab studies have shown that most leg loss occurs during molting, when legs may be stuck in the old carapace, or be eaten by conspecifics before the carapace hardens (Hobday, unpublished data). L. grandis appendages can only be regenerated during molting, and take several molts to return to normal size (Culver, 1991; Hobday unpublished data). In the red king crab, Paralithodes camischatica (a species with no terminal molt), five molts are required for the complete regeneration of a leg (Edwards, 1972, in Somerton and MacIntosh, 1983).

Juvenile L. grandis did not show any pattern in the appendages that were damaged, suggesting that they did not have an opportunity to react to potential leg damage, by either flight (increase in posterior leg loss frequency) or fight (increase in anterior leg loss frequency) responses. Adult male L. grandis had a higher overall frequency of leg damage than females, which may be related to their more aggressive behavior (personal observations). They may also encounter predators more often as they roam the sand plains. The front legs and claws were lost significantly more often than the rear ones, suggesting that they may face the threats to leg-damage. L. grandis also extend the first walking legs and use them as “feelers” (M. Wicksten, pers. comm.), which may expose them to damage more frequently than other legs. Animals with the ability to damage L. grandis legs in this study region may include bat rays (Myliobatis californica), harbor seals and sea lions, other crabs (Cancer spp.), as well as conspecifics. Male crabs of many species have been found to have chelae as the most common missing limb

(Juanes and Smith, 1995). Chelae loss has been shown to affect mating success (Abello et al., 1994; Juanes and Smith, 1995). Males are unable to hold females, or defend them from other undamaged males. The pattern of female leg damage suggests that they are more likely to lose in passive battles, where claws not used, or in mating embraces, when males often hold them by the legs. Competing males sometimes attempt to pull females away from another male by the legs. Abello et al. (1994) found that male Carcinus maenas had higher loss of chelae than females and that the percentage of animals with chelae damage increased with size class, a factor attributed to longer intermolt periods, rather than sexual maturity and an increase in intraspecific conflict among larger animals.

Leg damage has also been shown to affect the ability of crabs in feeding, growth, and defense (e.g. see Juanes and Smith, 1995). The effect of non-chelae leg loss has not been examined, but may affect walking speed, climbing ability, foraging success, and mate defense. Further ecological study is required to determine the effect of leg damage on L. grandis.

4.4. Carapace condition.

Patterns in carapace condition (CC) did not strongly support recruitment from juvenile populations as an explanation for adult abundance peaks. The time to move between carapace conditions was not examined here, but could be estimated from growth rates of epibionts (e.g. Gili et al., 1993).

Differences in CC between habitats were found. These differences are probably related to age of crabs, and the proximity to fouling organisms. The slight but significant increase in adult CC with CW was unexpected, as crabs above 10 cm (morphometrically mature) are not believed to molt again. Thus size classes above 10 cm CW should contain animals of similar age. Possible explanations include differential survival, as larger adults may live longer (and move to CC 4) than smaller adults (less likely to live long enough for the carapace to reach this condition), and habitat differences, with larger adults occupying more fouling habitats than the smaller adults.

4.5. Rhizocephalan Parasites.

Surprisingly, no animals with rhizocephalan parasites were observed in this study. Culver (1991) reported that approximately 11% of L. grandis were parasitized by the rhizocephalan Heterosaccus californicus in the Santa Barbara region. Parasitism levels were also low in two other species of majid crabs (Pugettia producta and Taliepus nutalli) studied at the same time in the Scripps region (Hobday, unpublished data). The explanation for the differences in parasite prevalence rates between this region and Santa Barbara is unknown. Differences in prevalence rates have been found between habitats and regions for other species, and have been attributed to differences in water quality that affect the cleaning abilities of the crabs (Hoeg, 1995; Watters, 1998).

4.6. Movement and speed.

Walking speeds of adult L. grandis measured in this study showed that these crabs can move quickly across a sandy bottom (> 0.4 km hr^{-1}), and would allow rapid onshore/offshore movements and large daily movements alongshore. Rapid local increases in population sizes may be due in part to the speed that these crabs can migrate. The speeds reported are probably faster than natural speeds as there was some handling effect, and no acclimation period prior to the trials. Estimates were also based on a limited sample size. Rapid movements of other majid crabs has been detected with long-term radio-tracking (e.g. Gonzalez-Gurriaran and Freire, 1994). Gonzalez-Gurriaran and Freire (1994) observed a maximum displacement of 10.7 km in 31 days. Radio-tracking of L. grandis should be the next step in explaining the seasonal peaks in abundance observed here, and determining the extent of the nearshore region used by this species.

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Table 1. Description of aggregations of Loxorhynchus grandis collected on the Sand Plain one kilometer southwest of the Scripps Pier, at a depth of 20 meters. The range of sizes (carapace width, CW (cm)) associated with males and females collected in the aggregations is shown, as is the percentage of females, and number and percentage of brooding females. The reproductive condition of the females was not determined in sampling the first two aggregations that were observed.

Date observed	Size of aggregation	Number of males (range of CW)	Number of females (range of CW)	% female	Number of females brooding (%)
Dec 5, 95	22	6 (8.8-14.7)	16 (10.0-14.0)	73	-
Dec 8, 95	27[1]	5 (7.0-11.6)	22 (7.5-14.3)	81	-
Oct 7, 96	24	3 (14.3-16.5)	21 (10.6-15.6)	86	7 (33)
Nov 12, 96	24	1 (16.3)	23 (10.6-17.9)	96	3 (13)
Average	24.25	3.75	20.50	84	5 (23)

1. An additional 11 crabs (7 males, CW 8.5-17 cm, and 4 females, CW 9.7-13 cm) were collected in the vicinity of the aggregation on the same date.

