New Zealand Fisheries Assessment Research Document 93/20

Estimates of growth, mortality, and yield per recruit for New Zealand surf clams

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December 1993

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EXECUTIVE SUMMARY

The growth of five species of surf clam, *Mactra murchisoni*, *M. discors*, *Spisula aequilatera*, *Paphies donacina*, and *Dosinia anus*, was studied by two methods at two locations, one in Cloudy Bay, Marlborough (South Island), the other along the Wellington west coast, (North Island). Length frequencies of sequential population samples were analysed using MULTIFAN to estimate the von Bertalanffy growth parameters. Incremental growth of recaptured marked clams at Cloudy Bay were analysed using GROTAG to compare growth rates. These estimates confirm the estimates of growth from MULTIFAN.

Mortality could not be estimated from the length frequency data. Estimates of maximum age from MULTIFAN analyses and shell sections were used to estimate the range of mortality.

The growth and mortality data were used in yield per recruit analyses to estimate the reference fishing mortality, $F_{0.1}$.

Each species occupies a different depth zone with little overlap with other species. As species can be targeted individually by fishers, species could be managed independently to avoid serial depletion by value. The wide differences between species in growth and mortality rates, age at exploitation, and $F_{0.1}$, and between areas for the same species, suggest that populations of each species at any location will respond to fishing differently. These data support the need to manage each species in each area independently.

1. INTRODUCTION

Sampling along New Zealand surf beaches suggests that the seven species of surf clams *Mactra murchisoni* (MMI), *M. discors* (MDI), *Spisula aequilatera* (SAE), *Paphies donacina* (PDO), *Dosinia anus* (DAN), *D. subrosea* (DSU), and *Bassina yatei* (BYA) have different ranges: at each site sampled, the species occupied different depth ranges with minimal overlap (Cranfield *et al.* 1993). Fishers will therefore be able to target individual species, and will tend to concentrate on the species of highest market value.

Initial management assumed that the life history strategies and productivity of the seven species would be comparable (Cranfield *et al.* 1993) so the yield for the first permit issued in this fishery was for the combined biomass of all species. The present document estimates rates of growth, mortality and $F_{0.1}$ for five species of surf clams in Cloudy Bay, Marlborough and on the Wellington west coast. As there are considerable differences between the individual species and locations, yields have been estimated by individual species at each location where adequate information is available (Cranfield *et al.* 1993). The differences in productivity indicate that populations of individual species will respond to fishing differently.

In this document, growth was estimated from analysis of sequential length frequency data and increment data from a mark-recapture experiment. Mortality was derived from estimates of the maximum age of each species at each location. Yield per recruit analyses were used to estimate $F_{0.1}$.

2. GROWTH RATE ESTIMATES

The maximum size of each species varied between locations in samples around New Zealand. Differences between locations in the North and the South Islands were not great compared with the differences between the two islands (Table 1). The differences in maximum size probably reflect differences in growth rates between locations. Two locations, the Wellington west coast in the North Island and Cloudy Bay in the South Island, were chosen to study growth of the five most abundant species of surf clams. At these locations the maximum size attained by surf clams was similar to other locations on that island.

2.1 Methods

2.1.1 Length frequency

Length frequency samples were collected from Cloudy Bay and the Wellington west coast, approximately every two months between February 1990 and September 1991. Two sites were sampled at each location (Figure 1) and one sample taken in each one metre depth interval between 1 and 7 m by hydraulic dredge. The hydraulic dredge was 0.8 m wide and built to similar specifications to the Rabbit Dredge (Michael *et al.* 1990). It was fitted with a fine grill (12 mm spacings between bars) to retain small (> 20 mm in length) surf clams. Sample tows were about 150 m in length along the beach contours. Sampling sites were relocated by landmarks and so were not very precise. Depth corrections for tide state were calculated from distant secondary ports so their precision is uncertain. Within these constraints, samples were taken as close as possible to the same location and depth each period.

Lengths of surf clams (the greatest distance along the anterior posterior axis) were measured with electronic callipers with an accuracy of 1% of the measurement.

Five species were sampled: *M. murchisoni*, *M. discors*, *S. aequilatera*, *P. donacina*, and *D. anus* (Figure 2). The relative proportions of these species at the two localities (Table 2) made it difficult to get large enough samples of some species to analyse satisfactorily. Nine length frequency samples were collected from each of the two sites at Cloudy Bay, Wairau and Fence (Figure 1), sampling from depths of 2–7 m. Eight length frequency samples were collected from each of the two sites on the Wellington west coast, Peka Peka and Otaki (Figure 1), sampling from depths of 1–6 m. Each species of surf clam dominated a discrete and narrow depth range, hence the bulk of the individuals of any one species were captured in only one or two depth strata. The length frequency data were grouped initially in 1 mm intervals. There was no difference in the length frequency distributions between the strata, so the data from all strata were combined. There was no difference in the length frequency distribution between the two sites at each location, so the data from both sites were combined.

2.1.2. Mark-recapture data

Length increment data from three mark-recapture experiments were used to estimate growth. Surf clams collected by hydraulic dredging were marked by notching, with tags alone and by notching and tagging together. Notches provided a permanent reference for length at release so the clams did not have to be measured before being returned to the sea bed. Grooves were ground from both notches, along both valves, to make the marked clams more visible at recapture. This method was faster and more efficient than tagging. Tags (8 mm Hallprint disc tags) were fixed with cyanoacrylate glue. Marked clams were reburied in the seabed by divers. The marked clams were recovered 1 year later by hydraulic dredging.

Cloudy Bay

A large scale mark-recapture experiment (4769 surf clams of five species (Table 3)) was established in Cloudy Bay in October 1991. The mark-recapture plot was 50 m wide and extended 170 m offshore covering depths from 3 to 6 m. The precise position of the plot was established by differential GPS (DGPS).

Marked clams were recovered in October 1992 by repetitive dredging. The vessel used DGPS to continuously track position with an accuracy of less than $\pm$ 2 m. HYDRO (survey software) was used to display the borders of the mark-recapture plot and the track of the vessel as it towed the dredge. The simultaneous display of the position of the vessel as well as the previous dredge tracks and mark recapture plot on the helmsman's monitor enabled the dredge to be towed as planned and ensured the complete coverage of the plot. Seventy tows were made in the plot and 14 at spaced intervals outside. Of 1027 (21.5%) marked clams recaptured 989 were alive and 38 dead. Almost all (1002) came from inside the plot. Tows made outside the plot to measure dispersion found no marked clams further than 50 m from the plot.

Wellington west coast

A pilot of the mark-recapture experiment was set up off Peka Peka in 1990. Transit marks and compass bearings were used to fix and relocate the position of the plot. Only 15 (2%) of the marked clams were recaptured from 20 dredge tows in October 1991 (Table 4). The dredge tracks were plotted with DGPS and HYDRO to better define the area where marked clams were caught. A further 21 marked clams were caught from 15 dredge tows in 1992. The pilot experiment highlighted the need for precise navigation (DGPS) and the marking of many clams to ensure sufficient recoveries for growth rates to be estimated reliably.

A mark-recapture experiment of similar scale and design to that in Cloudy Bay was planned in 1991, but inclement weather resulted in the experiment being abandoned after only a few clams were marked and reburied. Their precise position was established with DGPS.

In 1992, 36 marked clams were recovered from the 1990 experiment off Peka Peka and 6 from the 1991 experiment. Only specimens of *D. anus* were recaptured in sufficient number to analyse growth.

2.2 Analysis

2.2.1 Length frequency data

Von Bertalanffy growth curves were fitted to the length frequency distributions using the MULTIFAN model version 3.2. This model simultaneously analyses multiple sets of length frequency samples using a maximum likelihood method to estimate the proportion of clams in each age class and the von Bertalanffy growth parameters. The main assumptions of the MULTIFAN model and details of fitting the model are provided by Fournier *et al.* (1990) and Francis & Francis (1992).

Four models based on different growth hypotheses were fitted to the data: (1) constant length standard deviation across all length classes; (2) variable standard deviation across age classes; (3) constant standard deviation plus seasonal growth; and (4) variable standard deviation plus seasonal growth.

Following Fournier *et al.* (1990), the significance level of 0.10 has been used for testing whether there is any gain in introducing an additional age class in the length-frequency analyses.

Reliable results from MULTIFAN are dependent on length frequency distributions with clear modes which can be tracked through samples. The clear definition of modes of the first 2–3 year classes, in which the most rapid growth occurs, has the greatest effect on the estimate of K. A grouping factor (Fournier *et al.* 1990) of 5 (length frequency data grouped in 5 mm intervals) was used for samples containing few juveniles (the first two age classes) to define their modes better. This grouping also reduced the risk of gaps in the length frequency distribution affecting the reliability in tests of significance between models. Samples with more than 80 length intervals were analysed with a grouping factor of 2 so the number of length intervals would fit the limitations of the software.

Because year class 1 individuals for each species appeared in the samples at different times, nominal birth dates varied for each species. The incremental growth data from the mark-recapture study provided estimates of constraints for length at age to guide the MULTIFAN model.

2.2.2 Mark-recapture data

Incremental growth, the difference between length at release and recapture, was measured with an error of ± 0.88 mm. Incremental growth plotted against length at release for 45 tagged, 215 notched, and 33 notched and tagged *M. murchisoni* in Cloudy Bay recaptured after a year's growth, showed that the method of marking (especially notching) had no significant effect on growth rate (Figure 3). The similar proportions of tagged, notched, and notched and tagged surf clams of all species recovered in Cloudy Bay further indicate that survival was not significantly affected by the method of marking (see Table 3).

Growth increment data were analysed using GROTAG (Francis 1988), a computer program which uses a maximum-likelihood method to estimate growth rate. Francis & Francis (1992) outlined the method and described the growth parameters and significance testing. Francis

(1988) showed that two estimates of the mean annual growth of marked fish at the lower (g_α) and upper (g_β) end of the size range of recaptured fish were better descriptors of the growth information in tagging data than the more conventional von Bertalanffy growth parameters L_∞ and K. g_α and g_β were estimated for each of the five species in three ways. Francis & Francis (1992) showed that there are dangers in extrapolating beyond the range of the data. Here, most of the clams recaptured covered the entire size range of the population over 20 mm in length.

The fixed standard deviation of the measurement error (s) in the models used allowed estimates of the coefficient of variation of growth variability (ν) and the proportion of outliers (p) to be estimated. Confidence intervals for the parameters were estimated from the 95 percentiles of 200 simulations of the best fit models (Francis 1988).

2.3 Results and Discussion

MULTIFAN analyses

Some species were not abundant at the sample locations resulting in small sample sizes with either poorly defined or no juvenile modes. Grouping these data had a significant effect on parameter estimates; for example the same constraints were used for the *M. discors* data analysed with grouping factors of 2 and 5 but gave different estimates for K (0.20, 0.41), L_∞ (73.1, 68), and t_0 (2.9, 1.5) respectively. By increasing the grouping factor from 2 to 5 the modes were defined better so the number of year classes was better estimated. However, the higher grouping factor increased the average standard deviation from 2.25 to 4.04. Parameter estimates from this type of data should be used with caution.

