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NATIONAL ESTUARINE RESEARCH RESERVE

Brian S. Anderson

Rikk G. Kvitek

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SEA OTTER PREDATION AND THE DISTRIBUTION
OF BIVALVE PREY IN THE ELKHORN SLOUGH
NATIONAL ESTUARINE RESEARCH RESERVE

Brian S. Anderson*
Rikk G. Kvitek²

*Marine Pollution Laboratory
Coast Route 1, Granite Canyon
Monterey, CA 93940

²Zoology Dept., NJ-15
University of Washington
Seattle, WA 98195

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ABSTRACT

The California sea otter population is gradually expanding in size and geographic range and is consequently invading new feeding grounds, including bays and estuaries that are home to extensive populations of bivalve prey. One such area is the Elkhorn Slough, where otters have apparently established a spring and summer communal feeding and resting area. In anticipation of future otter foraging in the slough, an extensive baseline database on bivalve densities, size distributions, biomasses, and burrow depths has been established for three potential bivalve prey species, Saxidomus nuttalli, Tresus nutallii, and Zirphaea pilsbryi.

In 1986, the Elkhorn Slough otters were foraging predominately at two areas immediately east and west of the Highway 1 bridge (Skipper's and the PG&E Outfall). Extensive subtidal populations of Saxidomus nuttalli and Tresus nutallii occur in these areas. Shell records collected at these study areas indicated that sea otters were foraging selectively on Saxidomus over Tresus. The reason for this apparent preference was not clear. At the Skipper's study site, 51% of the shell record was composed of Saxidomus, yet this species accounted for only 16% of the in situ biomass, and only 39% of the available clams. Tresus represented 49% of the shell record at Skipper's, yet this species accounted for 84% of the in situ biomass and 61% of the available clams. There was no difference in mean burrow depth between the two species at this site so availability does not explain the disparity in consumption. At the PG&E Outfall, Saxidomus represents 66% of the in situ biomass and 81% of the available clams, while Tresus accounts for 34% of the in situ biomass and 19% of the available clams. Saxidomus accounts for 96% of the shell record at this

site vs. 4% for Tresus, again indicating that the otters were preying on Saxidomus out of proportion to their density or biomass..

High densities and biomasses of a third species, Zirphaea pilsbryi, occur in areas where sea otters were observed to be foraging, yet no cast-off Zirphaea shells were found. Although it is possible this species was not represented in the shell record because the otters were simply chewing up the shells, it is more likely this species is avoided by sea otters.

There were relatively few sea otters in the Elkhorn Slough in 1986 compared to the previous two years. This, coupled with high bivalve densities, precluded any quantitative comparison of bivalve densities before and after the 1986 sea otter occupation. Qualitative observations made during the course of this study, and quantitative observations from previous studies indicate that, after 3 years, sea otters are not yet significantly affecting bivalve densities in the Elkhorn Slough.

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PREFACE

The impact of sea otter foraging on soft-bottom bivalve populations is becoming increasingly relevant as sea otter populations continue to expand their range. This study represents a continuation of work begun in the Elkhorn Slough in 1984 to assess the impact of sea otter foraging on deep burrowing bivalve populations. The results of this study can be applied to other soft bottom marine systems to predict the impact of sea otter foraging on bivalve communities.

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INTRODUCTION

After recovering from near extinction since the termination of the fur trade, the California sea otter population is slowly expanding in size and geographic range and is consequently invading new feeding grounds (Kenyon 1969, Wild and Ames 1974, Estes et al. 1978). Sea otters are efficient predators with the potential for greatly impacting prey populations and their associated communities (Duggins 1980, Estes and Palmisano 1974, Estes et al. 1978, Garshelis 1983). This potential is of considerable interest to ecologists, particularly when the prey populations are commercially important (Estes and VanBlaricom 1985, Miller et al. 1975). The majority of ecological studies concerning sea otters have focused on their impact in rocky subtidal communities. Studies quantifying changes in community structure as a result of sea otter predation have concluded that sea otters can significantly alter prey abundance, especially populations of gastropod and echinoderm grazers which, as primary consumers, control macroalgae (Lowry and Pearse 1973, Estes and Palmisano 1974, Duggins 1980, Hines and Pearse 1982). Sea otters have been shown to function as optimal foragers in rocky subtidal communities (Estes et al. 1981, Ostfeld 1982). When a choice is available, otters feed primarily on prey with a higher caloric value (eg., ablaones, rock crabs and sea urchins) and broaden their diets to include less desirable prey (eg, turban snails, mussels, sea stars, and fish) only when preferred prey are less abundant or the larger size classes have been eliminated.

Sea otters are also important predators in soft-bottom subtidal

communities. Most soft bottom studies, however, have been limited to descriptive accounts of otter foraging behavior and prey selection (Ebert 1968, Shimek 1977, Calkins 1978, Hines and Loughlin 1980, Garshelis 1983). There have been few quantitative studies on otter foraging in soft-bottom communities (Miller et al., 1975, Stephenson 1977), and these have focused almost exclusively on the Pismo clam (Tivela stultorum) in central California.

Our earlier work in the Elkhorn Slough (Kvitek et al., in press) focused on the effects of sea otter foraging on populations of the deep burrowing bivalves Tresus nuttallii and Saxidomus nuttalli in the context of optimal foraging theory. We found that sea otters foraged optimally on these species not by selecting larger individuals as in previous studies, but by feeding in an area where the bivalves had shallower burrow depths. In the parlance of Pyke et al. (1977), the otters were selecting the optimal "patch type." In the part of the slough where this study was done, the sediments are typically stratified with a sand layer of variable thickness overlaying clay. The burrow depth of Tresus and Saxidomus was related to this stratigraphy; the bivalves burrowed deeper in less dense sediment (eg. sand vs. clay). Therefore, deep-burrowing bivalves were more easily excavated in areas where the clay layer was shallower (i.e.; the overlaying sand layer was thinner). We concluded that deeper burrowing bivalves may have a depth refuge from sea otters in the slough; especially in areas where the sand layer is thicker. This foraging pattern contrasts with that described for otters on other soft-bottom prey. For example, in studies on the shallow-burrowing Pismo clam, almost all of the larger individuals were eliminated by the foraging activities of otters (Miller et al., 1975; Stephenson, 1977).

Previous observations of the slough otters (Kvitek et al., in press) indicate that the invading otters were males associated with a migrating otter

front. Male otter movements are typically related to breeding activities. Male otters often form communal aggregations between breeding seasons. Otters are most numerous in the slough during the early months of the year, and absent during the late summer and fall. Male otters have been observed to leave communal male areas and set up territories with females during the breeding seasons in California (June - November; Jameson, in review) and in Prince William Sound, Alaska (September and October; Garshelis, 1984), returning to their communal areas after the breeding season. Elkhorn Slough, with its abundant supply of bivalve prey, and its central location between established otter populations (Santa Cruz and Monterey), may become such a seasonal communal male area.

The objectives of this work are to 1) complete a survey of the entire Elkhorn Slough system of all bivalve populations potentially available to foraging sea otters, and 2) test several hypotheses concerning the effects of sea otter predation on bivalve communities. The hypotheses addressed in this report are:

1) Sea otters do not significantly reduce the abundances of deep burrowing bivalves.

2) There is no relationship between bivalve burrow depth and susceptibility to sea otter predation.

3) Sea otters do not forage selectively on the largest available size classes of deep burrowing bivalves.

4) Sea otters show no preference in prey species.

METHODS

BASELINE STUDY

Initial surveys on the location and relative abundances of otter prey in the Elkhorn Slough were conducted using SCUBA. We surveyed the entire slough from the mouth (at the Moss Landing harbor), up the slough into the National Estuarine Research Reserve, mapping major bivalve populations. From these initial surveys we established six permanent study sites that encompassed both intensive foraging sites and less utilized areas. At each of these sites we set up permanent subtidal study areas in which we censused the density, size distribution, biomass, and burrow depth of all species of potential bivalve prey (specific methods below).

PERMANENT STUDY AREAS

Six permanent study sites were established in the slough. The six study sites were called: Skipper's, PG&E Outfall, Seal Bend, Shellfisheries, Reserve and Red House (see map page 23, and Cailliet et al., 1975). At each of the six study sites SCUBA divers swam stratified random transects parallel to the channel bottom and censused prey populations. The number of transects depended on the width, bottom topography, and prey distributions in the channel. For example, at the Reserve the channel bottom was narrow with steep sides and a relatively homogenous bottom topography. Only two transects were necessary to

effectively characterize the bivalve densities here. The Seal Bend site had a much wider channel bottom with a heterogenous topography consisting of a deep channel with sloping sides leading up to a wide flat bank. Because different bivalve species occupied different sections of the bottom, more transects were necessary to accurately characterize this site. Thus, the number of transects at each site study area are a reflection of the complexity of the site.

We compared two methods (tape vs toss) for censusing relative abundances of bivalves. The tape method involved establishing a 50m transect along which (10) 0.25m sq. quadrats were placed using a random numbers table. Bivalve counts were then made in each of the 10 quadrats. We compared this method statistically to simply tossing (10) 0.25m sq. quadrats haphazardly along the bottom. For the toss method, a diver simply swam along the length of the channel just above the visible range of the bottom (usually 2 to 3 feet), dropped the quadrat, followed it down to the bottom, and counted the bivalves in the quadrat. There was no significant difference in bivalve counts between the two methods (paired t-test, $p < .05$). The poor visibility in the slough effectively made the tossing method haphazard, thus eliminating bias. Because it was a simpler technique we opted to use it for all sampling, thus allowing us to effectively sample more area. Within each quadrat the diver counted all visible siphons of each of the larger bivalve species (those presumed or known to be potential sea otter prey). Bivalve siphons can be identified to species and provide a very accurate estimate of bivalve abundance (Fukuyama and Oliver 1985; Kvitek et al., in press). To test the accuracy of counting siphons to census bivalve density, we counted siphons and then excavated the bivalves in 5 quadrats at the PG&E study site. Bivalve siphons were first counted by species in circular 0.25 m sq. quadrats (an open-ended 55 gallon drum cut in half), then all bivalves in the quadrat were excavated to a depth

of 50 cm. To excavate the clams water was pumped through a 2.5" diameter fire hose by a 8h.p. Briggs and Stratton powered irrigation pump. The water pressure liquified the sediment within the barrels which dislodged the clams winnowing them to the surface where they were collected. Five replicates were counted and all bivalves were sorted to species, lengths measured, and wet meat weight recorded. (These latter measurements were used to describe regression relationships between siphon size and bivalve size, see methods below). There was no significant difference between the number of bivalves counted visually in the quadrats and the number excavated using the water pump (ANOVA $p < .05$), so visual counts were considered accurate.

In our previous work (Kvitek et al., in press) we found that there is a close correlation between siphon width and shell length for Tresus nuttallii. There is also a positive correlation between shell length and wet meat weight for this species. Tresus has rigid siphon plates which make it easy for a diver to accurately measure the width of its siphon. This correlation provided a regression equation enabling us to determine in situ size distributions and biomass for this species by simply measuring siphon widths. To determine whether there was a similar positive correlation between siphon size, shell length and biomass for Saxidomus and Zirphaea, we measured siphon sizes of each species in situ and then excavated the clams (either by digging by hand or with the water pump) and measured total shell length and wet meat weight. These data were used to derive regression equations (see results) similar to those derived for Tresus, allowing the determination of in situ size and biomass distributions for these species based on siphon measurements.

Burrow depths were measured by placing a meter rod down the burrow until it came into contact with the bivalve shell then recording the depth. We validated the accuracy of this method by measuring the depth of intertidal bivalves then excavating them to confirm their depth (Kvitek et al., in press).

SHELL RECORDS

Dead bivalve shells were collected from the sediment surface to determine the prey species and sizes eaten by otters. Shell records were collected at sites where otters were observed to be feeding. All fresh (not obviously fouled or discolored) shells showing signs of otter predation (cracked or torn apart at the hinge) were collected by divers swimming haphazardly over the study site. The shells were sorted to species and measured to the nearest millimeter. If two single Tresus valves could be paired, only one was measured to avoid duplication since otters were occasionally observed to open this species without breaking the shell. For a discussion of the validity of using cast-off shells to quantify predation, see Fukuyama and Oliver, 1985.

OBSERVATION DATA

Observations of feeding otters were made from land and boat using binoculars and a spotting scope. Observers recorded information on total otter numbers, where the otters were feeding, and the proportion of otters feeding.

RESULTS

SEA OTTER OBSERVATIONS

The total number of sea otters observed in Elkhorn Slough during the course of this study are given in Fig. 1. These data are presented as the mean number of sea otters per observation day (p.o.d.). The number of sea otter p.o.d. increased from a mean of 4 (+1, N=5) in January, 1987 to a mean high of 11 (+2, N=5) in May. The greatest densities of sea otters in the slough occurred in March, April and May in 1987, with a mean for these three months of 10.33 (+0.57, N=7) sea otters p.o.d.. No observations were made in June and only one was made in July; no otters were observed then. In August,

approximately 2 (\pm 2, N=4) otters p.o.d. were observed.

A map of the relative densities by location of sea otters in the slough is given in Fig.2. A greater density of otters were observed in the yacht harbor than in any other part of the slough (mean > 4 otters per observation day). Relatively large numbers of otters were also observed on either side of the highway one bridge at the Skipper's and PG&E Outfall study sites (mean = 1.4-1.5 otters p.o.d.). Only a few otters were observed at the Seal Bend and Shellfisheries sites (mean = 0.1-0.5 otters p.o.d.). No otters were observed at the other study sites.

SEA OTTER PREY DISTRIBUTION

The distribution maps for the three major potential bivalve prey species (Tresus nuttallii, Saxidomus nuttalli, and Zirphaea pilsbryi) in the Elkhorn Slough are given in Fig.'s 4, 5, and 6. The distribution of Saxidomus nuttalli is given in Fig. 4. The greatest density of Saxidomus occurred at the Skippers and Shellfisheries study sites. At Skipper's, a large bed of Saxidomus occur just west of the of the highway 1 bridge (mean = 5.0-7.5 per 0.25m sq.). All of the Saxidomus at the Shellfisheries site occur in the middle and south side of the slough channel, with the greatest density in the middle (mean = 5.0-7.5 per 0.25m sq.) and fewer on the south side (2.0-5.0 / 0.25m sq.). Relatively high densities of Saxidomus also occur just west of the Highway 1 bridge at the PG&E Outfall (2.0-5.0 / 0.25m sq.), all are on the north side and middle of the slough channel. The greatest density of Saxidomus at Seal Bend occur in the deepest part of the channel on the north/middle side (2.0-5.0 / .25m sq.). Lower densities of this species are also found on the banks of the north and south sides of the main channel at Seal Bend (0.1-2.0 / .25m sq.). No Saxidomus were found in the slough east of the Shellfisheries site.