Table 2. Monthly abundance and recapture rate of Loxorhynchus grandis collected at the Pier. The total number of crabs captured, recaptured, untagged (new) is shown for each sampling date, as are recapture, resident and male percentages.

Date sampled	Total captured	Total tagged previously	Total new	Tagged and captured previous month	Tagged but not captured previous month	Recaptures per month (%)	Recaptured from last month (% residents)	Males (%)
28-Mar-96	21	15	6	14	1	71.4	66.7	28.6
1-May-96	18	8	10	5	3	44.4	27.8	11.1
1-Jun-96	27	9	18	9	0	33.3	33.3	7.4
2-Jul-96	54	10	44	6	4	18.5	11.1	7.4
1-Aug-96	41	23	18	19	4	56.1	46.3	14.6
3-Sep-96	14	9	5	6	3	64.3	42.9	0.0
1-Oct-96	5	3	2	3	0	60.0	60.0	0.0
4-Nov-96	2	2	0	1	1	100.0	50.0	0.0
3-Dec-96	3	3	0	1	2	100.0	33.3	0.0
8-Jan-97	14	3	11	1	2	21.4	7.1	21.4
1-Feb-97	26	10	16	8	2	38.5	30.8	30.8
13-Mar-97	19	10	9	8	2	52.6	42.1	26.3
4-Apr-97	26	10	16	6	4	38.5	23.1	19.2
13-May-97	40	18	22	14	4	45.0	35.0	12.5
9-Jun-97	27	10	17	9	1	37.0	33.3	18.5
8-Jul-97	45	12	33	7	5	26.7	15.6	4.4
12-Aug-97	46	14	32	12	2	30.4	26.1	17.4
8-Sep-97	16	7	9	5	2	43.8	31.3	0.0
6-Oct-97	0	0	0	0	0			
7-Nov-97	0	0	0	0	0			
12-Dec-97	8	0	8	0	0	0.0	0.0	25.0
9-Jan-98	105	6	99	4	2	5.7	3.8	30.5
Feb-98[1]								
9-Mar-98	66	18	48	16	2	27.3	24.2	31.8
21-Apr-98	86	33	53	24	9	38.4	27.9	24.4
28-May-98	55	38	17	35	3	69.1	63.6	14.5
16-Jun-98	53	46	7	33	13	86.8	62.3	24.5
20-Jul-98	38	24	14	18	6	63.2	47.4	18.4
18-Aug-98	28	22	6	17	5	78.6	60.7	10.7
22-Sep-98	26	18	8	15	3	69.2	57.7	11.5
20-Oct-98	21	18	3	15	3	85.7	71.4	9.5
19-Nov-98	9	8	1	8	0	88.9	88.9	11.1

Average	30.29	13.13	17.16	10.29	2.84	51.54	38.75	14.9
SD	24.91	11.05	20.75	8.97	2.77	26.90	21.72	
Total	939	407	532	319	88			

1. Ocean too rough to permit sampling.

Table 3. Sex of Loxorhynchus grandis collected at Dike Rock and the Pier between February 1996 and November, 1998. The percentage of sexed crabs that were male is shown for three size classes at each site. Crabs smaller than 8 cm CW were never collected at the Pier. Animals larger than 10 cm CW were collected sporadically at Dike Rock. Each crab is included only once in this table.

Site and size	Unsexed	Females	Males	% Males
Dike Rock				
<4.20 cm CW	266	16	19	54.3
4.20-10 cm CW	-	86	98	53.3
>10 cm CW		16	14	46.6
Pier				
8-10 cm CW		2	11	84.6
>10 cm CW		419	130	23.7
Total	266	539	272	1077

Table 4. Recapture frequency for tagged Loxorhynchus grandis of each sex at the Pier between March 1995 and November, 1998.

Number of times recaptured	Total	Females (n)	Females (%)	Males (n)	Males (%)
0	343	230	54.4	113	80.1
1	114	95	22.5	19	13.5
2	50	45	10.6	5	3.5
3	26	25	5.9	1	0.7
4	19	19	4.5	0	0.0
5	8	6	1.4	2	1.4
6	3	2	0.5	1	0.7
7	1	1	0.2	0	0.0
8	0	0	0.0	0	0.0
Total	564	423	100	141	100

Table 5. Leg damage frequency for Loxorhynchus grandis collected from the Pier, Dike Rock and Sand Plain sites between December 1995 and November 1998. The frequency of crabs with different numbers of legs missing, regenerating or broken is shown by sex and size. Adult crabs are those with CW > 10 cm, while juveniles are those smaller than 10 cm CW.

Legs affected	Total	Juveniles	Adults	Adult females	Adult males
0	873	444	429	338	91
1	208	43	165	122	43
2	71	11	60	47	13
3	34	6	28	16	12
4	8	3	5	0	5
5	0	0	0	0	0
6	1	0	1	1	0
Total	1195	507	688	524	164
> 0 legs damaged	322	63	259	186	73
% crabs with leg damage	26.95	12.43	37.65	35.50	44.51

