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Distribution of Foveaux Strait oysters (*Tiostrea chilensis*) and prevalence of infection by *Bonamia* sp. in March 1995

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1. EXECUTIVE SUMMARY

Mean prevalence of infection by *Bonamia* sp. (percentage of oysters sampled that were infected) in legal-sized oysters in Foveaux Strait declined from 21% in 1990 to 8% in 1992 and 4.5 % in 1995. Intensity of infection (degree of infection of individual oysters graded from 1 to 5), and the likelihood of infection resulting in death of oysters, has also declined over this time.

A low prevalence of infection was found in oyster samples from most stations throughout Foveaux Strait. The positions of the four small patches of moderate prevalence of infection were not related in a clear pattern. Prevalence of infection was not related to oyster density or to recent mortality.

The number of legal-sized oysters in Foveaux Strait in 1995 was significantly greater than in 1992. Contouring oyster density suggests that density has increased most in the central area of Foveaux Strait. The number of immediate pre-recruits and small pre-recruits in Foveaux Strait in 1995 was similar to 1993.

There was some evidence of mortality of oysters since 1993 in the eastern and western extremities of oyster distribution. The cause of this mortality is unclear.

2. INTRODUCTION

In 1975, oysters in Foveaux Strait were distributed in some 50 discrete, small, and dense populations which in total covered some 7.5 square nautical miles of the sea floor (Allen 1979, Allen & Cranfield 1979) and contained 1140 million legal-sized oysters (Doonan *et al.* 1994). Oysters in Foveaux Strait were not surveyed between 1975 and the first appearance of mortality from the *Bonamia* sp. epizootic in the autumn of 1985. The CPUE data from the fishery and distribution of fishing effort between 1975 and 1985 suggest that oyster abundance and distribution of individual populations of oysters in 1985 were similar to those of 1975 (Cranfield *et al.* 1991, Doonan *et al.* 1994).

Investigations between 1986 and 1989 studied prevalence and intensity of infection (*see* Methods for definition of terms) around the site of the original mortality (Hine 1986a, 1986b, 1987a, 1987b, 1987c, 1987d, 1988a, 1988b, 1989, 1990a, Hine *et al.* 1986). Prevalence and intensity of infection throughout Foveaux Strait were studied in 1990 and 1992 (Hine 1990b, Cranfield *et al.* 1991, Doonan & Cranfield 1992, Hine & Wesney 1992). The impact of *Bonamia* sp. on the number and distribution of oysters in Foveaux Strait was studied in dredge surveys in 1990, 1992, and 1993 (Cranfield *et al.* 1991, Doonan & Cranfield 1992, Cranfield *et al.* 1993, Doonan *et al.* 1994).

The localised studies between 1986 and 1989 followed the build-up of prevalence of infection around the site of the original infection and established that *Bonamia* sp. spread steadily through oyster populations surrounding the site of original infection with prevalence of infection rising to 10% in the first year, 25 % in the second, and higher levels in the third year. Some mortality was seen in the second year, but mortality was high in the third year (*see* Hine 1986a, 1986b, 1987a, 1987b, 1987c, 1987d, 1988a, 1988b, 1989, 1990a, Hine *et al.* 1986).

A wave of infection of *Bonamia* sp. radiated through the oyster populations in Foveaux Strait in 1990 from the focus of infection. At the front of the wave, oysters had a light prevalence of infection (less than 10%) and did not die. In the middle of the wave, oysters had a moderate (between 10 and 25%) or heavy (over 25%) prevalence of infection which resulted in high mortalities. After the wave passed previously dense oyster populations were marked by dense accumulations of articulated shells of oysters that had been killed ("clocks") (Cranfield *et al.* 1991). Living oysters were reduced to very low densities.

Oyster density was high at the site of original infection in 1987 (Dinamani *et al.* 1987) and the prevalence of infection became high there between 1987 and 1989 (Dinamani *et al.* 1987, Hine 1987a, 1987b, 1987c, 1987d, 1988a, 1988b, 1989). By 1990, both oyster density and prevalence of infection were low and the density of clocks was similar to the difference in density of live oysters between 1987 and 1990 (Cranfield *et al.* 1991). These studies show that during the epizootic, widespread sampling was able to map the spread of infection through the population and the subsequent mortality resulting in the dense accumulation of clocks.

Sampling in 1992 showed that the wave of infection had reached the periphery of oyster distribution (Hine & Wesney 1992). Mortalities had destroyed most of the small discrete populations found in 1975 (Doonan & Cranfield 1992) and reduced oyster density in that area by 91% (Doonan *et al.* 1994). The oyster population (of an area considerably larger than that surveyed in 1975) had decreased to 297 million which was less than 10% of the estimated virgin stock (Doonan *et al.* 1994). A model of the oyster population suggested that recruitment would fail at this stock size (Allen 1979). Thus, in 1992, the area exploited and the catch permitted were reduced, and, in 1993, the fishery was closed to allow the population to rebuild.

The present study was conducted to map the distribution of *Bonamia* sp. and oysters throughout Foveaux Strait in 1995. Their distributions are compared with those of previous years to determine whether infection by *Bonamia* sp. is likely to continue causing death of oysters. The data collected were used to make a preliminary estimate of the oyster population; a further survey in October 1995, after all possibility of mortality from *Bonamia* sp. was past (*see* Hine 1991a), estimated the population more precisely.

3. METHODS

3.1 Size of oysters examined

In past surveys, prevalence and intensity of infection (*see* definitions below) were studied in the legal-sized oyster population only. Hine & Jones (1994) investigated the presence of infection in all oysters between 31 and 100 mm long (length is the greatest antero-posterior dimension normal to the dorso-ventral axis—the hinge to ventral margin) at one station sampled in the 1990 survey and found a similar prevalence of infection in all size groups. Hine (1989, 1990b, 1991a, 1991b) had established that *Bonamia* sp. proliferated most rapidly during the autumn in individual oysters in which female gonad material was being phagocytosed. The intensity of infection and the likelihood of death (Hine 1991a, Hine & Wesney 1992) was higher in such oysters than in those in which male gonad material was being phagocytosed. *Tiostrea chilensis* is a protandric hermaphrodite and in Foveaux Strait oysters as small as 41 mm long can breed as females (Cranfield & Allen 1977) so immediate pre-recruits (50–57 mm long, *see* below) fall within the size range we expect to breed as females. We therefore studied the prevalence and intensity of infection in samples of immediate pre-recruit oysters as well as legal-sized oysters in the February - March 1995.