The distribution of Tresus nuttallii in the slough is given in Fig.5. The greatest density of Tresus occurs at Skipper's (7.5-10.0 / 0.25m sq.). There is almost a continuous population of Tresus extending from the Highway 1 bridge east up the slough to the Shellfisheries study site. The density of Tresus in this population is 0.1-2.0 / 0.25m sq.. No Tresus occur in the main channel of the slough beyond the Shellfisheries site, except for a small population of Tresus discovered in the south section of the Reserve channel (0.1-2.0 / 0.25m sq.).

The distribution of Zirphaea pilsbryi in the Elkhorn Slough is given in Fig.6. Significant densities of Zirphaea begin to occur at Seal Bend and extend up the slough as far as the Red House study site. The greatest density of this species at Seal Bend occur on the north side of the channel (5.0-7.5 / 0.25m sq.). Significant densities also occur in the deepest part of the channel bottom near the middle of Seal Bend (2.5-5.0 / .25m sq.), and lower densities occur on the south side of Seal Bend (0.1-2.5 / .25m sq.). Relatively high densities of Zirphaea also occur on the middle and south sides of the Shellfisheries site (5-7.5 / .25m sq.). The highest density of Zirphaea occur at the Red House and in the Reserve (7.5-10.0 / .25m sq.). All of the Zirphaea at the Red House occur on the west side of the channel (Fig.6), while the majority of Zirphaea in the Sanctuary are found at the north end of the main channel. This species is associated with hard packed clay into which the animal burrows.

REGRESSION RESULTS

The results of the correlation studies comparing bivalve siphon width, shell length, and wet meat weight for the three species are given in Fig.'s 7,8, and 9. Size and weight regressions for Saxidomus nuttalli are given in Fig.7. There is a relatively high positive correlation between siphon width and shell length ($r^2 = 0.83$, Fig.7 a) and between siphon width and wet meat

weight ($r^2 = 0.81$, Fig.7 c) for Saxidomus. There is an extremely high positive correlation between shell length and wet meat weight for Saxidomus ($r^2 = 0.98$, Fig.7 c). These relationships allowed us to derive regression equations for siphon size vs shell length and wet meat weight for Saxidomus (Fig. 7 a,b, & c). These equations were used to determine in situ size frequency and biomass distributions for this species at each study site (see following results).

The size and weight regressions for Tresus nuttallii are given in Fig.8 (a,b & c). There is a high positive correlation between siphon width and shell length for Tresus ($r^2 = 0.85$, Fig.8 a), and between siphon width and wet meat weight ($r^2 = 0.87$, Fig.8 c). There is an extremely high positive correlation between shell length and wet meat weight for Tresus ($r^2 = 0.90$, Fig. 8 b).

The size and weight regressions for Zirphaea pilsbryi are given in Fig 9. There is a very high positive correlation between siphon width and shell length for Zirphaea ($r^2 = 0.93$, Fig.9 a). The relationship between siphon width and wet meat weight for Zirphaea, although positive, was the least significant of the three species ($r^2 = 0.74$, Fig 9 c). Shell length and wet meat weight was highly correlated for Zirphaea ($r^2 = 0.87$, Fig. 9 b).

The regression relationships of siphon width vs. shell length were used to determine the in situ size distributions for the 3 bivalve species at the six study sites. The in situ size distributions are given in Fig.'s 10-15 and summarized in Table 1. The size distributions for Saxidomus and Tresus at Skipper's are given in Fig. 10. The size distribution of Saxidomus at this site ranged between 5 and 12 cm., with the majority of individuals falling between 8 and 12 cm (mean = 9.1cm). The size distribution for Tresus at this site were larger than Saxidomus, ranging between 9 and 19cm. The majority of

Tresus at this site were between 13 and 16cm (mean=14.5cm).

The in situ size distribution of Saxidomus and Tresus at the PG&E Outfall are given in Fig. 11. The size distributions of Saxidomus at this site ranged between 8 and 14cm with the majority of individuals between 10 and 12cm (mean=10.4cm). The size distribution for Tresus at this site were clustered between the 16 and 20cm range (mean= 16.4cm), with a few smaller individuals in the 9cm range.

The in situ size distributions of Saxidomus and Zirphaea at Seal Bend are given in Fig.12. Saxidomus ranged in size between 5 and 14cm with the majority of individuals falling between 10 and 13cm (mean= 11.1). Zirphaea ranged between 3 and 11cm at Seal Bend, with the majority between 7 and 9 cm (mean = 6.9cm). The mean length of the small number of Tresus counted at this site was 13.3cm (Table 1).

The size distributions for Saxidomus, Tresus, and Zirphaea at the Shellfisheries are given in Fig.13. Saxidomus ranged between 7 and 16cm at this site (mean- 11.0cm), while Tresus ranged between 12 and 18cm. (mean=15.1cm). The majority of Zirphaea at this site were fairly large for this species (mean-6.7cm).

The size distribution for Tresus and Zirphaea in the Sanctuary are given in Fig.14. Most of the Tresus in the Sanctuary were relatively smaller individuals ranging between 8 and 14cm. (mean= 9.8cm). All of the Zirphaea at this site were smaller (mean = 4.1cm).

The only bivalve species, of the three censused in this study, at the Red House was Zirphaea. These were relatively small individuals ranging between 3 and 7cm (mean=4.5cm).

The in situ biomass distributions for Saxidomus, Tresus, and Zirphaea are summarized in Table 1. Histograms of bivalve biomass for 4 of the study sites (Skipper's, PG&E outfall, Seal Bend, and Shellfisheries) are given in Fig.'s

16-19. The results of the biomass estimates by species (Table 1) show that Saxidomus had the greatest biomass at the PG&E outfall (407 g/ 0.25m sq) and significant biomass at Skipper's (360 g/ 0.25m sq.) and the Shellfisheries (338 g/ 0.25m sq.). Saxidomus biomass began to decline at Seal Bend (147 g/ 0.25m sq.). No Saxidomus were found beyond the Shellfisheries. Tresus had the greatest biomass at Skipper's (1,909 g/ 0.25m sq.) and slowly declined in biomass up into the slough (206, 84, 47, 31, and 0 grams / 0.25m sq. at PG&E, the Shellfisheries, Seal Bend, The Reserve and Red House respectively). Zirphaea (which was not found at the two western most sites at Skipper's and the PG&E Outfall) had significant biomasses at Seal Bend (159 g/ 0.25m sq.), the Shellfisheries (156 g/ 0.25m sq.), and the Red House (149 g/ 0.25m sq.). Lower biomasses of Zirphaea occur in the Reserve restoration channel (90g / 0.25m sq.).

BIVALVE BURROW DEPTHS

The mean burrow depth of Saxidomus and Tresus in the slough is given in Table 1. Burrow depths were generally not taken for Zirphaea because this species has a curved burrow. Burrow depths for Tresus could not be obtained at Seal Bend and the Shellfisheries. At Skipper's, the mean burrow depths for Saxidomus and Tresus were 32.4 and 31.4cm respectively. At the PG&E outfall, the mean burrow depths for Saxidomus and Tresus were 25.4 and 27.4cm respectively. The mean burrow depth for Saxidomus at Seal Bend was 23.3cm, and at the Shellfisheries the mean burrow depth was 26.8cm. In the Reserve channel Tresus occurred at the sediment surface probably as a result of scour (personal observations, the authors). Although limited depth measurements were taken for Zirphaea, this species is in most cases a relatively deep burrower. In some cases it is found with the tip of its shell exposed (personal observations, the authors). This generally occurs in areas where scouring of the bottom occurs

due to fast moving water.

SHELL RECORDS

The size distribution of discarded prey shells found at Skipper's and the PG&E outfall are given in Fig. 20. The size distribution for otter predated Tresus at the PG&E Outfall was not included in this figure because only 2 shells were found at this site. The size range of the shell record found at Skipper's was 9-14cm for Saxidomus (mean =11.6cm) and 10-17 cm for Tresus (mean =13.6cm). The size range for Saxidomus at the PG&E Outfall was 10 -15cm (mean = 12.6cm). The mean size of the 2 Tresus found at the PG&E Outfall was 13.7cm. These data are summarized in Table 2. Saxidomus represented 51% of the shell record at Skipper's, and Tresus 49% of the record at this site. Saxidomus dominated the shell record at the PG&E outfall (96%). Few otter predated Tresus were found at this site (4%).

DISCUSSION

The results of this study indicate that California sea otters are continuing to exploit bivalve populations in Elkhorn Slough on a seasonal basis. Although there are usually at least a few otters present in the slough throughout the year, sea otter numbers in the slough typically increase in the late winter and spring and decline in the summer. In 1986 otter numbers increased from approximately 4 animals (p.o.d.) in January and February (Fig. 1) to a mean of 11 sea otters (p.o.d) in March, April, and May. By June, most of the sea otters had departed from the slough. This pattern of a seasonal increase in sea otter numbers in the slough in the springtime followed by a decline in summer and winter has been observed since our observations began in 1984, when sea otter numbers in the slough reached a high of 25 animals (Fig.

2, Kvitek et al., in press). The reason for this fluctuation in sea otter numbers is not clear. The most likely explanation is that the Elkhorn Slough otters are members of a male otter "front" who use the slough as a spring communal area and depart during the breeding season (Kvitek et al., in press).

The sea otters changed their foraging and rafting areas in the slough in 1986 compared to 1984. In 1984, the sea otters spent most of the time rafting in the harbor area at the mouth of the slough and foraged in front of the PG&E intake pipes (Fig.1, Kvitek et al., in press). In 1986, the sea otters rafted in the yacht basin and foraged most of the time in front of Skipper's and just east of the highway one bridge at the PG&E Outfall (Fig.2). Less than 4% of the sea otters in the yacht harbor were feeding at any one time (Fig.3), while of those observed at Skipper's and the PG&E Outfall, 60-70% were feeding. Four otters were observed at Seal Bend, and of these 3 or 75% were feeding. Foraging sea otters were rarely observed beyond Seal Bend (Fig 3).

Our subtidal survey of the Elkhorn Slough system revealed an extensive community of bivalves in the front half of the slough that represent an abundant biomass for potential sea otter predation. Most of the larger species that are known otter prey are found just west of the highway 1 bridge at Skipper's, and east of the bridge up the slough as far as the Shellfisheries (There are also large populations of Saxidomus and Tresus in the harbor in front of the PG&E intake pipes, Kvitek et al., in press). Beyond the Shellfisheries, the larger bivalve species decline in numbers.

In terms of overall density of individual species, Saxidomus dominate from the highway 1 bridge east through the Shellfisheries site (Fig.4). There is also a high density of Saxidomus at Skipper's (Fig.4). Tresus is the dominant species at Skipper's (7.5-10 / 0.25m sq.), but this species occurs in lower densities east of the bridge (Fig.5). Surprisingly, there is also a limited population of Tresus in the southern part of the Reserve channel. These Tresus

evidently began to settle there when the channel was restored to tidal action in 1983. There are now three size classes present which apparently correspond to the three years since the channel's opening. It is interesting to note that no Tresus were found in the main slough channel east of the Shellfisheries site, but this species is able to persist in the Sanctuary. Populations of Zirphaea pilsbryi first begin to appear at Seal Bend and this species is present in high densities from this site east. High densities of Zirphaea and Saxidomus overlap at Seal Bend and the Shellfisheries but the two species are segregated at these two sites with Saxidomus occurring predominantly in the deepest part of the main channel (Fig.4), and Zirphaea occurring on the banks of the channel at Seal Bend and the Shellfisheries (Fig.6). Zirphaea dominates in densities east of the Shellfisheries.

Data on in situ size distributions for the 3 species (Fig.'s 10-15, & Table 1) show that the largest individual Saxidomus occur at Seal Bend and the Shellfisheries followed by the PG&E Outfall. The Saxidomus at Skipper's were the smallest. The largest Tresus occurred at the PG&E Outfall, followed by the Shellfisheries, Skipper's, and Seal Bend. The smallest Tresus were found in the Reserve channel, which reflects their younger age. Zirphaea found in the western part of the slough (Seal Bend and the Shellfisheries) were significantly larger than those in the eastern part of the slough the (Red House and the Reserve).

The greatest biomass of bivalves occurs at Skipper's. Most of this biomass is composed of Tresus. There is also a large biomass of Saxidomus and Tresus east of the Highway 1 bridge, in front of the PG&E Outfall. There is an equally large biomass of bivalves at the Shellfisheries, composed predominately of Saxidomus. We found significant bivalve biomasses at Seal Bend and to a lesser extent up the slough at the Red House and in the Reserve.

It is interesting to note that although there is a definite positive correlation between shell length and biomass for all 3 species, there does not appear to be any relationship between in situ density, length, and biomass at any one site. For example, although the greatest density of Saxidomus occurred at Skipper's, the greatest biomass for this species occurred at the PG&E Outfall and the largest in situ size distribution of this species occurred at Seal Bend (Table 1). Similarly, the greatest biomass and density of Tresus occurred at Skipper's, but the largest mean in situ size distribution occurred at the PG&E Outfall.

The regression equations for relating shell length and wet meat weight from siphon width for Saxidomus in Fig.7 indicate that although there is a significant positive correlation between siphon width, length, and weight for this species, there is quite a bit of variability about the regression lines, particularly for siphon width vs. weight. This variability is probably a reflection of the relatively low number of individuals used to describe the relationship. There is a higher positive correlation between siphon width, length, and weight for Tresus (Fig.8), which likely reflects a larger sample size. The hard plates covering the siphon of Tresus also allow for a more accurate measure of siphon width (Kvitek et al., in press). The relationship between siphon width and shell length for Zirphaea is highly correlated ($r^2 = 0.93$, Fig. 9a), but the relationship between siphon width and bivalve weight is more variable for this species ($r^2 = .74$, Fig.9c. Note: $n=23$).