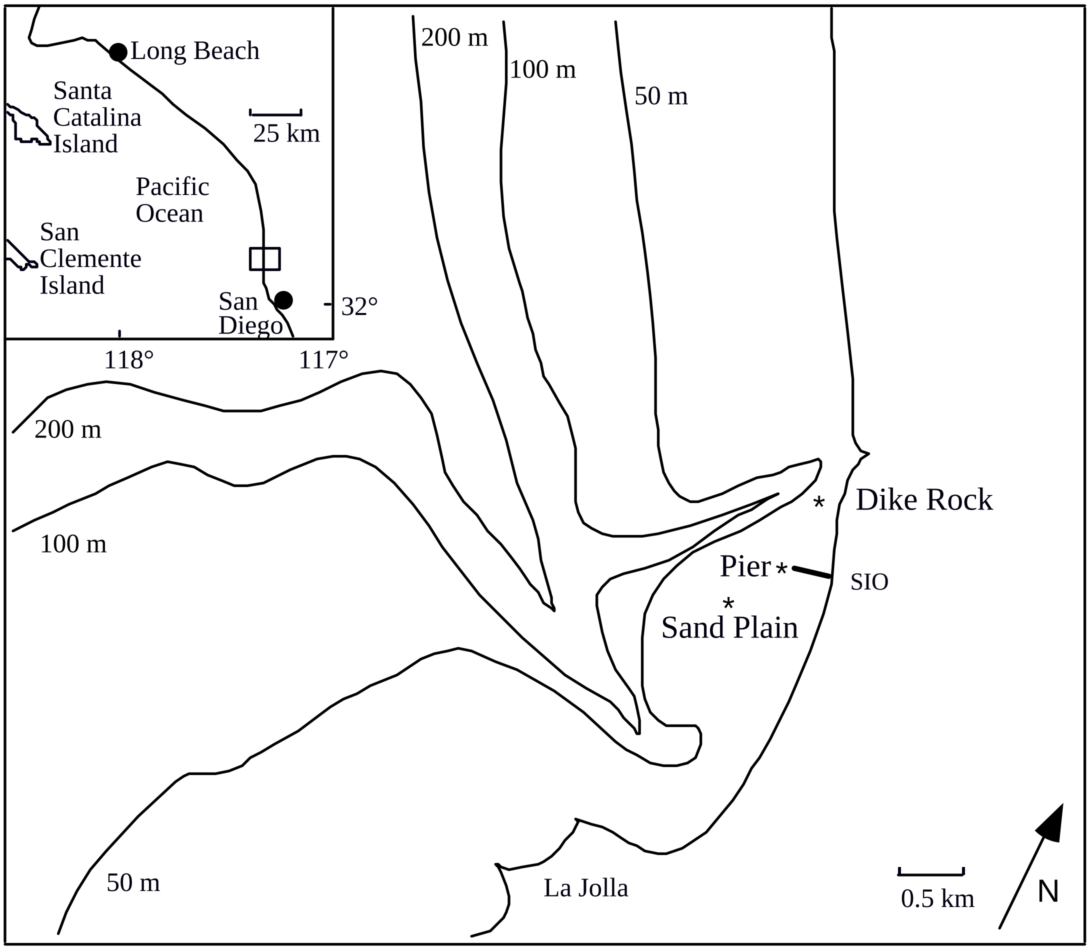

Figure 1. Map of the three Loxorhynchus grandis survey sites (*); the Sand Plain, approximately one km southwest of the Scripps Institution of Oceanography (SIO), the Pier at SIO, and Dike Rock, approximately one km north of the Pier. Depth contours (50 m, 100 m, and 200 m) are also shown to indicate the positions of the nearby submarine canyons. The inset shows the study site location (box) in the southern California region.

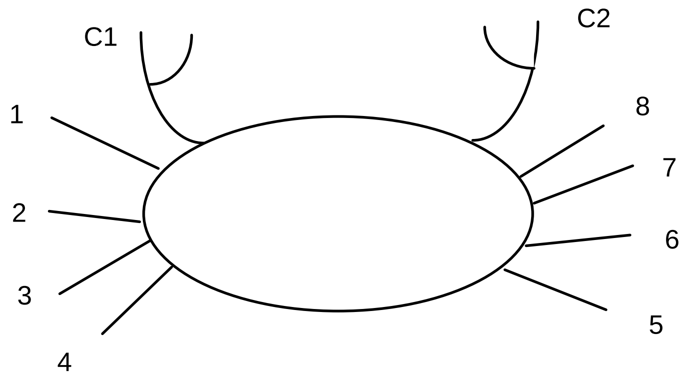

Figure 2. Dorsal view of <u>Loxorhynchus grandis</u> showing the numbering scheme for determining which appendages were damaged. Legs 4 and 5 were tagged with numbered tags in the last two years of the study. Prior to that, different combinations of zip ties were attached to the legs to provide a unique code for each individual.