3.2 Station selection

We randomly allocated 50 stations within the area of Foveaux Strait sampled in 1992 and 1993 (Doonan & Cranfield 1992, Cranfield *et al.* 1993). Mapping the distribution of oysters and of the prevalence of infection was the main aim of this investigation. For this we required an even spread of sampling stations which was most readily achieved by sampling in a uniform grid pattern. Estimating the size of the oyster population was a secondary objective, but grid pattern sampling gives rise to a technical problem in estimating variance (Doonan *et al.* 1994). We avoided this problem, without sacrificing the advantage of a uniform dispersion of stations for mapping purposes, by choosing stations randomly and using a wide exclusion zone to spread them evenly throughout Foveaux Strait (stations 1—50, Figure 1). The 1.75 n. miles (3.24 km) exclusion zone used is outside the approximate 1 n. miles (1.8 km) distance at which oyster catches would be spatially correlated (*see* Allen & Cranfield 1979). A further 10 stations were selected to increase the coverage for mapping prevalence of infection (stations 100–107, 110, and 111, Figure 1). These stations were not included in the estimate of population size.

3.3 Dredging

We followed the procedures used in the 1993 survey (Cranfield *et al.* 1993) so oyster abundance and distribution could be compared with that in 1993. The survey took 8 days between 26 February and 31 March 1995. The *Torea* (a sister ship to the *Hirere* and *Toiler*, both used in earlier surveys), operated by a skipper who had taken part in previous surveys, towed one standard commercial dredge (3.35 m wide) in a straight line 0.2 n. miles (370 m) down-tide at each station. GPS was used to position the vessel for the start of the tow and to control the length of the tow.

All oysters caught were sorted and counted in three categories: legal-sized oysters (≥ 58 mm in length), immediate pre-recruits (50–57 mm in length), and pre-recruits (10–49 mm in length). Clocks of legal-sized oysters and of both sizes of pre-recruits were counted as either clean or fouled (new clocks or old clocks). New clocks, the clean articulated shells of oysters that have died since settlement of fouling organisms during the last summer, indicate mortality in the year of sampling. The ligament of old clocks (the fouled articulated shells of dead oysters) remains intact for up to 3 years in Foveaux Strait and indicates oyster mortality in the past years (Cranfield *et al.* 1991).

3.4 *Bonamia* sp.

3.4.1 Prevalence of infection

Prevalence of infection is the percentage of oysters in a sample in which *Bonamia* sp. can be detected. In 1995, prevalence was estimated in samples of 50 legal-sized and 50 immediate pre-recruit oysters taken randomly from catches of over 50 oysters at each station. All oysters were taken where the catches contained 50 or less of each size range. Samples were flown to Greta Point where the oysters were held in running sea water until they could be examined. The longest delay in the aquarium before a sample was examined was 7 days. The intensity of infection in individual oysters would be unlikely to change in this period as at the low intensities prevailing in 1995 there were no lesions to allow the loss of *Bonamia* sp. No new putative infection could arise within a 7 day period so prevalence of infection would also remain the same. The length of each oyster was measured, the oyster opened, heart removed, and 8—10 air dried imprints were made. The imprints were stained with the Merck Hemacolor system and examined by oil-immersion light microscopy to determine the presence of *Bonamia* sp. Blocks of tissue from a number of samples were fixed for later histological examination.

Infection was determined from examination of all the blood cells in one imprint. If no blood cells in that imprint contained *Bonamia* sp., all the other imprints on the slide were examined. For mapping, prevalence of infection was graded in four levels: absent, light (1—10%), moderate (11—25%), and heavy (over 25%) (after Cranfield *et al.* 1991). Prevalence of infection was contoured in new "S" (Becker *et al.* 1989) at the 10% and 25% levels.

3.4.2 Intensity of infection

Intensity of infection was scored from 1 to 5 from the histopathology of all oyster tissues (Hine 1991a). Hine & Wesney (1992) correlated heart smear data with histological changes: at intensity 1, one oyster blood cell was infected in one imprint; at intensity 2, several blood cells were infected in each imprint; at intensity 3, about 25% of the blood cells in one imprint contained *Bonamia* sp.; at intensity 4, 30—50% of blood cells contained *Bonamia* sp. and few or no parasites were found outside haemocytes; at intensity 5, over 50% of blood cells were infected, most infected blood cells were disrupted, and many *Bonamia* sp. were extracellular. The intensity of infection determined from blood smears has also been correlated with histopathological changes in oyster tissues. At intensities of 4 and 5, hyperplasia of epithelia of the mantle, kidneys, and to a lesser extent the gills was common. Tissue lesions occurred following the breakdown of basal membranes at intensity 5 (Hine 1991a, Hine & Thorne in press). Oysters infected at intensity 5 cannot maintain turgor, extend the gills and feed, and die within a short time (Hine, pers. comm.).

3.5 Oyster population

Catches were standardised to a tow length of 0.2 n. miles (370 m) from the actual tow lengths determined from GPS positions of the beginning and end of each tow. The numbers of legal-sized, immediate pre-recruit, and small pre-recruit oysters in 1995 were contoured at 100 and 400 oysters in new "S". In 1990, a catch of 400 legal-sized oysters in a 370 m straight line tow was equivalent to a commercially acceptable catch rate in the oyster fishery (then 6—8 sacks per hour, *see* Cranfield *et al.* (1991)). The correlation coefficient of oyster density and prevalence of infection by *Bonamia* sp. at all stations was tested for significance.

The population of oysters in 1995 in each size group in the area sampled was estimated using the simple random survey formula. Although the stations were chosen randomly, the very regular spacing of stations achieved by using a 1.75 n. mile exclusion zone will probably result in sampling variance being overestimated in a similar manner to that of a simple grid survey (*see* Doonan *et al.* 1994).

The correlation coefficient of density of new clocks (numbers of greater than 50 mm long new clocks per standardised tow) and prevalence of infection by *Bonamia* sp. at each station was tested for significance. The distribution of mortality since summer 1994 was analysed as the ratio of new clocks to new clocks and live oysters combined. This mortality was contoured at the 1% and 8% levels. The distribution of old clocks in 1995 was analysed by contouring the catch data at 100 clocks per tow.

4. RESULTS

4.1 *Bonamia* sp.

4.1.1 Impact of size of oysters on infection

The mean prevalence of infection by *Bonamia* sp., 4.7% in legal-sized oysters and 4.2% in immediate pre-recruits, was not significantly different ($t = 0.15$, n.s.). The mean intensity of infection in infected oysters in the two size groups was 1.15 in legal-sized oysters and 1.12 in immediate pre-recruits and was also not significantly different ($\chi^2 = 0.5$, n.s.). The data on prevalence of infection in both size groups have been combined in the following analyses.

4.1.2 Prevalence of infection

Mean prevalence of infection in oysters from all stations sampled in 1995 (3898 oysters examined for infection) was 4.5%. A low prevalence of infection by *Bonamia* sp. is apparent throughout Foveaux Strait (Figure 2). The seven stations at which no infection was found were surrounded by stations at which infection was present. Four foci of moderate prevalence of infection occurred between Ruapuke Island and Saddle Point. At the single station with a high prevalence of infection we caught only five oysters.

4.1.3 Intensity of infection

The intensity of infection of the 174 infected oysters is shown in Figure 3. Mean intensity was 1.13.