SEA OTTER PREY

The surface observations of feeding sea otters showed that during the course of this study the majority of the sea otters in the Elkhorn Slough were foraging at the Skipper's and PG&E Outfall study sites (Fig. 3). The shell records of otter predated bivalves revealed that all of the prey taken at these two sites were either Saxidomus or Tresus. However, the proportion of Saxidomus and Tresus eaten differed dramatically between the two sites. Saxidomus was the preferred prey at both sites (Table 2). At Skipper's, 51% of the shell record was composed of Saxidomus, yet this species accounted for only 16% of the in situ biomass, and only 39% of the density (Table 1). Tresus represented 49% of the shell record at Skipper's, yet this species accounted for 84% of the in situ biomass and 61% of the density. Given its superiority in size and numbers at this site, one would expect to see a higher proportion of Tresus in the shell record than Saxidomus. There was no difference in mean burrow depth between the two species at this site (Table 1), so accessibility does not explain the disparity. It appears that the otters were preferentially preying on Saxidomus at Skipper's. It is interesting to note that the mean length of the otter-predated Saxidomus at Skipper's was 11.6cm (Table 2) but the calculated mean in situ size distribution for Saxidomus at this site was just 9.1cm (Table 1). This suggests that the otters were preying on the larger size classes of this species. Although possible, this seems unlikely, especially considering the fact that the mean size of the otter-predated Tresus at Skipper's (13.6cm, Table 2) was smaller than the mean in situ size of this species (14.5cm, Table 1). It is more likely that Saxidomus size classes are patchily distributed. Alternatively, the regression equations for Saxidomus might not be an accurate representation of the population; the in situ sizes

for Saxidomus might be larger than was predicted based on the regressions. We found no evidence in our previous work to suggest that the Elkhorn Slough otters were preferentially selecting the largest individual bivalves (Kvitek et al., in press). Our studies in Alaska, however, indicate that otters preying on Saxidomus giganteus in the Kodiak island archipelago were selecting the largest size classes (Kvitek et al., 1987, Fig.2).

At the PG&E Outfall, Saxidomus represents 66% of the in situ biomass and, more importantly, 81% of the available clams while Tresus accounts for 34% of the in situ biomass, and 19% of the available clams. Although it is not surprising that a higher proportion of Saxidomus were found in the shell record at this site it is not clear why a greater percentage of Tresus were not found in the shell record here (96% for Saxidomus vs. 4% for Tresus). Tresus is more conspicuous than Saxidomus because its siphon extends farther out of the substrate and its plates are often covered with algae. Both species had similar burrow depths at this site (Table 1). It appears that the otters were again selecting Saxidomus disproportionate to their density or biomass at the PG&E Outfall. Moreover, the only times otters were observed feeding at Seal Bend or the Shellfisheries, they were feeding over areas dominated by Saxidomus (Fig.'s 3 & 4). The only shell records found at these two sites were Saxidomus, but they were never whole shells (shells that were obviously otter-predated with at least one measureable valve) and so were not counted.

Contrary to our findings in 1984 (Kvitek et al., in press), the burrow depths of Tresus and Saxidomus played no role in prey selection by sea otters in 1986. Unlike the previous (1984) study site, the bivalve populations on which the sea otters were foraging in 1986 burrowed to similar depths in the sediment (perhaps because the sediment stratigraphy at the 1986 study sites was more homogeneous than the 1985 study sites).

At no times were sea otters observed feeding on Zirphaea pilsbryi, or

feeding over Zirphaea rich areas. No Zirphaea shells were ever found in the shell record. Although it is possible that the Zirphaea were simply chewed up whole, preventing the deposition of a shell record, it is more likely that they were being avoided. This species was abundant between two sites used by otters and dominated by Saxidomus (Fig.'s 3 & 6). Zirphaea was the most numerous species at Seal Bend and the Shellfisheries (Table 1), and represented a significant biomass at both sites.

Zirphaea is a deep burrowing, but easily excavated species (personal observation, the authors), and at some sites animals can be found simply laying on the bottom, evidently dislodged by the current. This occurs in sections of the channel where the water moves faster and scours the bottom (usually the narrow parts of the channel or around the bends). This species represents a potentially great biomass of easily obtainable bivalves, yet the otters did not appear to prey on them. The nature of the sediment in which Zirphaea occurs, may dissuade otters from foraging for them. At Seal Bend the most of the larger Zirphaea occur in a very soft, sticky clay substrate that could conceivably foul the fine pelage that otters depend on for thermal insulation. It is also possible that the taste of Zirphaea is repugnant to otters. However, a food preference test using the three bivalve species in this study, was conducted on captive otters at the Monterey Bay Aquarium. This showed that all 3 species were readily consumed by the captive otters; there was no preference or avoidance evident (Anderson and Kvitek, unpublished data). Zirphaea is the most visibly conspicuous of the three bivalve species followed by Tresus then Saxidomus, but the preference of these three species is apparently not related to their conspicuousness.

CONCLUSION

California sea otters have apparently established a spring and early

summer feeding area in the Elkhorn Slough. Sea otter numbers in the slough generally increase in early spring then decline back to a yearly mean of 2 or 3 in the late summer through winter. The continued utilization of the Elkhorn Slough otters provides a unique opportunity to document the long term effects of sea otter predation on deep burrowing bivalve communities. In anticipation of this continued presence we have established a complete baseline database on the density, size distribution, biomass, burrow depth, and locations of 3 species of potential sea otter prey. This information will be useful to managers of the Elkhorn Slough National Estuarine Research Reserve, not only for assessing the future impact of sea otters, but for other studies on estuarine ecosystems (eg., population biology and pollution impact studies).

Our studies of sea otter foraging activities on deep burrowing bivalve populations indicate that there has been no significant decrease in bivalve numbers in the slough since our observations began in 1984. In 1986, in particular, there were relatively lower numbers of sea otters foraging on extensive populations of Saxidomus and Tresus (The otter numbers were too few to warrant a formal statistical test of changes in bivalve densities). This situation is similar to that described for Monterey Harbor by Hines and Loughlin (1980), who found no significant decrease in densities of Saxidomus and Tresus during one year of study at a site occupied by sea otters for 10 years. Given enough time or numbers, sea otters could possibly deplete deep burrowing bivalve densities in the Elkhorn Slough. However, this remains to be seen.

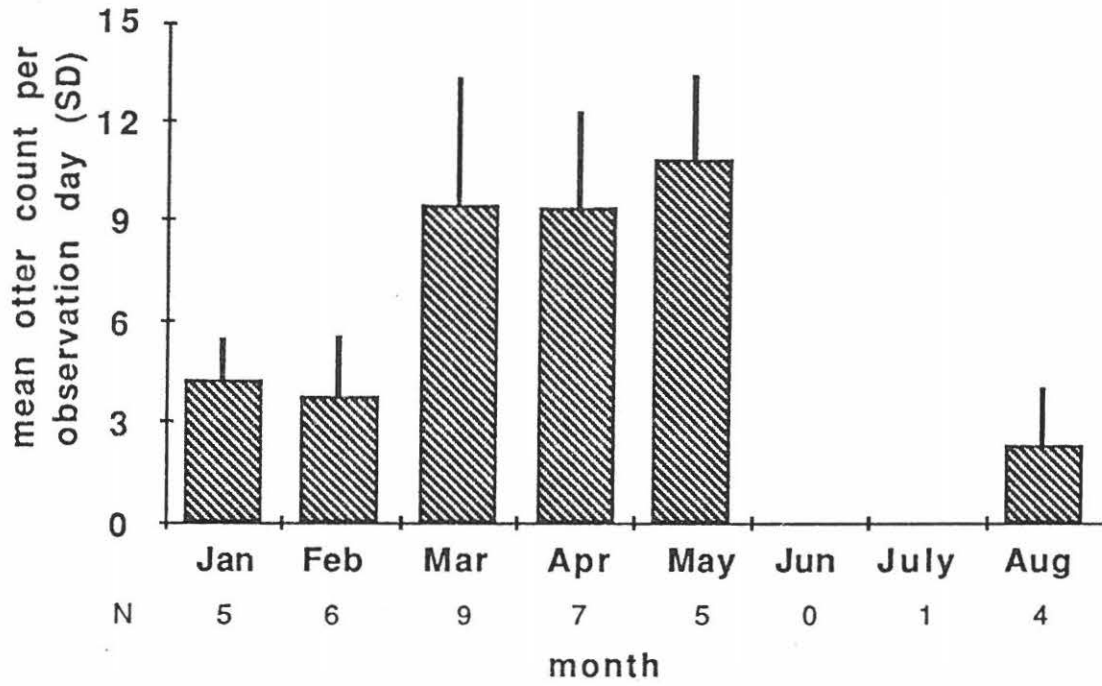
The results of our work in 1986 indicate that the sea otters selected Saxidomus over Tresus at two study sites, and apparently avoided Zirphaea altogether. The reason for this apparent preference is not clear. More research into the foraging behavior of sea otters on deep burrowing bivalves is needed to fully answer this question. As sea otters populations continue to expand into other soft-bottom habitats these questions will become increasingly important.