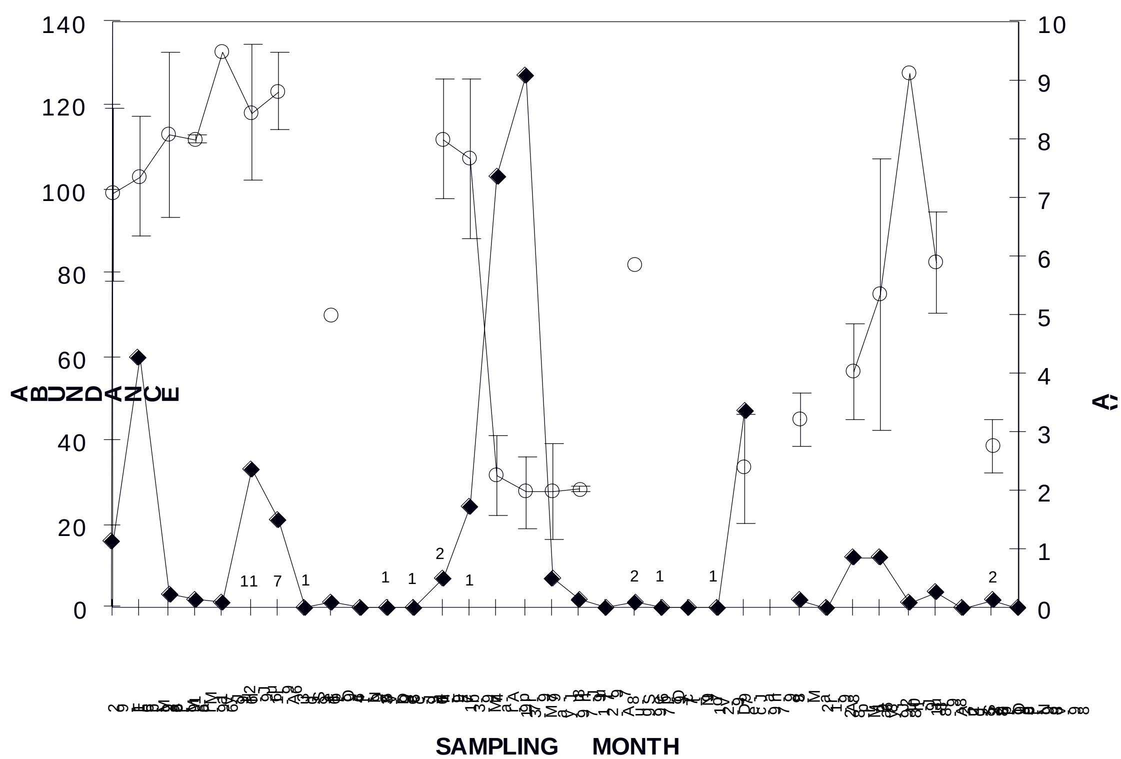

Figure 3. Abundance and average size of juvenile (<10 cm CW) <u>Loxorhynchus grandis</u> collected at Dike Rock at a depth of 10-20 meters between February 1996 and November 1998. Diamonds represent the number of crabs collected on each date (see text for methods) while the open circles represent the average CW of the juvenile crabs collected. The number of adult crabs (>10 cm CW) collected is shown by the numbers above each sampling date. Vertical bars represent ± 1 SD. In February 1998 the ocean was too rough to permit sampling.