4.2 Oyster population

4.2.1 Distribution of oysters, prevalence of infection by *Bonamia* sp., and mortality

Contours of density of legal-sized oysters (*see* Figure 7d), immediate pre-recruits, and smaller pre-recruits (Figures 4a, 4b) show four concentrations (two large and two small) of commercial densities of legal-sized oysters (assumed to be the same as in 1990, 400 per tow). Immediate pre-recruits and small pre-recruits were distributed in a pattern similar to the legal-sized oysters. Contours of prevalence of infection by *Bonamia* sp. in 1995 were unrelated to those of oyster density (Figures 3, 4, 7d) and there was no correlation between the two at each station ($r = 0.17$, n.s.).

New clocks of both legal-sized and immediate pre-recruit size groups were combined and the new mortality contoured (Figure 5). The distribution of new mortality covered large areas of low to moderate oyster density (cf. Figures 7d, 4) and show little or no relationship with distribution of *Bonamia* sp. (*see* Figure 3). The prevalence of infection by *Bonamia* sp. and new mortality at each station were also not correlated ($r = 0.08$, n.s.).

The distribution of old clocks of legal-sized and immediate pre-recruit size was similar and the two size groups were combined in contouring these data (Figure 6). The two patches of old clocks coincided with the two patches of highest oyster density (Figure 4, 7d).

Contours of legal-sized oysters over the same area in 1990, 1992, 1993, and 1995 are shown in Figures 7 a–d. Immediate pre-recruits were sampled for the first time in the 1993 survey. The distribution in 1993 and 1995 of immediate pre-recruits and legal-sized oysters combined are shown in Figure 8.

4.2.2 Population size

The estimates of the size of the population of legal-sized oysters has increased steadily since 1992; the size of the population of immediate pre-recruits and small pre-recruits were similar in 1993 and 1995 (Table 1).

Table 1: Estimates of the size of the population of legal-sized (≥ 58 mm in long), immediate pre-recruit (50–57 mm in length), and smaller recruit (10–49 mm in length) oysters in in the area surveyed in 1993 in 1992 (legal-sized oysters alone) and 1995. Units, millions of oysters; CI, Confidence intervals include error in the estimate of dredge efficiency by bootstrapping.

	≥ 58 mm	95% CI	50–57 mm	95% CI	10–49 mm	95% CI
1992	238	155-366	*		*	
1993	283	178–402	273	171–390	443	282–630
1995	543	255–875	377	174–617	370	189–581

* Only numbers of legal-sized oysters estimated in this year.

5. DISCUSSION

5.1 *Bonamia* sp.

The prevalence and intensity of infection by *Bonamia* sp. was similar among legal-sized and immediate pre-recruit oysters and confirms the observations of Hine & Jones (1994).

Mean prevalence of infection in Foveaux Strait was 21% in 1990 (Hine 1990b), 8% in 1992 (Hine & Wesney 1992), and 4.5% in 1995. Mean intensity of infection of infected oysters (Hine 1991a, Hine & Wesney 1992), was 2.75 in 1990, 2.35 in 1992, and 1.13 in 1995. Stations sampled in the 1990 survey to determine prevalence of infection by *Bonamia* sp. were selected on known oyster populations; stations in the 1993 survey were sampled on a regular grid, and stations in the in 1995 survey were selected randomly. The mean calculated for the 1990 survey is probably overestimated, so the decreasing trend in prevalence and intensity of infection over this period may overestimate the real changes.

In 1995, oyster densities over 100 per tow were found in areas devastated by *Bonamia* sp. One of these areas was reduced well below 100 oysters per tow by 1990, the other below this density by 1992. Subsequent levels of infection were low or undetectable by 1992. In 1995, not only were oyster densities recovering, but a patch of moderate infection was also found in the area. These data suggest that infection by *Bonamia* sp. can recur in previously infected oyster populations as density rebuilds.

Infection by *Bonamia* sp. is probably transmitted by waterborne infective particles (Hine 1990b). Models of epizootics in which infections were transmitted directly between hosts suggest that the epizootic could recur as oyster density rebuilds (*see* Dobson & May 1986, Murray *et al.* 1986). There was no sign of increased prevalence of infection at stations with high oyster density. The general picture of the distribution of infection by *Bonamia* sp. was of a light prevalence of infection with unrelated patches of moderate prevalence. The lack of correlation of infection with oyster density suggests that there is little likelihood of any recurrence of the epizootic in Foveaux Strait with rebuilding oyster density, but localised random outbreaks of mortality may persist.

5.2 Changes in the oyster population

5.2.1 Changes in the distribution of oysters and mortality

In the central area of western Foveaux Strait the oyster population was reduced to low densities by the epizootic before 1990 (Doonan *et al.* 1994). Changes in the distribution of legal-sized oysters since 1990 are shown in Figures 7 a–d. The first change was the reduction of oyster densities below commercial levels (400 oysters per tow) around the periphery of oyster distribution between 1990 and 1992 (Figures 7 a, b) and in the western and eastern extremes of oyster distribution between 1993 and 1995 (Figures 7 c, d). Contours (Figure 8) suggest that the population decrease in the eastern and western extremes of oyster distribution may have involved pre-recruit mortality as well as mortality of legal-sized oysters. The second change was a rebuilding of oyster density in central Foveaux Strait. In 1995 moderate densities (100–200 oysters per tow) were found to the north and west of central Foveaux Strait where only very low densities were present in 1990 and 1992 after the passage of the epizootic.

The distribution of recent mortality shows little relationship (other than in the western extremes of oyster distribution, *see* Figure 7d) with the areas of moderate prevalence of *Bonamia* sp. in 1995 (compare Figures 3, 5). There was little correlation between the prevalence of infection and recent mortality in 1995 whereas in 1987 they were strongly correlated (Cranfield *et al.* 1991). The distribution of infection by *Bonamia* sp. shows a background of low prevalence and only small patches of moderate prevalence of infection with no pattern or relationship between them. Although some of the mortality reflected by new clocks in 1995 may not be the result of infection by *Bonamia* sp., other causes are difficult to identify. The extremely low mortality of adult oysters in Foveaux Strait before the epizootic (a mark-recapture experiment indicated a natural mortality rate between 0.009 and 0.015, Cranfield & Allen (1979)), indicates that there are few sources of natural mortality here. Although numbers of oysters appear to have died since 1993 in the western and eastern extremes of oyster distribution (Figure 8), there is no evidence that infection by *Bonamia* sp. was the cause.

5.3 Changes in size of the population

The population of legal-sized oysters has increased over the last the 3 years (*see* Table 1). The population estimates of 1995 and 1992 are significantly different ($t = 3.68$ $p = 0.0003$) as are those of 1995 and 1993 are ($t = 2.77$, $p = 0.006$). The numbers of immediate pre-recruits and small pre-recruits in 1993 and 1995 were not significantly different.