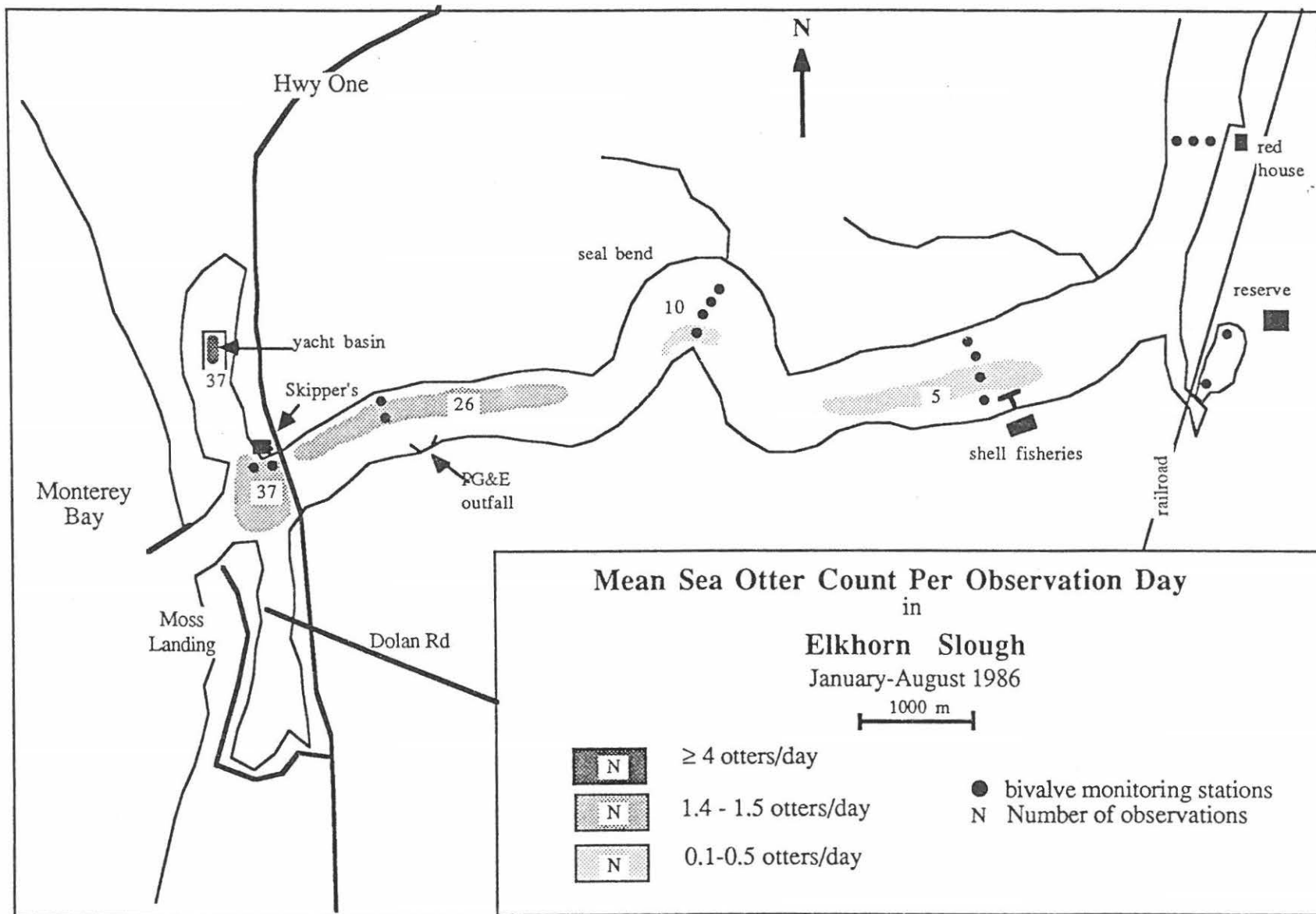
LITERATURE CITED

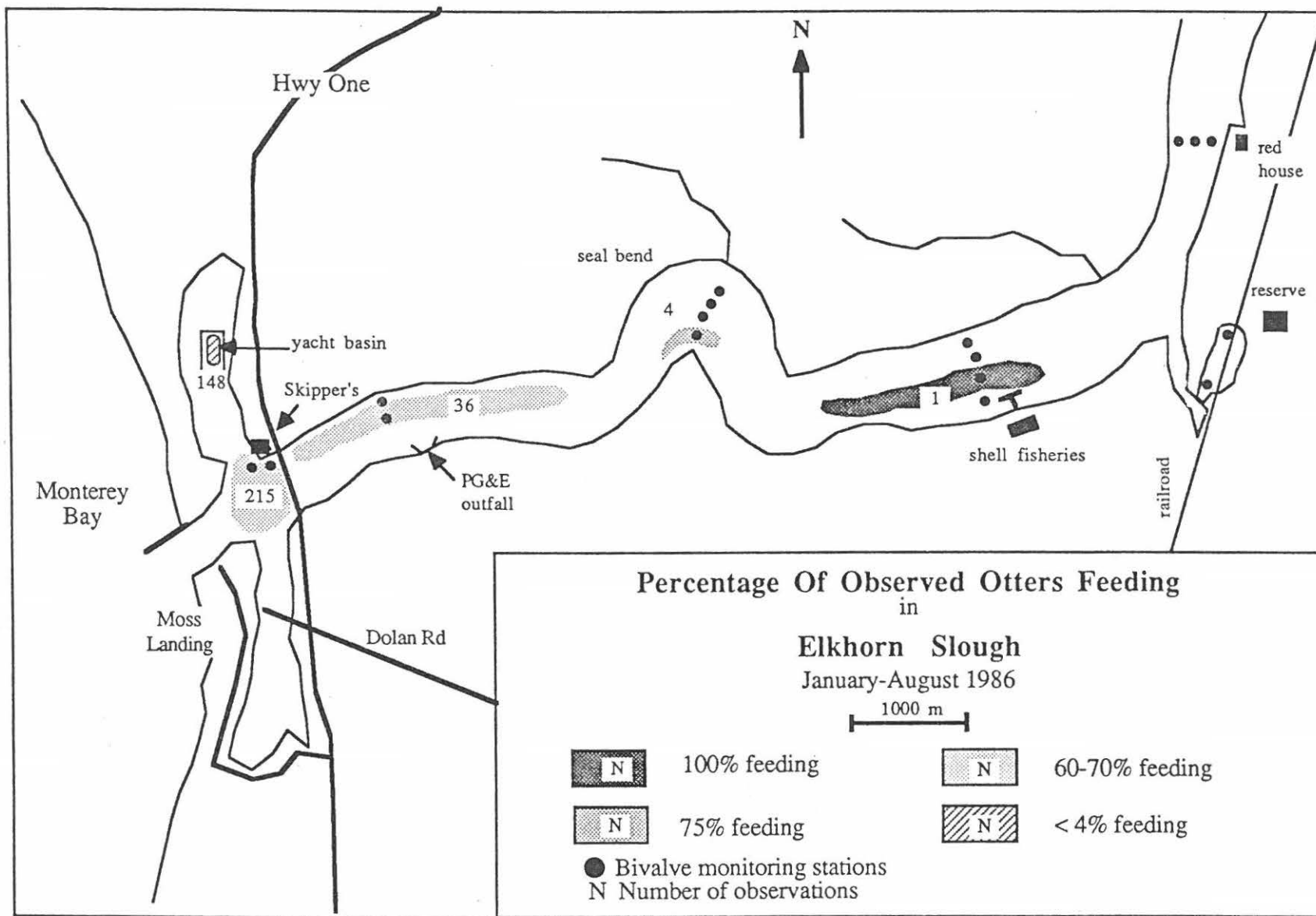
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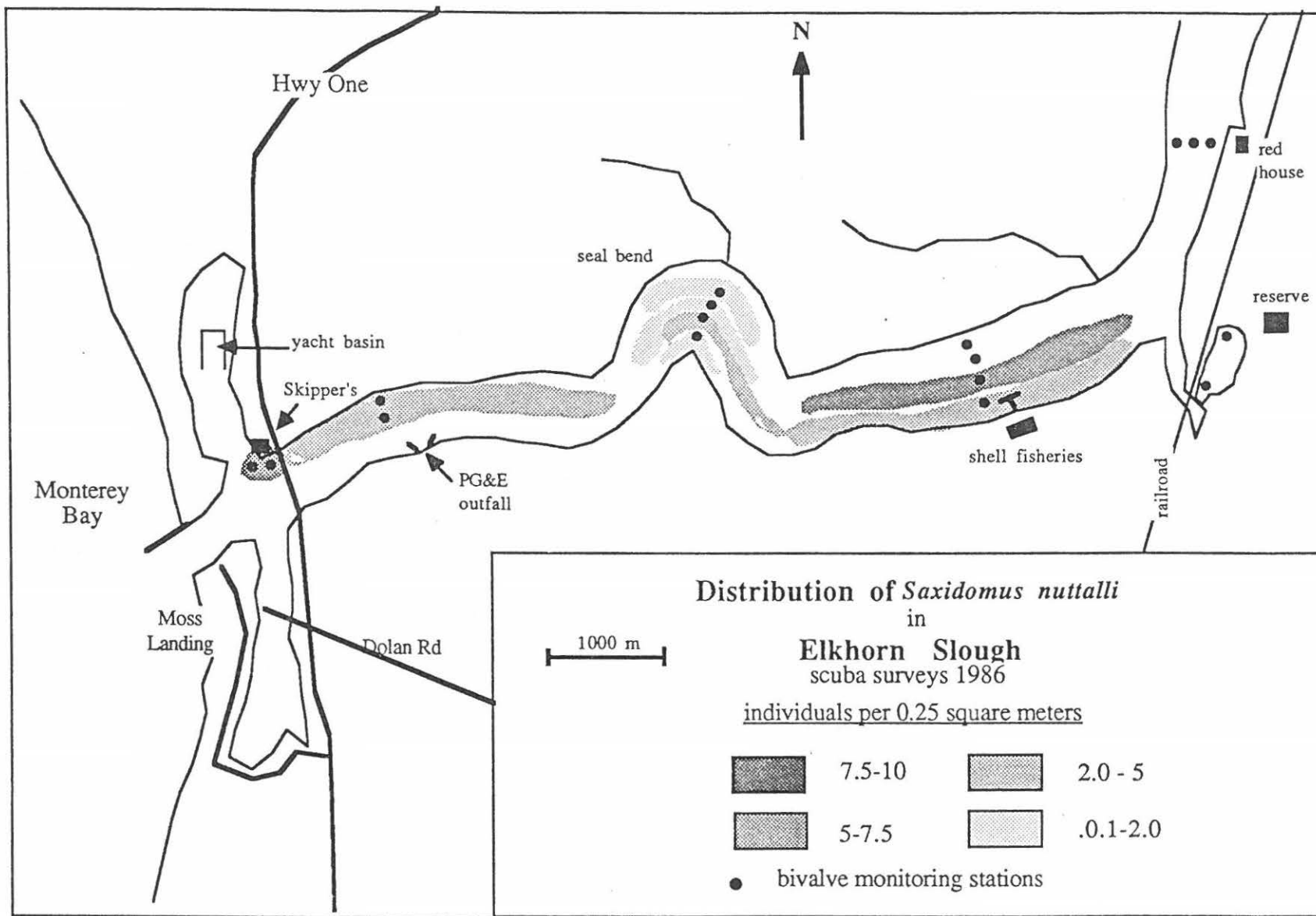
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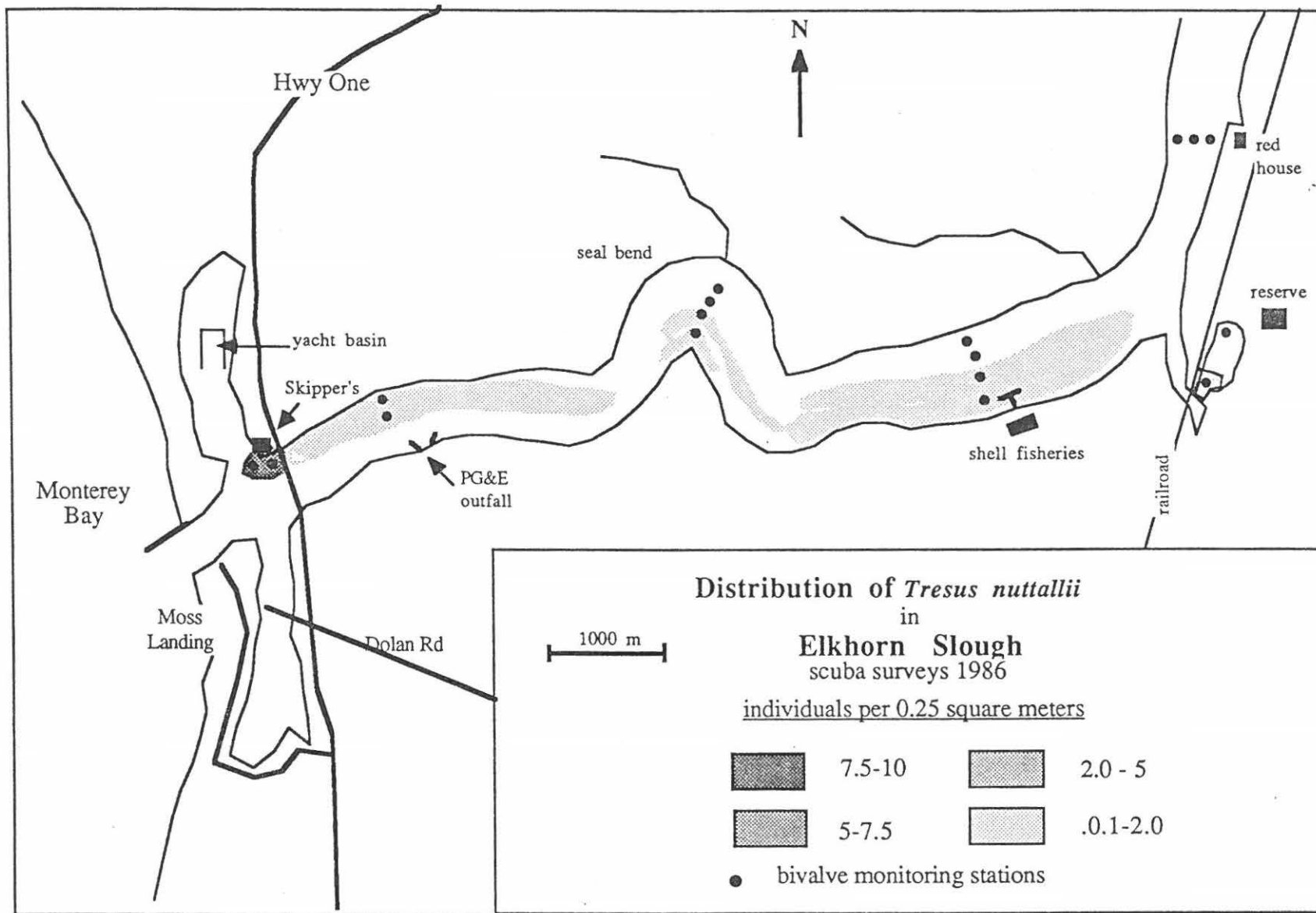
Figure 1. Sea otters in Elkhorn Slough
1986