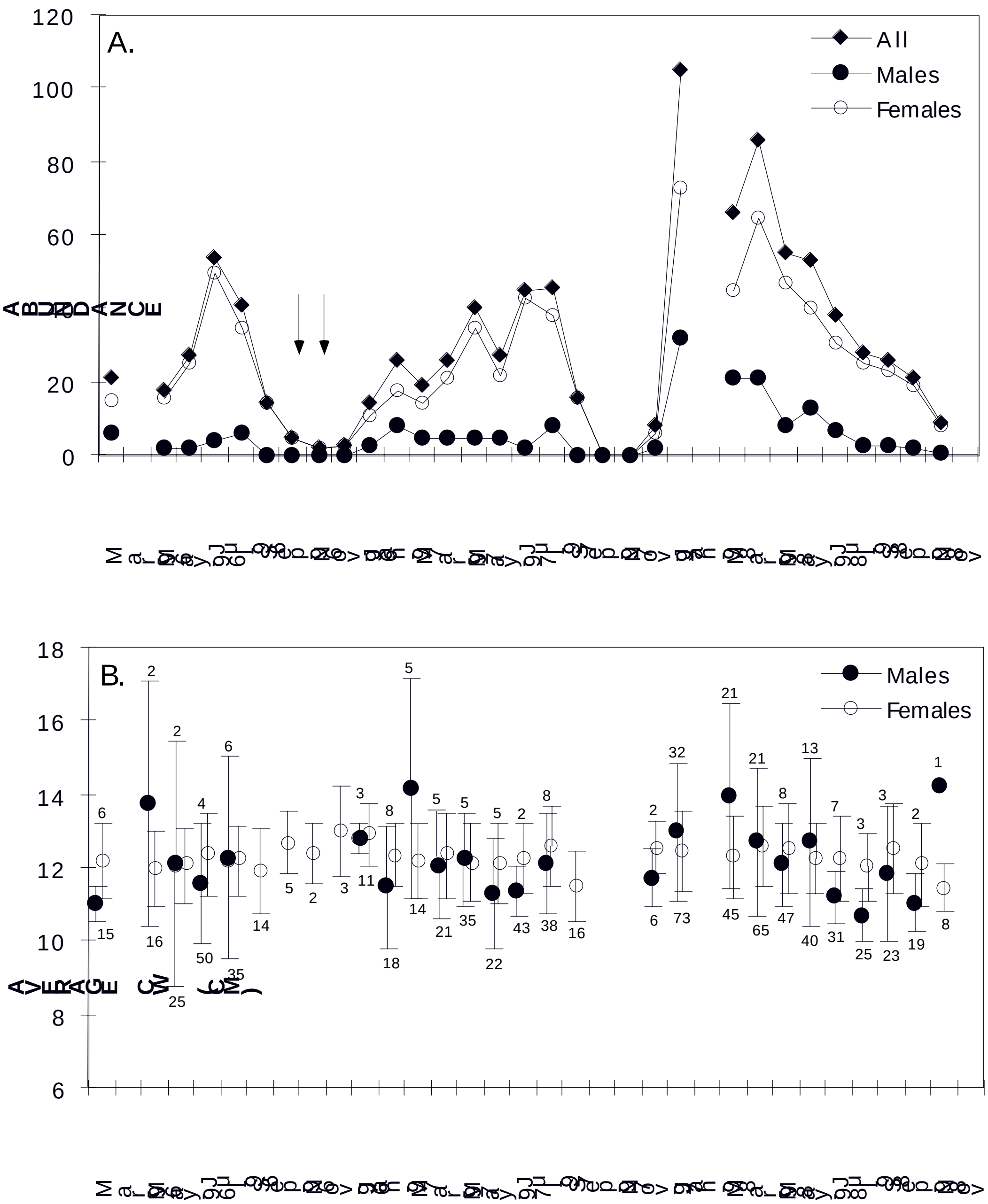

Figure 4. Abundance and size of <u>Loxorhynchus grandis</u> collected at the Pier between March 1996 and November 1998. Exact sampling dates are shown in **Table 2**. **A**. Abundance of all, male, and female crabs collected. The months in which aggregations were observed at the Sand Plain site are indicated by the vertical arrows. Two additional aggregations were observed before the Pier sampling began, and are not indicated on this figure. **B.** Average size (vertical bars are ±1 SD) of male and female crabs at each sampling month. Number of males (females) is shown above (below) the symbols for each month.

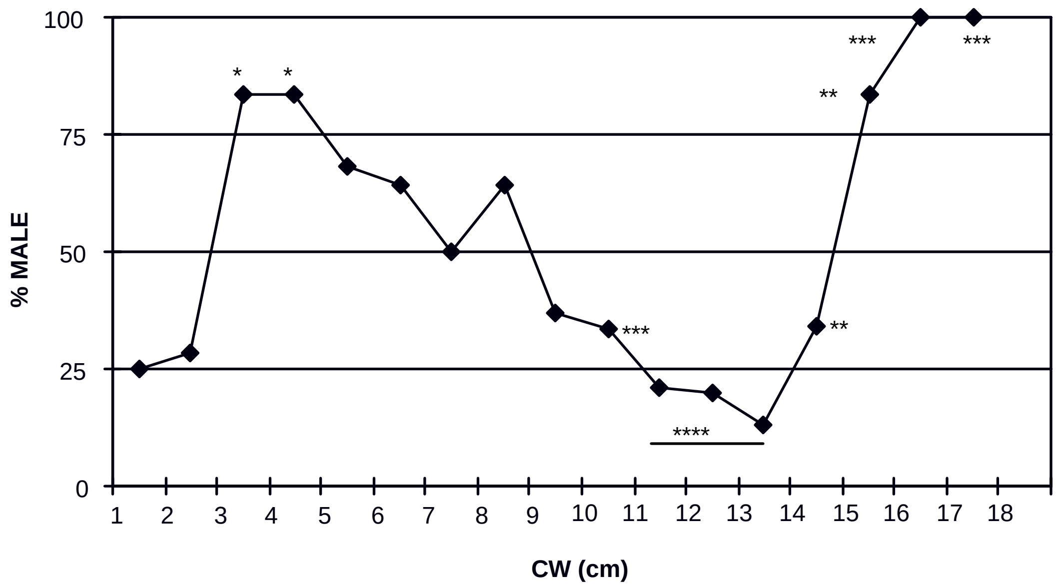

Figure 5. Percentage of male Loxorhynchus grandis by size class collected at Dike Rock and the Pier between February 1996 and November 1998. The percentage of male crabs of known sex is shown by 1 cm CW intervals (total n = 1077). Significant chi-square differences in the frequency of sexes in each size class are indicated by * ($p<0.05$), ** ($p<0.01$), *** ($p<0.001$), and **** ($p<0.005$).