6. CONCLUSION

We sampled oysters in late March when infection by *Bonamia* sp. is most readily detected (*see* Hine 1991a). *Bonamia* sp. was still present at low levels throughout Foveaux Strait, but the mean prevalence and intensity of infection was less than in 1992 and 1993. Although mortalities had occurred since 1993, the cause is unknown. Oyster density (especially in central and southern Foveaux Strait, *see* Figure 7d) has increased, and the population is now significantly larger than in 1992.

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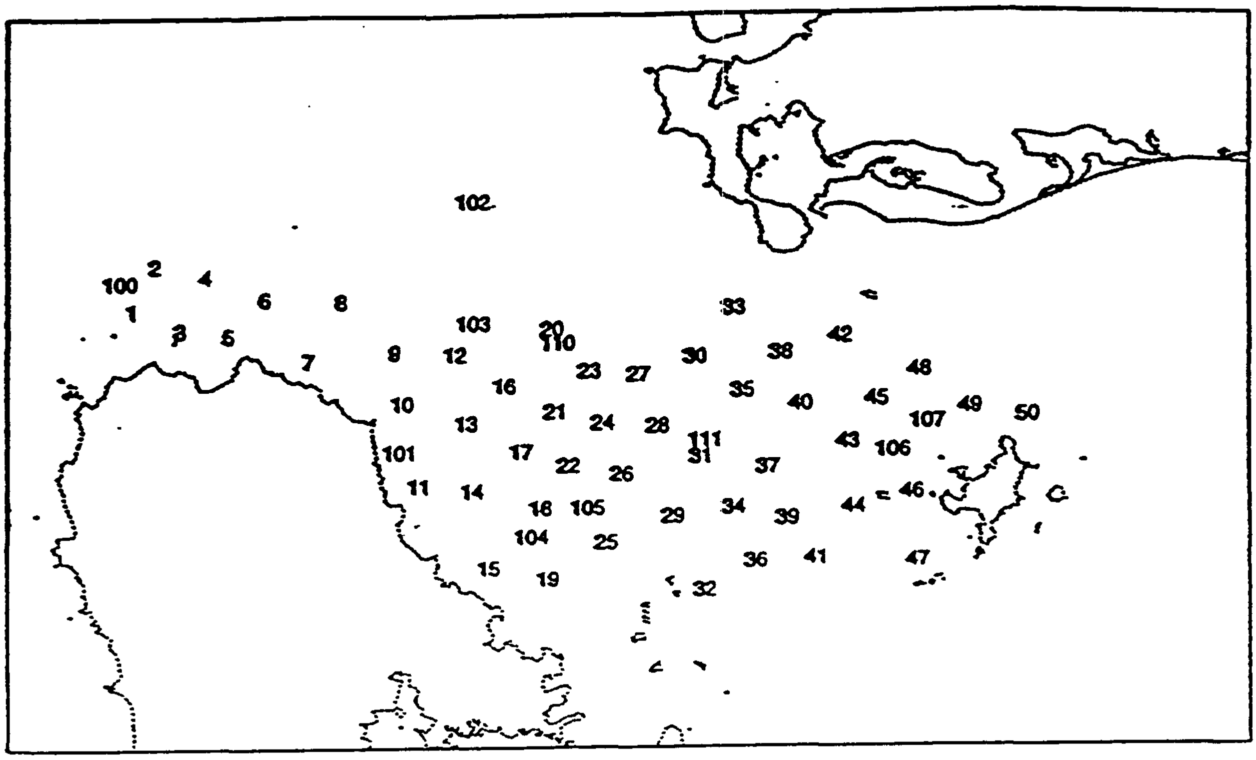

Figure 1: Station positions sampled in 1995 to determine changes in distribution of oysters and distribution of prevalence of infection by *Bonamia* sp. in Foveaux Strait.

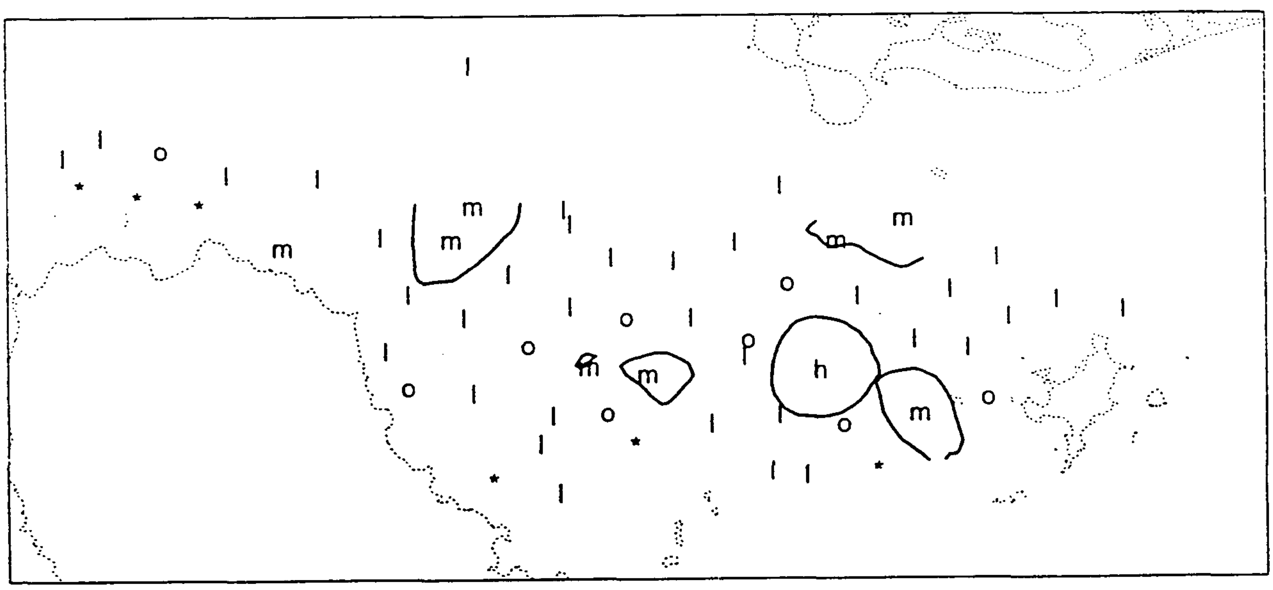

Figure 2: The prevalence of infection by *Bonamia* sp. in 1995 contoured at low ("l", 1–10%) and medium ("m", 11–25%) levels. A single station with high prevalence of infection (26+%) is shown as "h". Stations with no *Bonamia* ("o") and those with no oysters ("•") are also shown.