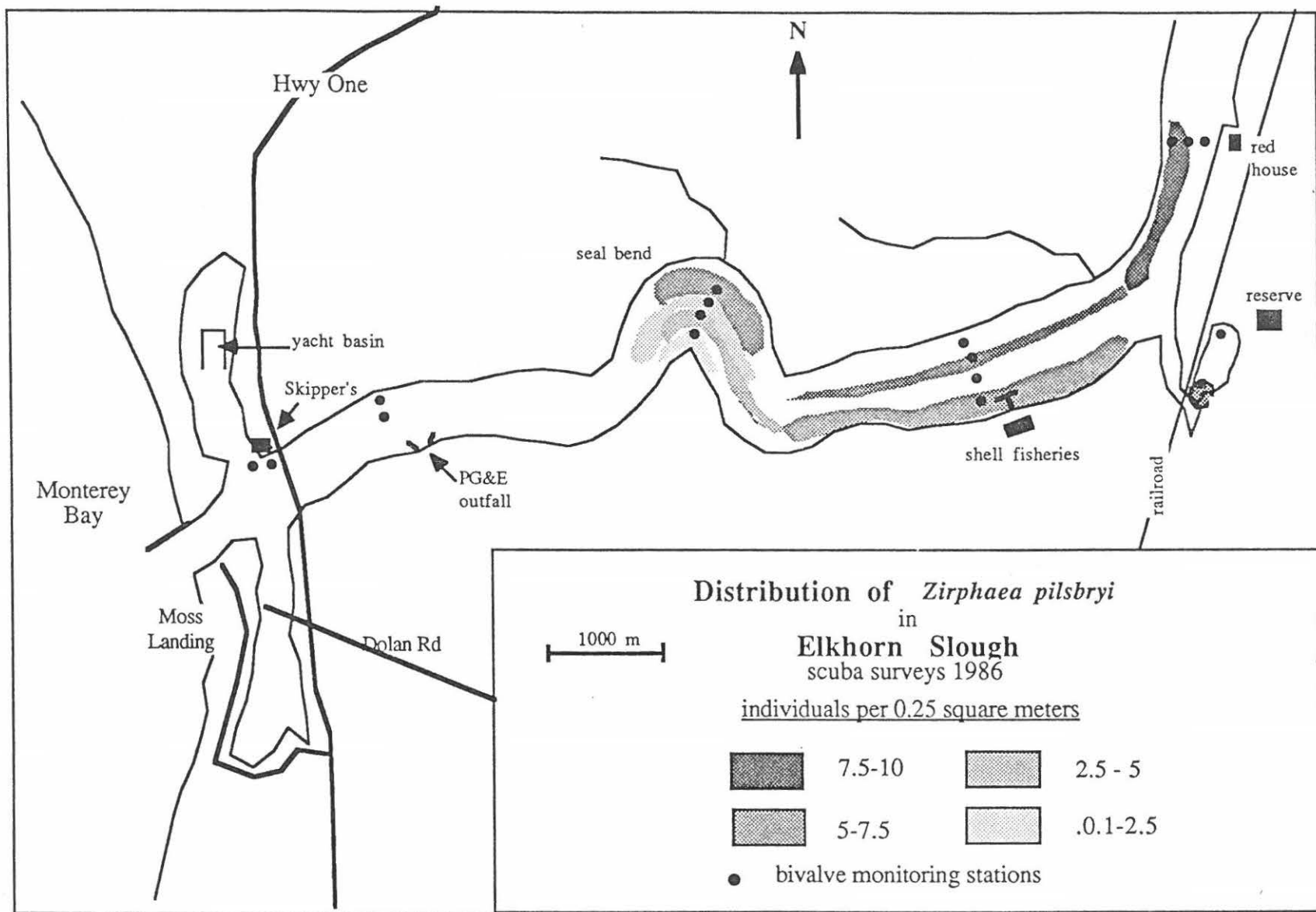




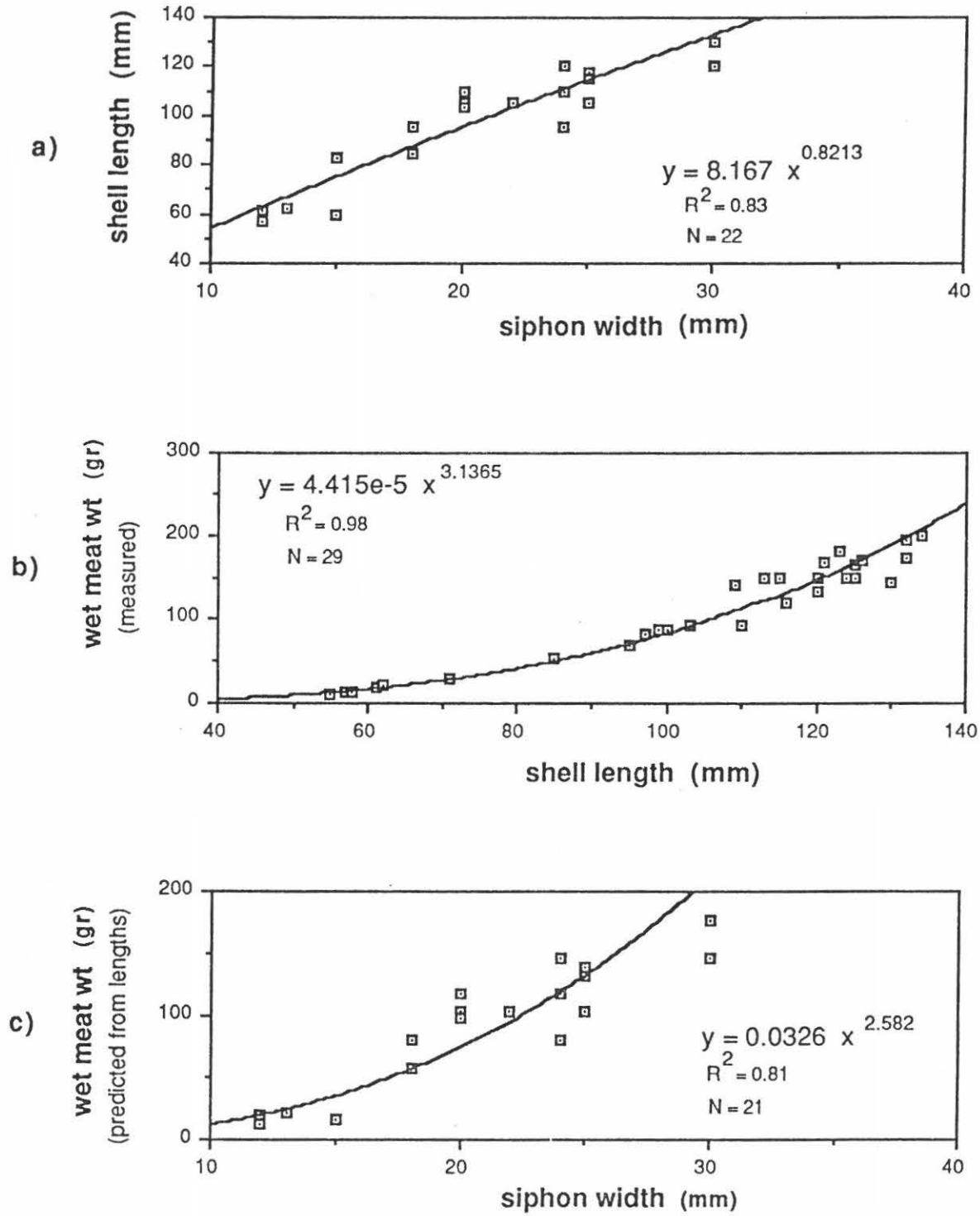




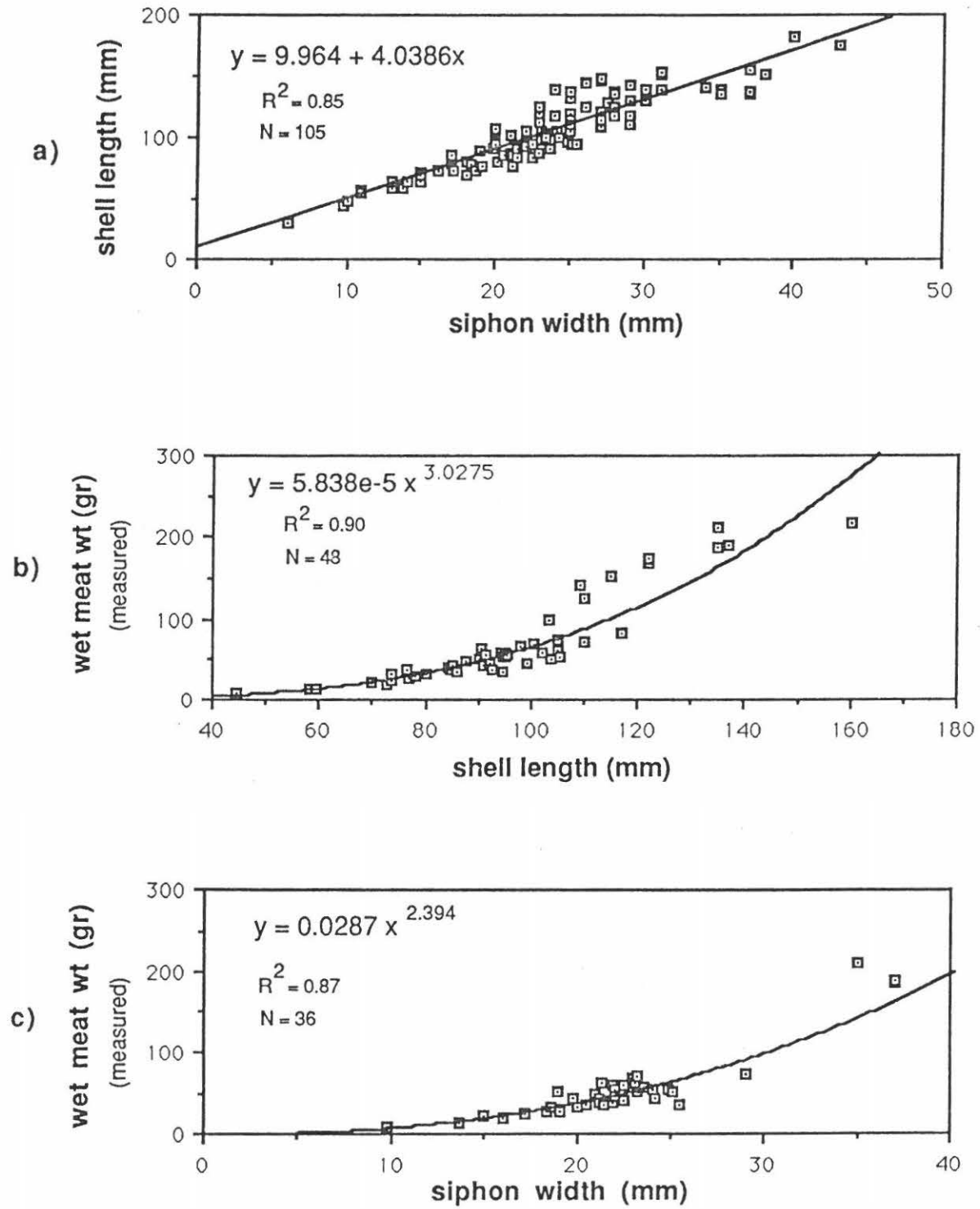




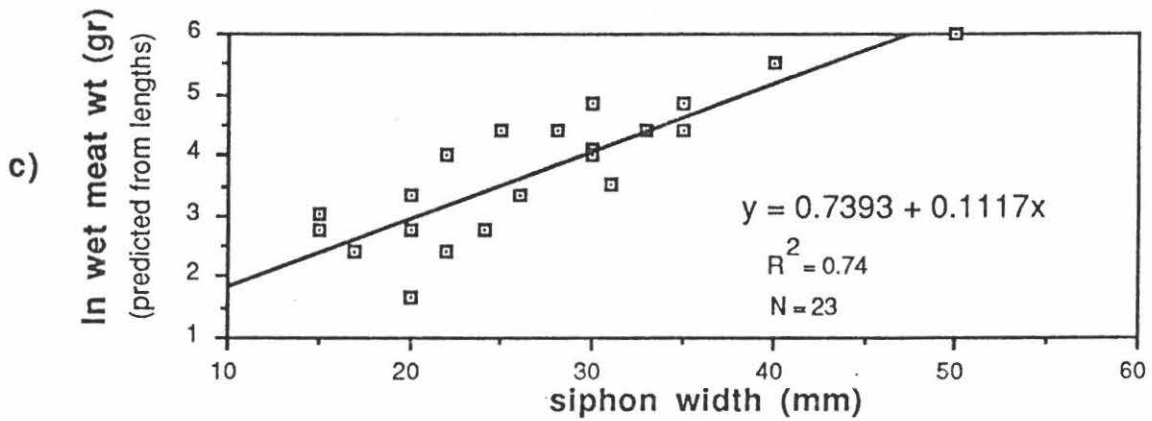
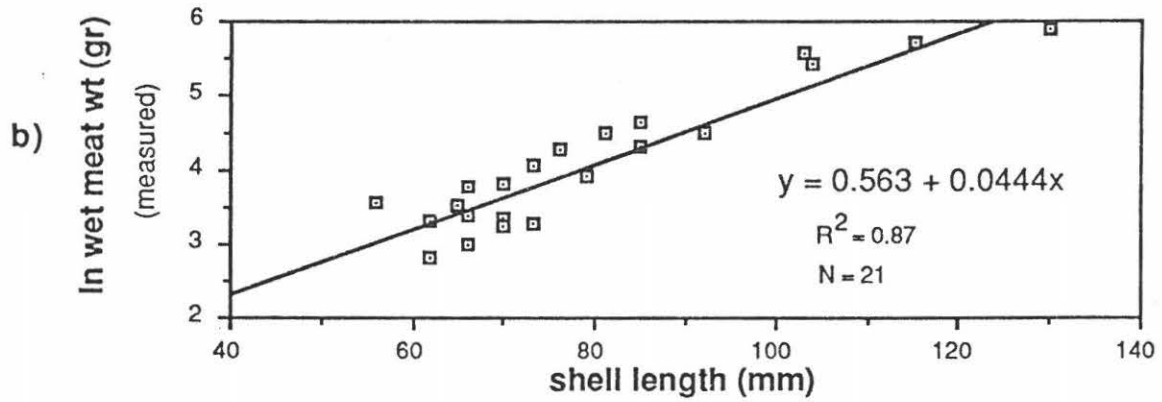
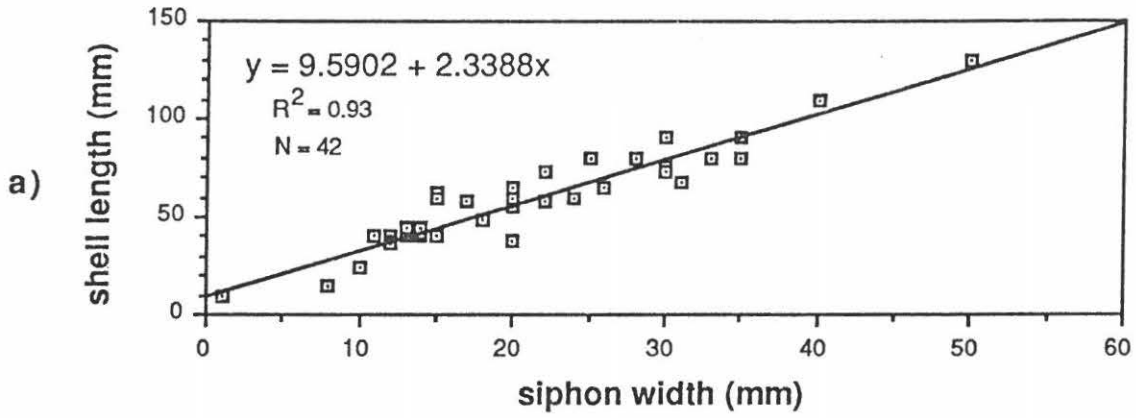
Saxidomus nuttalli
size and weight regressions



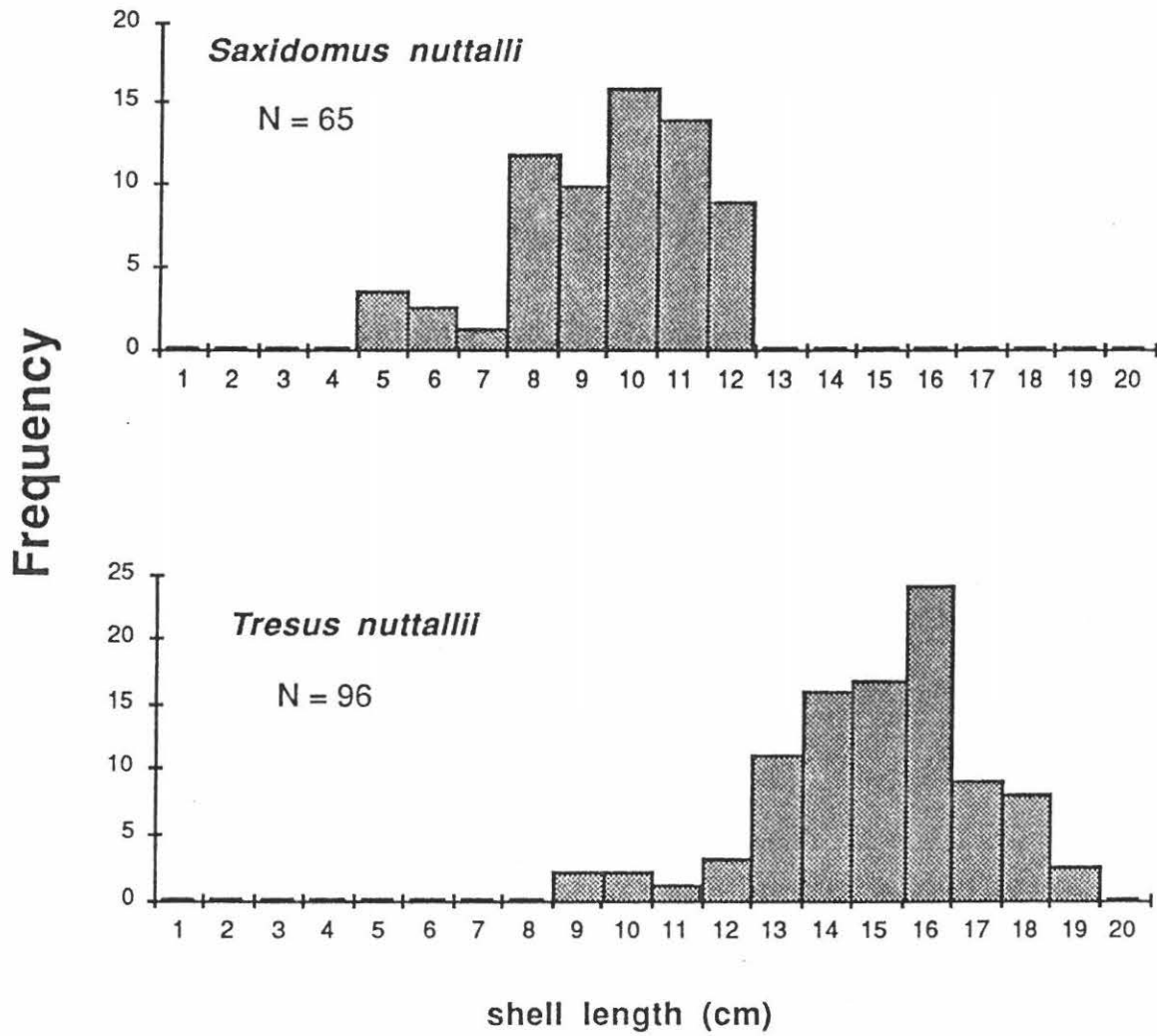
Tresus nuttallii
size and weight regressions