The log likelihood values, the number of parameters, the best fit for each model, and the best fit overall are shown by location and species in Tables 5 and 6. The von Bertalanffy parameter estimates with standard errors for the best fit MULTIFAN models, for all species from the Wellington west coast and Cloudy Bay are given in Table 7. Penalty weight, a measure of how well the best fit model fitted the data within the constraints for mean length at age, was used to adjust the bounds on constraints. In initial runs of the data, the bounds were relaxed where the penalty weight was high. For sparse data, relaxing the bounds did not reduce the penalty weight.

GROTAG analyses

Three methods were used to describe growth in surf clams using two models. A linear model of the von Bertalanffy growth function was fitted to all the data for each species (method 1), the same model was fitted to data truncated to contain only individuals which grew over the time at liberty (method 2); and a modified model (method 3) which used an additional exponential function to describe the growth of larger clams above a length where their growth departed from the linear model (Par10, Table 8).

Method 1. A simple linear model of GROTAG, which incorporated an estimate of measurement error as a fixed parameter, generally did not fit the data well. The distribution of plotted residuals against expected increment was heavily skewed at the point where numerous large clams showed no growth in length. The model under-estimated the growth of small clams and over-estimated the growth of the larger.

Method 2. Plots of size at release against annual increment showed growth to be highly variable in large clams. To investigate the effect of this increased variability on the estimates of growth, the lengths at release were ranked and the data truncated at a size below which all individuals grew over the time at liberty. These data were analysed with the same linear model. The distribution of residuals plotted against expected increment was not skewed. The model fitted the data well, and predicted growth of the smaller clams was higher than predicted from the whole data set. The model can give no information on the growth of the largest clams.

Method 3. The data were fitted to a second model that incorporated an exponential function which located the length at which clam growth increased in variability and departed from the linearity of the von Bertalanffy growth parameters. The distribution of residuals was not skewed and this model predicted growth for all clams in the sample.

The growth parameter estimates from GROTAG (g_α, g_β, v, s, p, and Par10) and the 95% confidence intervals for all species from the Wellington west coast and Cloudy Bay are given in Table 8. For all species except *S. aequilatera* from Cloudy Bay, model 2 described growth better than model 1.

Growth rates estimated from length frequency analysis and tagging data are not directly comparable. Francis & Francis (1992) proposed a method of graphical comparison and the expected mean annual growth derived from MULTIFAN lengths at age is included in the graphs of mark recapture data and model fits.

2.3.1 *Mactra murchisoni*

Cloudy Bay

The length frequency samples (Figure 4) were large (n = 233–1606) and had well defined modes that could be tracked through the samples. The smallest juveniles appeared in December 1990 (sample 5) which was assigned as month 1 in the MULTIFAN analysis. The data had to be grouped by a factor of 2 so there were less than 80 length intervals. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The mode at 23.1 mm (width 18-33 mm) in December 1990 (sample 5) was assigned to year 1 (0+ year class) and a mode at 51.0 mm (39–61 mm) in the same sample to year 2 (Figure 4). The low penalty weight (-0.07) in the best-fit model (constant standard deviation and seasonal growth with eight fitted year classes) showed the model fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7). The parameter estimates are precise and fit the data well. The von Bertalanffy growth curve is shown in Figure 5. The large standard deviation of the modes (particularly the first two) could indicate protracted spawning in this species.

Large numbers of marked clams were recaptured and the data was well spread over all sizes larger than 35 mm. Plots of length at release against increment showed little variation in growth of smaller clams but greater variation in those over 70 mm in length, many of which did not grow at all (Figure 6). Plots of residuals against expected increment and the difference in the estimates of mean growth for g_{45} from all data and truncated data (Table 8) indicate that model 1 of GROTAG did not describe growth well. Model 2 described growth precisely with tight 95% confidence limits for the parameters. Up to a length of 78 mm, growth follows the linear von Bertalanffy functions, but thereafter is better described by an exponential function.

MULTIFAN gave a higher estimate of growth than GROTAG (Figure 6).

Wellington west coast

The length frequency sample sizes were small (n = 63–250), particularly in 1990 when samples contained few juveniles (< 55 mm) (Figure 7). In 1991 (January to September) samples had a large cohort of recently recruited juveniles. Length frequency samples were analysed using a grouping factor of 1. The smallest juveniles appeared in January 1991 (sample 5) which was assigned as month 1. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The mode of newly recruited juveniles at 23.1 mm (width 16–34 mm) in sample 5 was assigned to year 1 (0+ year class) and the same mode at 33.2 mm (24–44 mm) in sample 8 to year 2 (Figure 7). Year 2 was used for the recruits in sample 8 because they had passed the anniversary of their estimated settlement date (mid February) to become 1+ age group. The low penalty weight (0.02) in the best-fit model (constant standard deviation and seasonal growth with eight fitted year classes) showed the model fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7). The parameter estimates are precise and fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

Only three marked *M. murchisoni* have been recaptured, all from the 1990 experiment off Peka Peka. One (released at 73.2 mm) was recaptured after a year and the other two (70.8 mm and 69.6 mm) after 2 years. None had grown in that time.

Differences in growth between locations

MULTIFAN estimates give slower growth for the Wellington west coast than for Cloudy Bay (see Figure 5). Maximum size and L_{∞} were also about 20% lower, but the number of fitted age classes are the same (eight).

2.4.2 *Mactra discors*

Cloudy Bay

Length frequency samples were small (n = 46–133) and had few juveniles (Figure 8). The smallest juveniles appeared in December 1990 (sample 5) which was assigned to month 1 in the MULTIFAN analysis. The data were grouped by a factor of 5 to better define modes in the juveniles. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The mode at 30.0 mm in sample 8 was assigned to year 1 (0+ year class) and the modes at 38.8 and 48.6 mm in the same sample to years 2 and 3 respectively (Figure 8). The penalty weight (3.35) is relatively high and is probably the result of the small sample sizes and the lack of well defined modes among the juveniles. The best-fit model (constant standard deviation and seasonal growth with seven fitted year classes) fitted the data poorly with these constraints. This did not appear to have affected the precision of estimates of the number of fitted year classes or the estimate of K as the standard error of the von Bertalanffy parameters is small (see Table 7). The parameter estimates are precise and fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

Few marked clams were recaptured and only 10 had grown measurably. The recaptured clams ranged from 30 to 73 mm in length. Plots of length at release against increment showed little variation in growth of smaller clams. None of the clams over 59 mm grew over the time at liberty (Figure 9). Plots of residuals against expected increment and the large difference in the estimates of mean growth for g_{33} from all data and truncated data (Table 8) indicate that model 1 of GROTAG did not describe growth well. Model 2 described growth better. Up to a length of 61 mm, growth followed the linear von Bertalanffy functions, but thereafter was better described by an exponential function.

MULTIFAN gave a lower estimate of growth than GROTAG (Figure 9).

Wellington west coast

The length frequency samples were large (n = 231–942). Samples taken in 1990 contained a large number of juveniles (< 40 mm) which did not show well defined modes. Samples taken in 1991 (January to September) contained very few juveniles (Figure 10). The smallest juveniles appeared in January 1991 (sample 5) which was assigned to month 1 in the MULTIFAN analysis. The data were grouped by a factor of 2 to better define the juvenile modes. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The mode at 27.2 mm in sample 1 was assigned to year 2 (1+ year class) and constrained to 19–33 mm (Figure 10). The penalty weight (-0.05) is low and the best-fit model (variable standard deviation and seasonal growth with nine fitted year classes) fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7) and fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

Only one marked *Mactra discors* (from the 1990 experiment off Peka Peka) was recaptured. It was released at 39.2 mm and grew 8.5 mm in a year. This length increment is similar to growth predicted from the MULTIFAN model.

Differences in growth between locations

MULTIFAN estimates show Cloudy Bay clams grow faster than those on the Wellington west coast. Less confidence can be placed on the Cloudy Bay estimate from MULTIFAN because of the small sample sizes and lack of juveniles. The number of fitted age classes were lower at Cloudy Bay.

2.4.3 *Spisula aequilatera*

Cloudy Bay

Length frequency samples varied in size (n = 33–466) but had well defined modes that could be tracked through the samples (Figure 11). The smallest juveniles appeared in September 1990 (sample 4) which was assigned as month 1 in the MULTIFAN analysis. The data were grouped by a factor of 5 to prevent problems with the MULTIFAN analysis caused by gaps in the distribution. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The mode at 31.0 mm in sample 6 was assigned to year 1 (0+ year class) with constraints of 17-39 mm (Figure 11). The penalty weight (0.08) is low and the best-fit model (variable standard deviation and seasonal growth with five fitted year classes) fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7). The von Bertalanffy growth curve is shown in Figure 5.

Large numbers of marked clams were recaptured and, apart from the size range 45-50 mm, they were well spread over all sizes over 28 mm. Plots of length at release against increment showed little variation in growth of smaller clams. Growth became more variable above 40 mm and many individuals over 48 mm did not grow at all (Figure 12). Plots of residuals against length at release and the difference in the estimates of mean growth from all data and truncated data (Table 8) indicate that model 1 of GROTAG did not describe growth well: nor did Model 2. It appears that the pattern of growth changes significantly over the 45-50 mm range. The growth of smaller individuals (< 45 mm) was well described by model 1 whose parameters had tight 95% confidence limits. Growth over the whole length range could not be estimated reliably from these data.
A graphical comparison of expected annual growth from MULTIFAN and GROTAG data showed MULTIFAN gave a slightly lower estimate of growth (Figure 12).

Wellington west coast

The length frequency samples were large (n = 226–2298, except sample 7, August 1991, n = 73) and contained large numbers of juveniles (> 20 mm). 1991 samples contained a large well defined cohort of recently settled juveniles which was readily tracked through time. The proportion of these juveniles decreased significantly over the winter period (Figure 13). The smallest juveniles appeared in January 1991 (sample 5) which was assigned as month 1 in the MULTIFAN analysis. The original data in 1 mm intervals were used in the MULTIFAN analysis. No increment data was available from the mark–recapture experiment to guide the length at age constraints for MULTIFAN. The mode at 24.9 mm in sample 6 was assigned to year 1 (0+ year class) and used in the analysis without constraints. The penalty weight (-0.10) is low and the best-fit model (variable standard deviation and seasonal growth with three fitted year classes) fitted the data well with these constraints. Except for L_∞, the standard errors of the von Bertalanffy parameters are small (see Table 7). MULTIFAN could not estimate L_∞ precisely because the fast growing juvenile modes merge in to the one mode in the third year while they are still growing relatively fast (Figure 13). The parameter estimates are precise and fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

No marked *S. aequilatera* were recaptured on the Wellington west coast.

Differences in growth between locations

MULTIFAN estimates of growth on the Wellington west coast are slower than for Cloudy Bay. Maximum size and L_∞ were similar. The number of fitted age classes was lower on the Wellington west coast.