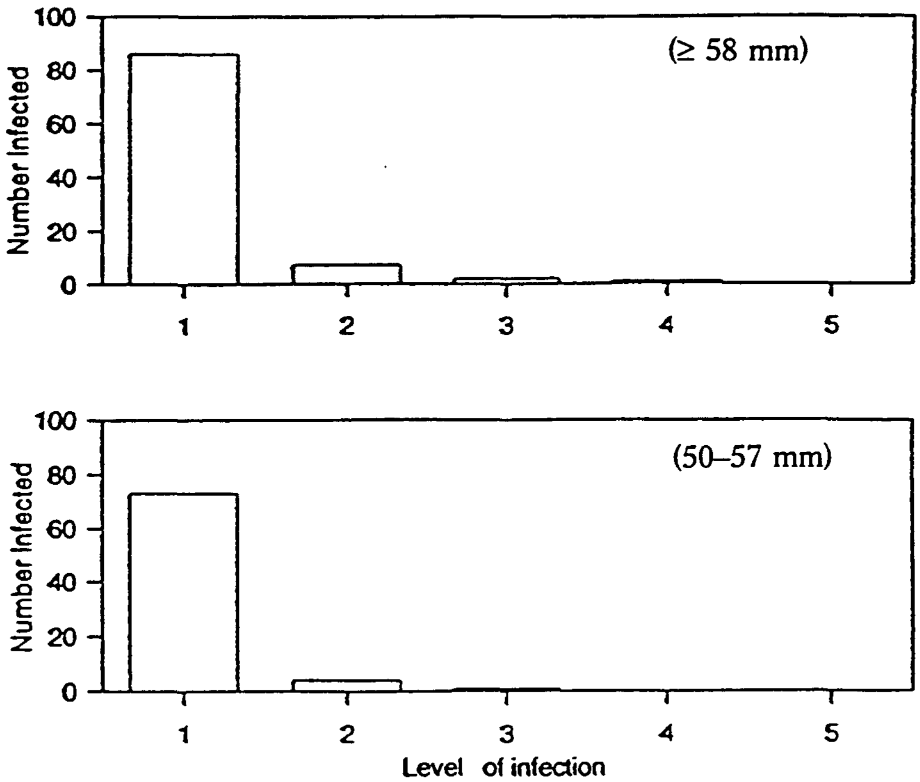

Figure 3: Intensity of infection (levels 1–5, see text) of recruited (≥ 58 mm in length) and immediate pre-recruit (50–57 mm in length) oysters in 1995.

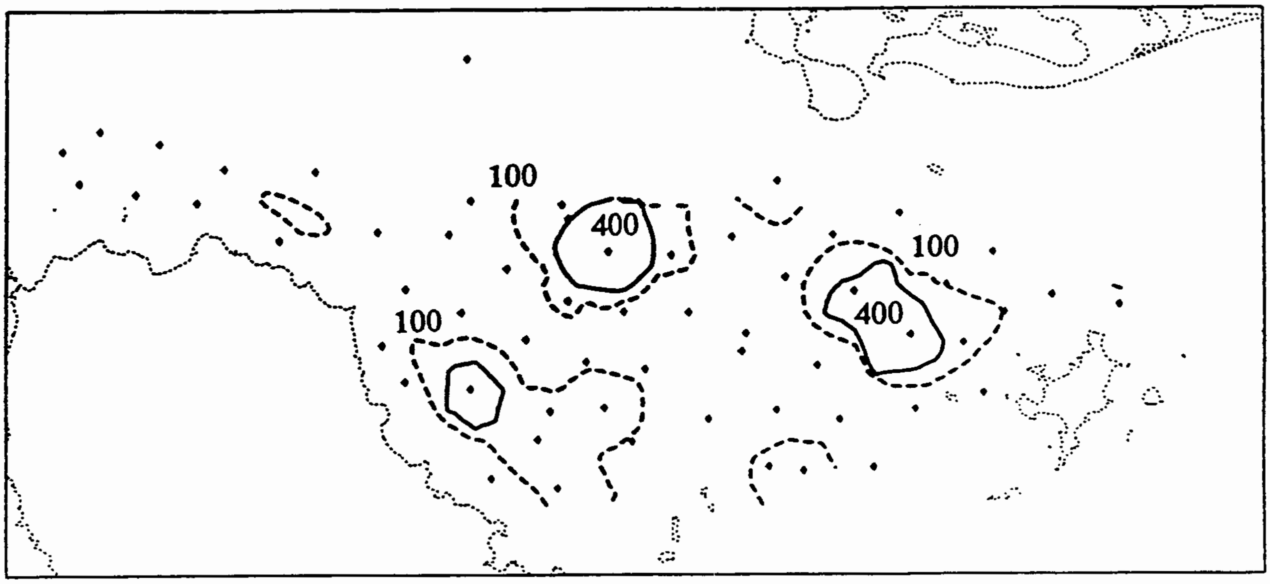

Figure 4a: The distribution of live oysters (50–57 mm in length) in 1995 contoured at 100 and 400 oysters per tow. Diamonds denote sample stations.

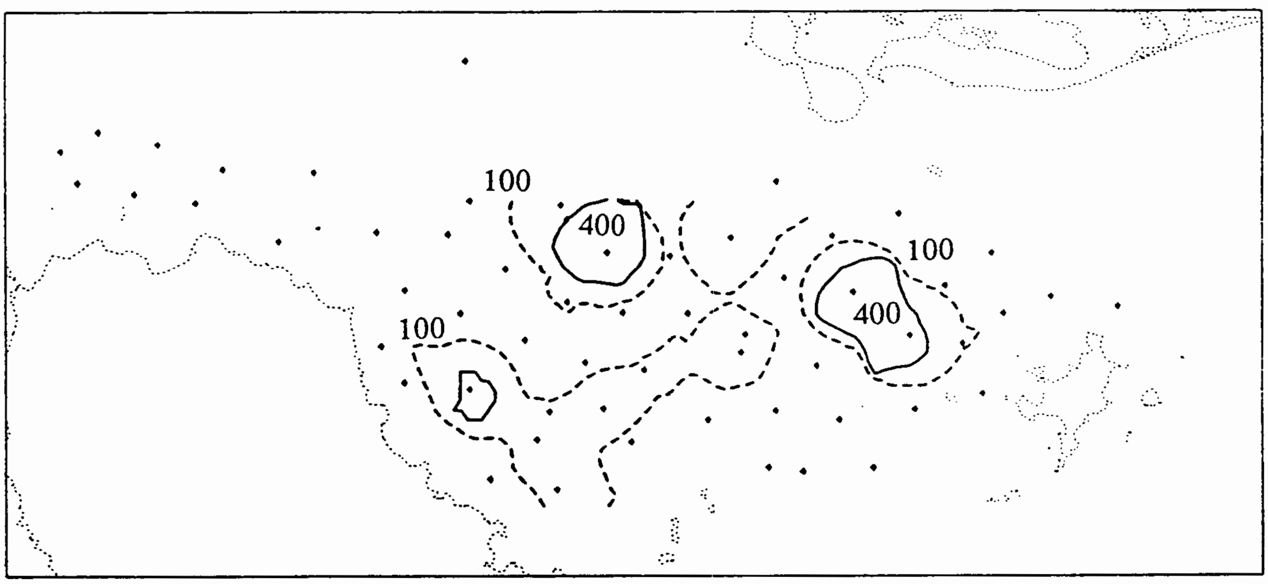

Figure 4b: The distribution of live oysters (⟨ 50 mm in length) in 1995 contoured at 100 and 400 oysters per tow. Diamonds denote sample stations.