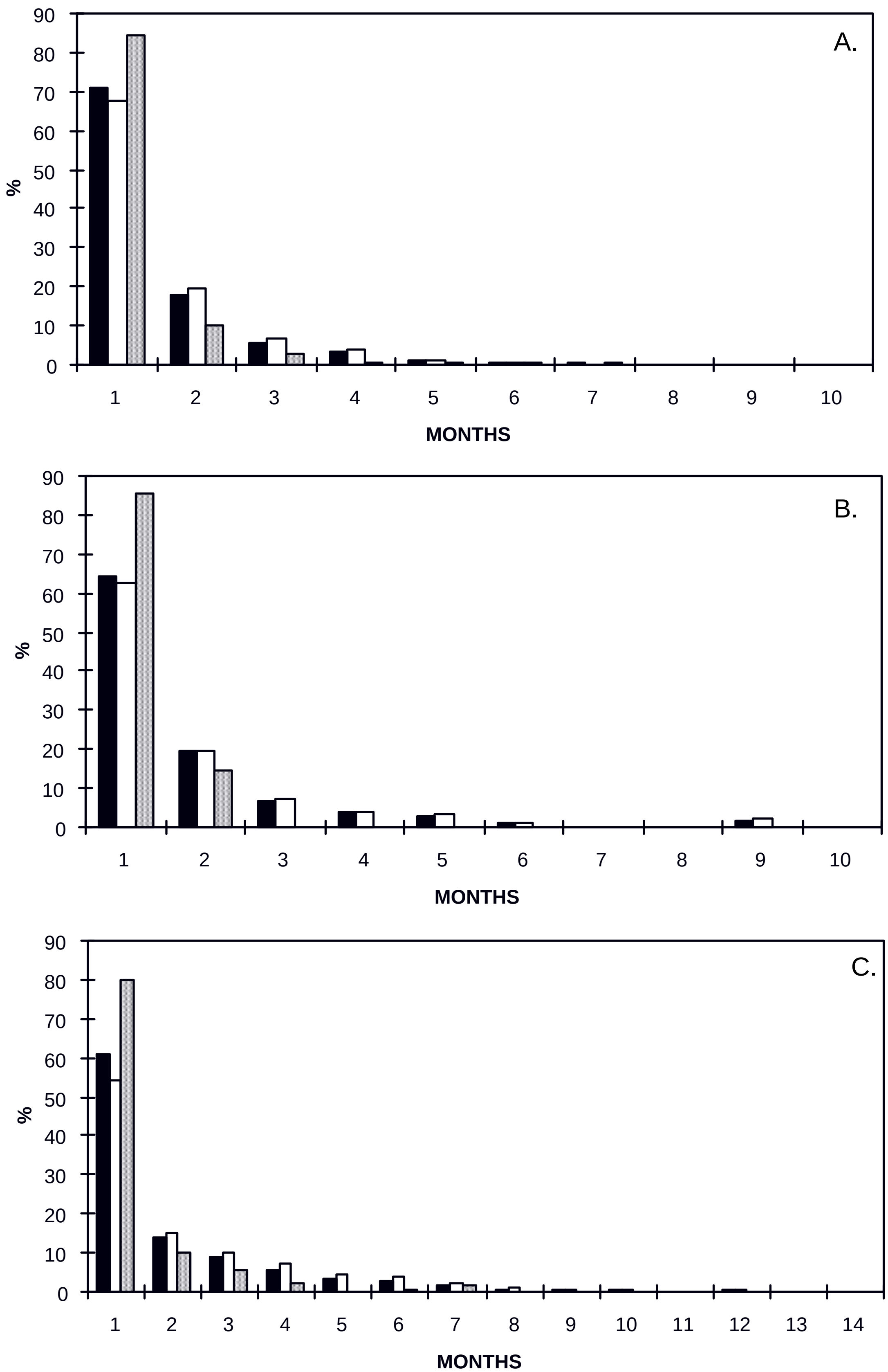
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Figure 6. Capture summary for tagged Loxorhynchus grandis at the Pier between March 1995 and November 1998. All crabs are represented by black bars, females by white bars, and males by dotted bars. **A**. The percentage of consecutive months (including first and last month) that a crab was seen. A single crab could be seen one month, then be absent the next month, before being captured in two consecutive months. It would then included in both the one and two month consecutive capture category. This summary also includes animals captured only once (i.e. one consecutive month). **B.** Percentage of time between captures, which is the number of months that a crab was absent from the Pier. For example, a crab may have been tagged, then been absent for two months, then reappeared for one month, been absent for one month, before being recaptured the following month. It would appear in both the one and two month category. **C.** The study lifetime is the total number of months (including first and last) that a crab was in the study. Crabs that had a study lifetime of one month were those that were captured only once.

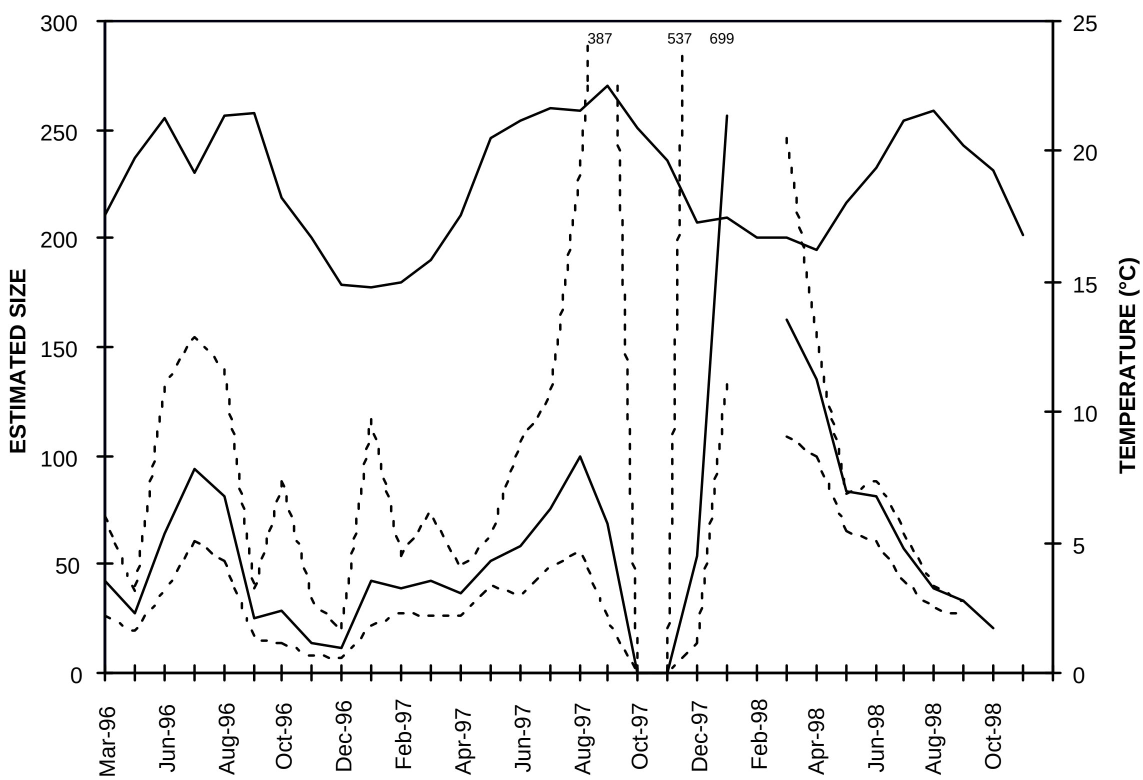

Figure 7. Estimated Loxorhynchus grandis population size in the vicinity of the Pier, calculated from mark-recapture data using the Jolly-Seber method. The lower solid line is the estimated population size, with upper and lower 95% confidence limits (doted lines). The upper 95% confidence limits for September 1997, December 1997 and January 1998 are 387, 537, and 699 crabs respectively. The upper solid line is the average monthly surface temperature at the Pier.