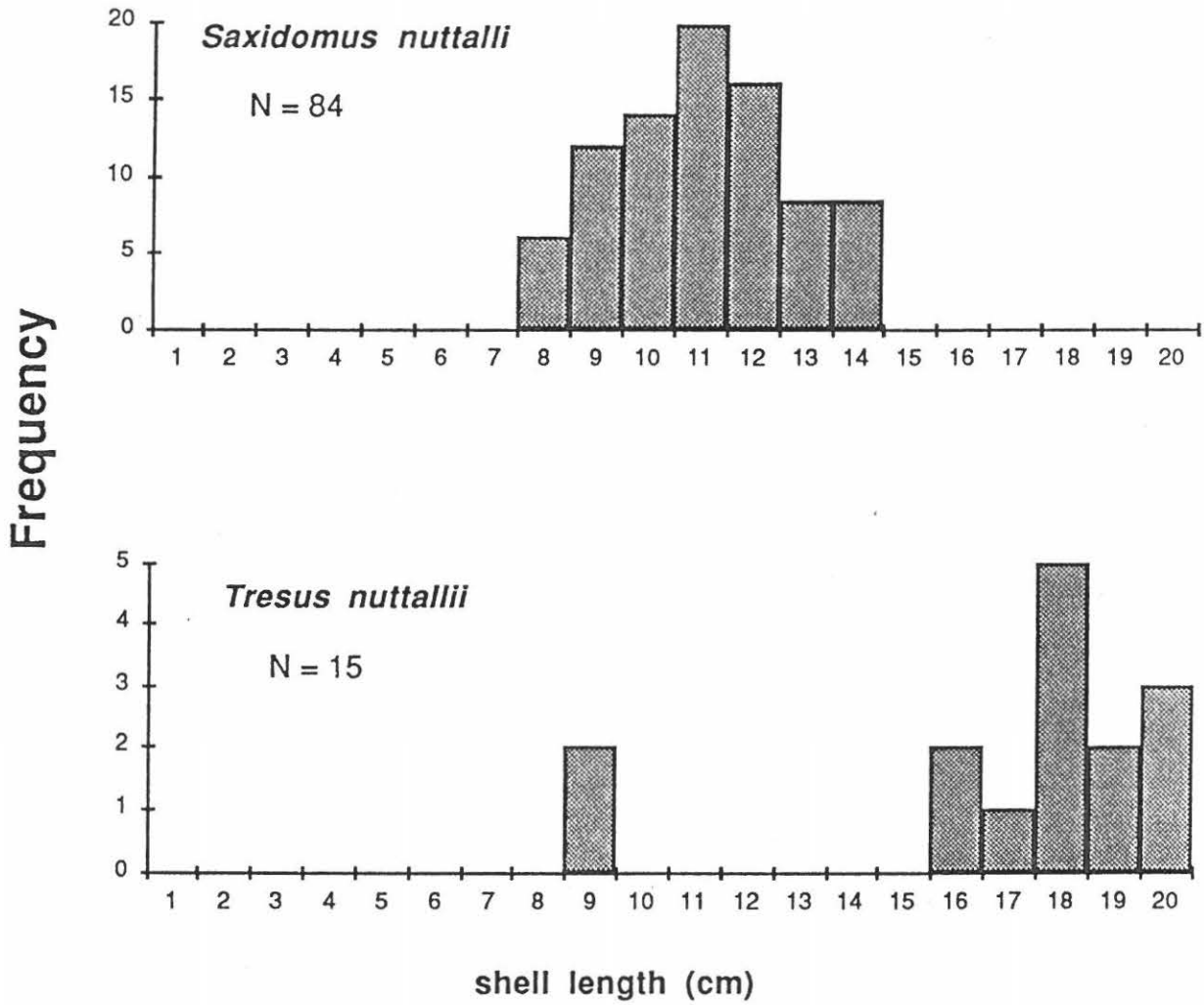
Zirphaea pilsbryi
size and weight regressions