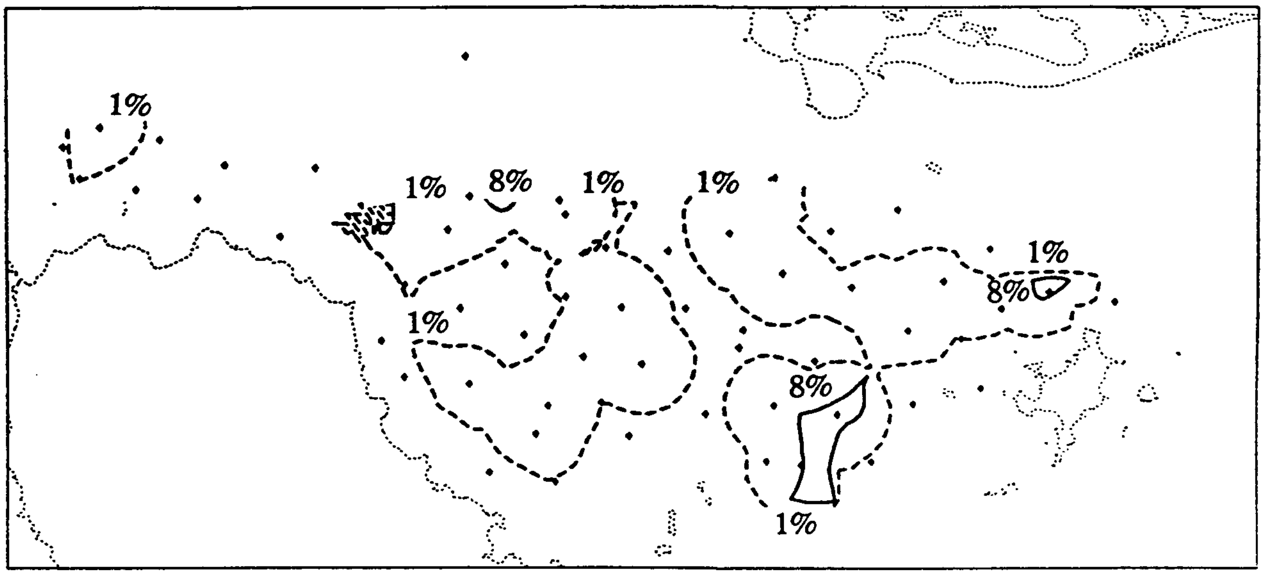

Figure 5: The distribution of mortality since last summer in 1995 expressed as the percentage of new clocks (> 50 mm in length) to new clocks and live oysters (> 50 mm in length), contoured at 1% and 8% levels. Diamonds denote sample stations.

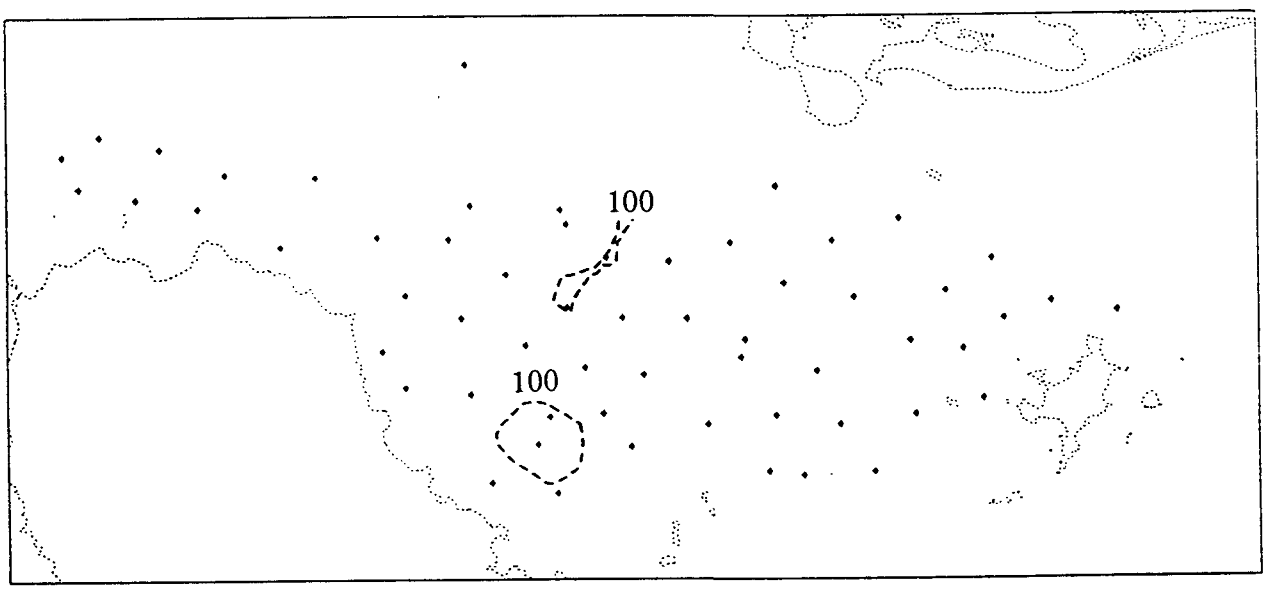

Figure 6: The distribution of old clocks (> 50 mm in length) in 1995 contoured at 100 clocks per tow. Diamonds denote sample stations.