2.4.4 *Paphies donacina*

Cloudy Bay

Although length frequency samples were moderately large (n = 197–744) they contained few juveniles. There appear to be five juvenile year classes before the size classes merge into one adult mode (Figure 14). The smallest juveniles appeared in February 1990 (sample 1) which was assigned as month 1 in the MULTIFAN analysis. The data was grouped by a factor of 2 to better define modes among the sparse juveniles. Increment data from the mark–recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. Modes at 30.2, 53.8, and 63.1 mm in sample 1 were assigned to years 2, 4, and 5 (1+, 3+ and 4+ year classes) respectively without constraints. The penalty weight (-2.69) is relatively high and probably reflects the lack of juveniles and the absence of well defined juvenile modes. The best-fit model (variable standard deviation and seasonal growth with 10 fitted year classes) did not fit the data well with these constraints. Nevertheless, the standard errors of the von Bertalanffy parameters are small (see Table 7). The von Bertalanffy growth curve is shown in Figure 5.

Only a small proportion (27:170) of the marked clams recovered grew. No clams under 50 mm in length were recaptured (very few of this size were marked because so few were present). Plots of length at release against increment showed growth increments for recovered clams of a given length were highly variable (Figure 15). Plots of residuals against expected increment, and the large difference in the estimates of mean growth from all data and truncated data (Table 8), indicate that model 1 of GROTAG did not describe growth well. Model 2 described growth better. Up to a length of 83 mm growth followed the linear von Bertalanffy function, but thereafter is better described by an exponential function.

The graphical comparison of expected annual growth from MULTIFAN and GROTAG data showed MULTIFAN gave a higher estimate of growth (Figure 15). Growth of individual *P. donacina* appears to be highly variable at all sizes.

Wellington west coast

Despite the very large samples (n = 1402-3200) virtually no juveniles were caught and the length frequency distributions were unimodal (Figure 16). These data could not be analysed to estimate growth.

No marked *P. donacina* were recaptured from the Wellington west coast.

Differences in growth between locations

We are unable to compare of growth rates for *P. donacina* at present.

2.4.5 *Dosinia anus*

Cloudy Bay

Length frequency samples were small (n = 45–446) and juveniles were largely absent (Figure 17). The smallest juveniles appeared in July 1991 (sample 8) which was assigned as month 1 in the MULTIFAN analysis. The data were grouped by a factor of 2 to better define modes among the sparse juveniles. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. The same year class, represented by a mode at 44.1 mm in sample 4 and 50.0 mm in sample 6 was used without constraints in the analysis. The penalty weight (0.01) is low and the best-fit model (variable standard deviation with no seasonal growth and 16 fitted year classes) fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7) and the parameter estimates fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

Less than 5% (5/129) of marked clams recovered grew (Figure 18). Only one of those over 58 mm grew over the time at liberty. These clams biased the estimate of the growth rate of smaller clams substantially. Plots of residuals against expected increment indicate that model 1 of GROTAG did not describe growth of larger clams well. Model 1, however, described the growth of *D. anus* < 58 mm better than model 2. Model 2 gave much higher estimates of growth for small individuals and about the same for larger clams (see Table 8) but the 95% confidence limits for the parameters were quite wide. Up to a size of 60 mm, growth follows the linear von Bertalanffy function, but thereafter is better described by an exponential function.

Graphical comparison of expected annual growth from MULTIFAN and GROTAG data showed MULTIFAN gave a slightly higher estimate of growth to model 1 and slower estimate of growth to model 2 (Figure 18).

Wellington west coast

The large length frequency samples collected (n = 1130–3322) contained many juveniles (> 20 mm). Samples had a large cohort of recently recruited juveniles which was well defined and a proportion of juveniles which did not fall into clearly defined modes. The juvenile modes did not move appreciably over time and their proportions decreased significantly, particularly over the winter period (Figure 19). The smallest juveniles appeared in July 1990 (sample 3) which was assigned as month 1 in the MULTIFAN analysis. The data were analysed in the original 1 mm grouping. Increment data from the mark-recapture experiment provided a guide to length at age for constraining the MULTIFAN analysis. Modes of 18.5, 29.5, and 35.7 mm were assigned to years 2, 3, and 4 respectively without constraints. The penalty weight (0.20) is moderately low and the best-fit model (variable standard deviation and seasonal growth with 19 fitted year classes) fitted the data well with these constraints. The standard errors of the von Bertalanffy parameters are small (see Table 7) and the parameter estimates fit the data well. The von Bertalanffy growth curve is shown in Figure 5.

Altogether 42 marked *D. anus* have been recaptured from three separate periods, but only 11 grew in the period of liberty. All the data were analysed, but only those for the 18 marked clams at liberty for 1 year are shown in Figure 20. Plots of residuals against expected increment, and the large difference in the estimates of mean growth for g_{25} from all data and truncated data (Table 8), indicate that model 1 of GROTAG did not describe growth well. Model 2 described growth better. Up to a length of 44 mm growth followed the linear von Bertalanffy growth function, but thereafter is better described by the exponential function.

MULTIFAN indicated a lower rate of growth than GROTAG (Figure 20).

Differences in growth between locations

MULTIFAN estimates of growth for the Wellington west coast are similar to those for Cloudy Bay, but in Cloudy Bay *D. anus* continue growing at the same rate for longer to attain a larger L_∞ of 77.5 mm compared with 58.7 mm. GROTAG estimates are faster for both models from Cloudy Bay than the Wellington west coast, e.g., g_{30} 12.5 mm compared with 5.2. Growth in large *D. anus* on the Wellington west coast departed from the linear model and became more variable at 44 mm compared to 58 mm in Cloudy Bay.

2.5 General

Growth rate (estimated from MULTIFAN) in surf clams is fastest in the mactrids (*Mactra murchisoni*, *Mactra discors*, and *Spisula aequilatera*) followed by the mesodesmatid (*Paphies donacina*) and slowest in the venerid (*Dosinia anus*). This trend was found at both sample locations. Surf clams grew as fast, or faster, at Cloudy Bay as on the Wellington west coast.

Species which showed a clear seasonal component in growth rates (i.e., the best fit models overall that included seasonal growth, see Table 7) grew rapidly between October and April, and hardly at all between May to September.

3. MORTALITY RATE

The instantaneous natural mortality rate, *M*, is one of the hardest biological parameters to estimate in a fishery. We have no information that will allow us to estimate *M* precisely. *M* could not be calculated from the length frequency data using MULTIFAN because assumptions of the model were not met.

A number of techniques that use estimates of the maximum life span are available, however, and indicate the likely magnitude of *M*. MULTIFAN disaggregates a number of year classes in calculating the growth rates. In each of the species discussed below this has given an estimate of the minimum number of year classes present in the population. Sections of

M. murchisoni shells from Cloudy Bay show that rings are laid down annually (at the same period April–July) in small clams (up to 4 years old). The growth rate indicated by length at age from these rings is comparable to that estimated by MULTIFAN and GROTAG. Assuming that rings in shell sections of other species are annual, as indicated for *M. murchisoni*, counts of the rings in the largest and heaviest shells have been used to estimate the maximum age of each species in Cloudy Bay. Shells from the Wellington west coast have not been sectioned and their maximum age has been inferred from the relationship between age classes estimated by MULTIFAN and maximum age estimated from shell sections in Cloudy Bay. A ratio of the number of rings counted from shell sections to the number of fitted year classes from MULTIFAN was calculated for each species from Cloudy Bay. The ratio was then applied to the number of fitted year classes for surf clams of the same species from the Wellington west coast to estimate maximum age.

Hoenig (1983) compared published estimates of mortality rate and life span in crustacea, molluscs, and fish. The regression of mollusc life span on mortality was $\ln M = 1.23-0.832 \ln(t_{max})$. The combined regression for crustacea, molluscs, and fish was $1.44-0.982 \ln(t_{max})$ and he (1983) recommended that it be used for predicting M for all three groups. The range of M predicted by both regressions is shown in Table 9.

M is frequently estimated from the equation $M = \ln 100/$ maximum life span (Annala 1992). This equation was derived from the suggestion of Hoenig (1983) that life span could be taken as the age reached by 1% of the population. The values of M estimated with this equation fall within the range predicted by Hoenig's regressions (Table 9).

3.1 Discussion

The estimates of natural mortality rate of surf clams within the two localities varies from 0.17 to 0.92. These estimates have different levels of reliability, but show a consistent pattern of variation:

Inshore/offshore. Each clam species is dominant over a narrow depth range, so they tend to be distributed in successive bands along the beach contours (Cranfield *et al.* 1993). The order of succession of species (inshore–offshore) is *P. donacina*, *S. aequilatera*, *M. murchisoni*, *M. discors*, and *D. anus*. *P. donacina* has a low mortality rate, mortality is highest in *S. aequilatera* and progressively decreases in species found offshore to the lowest in *D. anus*. This pattern is consistent between the two locations.

S. aequilatera and *M. murchisoni* are distributed within the primary wave break area where most of the wave energy is dissipated. *P. donacina* is distributed inshore of this among the smaller waves of the secondary wave break. *M. discors* and *D. anus* tend to be outside the influence of breaking waves. Breaking waves re-suspend sediment, particularly during storms, and may wash clams out of the sea bed. The differences between the mortality rates of clam species is closely related to their exposure to waves and suggests erosion may be a major factor in mortality.

Between locations. The estimates of mortality on the Wellington west coast are based on less reliable data, but *S. aequilatera* at least has a higher mortality than in Cloudy Bay. The beach along the Wellington west coast is much more exposed than that at Cloudy Bay and has a higher energy wave climate (Harris 1990). The difference between locations is consistent with the different probability of erosion of the sea bed by storms. The dramatic reduction in abundance of the first year class shown in the length frequency data for *M. murchisoni* (reduced to 1/5) and *S. aequilatera* (reduced to 1/10) on the Wellington west coast in the winter of 1991 (Figure 7, 13) was due to mortality as large numbers of shells of recently dead individuals of this size group were captured at the same time. Erosion may have been the major contributor to this mortality of the shallow buried juveniles.

Estimates of the rate of natural mortality in offshore populations of *Spisula solidissima* in the eastern US ranged from 0.20 to 0.25 (Ropes 1980), a similar level to that found for offshore surf clams here. However, Cerrato & Keith (1992) found that inshore populations of *S. solidissima* along estuarine beaches had a life span of 10 years, with a natural mortality of 0.46, similar to that found here for *M. murchisoni*. These data suggest that the mortality rate of different stocks of the same species may depend on the environment.

The estimates of M in the relatively short-lived surf clam species are extremely sensitive to errors in the estimate of maximum age. Clearly, a high priority should be given to complete validation of the age rings in all species, more precise estimates of maximum age, and the estimates of M from comparisons of age structure of populations a year apart following the method of Ricker (*see* Hughes & Bourne 1983).

4. YIELD PER RECRUIT

4.1. Methods

In 1992 the lengths and weights of each species of surf clam from both localities were measured (Figure 21, 22). The regressions of ln (length) on ln (weight) were calculated (Table 10) and used to estimate the weight of surf clams from length at age estimates derived from the von Bertalanffy curve. The absence of individuals of the first three year classes of *P. donacina* at Peka Peka, which made the length frequency data for 1990 and 1991 impossible to analyse with MULTIFAN, was still apparent in 1992 and the data set was inadequate to estimate a robust relationship between length and weight ($r = 0.56$).