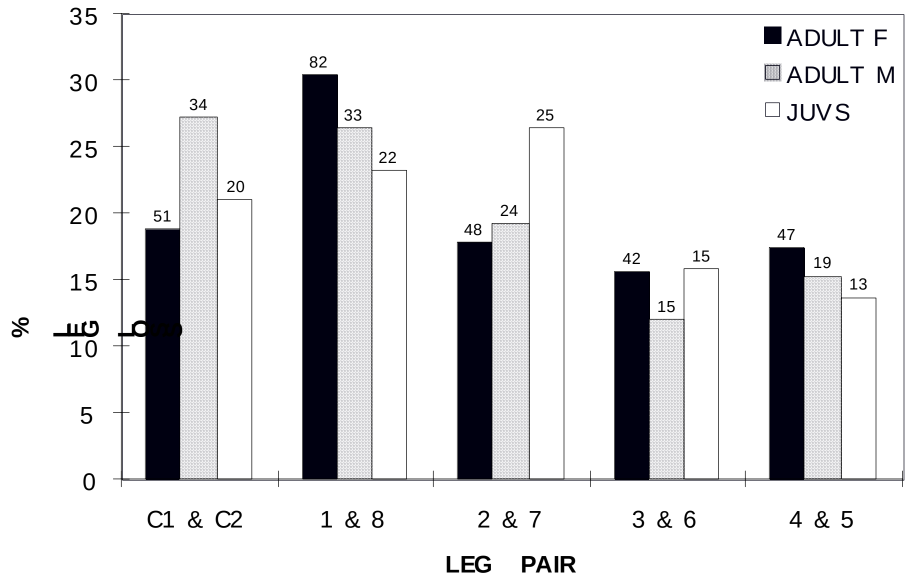

Figure 8. Percentage of <u>Loxorhynchus grandis</u> legs damaged by leg pair, for adult males, adult females, and juveniles (<10 cm CW) collected at all sites between February 1996 and November 1998. Sample size is shown above each bar. Leg pairs are shown in **Figure 2.**

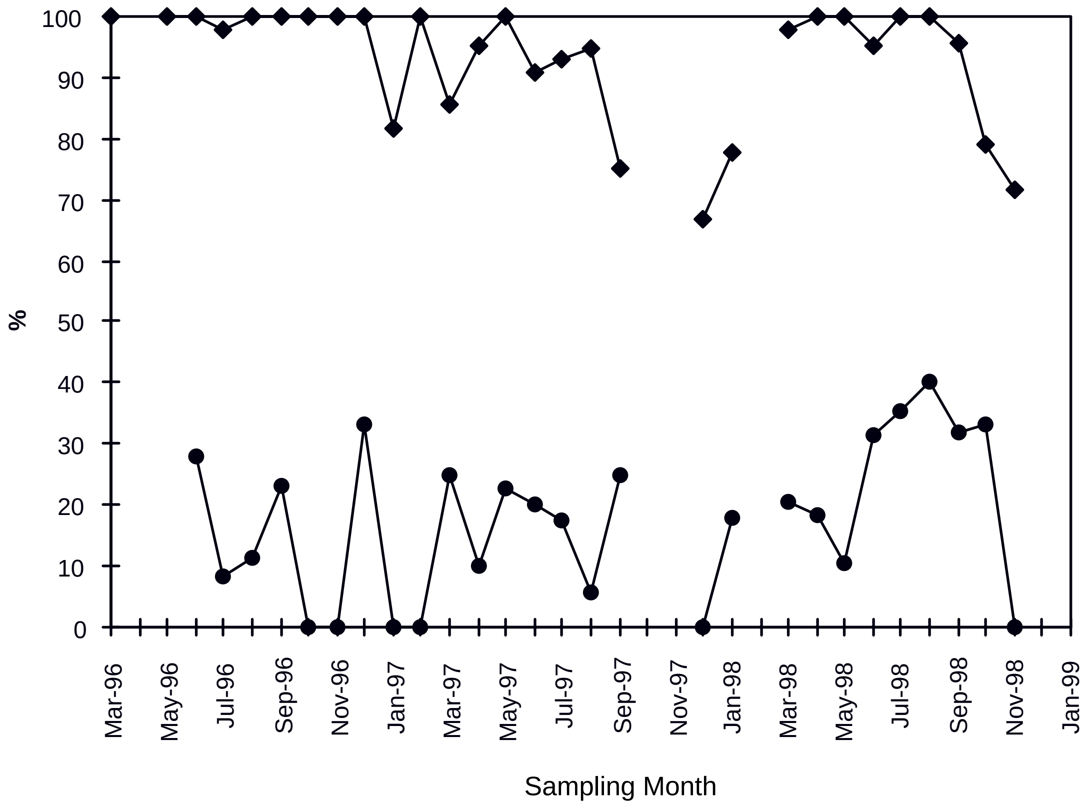

Figure 9. Brooding condition of Loxorhynchus grandis females collected at the Pier each month between February 1996 and November 1998. The stage of eggs was not recorded for females collected prior to June, 1996. Diamonds represent the percentage of females brooding eggs each month, while the circles indicate the percentage of females brooding brown (eyed) eggs. Brown eggs indicate the final developmental stage prior to release of larvae, and may identify the period just prior to spawning. Exact sampling dates are shown in **Table 2,** and the sample size each month is given in **Figure 4**.