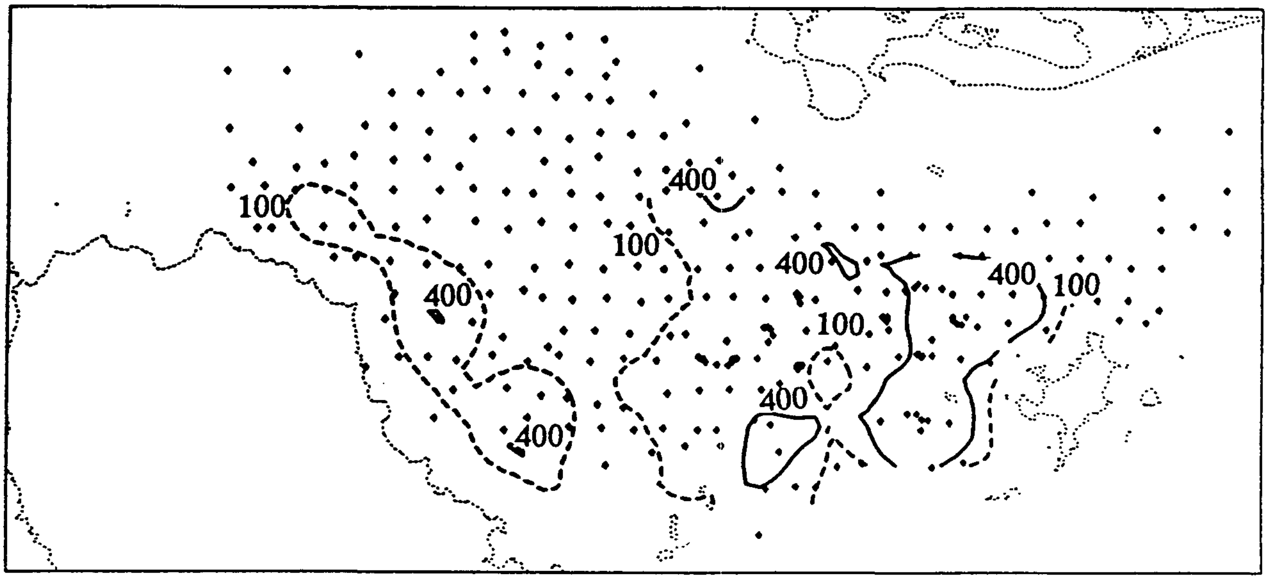

Figure 7a: The distribution of live oysters (≥ 58 mm in length) in 1990 contoured at 100 oysters per tow. Diamonds denote sample stations.

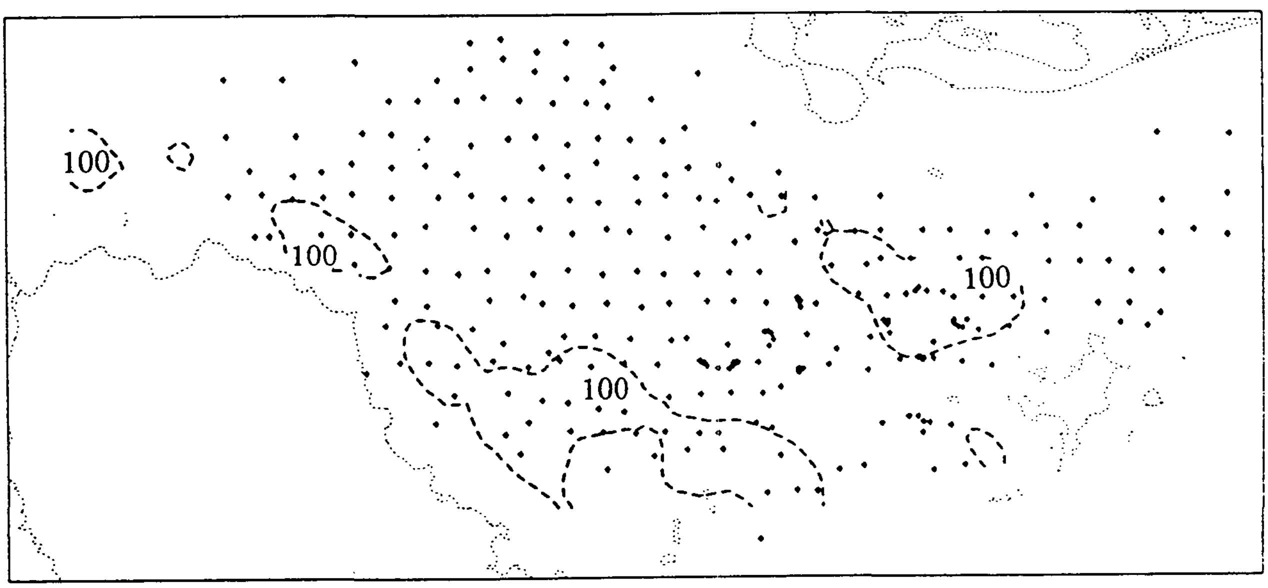

Figure 7b: The distribution of live oysters (≥ 58 mm in length) in 1992 contoured at 100 oysters per tow. Diamonds denote sample stations.

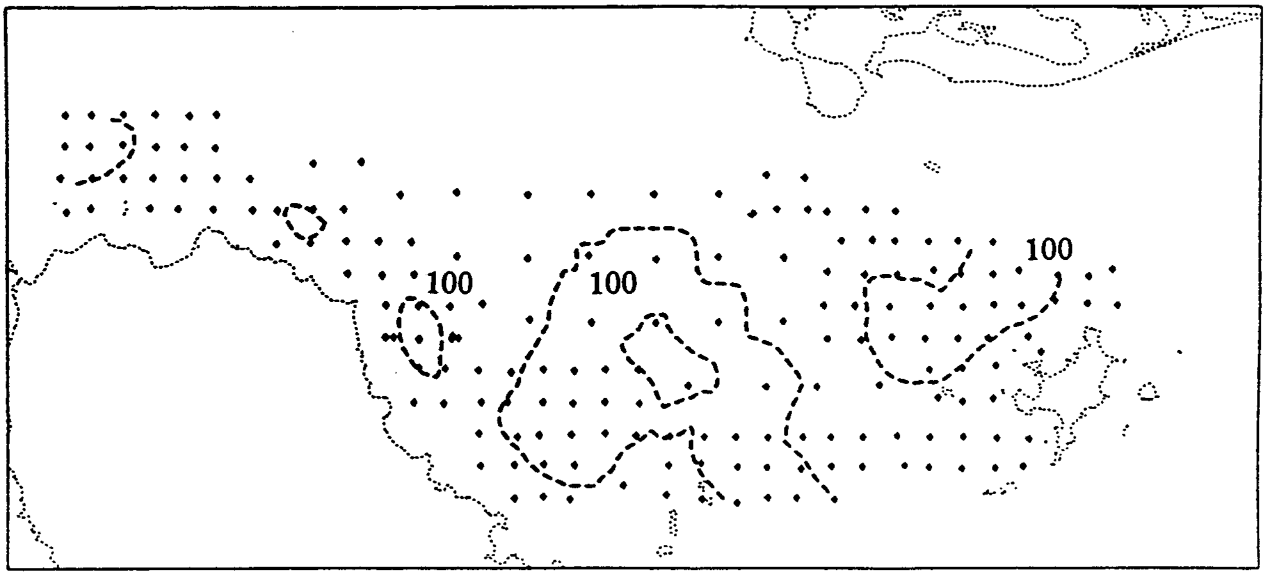

Figure 7c: The distribution of live oysters (≥ 58 mm in length) in 1993 contoured at 100 oysters per tow. Diamonds denote sample stations.