4.2. Analysis

The estimates of growth and mortality were used to carry out yield per recruit analyses to estimate $F_{0.1}$. As the fishery for surf clams is not developed (Cranfield *et al.* 1993,) the size at exploitation (marketable size) has been inferred from existing market preferences. The age at first exploitation for the same species differs at the two locations (Table 11).

The YPR model (M.J. Fogarty, National Marine Fishery Service, Northeast Fisheries Center, Woods Hole, USA) is:

$$Y/R = \Sigma_i \{p_i F/(p_i F + M)\} \{1 - e^{-p(i)F + M)}\} \{\Pi_j e^{-(p(j)F + M)}\} W_i$$

where R is the number of recruits entering the fishery and the product is evaluated over the previous age classes $j = 1$ to $i-1$. The age specific fishing mortality components have been split into two parts, an overall fishing mortality (F) and a partial selection factor (p_i) which represents the vulnerability at age to harvest. An arbitrary 1000 recruits were assigned at year one and the weight at length half way through each year calculated by MULTIFAN used as the mean weight of each year class. The model assumes that the natural mortality (M) and *fishing mortality* (F) are spread uniformly through the year.

The yield per recruit model was used to estimate $F_{0.1}$ for five species in Cloudy Bay and four on the Wellington west coast (Table 12).

As the yield per recruit model is very sensitive to the estimates of M used, it is important to know whether M was likely to be under-or over-estimated. The estimates of M have been derived from estimates of maximum age from rings seen in shell sections. These are demonstrably annual in the first 4 years, but the annual pattern becomes obscured in older shells with what appear to be numerous spawning rings, several of which are laid down each summer. These extra rings make it likely that maximum age has been over-estimated rather than under-estimated and M is likely to have been under-estimated. The YPR model was probably run with under-estimates of M. The estimates of $F_{0.1}$ are therefore likely to be conservative.

5. MANAGEMENT IMPLICATIONS

Each species occupies a different depth zone with little overlap with other species. As species can be targeted individually by fishers, species could be managed independently to avoid serial depletion by value. The wide differences between species in growth and mortality rates, age at exploitation, and $F_{0.1}$, and between areas for the same species, suggest that populations of each species at any location will respond to fishing differently. These data support the need to manage each species in each area independently.

6. ACKNOWLEDGMENTS

Thanks to Chris Francis for his assistance with GROTAG and providing a modified model to fit the surf clam data. Also to Malcolm Francis for his assistance with MULTIFAN and to Nick Davies and John Annala for refereeing this document. We are grateful to Bosun Huntley and Ant Piper for the return of marked surf clams from Cloudy Bay.

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Table 1: Maximum length of surf clam species from various sites in the North and South Islands and mean lengths with standard deviations (s.d.). Abbreviations of species are: *Mactra murchisoni* (MMI), *M. discors* (MDI), *Spisula aequilatera* (SAE), *Paphies donacina* (PDO), *Dosinia anus* (DAN), *D. subrosea* (DSU) and *Bassina yatei* (BYA)

		Maximum length (mm) of each species at each location						
Location	Latitude ° 'S	MMI	MDI	SAE	PDO	DAN	BYA	DSU
North Island								
Great Exhibition Bay	34 41'					63		56
Te Arai	36 08'			39		70	58	65
Matakana	37 34'	76	65	46		75	55	75
Ohope	37 59'	77	65	57		76	60	50
Nuhaka	39 04'	63		50	80	58		41
Waitarere	40 34'	80	71	42	73	61	58	50
Otaki	40 45'	82	64	63	85	65	48	49
Peka Peka	24 50'	84	63	59	88	60	52	52
Mean		77.0	65.6	50.9	81.5	66.0	55.2	54.7
s.d.		7.5	3.1	9.1	6.6	6.9	4.5	10.6
South Island								
Fence	41 28'	100	95	66	109	81	65	68
Wairau	41 30'	102	77	67	105	82	66	68
Leithfield	43 09'	93		66	95	72	88	60
Waikuku	43 18'	95		68	96	72		
Kainga	43 24'	92		67	95	68		56
Blueskin*	45 43'		73	65	102			58
Te Waewae	46 09'	94		74		80		
Oreti	46 21'	80	77	65				
Mean		93.7	80.5	67.2	100.3	75.8	73.0	62
s.d.		7.1	9.8	2.9	5.9	5.9	13.0	5.6

* Survey not completed

Table 2: The percentage of each species (by number) at each location.

	Species				
Location	MMI	MDI	SAE	PDO	DAN
Wellington west coast	3.1	10.8	2.6	26.4	57.1
Cloudy Bay	59.4	4.1	6.3	9.3	20.9

Table 3. The number of notched, notched and tagged, and tagged clams of each species released in Cloudy Bay, 1991 and recaptured in 1992. Number of clams recaptured is for live and dead combined.

Species	Number released in 1991				Total number recaptured				Percentage recaptured			
	Notched	Notched & tagged	Tagged	Total	Notched	Notched & tagged	Tagged	Total	Notched	Notched & tagged	tagged	Total
MMI	899	99	200	1 198	215	33	46	294	23.9	33.3	23.0	24.5
MDI	376	0	0	376	74	0	0	75	19.7	-	-	19.7
SAE	850	100	203	1 153	276	33	55	364	32.5	33.0	27.1	31.6
PDO	976	0	95	1 071	149	0	14	163	15.3	-	14.7	15.2
DAN	971	0	0	971	132	0	0	132	13.6	-	-	13.6
Total	4 072	199	498	4 769	846	66	115	1 027				21.5

Twenty-two marked clams (12 MMI, 5 MDI, 2 SAE, and 3 DAN) were caught by a commercial fisher 6 months after release.

Table 4. The number of notched, notched and tagged, and tagged clams of each species released at Peka Peka in 1990 and recaptured in 1991 and 1992. Number of clams recaptured is for live and dead combined.

Species	Number released in 1990				Number recaptured 1991				Number recaptured 1992			
	Notched	Notched & tagged	Tagged	Total	Notched	Notched & tagged	Tagged	Total	Notched	Notched & tagged	tagged	Total
MMI	63	0	0	63	1	0	0	1	2	0	0	2
MDI	173	0	0	173	0	0	1	1	1	0	0	1
SAE	92	0	0	92	0	0	0	0	0	0	0	0
DAN	260	0	40	300	12	0	1	13	15	0	3	18
Total	588	0	40	628	13	0	2	15	18	0	3	21

Table 5: Length-frequency (MULTIFAN) growth models for Cloudy Bay. Maximum log-likelihoods (2λ) and the number of parameters estimated (Param) for each model are shown. Models are based on constant or variable standard deviation (s.d.) and with or without seasonal growth. The best fit for each model is shown in bold type, and the overall best fit is underlined.

Age classes	Model 1 (without seasonal growth, constant s.d.)		Model 2 (without seasonal growth, variable s.d.)		Model 3 (seasonal growth, constant s.d.)		Model 4 (seasonal growth, variable s.d.)	
	Param	2λ	Param	2λ	Param	2λ	Param	2λ
Mactra murchisoni								
6	2578.06	11	2578.55	12	2631.73	13	2634.82	14
7	2586.01	12	2586.13	13	2637.51	14	2639.48	15
8	2590.34	13	**2590.43**	14	**2640.85**	15	**2642.24**	16
9	**2593.10**	14	2593.10	15	2643.08	16	2644.10	17
10	2594.91	15	2594.92	16	2644.40	17	2645.28	18
Mactra discors								
6	1687.55	11	1690.64	12	1710.28	13	1711.34	14
7	**1696.46**	12	**1696.88**	13	**1714.38**	14	**1714.41**	15
8	1698.13	13	1697.13	14	1711.64	15	1715.14	16
9	1700.45	14	1699.77	15	1714.66	16	1714.66	17
10	1699.55	15	1700.49	16	1714.67	17	1714.74	18
11	1699.91	16	1701.36	17	1716.08	18	1716.12	19
Spisula aequilatera								
4	1172.69	10	1202.76	11	1226.73	12	1250.63	13
5	1188.79	11	1216.97	12	**1238.48**	13	**1262.48**	14
6	**1194.36**	12	**1220.31**	13	1240.91	14	1263.03	15
7	1196.78	13	1221.64	14	1241.44	15	1263.08	16
8	1198.09	14	1222.35	15	1241.67	16	1263.02	17
Paphies donacina								
9	6266.95	14	6282.50	15	6285.39	16	6301.21	17
10	6273.17	15	**6287.98**	16	6288.74	17	**6305.33**	18
11	6277.83	16	6290.67	17	6290.31	18	6307.58	19
12	**6281.56**	17	6293.15	18	6294.12	19	6308.73	20
13	6282.41	18	6293.34	19	**6296.86**	20	6309.46	21
14	6285.12	19			6293.69	21	6310.04	22
Dosinia anus								
14	4454.28	20	4469.76	21	4459.23	22	4474.01	23
15	4459.49	21	4457.85	22	4459.20	23	4455.39	24
16	**4464.83**	22	**4475.54**	23	**4470.34**	24	**4479.21**	25
17	4433.48	23	4463.49	24	4471.56	25	4456.39	26
18	4433.52	24	4463.80	25	4434.97	26	4462.84	27

Table 6. Length-frequency (MULTIFAN) growth models for Wellington west coast. Maximum log-likelihoods (2λ) and the number of parameters estimated (Param) for each model are shown. Models are based on constant or variable standard deviation (s.d.) and with or without seasonal growth. The best fit for each model is shown in bold type, and the overall best fit is underlined.

Age classes	Model 1 (without seasonal growth, constant s.d.)		Model 2 (without seasonal growth, variable s.d.)		Model 3 (seasonal growth, constant s.d.)		Model 4 (seasonal growth, variable s.d.)	
	Param	2λ	Param	2λ	Param	2λ	Param	2λParam
Mactra murchisoni								
6	4050.26	11	4055.75	12	4103.71	13	4105.67	14
7	4070.96	12	4076.36	13	4094.92	14	4100.87	15
8	4081.07	13	4085.01	14	**<u>4115.65</u>**	15	**4115.69**	16
9	**4095.38**	14	**4092.65**	15	4116.69	16	4116.63	17
10	4091.45	15	4094.24	16	4103.57	17	4117.71	18
Mactra discors								
7	2959.83	12	2961.36	13	2986.86	14	2991.97	15
8	2974.85	13	2979.97	14	2995.71	15	3002.65	16
9	2983.57	14	2988.39	15	**2999.28**	16	**<u>3007.21</u>**	17
10	2987.70	15	2992.54	16	3001.25	17	3009.34	18
11	2993.12	16	2994.99	17	3002.27	18	3009.38	19
12	**2996.89**	17	**2998.90**	18	3002.52	19	3009.83	20
13	2999.16	18	3000.51	19	3002.45	20	3010.12	21
Spisula aequilatera								
2	4739.97	7	*	*	5439.54	9	5440.38	10
3	**5461.29**	8	*	*	**5516.80**	10	**<u>5589.19</u>**	11
Dosinia anus								
15	6465.62	21	6466.60	22	6499.31	23	6524.15	24
16	6476.06	22	6480.18	23	**6512.72**	24	6503.86	25
17	6483.02	23	6449.53	24	6514.68	25	6517.12	26
18	6485.71	24	6486.89	25	6515.26	26	6512.33	27
19	**6488.42**	25	**6521.73**	26	6517.67	27	**<u>6534.92</u>**	28
20	6489.39	26	6523.52	27	6506.81	28	6517.57	29

* Unable to run model.