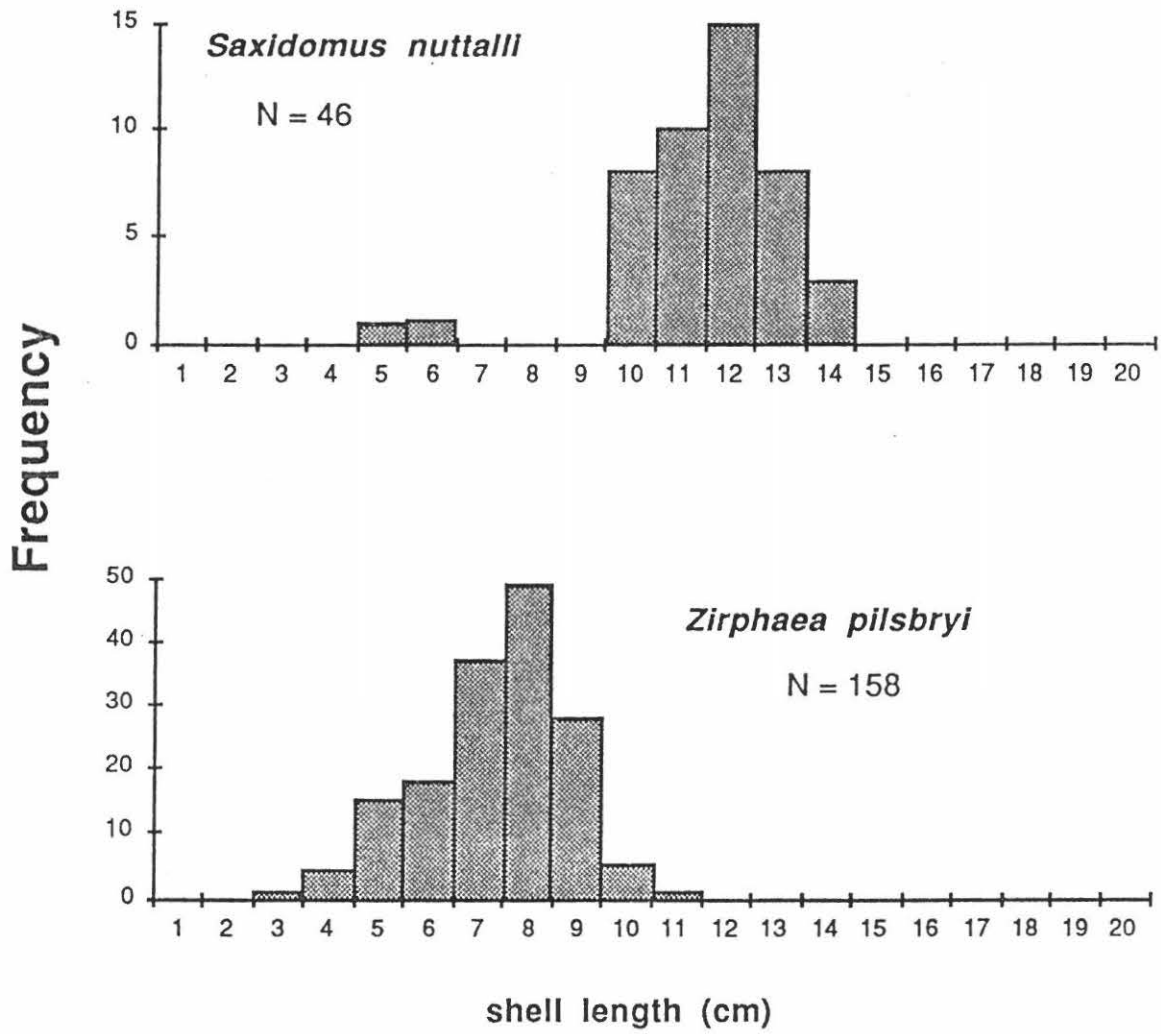
Skipper's Live Bivalve Sizes



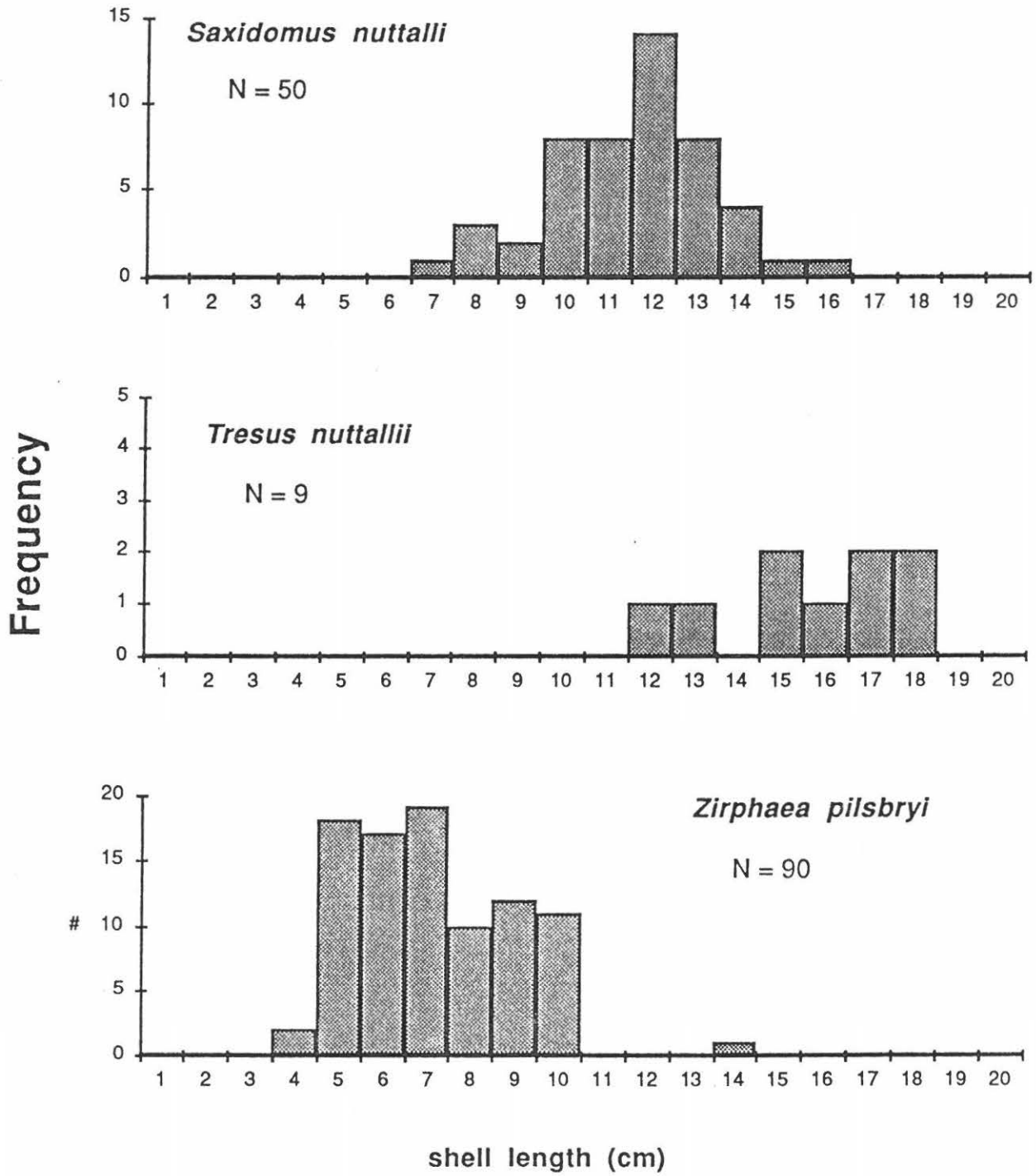
PG&E Outfall
Live Bivalve Sizes



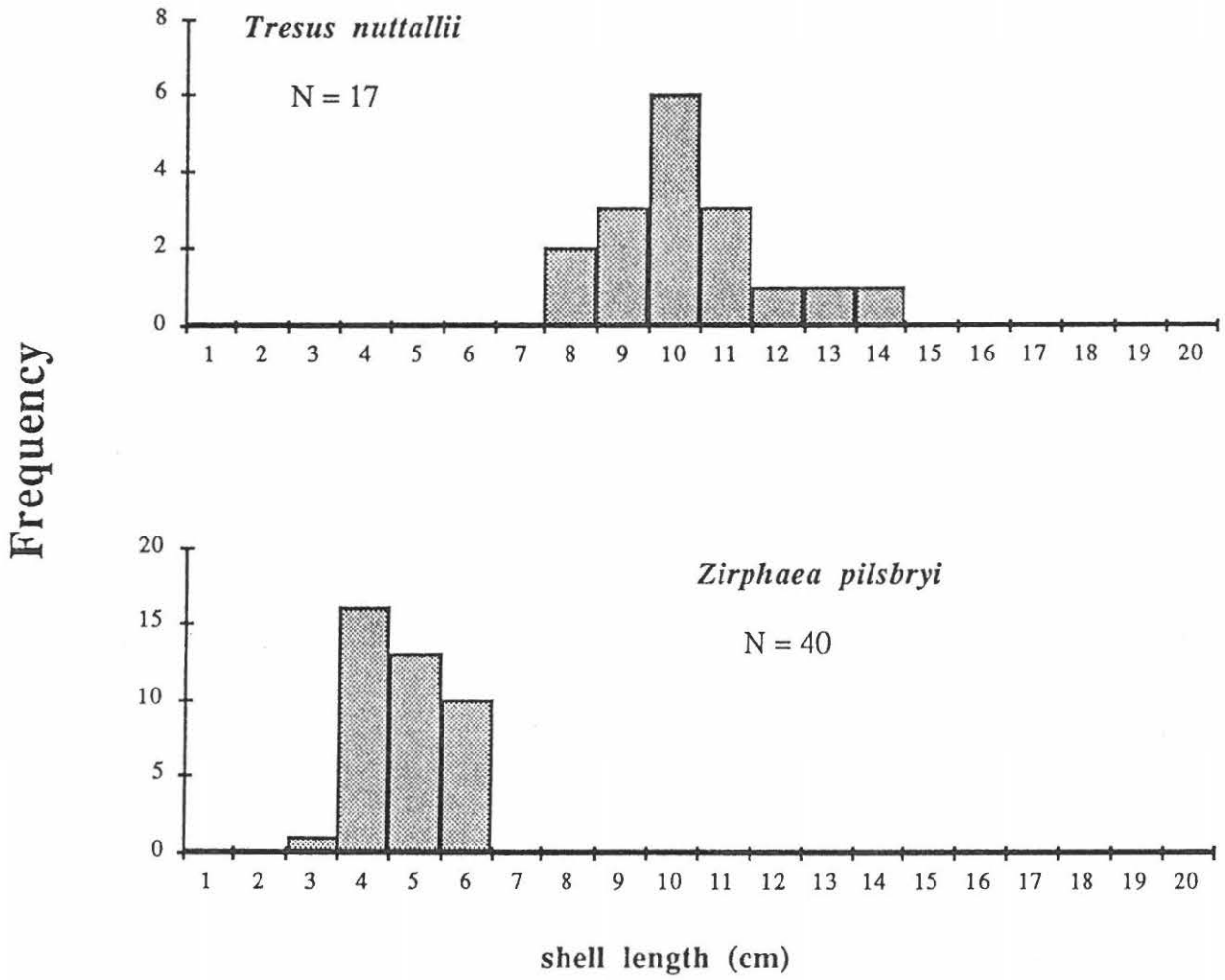
Seal Bend Live Bivalve Sizes



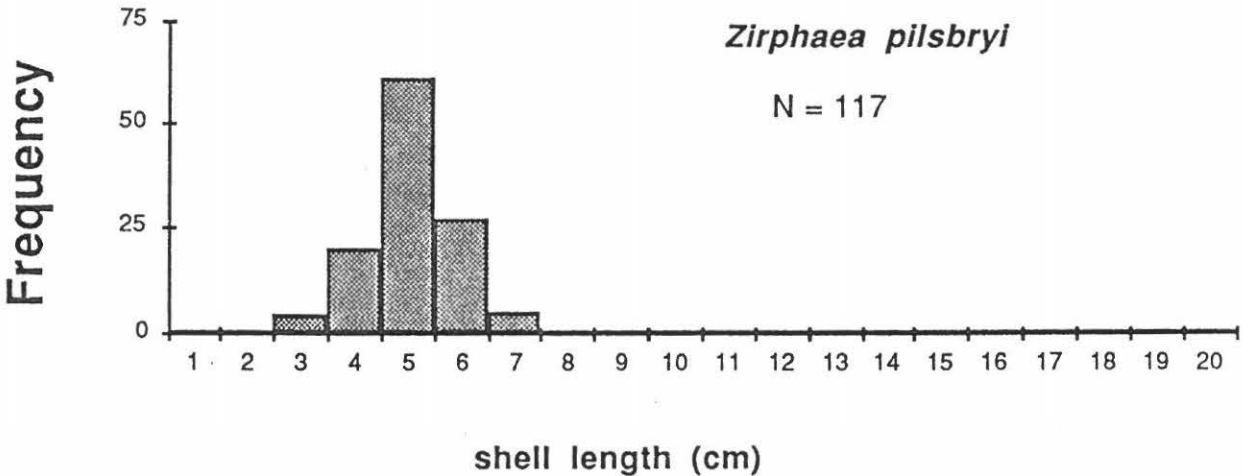
Shellfishery Live Bivalve Sizes



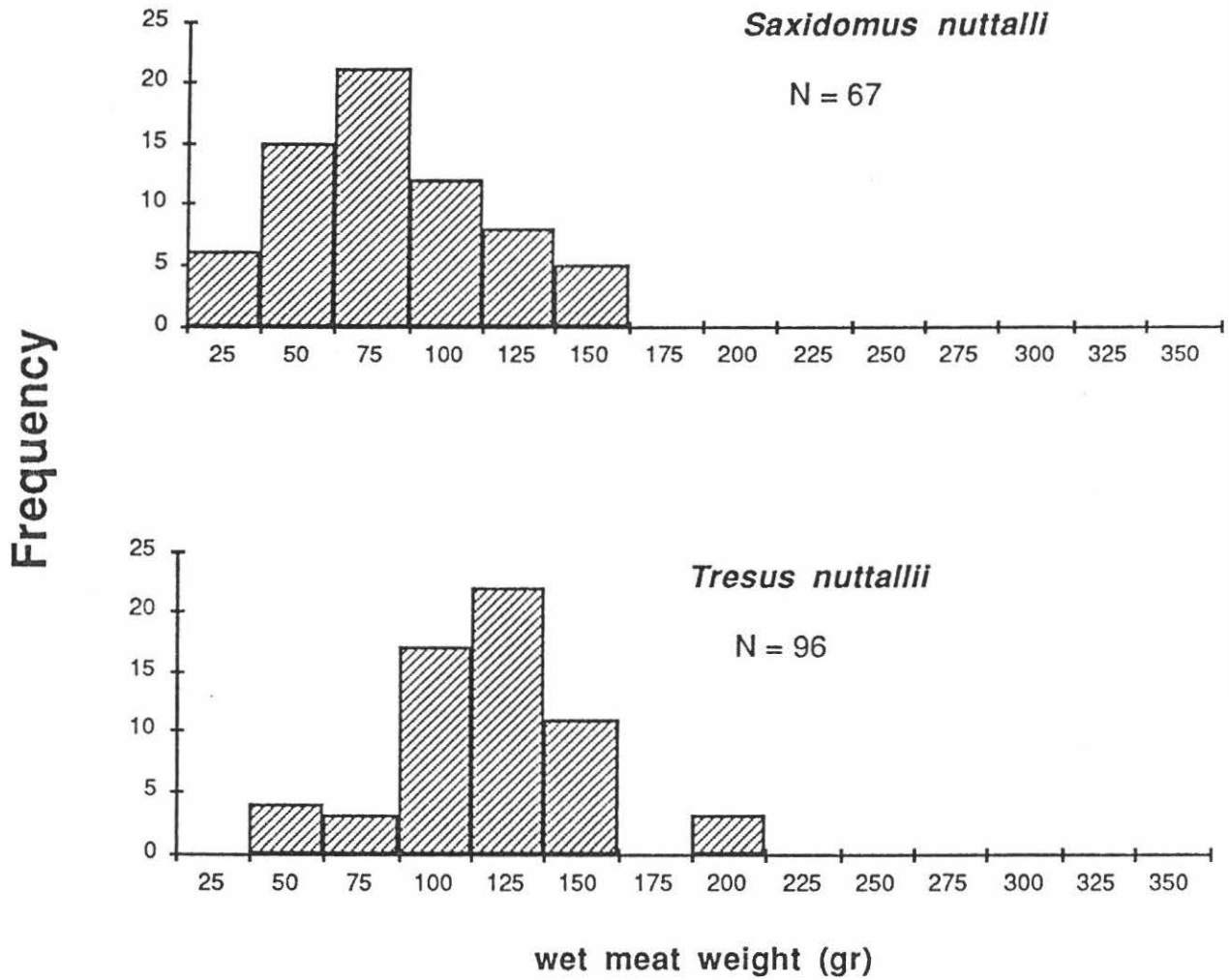
RESERVE
LIVE BIVALVE SIZES



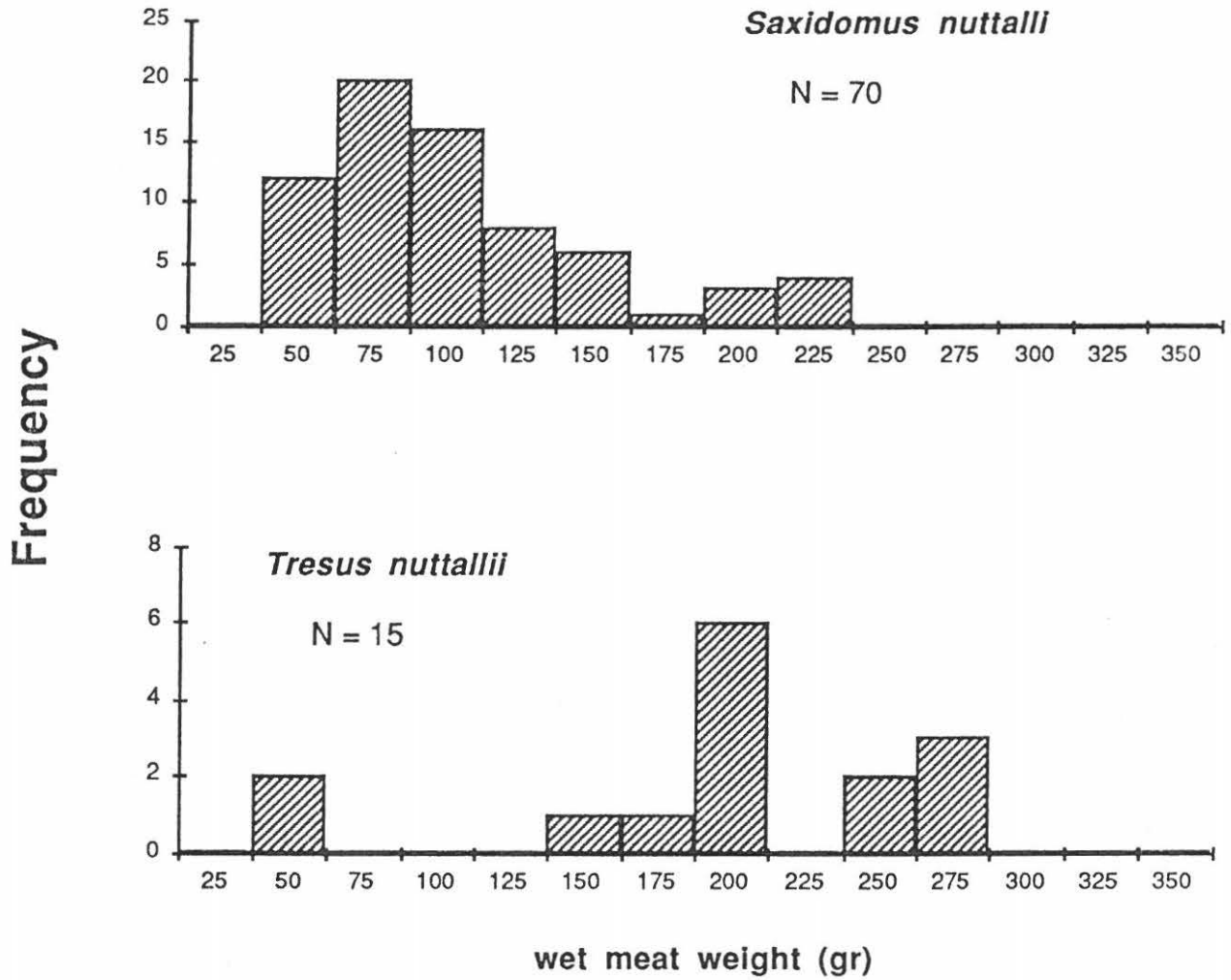
**Red House
Live Bivalve Sizes**



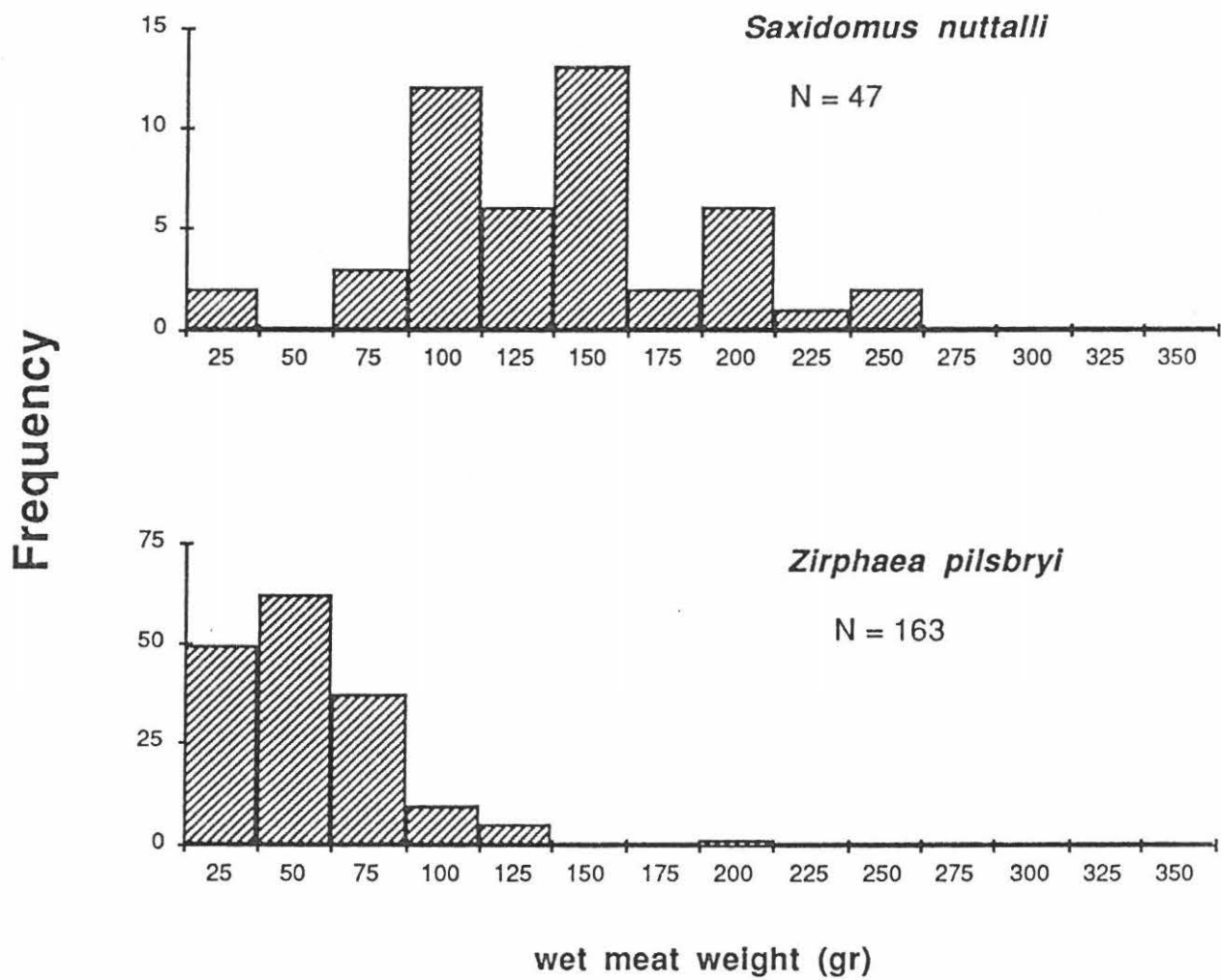
Skipper's Bivalve Wet Meat Weights



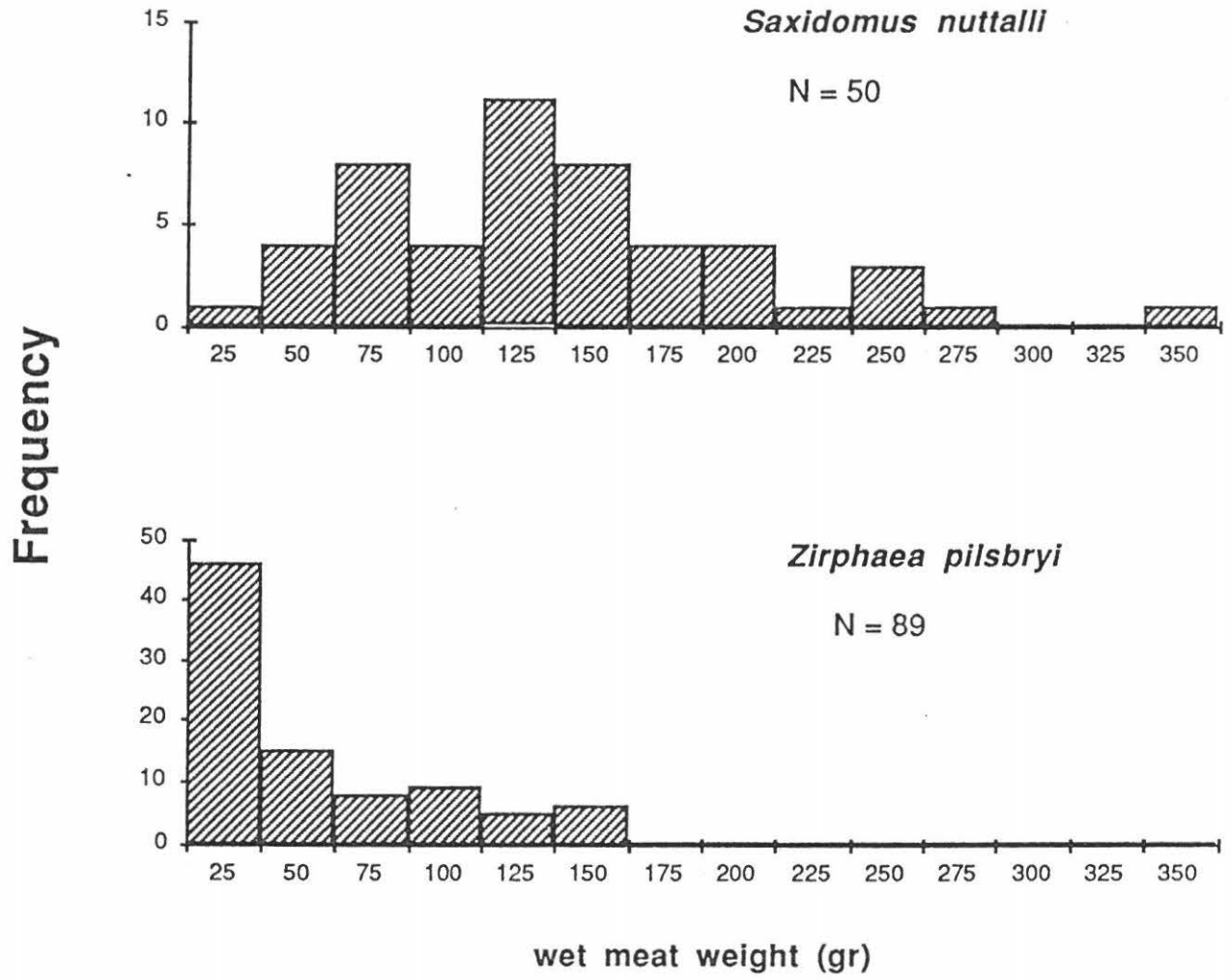
PG&E
Bivalve Wet Meat Weights



Seal Bend
Bivalve Wet Meat Weights



Shell Fishery Bivalve Wet Meat Weights



Dead Shell Records

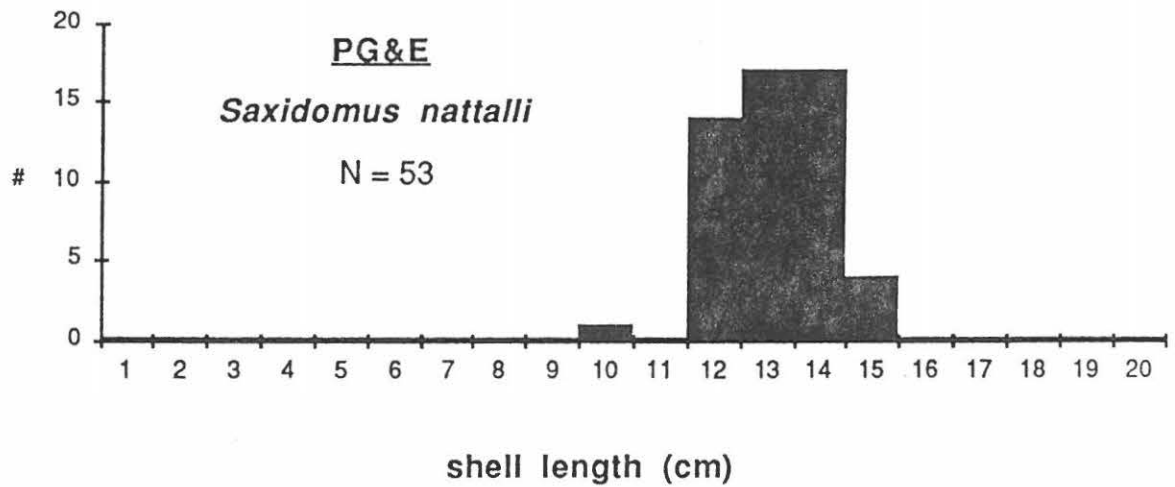
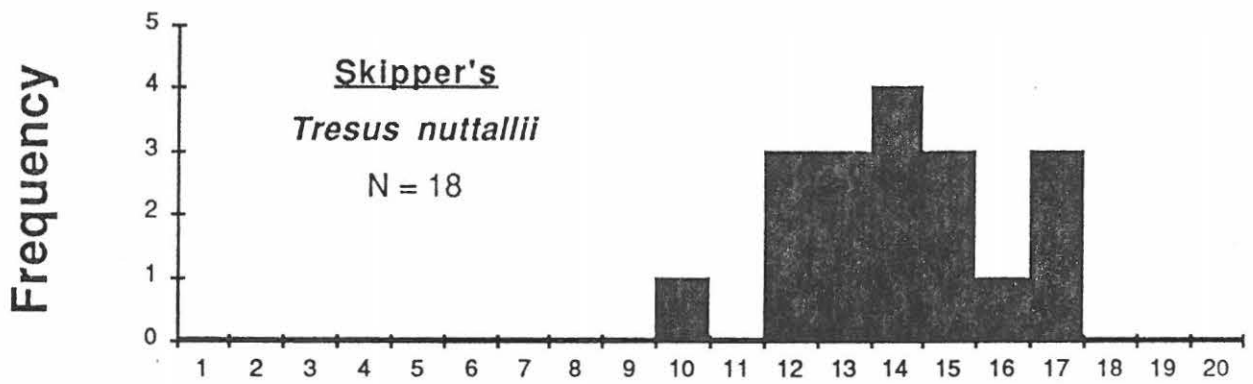
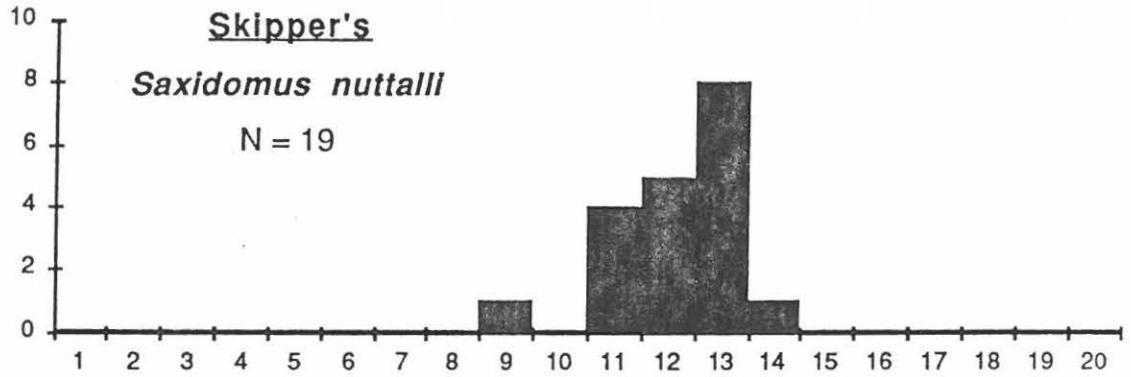


Table 1. Sea otter bivalve prey census results from all Elkhorn Slough study sites. General study areas are underlined, and their figures represent a composite of the constituent subsites, each listed individually. Means, (SD) and sample sizes are given when available for abundance (ind/.25m²), shell length and burrow depth of the three dominant species of large bivalves found in the slough. Biomass estimates (grams/.25m²) are the product of abundance and mean wet meat weight (obtained from shell length to weight regressions shown in figures 2,3 and 4).

Site subsite	<u><i>Saxidomus Nuttalli</i></u>				<u><i>Tresus nuttalli</i></u>				<u><i>Zirphaea pilsbryi</i></u>			
	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (mm)	burrow depth (cm)
<u>Skipper's</u>	<u>5.9</u>	<u>360</u>	<u>9.1</u>	<u>32.4</u>	<u>9.3</u>	<u>1909</u>	<u>14.5</u>	<u>31.4</u>	<u>0</u>			
SD	(6.47)		(1.75)	(10.61)	(11.41)		(2.08)	(7.68)				
N	40		67	13	40		96	33	40			
<u>west</u>	<u>0.8</u>				<u>4.5</u>				<u>0</u>			
SD	(0.97)				(3.87)							
N	20				20				20			
<u>east</u>	<u>11.1</u>				<u>14.1</u>				<u>0</u>			
SD	(5.36)				(14.25)							
N	20				20				20			
<u>PG&E outfall</u>	<u>3</u>	<u>407</u>	<u>10.4</u>	<u>25.4</u>	<u>0.7</u>	<u>206</u>	<u>16.4</u>	<u>27.4</u>	<u>0</u>			
SD	(0.95)		(1.64)	(4.98)	(0.82)		(3.38)	(7.01)				
N	45		84	16	45		15	8	45			
<u>north bank</u>	<u>2.9</u>				<u>0.75</u>				<u>0</u>			
SD	(0.81)				(0.91)							
N	20				20				20			
<u>channel</u>	<u>3.1</u>				<u>0.7</u>				<u>0</u>			
SD	(1.05)				(0.75)							
N	25				25				25			
<u>south bank</u>	<u>0</u>	<u>0</u>			<u>0</u>	<u>0</u>			<u>0</u>	<u>0</u>		
SD	(0.00)				(0.00)				(0.00)			
N	10				10				10			

Table 1. (continued)