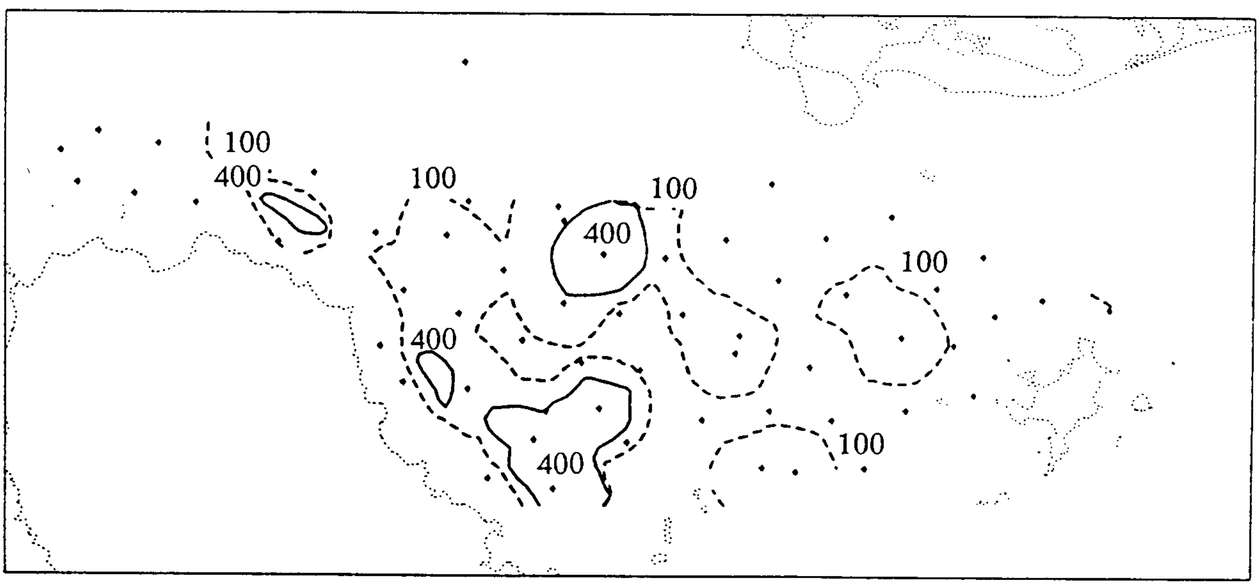

Figure 7d: The distribution of live oysters (≥ 58 mm in length) in 1995 contoured at 100 and 400 oysters per tow. Diamonds denote sample stations.

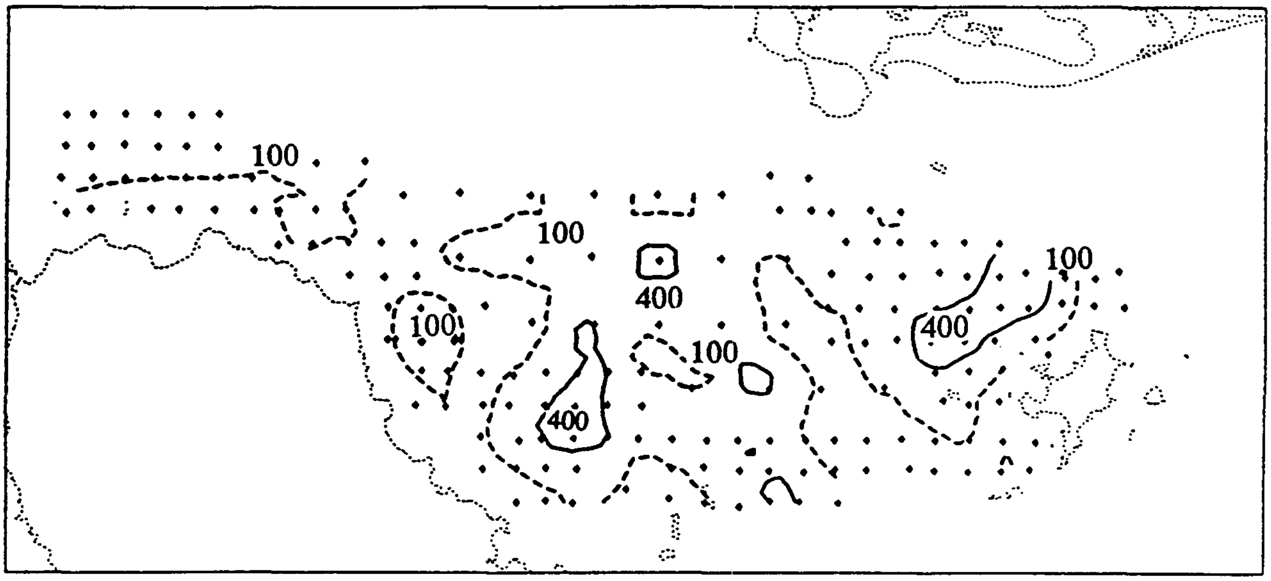

Figure 8a: The distribution of live oysters () 50 mm in length) in 1993 contoured at 100 and 400 oysters per tow. Diamonds denote sample stations.

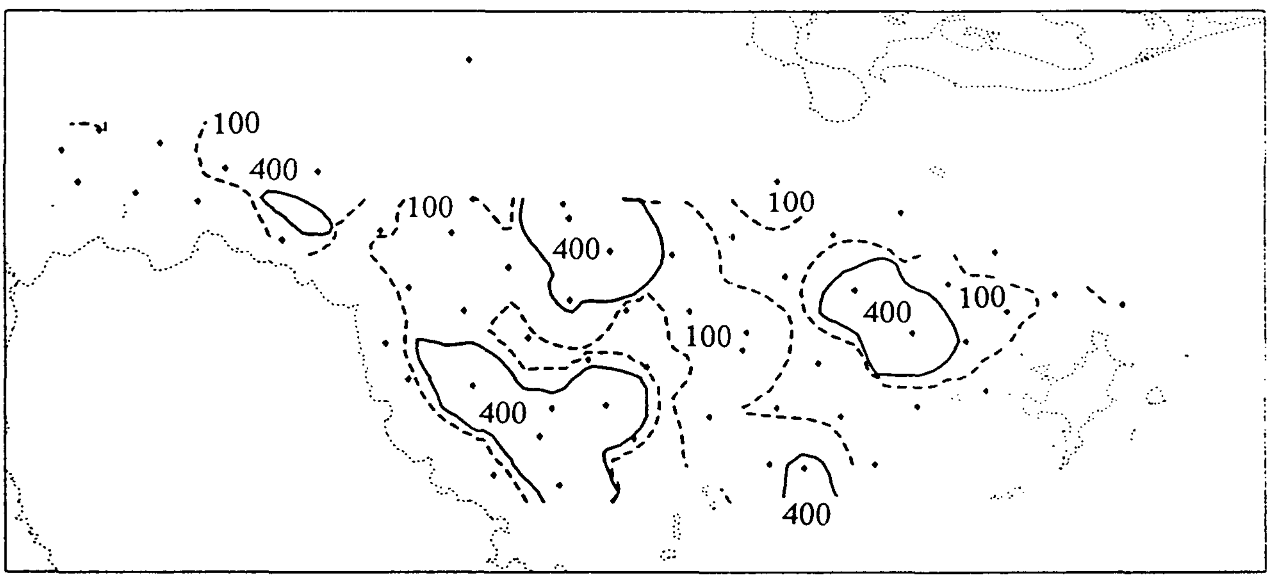

Figure 8b: The distribution of live oysters () 50 mm in length) in 1995 contoured at 100 and 400 oysters per tow. Diamonds denote sample stations.