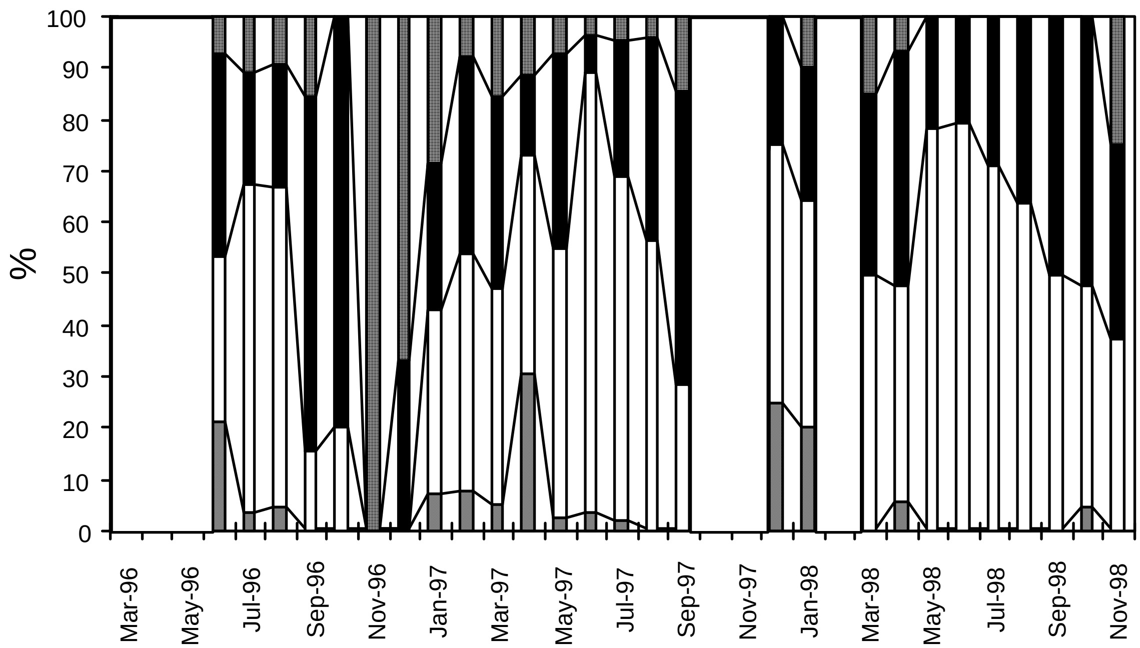

Figure 10. Percentage carapace condition (CC) of the <u>Loxorhynchus grandis</u> population collected at the Pier between June 1996 and November 1998. Crabs were divided into four categories depending on the condition of the carapace (see text). CC 1 (dotted bars), CC 2 (open bars), CC 3 (filled bars), and CC 4 (hatched bars). No crabs were found at the Pier in October and November 1997, while sampling did not occur in February, 1998. See **Table 2** for sample size each month.

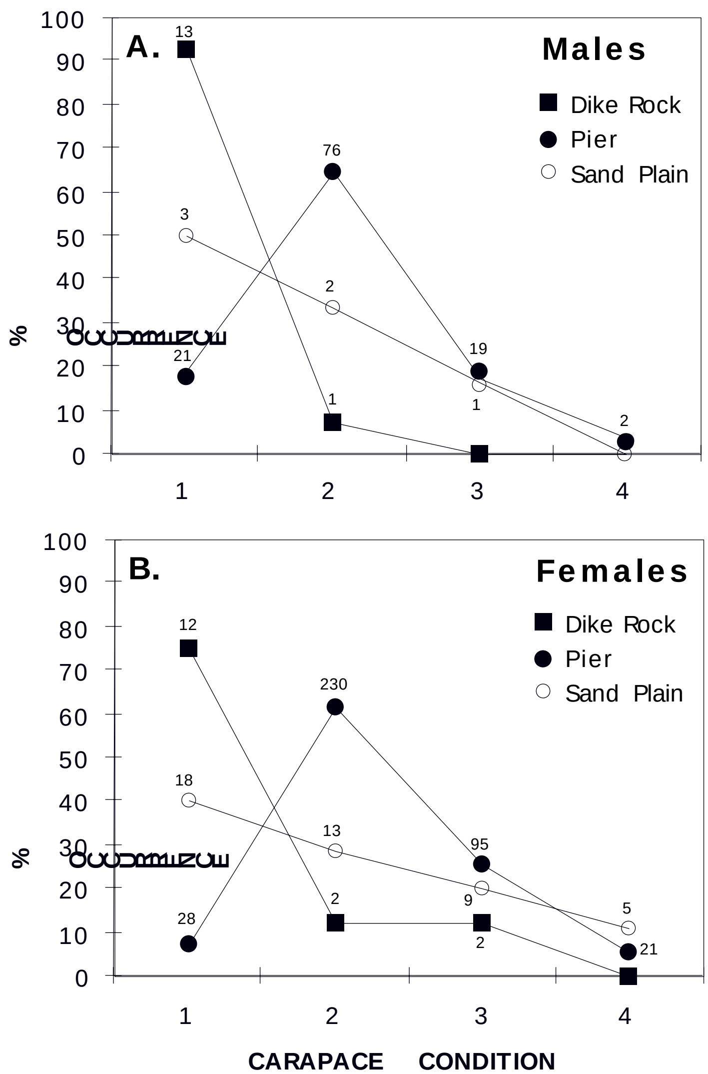

Figure 11. Frequency of carapace condition (CC) by location for adult (>10 cm CW) Loxorhynchus grandis collected between June 1996 and November 1998. **A**. Males. **B**. Females. Sample sizes are given above each symbol. Each crab was included only the first time it was captured. Crabs collected at the Sand Plain prior to July 1996 were not scored for CC.