Site subsite	<i>Saxidomus Nuttalli</i>				<i>Tresus nuttalli</i>				<i>Zirphaea pilsbryi</i>			
	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)
Seal Bend	1.3	147	11.1	23.3	0.3	47	13.3		4.4	159	6.9	21.8
SD	(2.00)		(1.71)	(3.72)	(0.71)		(1.66)		(4.97)		(1.40)	(10.66)
N	66		47	6	66		8		65		163	25
north bank	0.1				0				8.1	491	8.1	
SD	(0.30)								(5.87)		(0.71)	
N	11				11				11		59	
north slope	0.6	85	11.9		0.1				7.3	307	7.2	
SD	(1.90)		(1.32)		(0.32)				(6.26)		(0.74)	
N	10		5		10				10		34	
channel	2.1	230	10.9		0.5	81	13.4		2.5	48	5.4	
SD	(1.22)		(1.79)		(0.52)		(1.12)		(3.24)		(1.28)	
N	11		39		11		5		11		23	
south slope	0.1				0.4				5	111	5.8	
SD	(0.30)				(0.92)				(3.46)		(0.99)	
N	11				11				10		43	
south bank	0.2				0.1				0.4	10	6.0	
SD	(0.42)				(0.32)				(0.70)		(1.3)	
N	10				10				10		4	
Shellfishery	3	338	11.0	26.8	0.4	84	15.1		4.7	156	6.7	21
SD	(3.27)		(1.87)	(5.70)	(0.99)		(2.17)		(4.45)		(1.93)	(11.27)
N	31		50	15	31		9		31		90	3
north bank	0	0			0	0			0	0		
SD	(0.00)				(0.00)				(0.00)			
N	10				10				10			
north slope	0	0			0				6.6	112	5.2	
SD	(0.00)				(0.00)				(3.47)		(0.70)	
N	10				10				10		45	
channel	6.4	748	11.2	26.8	0.2	41	14.5		0			
SD	(2.41)		(1.62)	(5.70)	(0.42)							
N	10		26	15	10		2		10			
south slope & bank	3	325	10.9		0.9	216	15.3		8.0	518	8.2	
SD	(2.45)		(2.13)		(1.60)		(1.76)		(3.30)		(1.52)	
N	10		24		10		7		10		45	

Table 1. (continued)

Site subsite	<i>Saxidomus Nuttalli</i>				<i>Tresus nuttallii</i>				<i>Zirphaea pilsbryi</i>			
	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)	Ind/ .25/m ²	gr/ .25m ²	shell length (cm)	burrow depth (cm)
<u>Reserve</u>												
front channel	0				0.5	31	9.8	all clams at surface	8.4	90	4.1	
SD	(0.00)				(0.80)		(1.50)		(5.48)		(0.89)	
N	32				32		17		20		40	
back channel	0	0			0	0			0	0		
<u>Red House</u>												
SD	0	0			0	0			10.8	142	4.5	
SD	(0.00)				(0.00)				(4.90)		(0.77)	
N	22				22				22		117	
west slope	0				0				9.2	137	4.9	
SD	(0.00)				(0.00)				(3.55)		(0.73)	
N	10				10				10		65	
channel	0				0				13.5	153	4.2	
SD	(0.00)				(0.00)				(4.10)		(0.67)	
N	10				10				10		52	
east bank & channel	0				0				0.0			
SD	(0.00)				(0.00)				(0.00)			
N	10				10				10			

Table 2. Bivalve shell records of recent origin collected at Skipper's and PG&E outfall sites in the Elkhorn Slough. Shell lengths given as mean (SD).

Site	<u><i>Saxidomus nuttalli</i></u>		<u><i>Tresus nuttalli</i></u>		N
	percent of record	shell length (cm)	percent of record	shell length (mm)	
Skipper's (SD)	51%	11.6 (1.11)	49%	13.6 (1.96)	37
PG&E outfall (SD)	96%	12.6 (1.0)	4%	13.7	55