Table 7. Von Bertalanffy parameter estimates (with standard errors) for MULTIFAN best-fit models for all species from Cloudy Bay and the Wellington west coast, 1990-91. Amplitude and phase parameters describe seasonal growth. s.d. = standard deviation, c = constant, v = variable.

Species	MMI		MDI		SAE		PDO		DAN	
Cloudy Bay										
s.d.	c		c		v		v		v	
Age classes	8		7		5		10		16	
K (year^{-1})	0.57	(0.01)	0.41	(0.03)	1.01	(0.02)	0.33	(0.01)	0.10	(0.03)
L_∞ (cm)	88.00	(0.44)	68.00	(0.35)	60.3	(0.92)	94.10	(0.29)	77.5	(0.71)
t_0 (years)	0.62	(0.02)	1.48	(0.09)	0.13	(0.02)	1.13	(0.03)	9.72	(0.35)
Amplitude ϕ_1	0.95	(0.01)	0.95	(0.01)	0.95	(0.01)	0.95	(0.01)	-	-
Phase ϕ_2 (yr)	0.12	(0.01)	0.06	(0.03)	0.30	(0.01)	0.00	(0.02)	-	-
Average s.d. (S_A)	5.74	(0.58)	4.04	(0.20)	5.40	(0.57)	4.37	(0.47)	2.71	(0.03)
Ratio s.d. (S_R)	1.00		1.00		0.52		1.89		1.93	
Wellington west coast										
s.d.	c		v		v		*		v	
Age classes	8		9		3		*		19	
K (year^{-1})	0.35	(0.01)	0.42	(0.02)	0.48	(0.03)	*	*	0.13	(0.02)
L_∞ (cm)	75.2	(0.30)	56.0	(0.95)	60.8	(1.23)	*	*	58.7	(0.28)
t_0 (years)	0.96	(0.02)	0.42	(0.07)	0.97	(0.05)	*	*	4.02	(0.01)
Amplitude ϕ_1	0.78	(0.02)	0.95	(0.01)	0.95	(0.01)	*	*	0.95	(0.01)
Phase ϕ_2 (yr)	0.00	(0.01)	0.90	(0.04)	0.88	(0.01)	*	*	0.26	(0.02)
Average s.d. (S_A)	3.47	(0.18)	3.68	(0.72)	3.85	(0.30)	*	*	1.64	(0.01)
Ratio s.d. (S_R)	1.00	-	0.55	(0.03)	0.57	(0.01)	*	*	0.52	(0.00)

* Data could not be analysed.

- Best fit model had no seasonal growth.

Table 8: GROTAG models with 95% confidence limits for parameters. Method 1, model 1 (von Bertalanffy growth function) using all data; method 2, model 1 using truncated data of only individuals that grew over the time at liberty; and method 3 using model 2 including an exponential function to describe the data where it diverges from the linear model of the von Bertalanffy growth function (at length Par 10). Parameters given are: maximum log-likelihoods (2λ), estimates of the mean annual growth of clams of a length (g_α) and (g_β), standard deviation of the measurement error (s), the coefficient of variation of growth variability (v) and the proportion of outliers (p).

Parameter		Method 1	Method 2	Method 3	
Cloudy Bay					
Mactra murchisoni					
Log-likelihood	2λ	538.57	256.92	418.15	
Mean growth rate	g_{45}	11.55	15.10	15.46	(14.84–16.06)
	g_{70}	4.52	4.84	4.30	(4.04–4.52)
Growth variability	v	0.40	0.16	0.17	(0.13–0.19)
s.d. measurement error	s	0.88	0.88	0.88	
Outlier contamination	p	*	*	*	
Par10				78	
		Mactra discors			
Log-likelihood	2λ	83.17	15.38	66.50	
Mean growth rate	g_{33}	4.92	11.26	11.84	(9.71–15.43)
	g_{50}	2.39	5.45	4.51	(3.62–5.37)
Growth variability	v	0.86	0.00	0.26	(0–0.41)
s.d. measurement error	s	0.88	0.88	0.88	
Outlier contamination	p	0	0.20	0.00	
Par10				61	
		Spisula aequilatera			
Log-likelihood	2λ	810.87	169.46		
Mean growth rate	g_{30}	18.00	21.67(g_{28})	(20.49–22.74)	
	g_{50}	6.56	12.95(g_{44})	(12.35–13.62)	
Growth variability	v	0.52	0.11	(0.01–0.13)	
s.d. measurement error	s	0.88	0.88		
Outlier contamination	p	*	*		
Par10			*		
		Paphies donacina			
Log-likelihood	2λ	245.65	47.66	221.38	
Mean growth rate	g_{50}	5.95	8.32(g_{55})	9.49	(8.33–10.73)
	g_{80}	1.80	5.57(g_{65})	1.35	(0.93–1.63)
Growth variability	v	0.61	0.16	0.60	(0.17–0.37)
s.d. measurement error	s	0.88	0.88	0.88	
Outlier contamination	p	0	0.03	0.61	
Par10				83	
		Dosinia anus			
Log-likelihood	2λ	149.27	11.00	109.87	
Mean growth rate	g_{21}	11.00	10.09	16.49	(12.91–20.78)
	g_{50}	4.14	4.00	4.12	(2.99–5.17)
Growth variability	v	0.31	0.61	0.36	(0–0.63)
s.d. measurement error	s	0.88	0.88	0.88	
Outlier contamination	p	*	*	*	
Par10				60	
Wellington west coast					
		Dosinia anus			
Log-likelihood	2λ	52.62	15.27	40.26	
Mean growth rate	g_{25}	3.66	6.33	6.38	(5.23–8.11)
	g_{35}	2.13	2.74	2.90	(2.07–3.40)
Growth variability	v	0.61	0.17	0.22	(0–0.32)
s.d. measurement error	s	0.88	0.88	0.88	
Outlier contamination	p	*	*	*	
Par10		44			

Table 9. Estimates of the instantaneous natural mortality rate, M.

A: minimum number of year classes indicated by MULTIFAN.
B: maximum age indicated by shell sections.
M_1: mortality range estimated from $\ln M = 1.23-0.832\ln(t_{max})$ and $\ln M = 1.44-0.982\ln(t_{max})$, formulae for molluscs, fish, and crustaceans combined (Hoenig 1983).
M_2 mortality estimated from $M = \ln 100/(t_{max})$; t_{max} is the estimate of maximum age.

Cloudy Bay

	A	B	M_1	M_2
Mactra murchisoni	8	11	0.40–0.46	0.42
Mactra discors	7	14	0.32–0.38	0.33
Spisula aequilatera	5	7	0.63–0.68	0.66
Paphies donacina	10	17	0.26–0.32	0.27
Dosinia anus	16	22	0.20–0.26	0.21

Wellington west coast

	A	B*	M_1	M_2
Mactra murchisoni	8	11	0.40–0.46	0.42
Mactra discors	8	16	0.28–0.34	0.29
Spisula aequilatera	3	5	0.87–0.89	0.92
Paphies donacina†				
Dosinia anus	19	26	0.17–0.23	0.18

*Shell sections not yet examined. Ages are inferred from Cloudy Bay data.
†Growth data could not be analysed.

Table 10. Regressions of ln length (x) on ln weight (y) of samples of each of five surf clam species at Peka Peka, Wellington west coast and Cloudy Bay, Marlborough

	Cloudy Bay			Peka Peka		
Species	Regression y =	*r*	*n*	Regression y =	*r*	*n*
M. murchisoni	3.29x–9.58	0.99	328	3.29x–9.47	0.98	225
M. discors	3.39x–9.67	0.99	223	3.43x–9.73	0.99	291
S. aequilatera	3.09x–8.65	0.96	270	3.16x–8.85	0.98	243
P. donacina	2.70x–7.52	0.98	231	1.31x–1.68	0.56	209
D. anus	2.87x–7.51	0.99	218	2.99x–8.03	0.99	241

Table 11: Estimates of age at which individual surf clams reach exploitable size, (inferred from market preferences)

	Cloudy Bay	Wellington west coast
Mactra murchisoni	3	5
Mactra discors	5	7
Spisula aequilatera	3	4
Paphies donacina	5	*
Dosinia anus	10	14

* Growth data could not be analysed to estimate this figure.

Table 12. Estimates of $F_{0.1}$ obtained from yield per recruit analyses for the five species of surf clams using figures for natural mortality that bracket those estimated from maximum ages (see Table 9). Data for *P. donacina* on Wellington west coast were inadequate to run yield per recruit analysis.

Cloudy Bay

M. murchisoni		*M. discors*		*S. aequilatera*		*P. donacina*		*D. anus*	
M	$F_{0.1}$	M	$F_{0.1}$	M	$F_{0.1}$	M	$F_{0.1}$	M	$F_{0.1}$
0.35	0.43	0.30	0.46	0.55	1.06	0.25	0.36	0.20	0.25
0.40	0.50	0.35	0.54	0.60	1.16	0.30	0.44	0.25	0.33
0.45	0.57	0.40	0.64	0.65	1.26	0.35	0.52	0.30	0.42
				0.70	1.37				

Wellington west coast

M. murchisoni		*M. discors*		*S. aequilatera*		*D. anus*	
M	$F_{0.1}$	M	$F_{0.1}$	M	$F_{0.1}$	M	$F_{0.1}$
0.40	0.70	0.30	0.56	0.7	1.12	0.15	0.27
0.45	0.79	0.35	0.66	0.8	1.34	0.20	0.35
0.50	0.89	0.40	0.77	0.9	1.56	0.25	0.44
		0.45	0.87			0.30	0.54

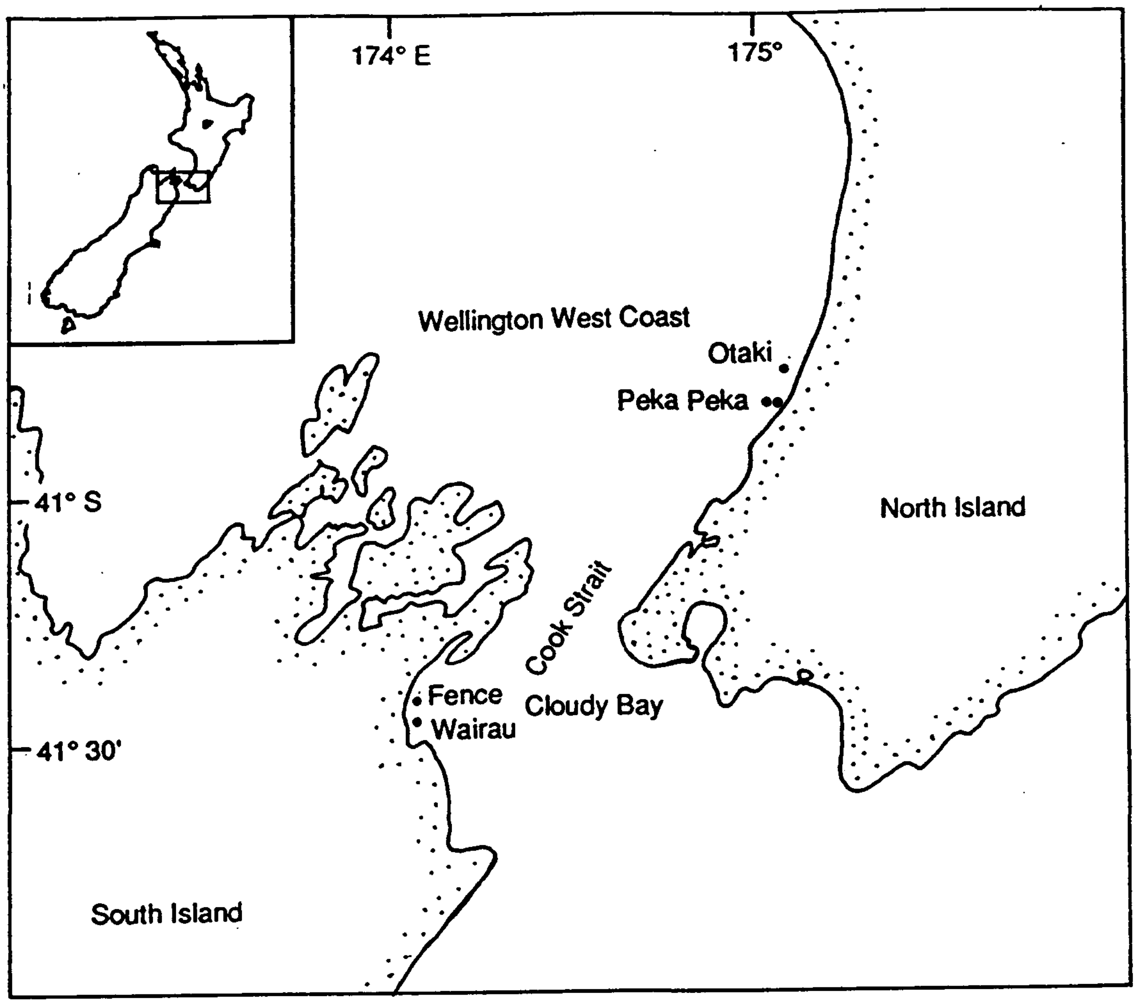


Figure 1: Location of sampling sites for the mark-recapture experiments and length frequency sampling, Cloudy Bay, Marlborough and the Wellington west coast.

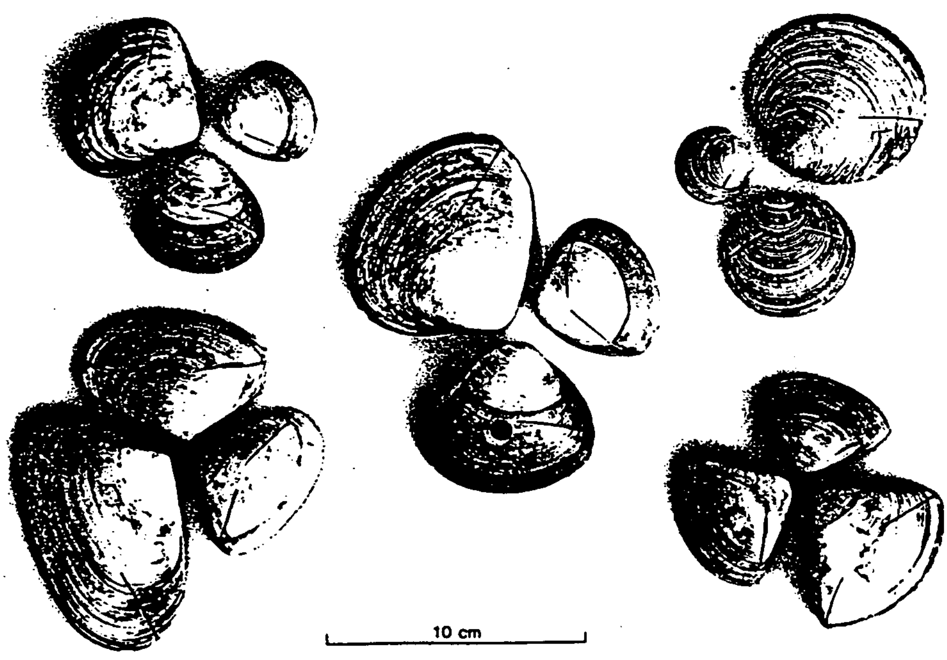


Figure 2: The five surf clam species studied, top left *Mactra discors*, centre *Mactra murchisoni*, top right *Dosinia anus*, bottom left *Paphies donacina* and bottom right *Spisula aequilatera*. Lines on the shells show length at release and the incremental growth of different size surf clams is also shown.

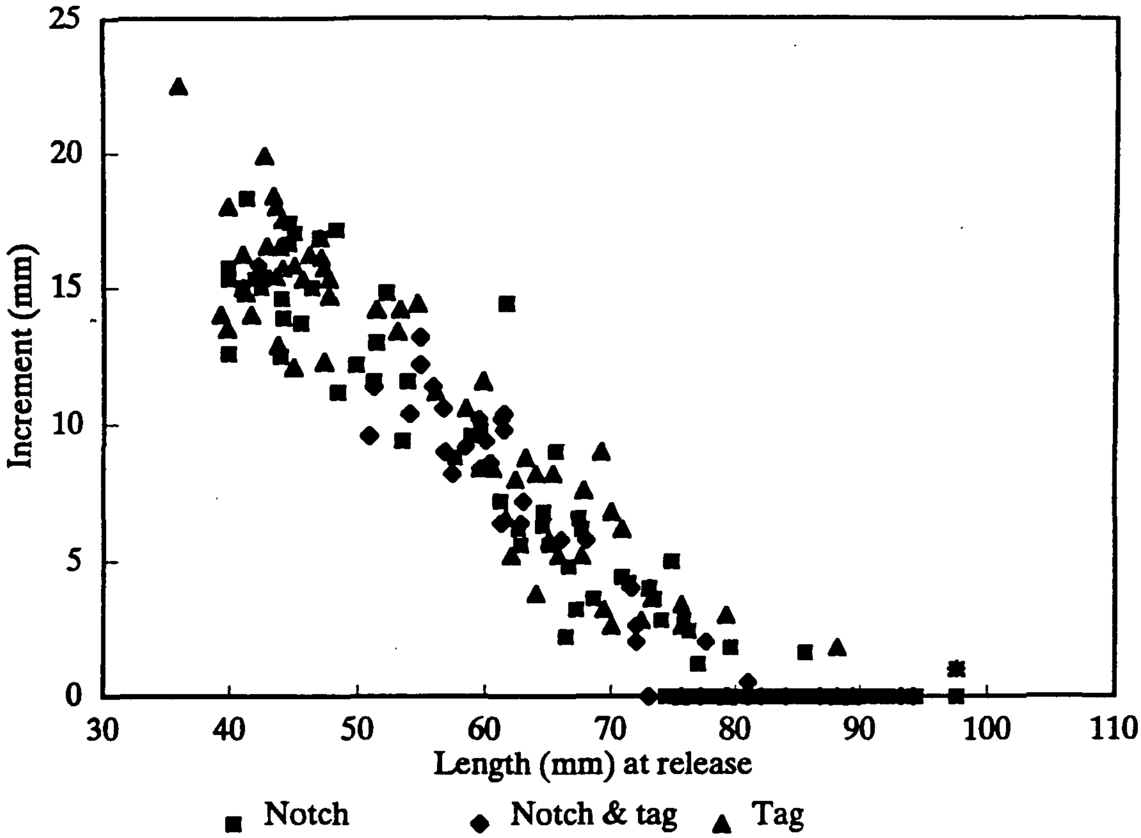


Figure 3: Plots of length at release against growth increment for notched, tagged and notched, and tagged *Mactra murchisoni* from Cloudy Bay.

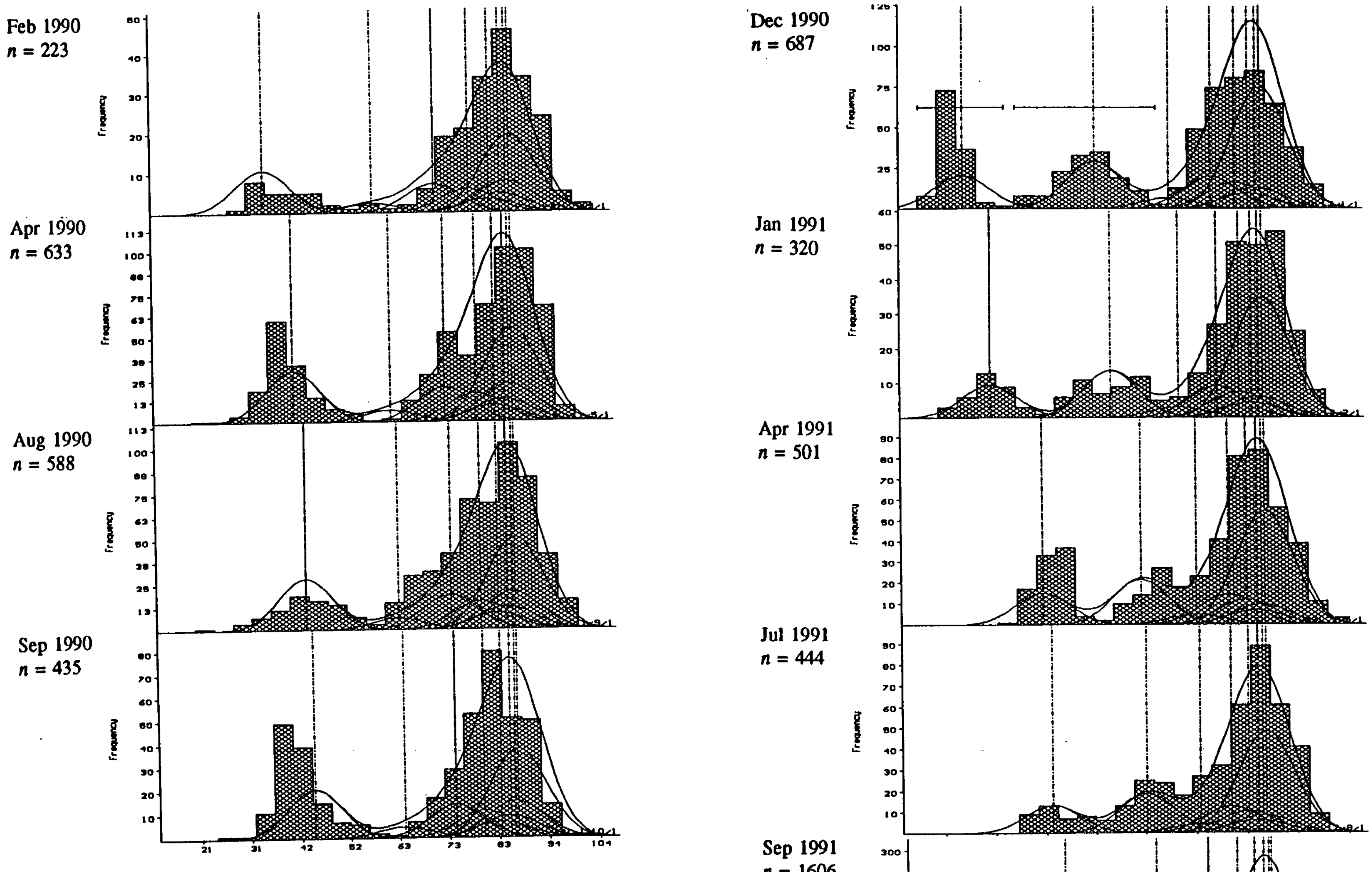


Figure 4: Length frequency histograms of *Mactra murchisoni* from Cloudy Bay, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

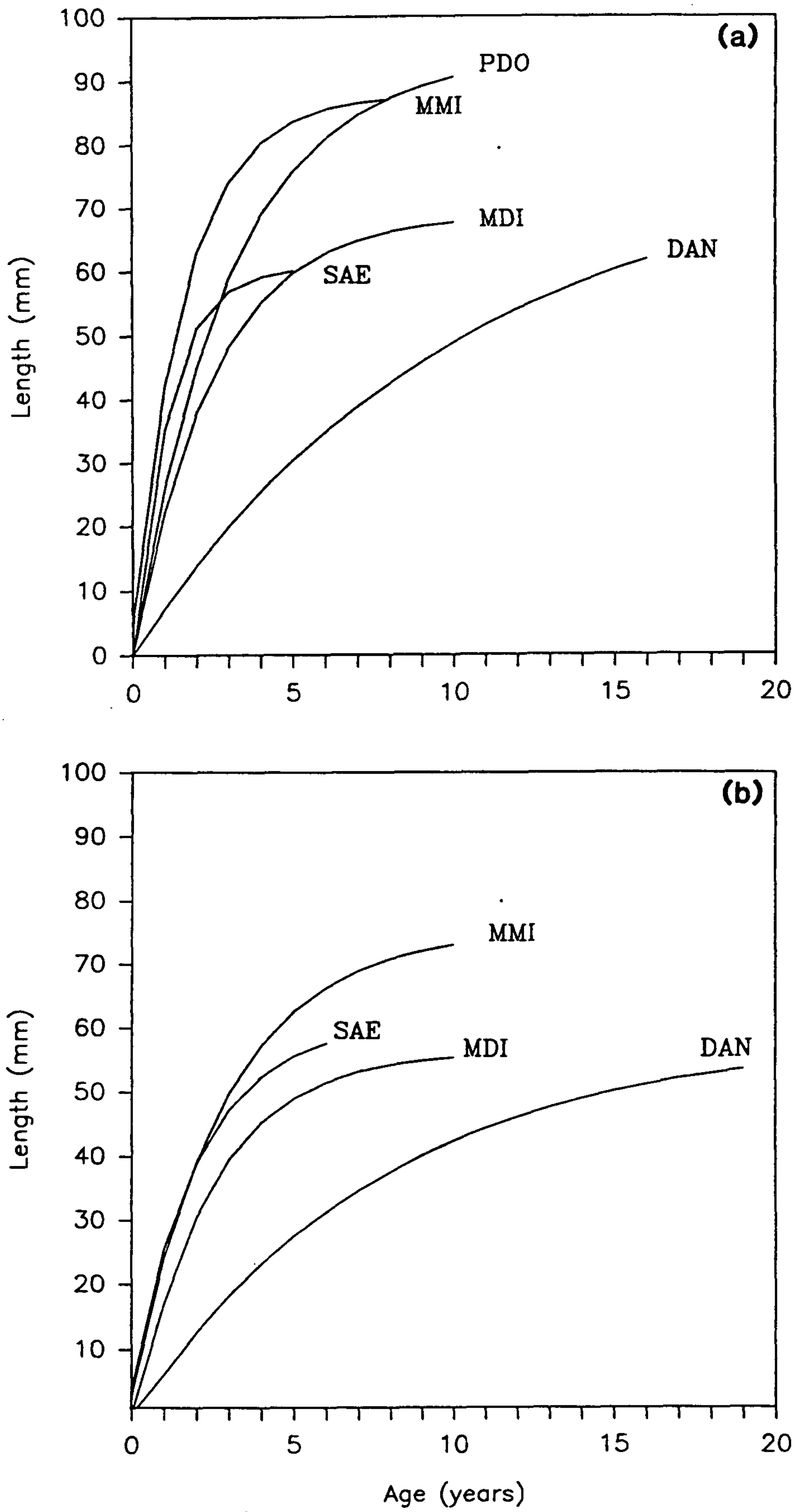


Figure 5: Growth curves for all species from (a) Cloudy Bay and (b) Wellington west coast. *Mactra discors* (MMI), *Mactra murchisoni* (MDI), *Dosinia anus* (DAN), *Paphies donacina* (PDO) and *Spisula aequilatera* (SAE).

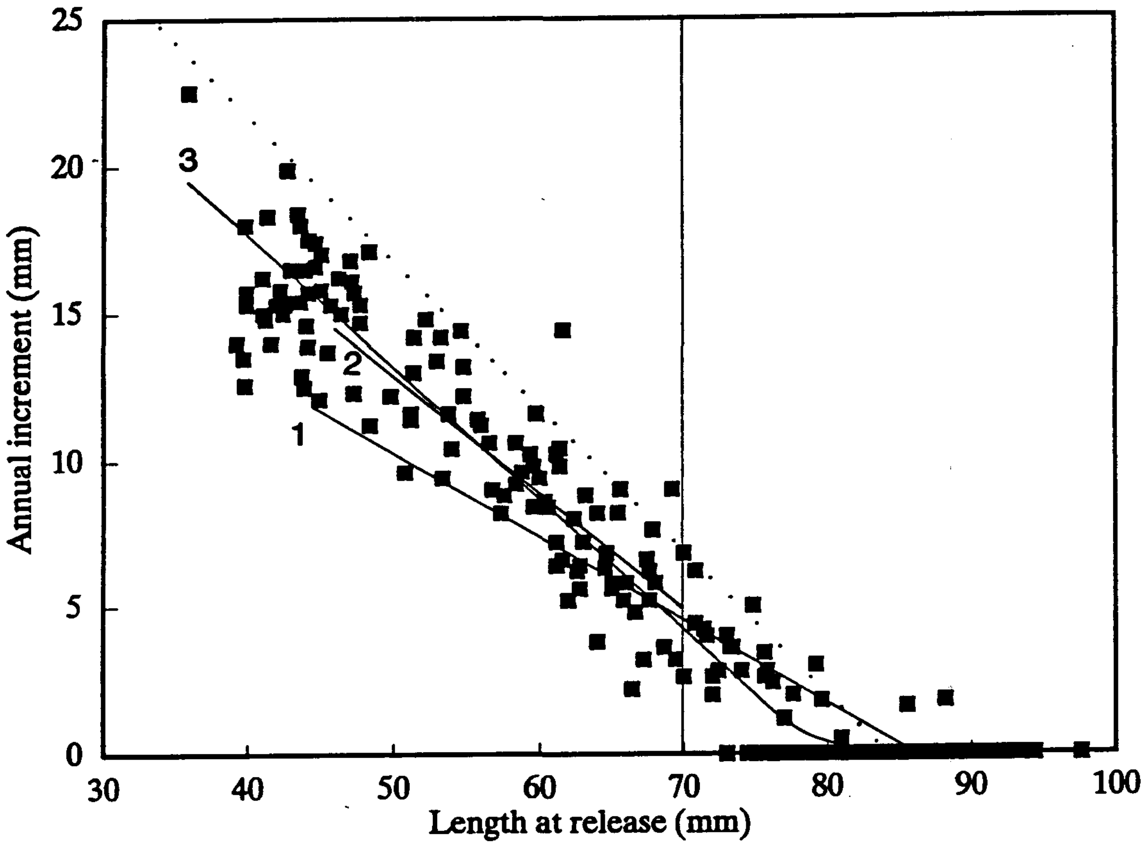


Figure 6: Length at release against growth increment for *Mactra murchisoni* from Cloudy Bay. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 70 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

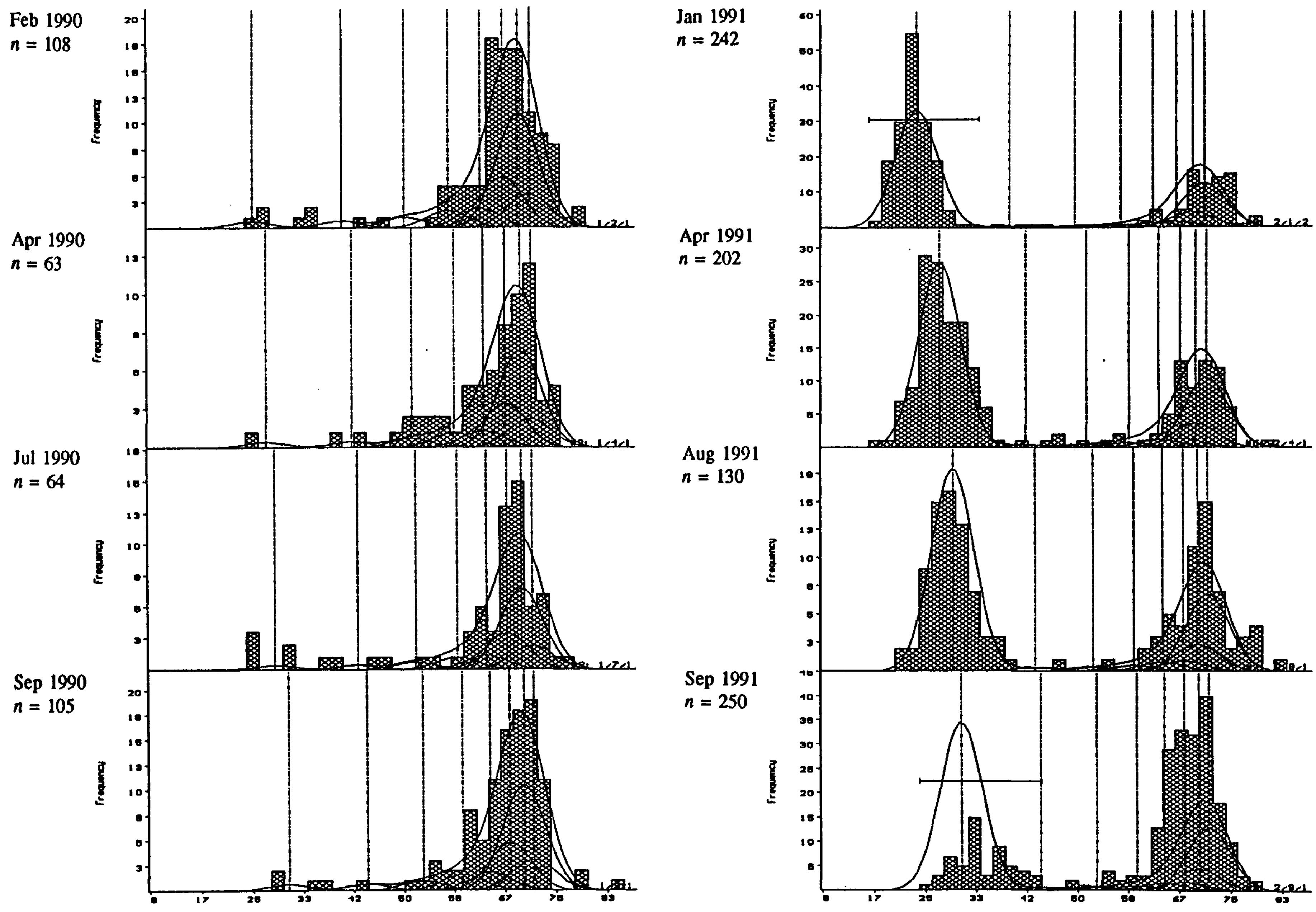
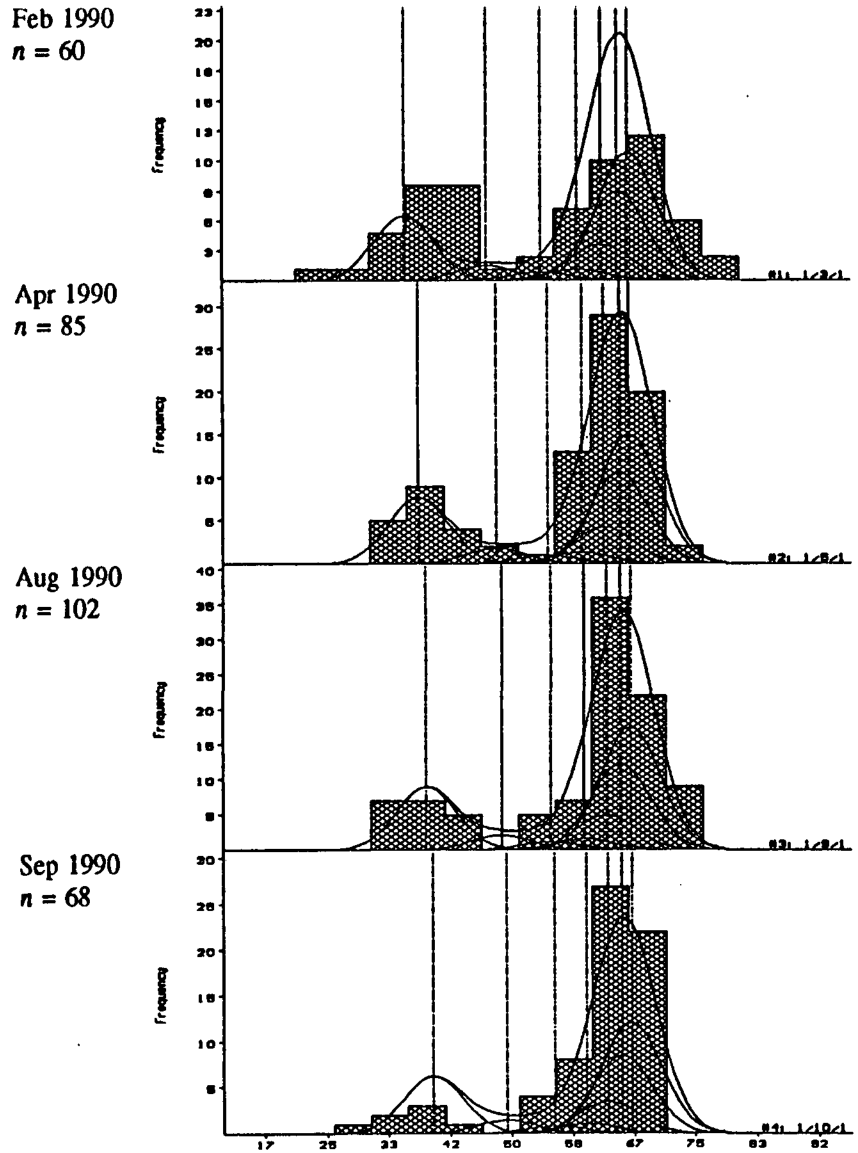


Figure 7: Length frequency histograms of *Mactra murchisoni* from the Wellington west coast, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.



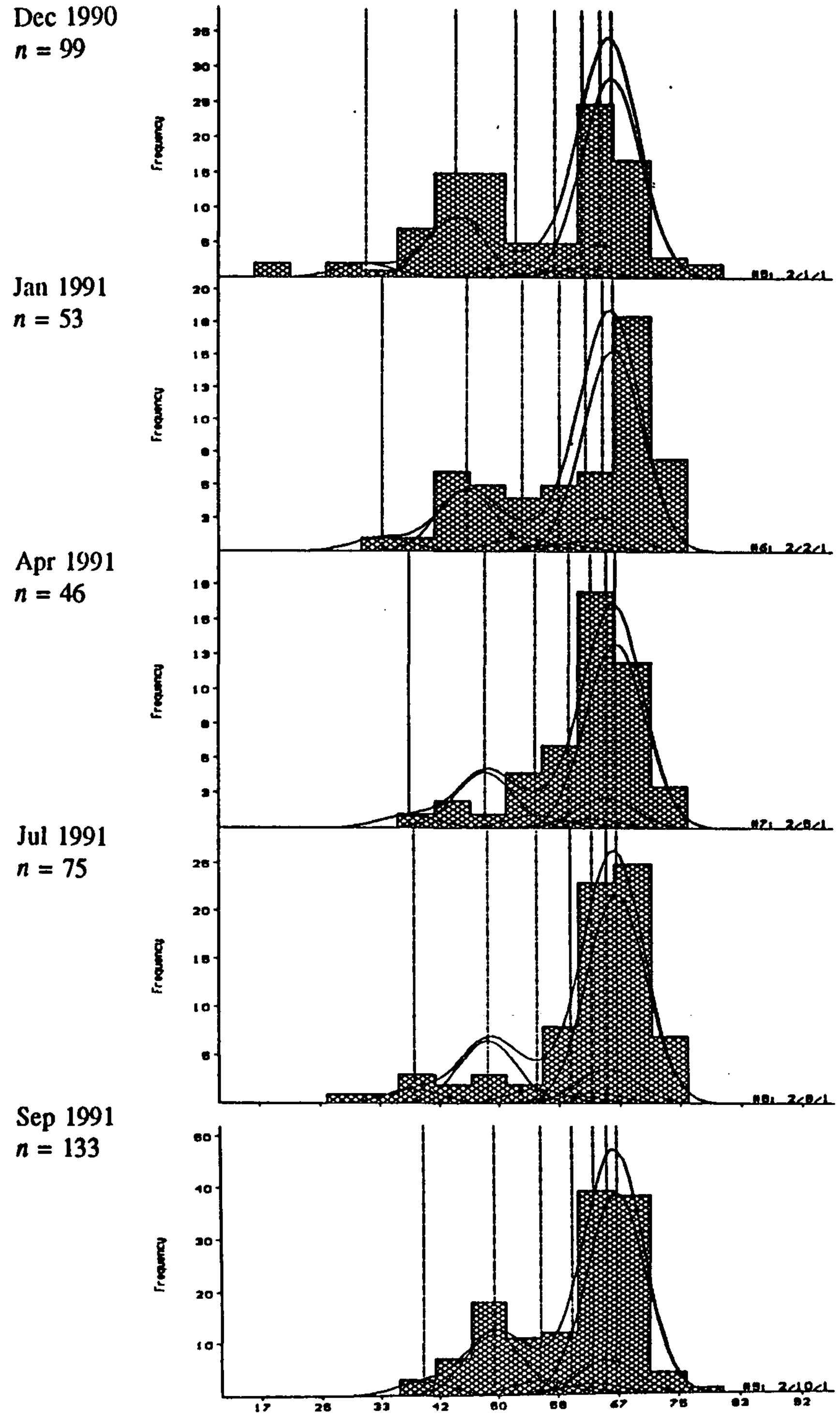


Figure 8: Length frequency histograms of *Mactra discors* from Cloudy Bay, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

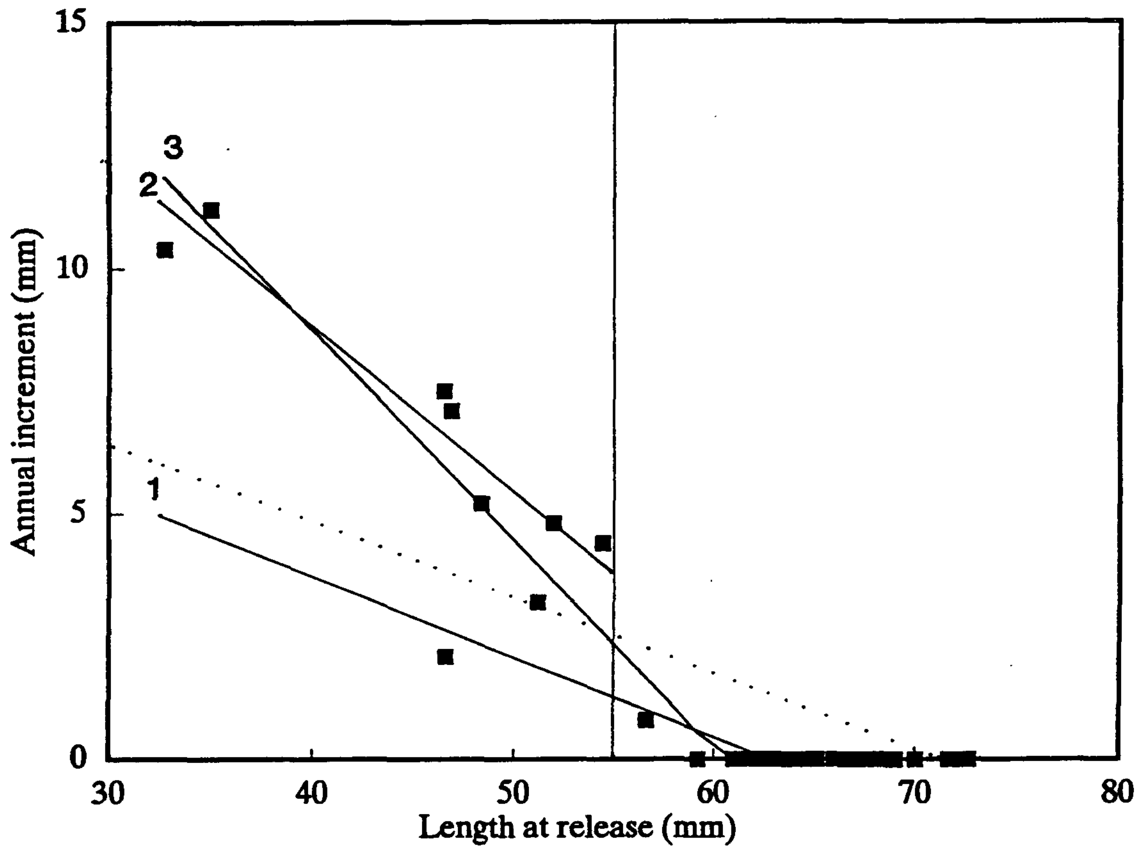


Figure 9: Length at release against growth increment for *Mactra discors* from Cloudy Bay. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 55 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

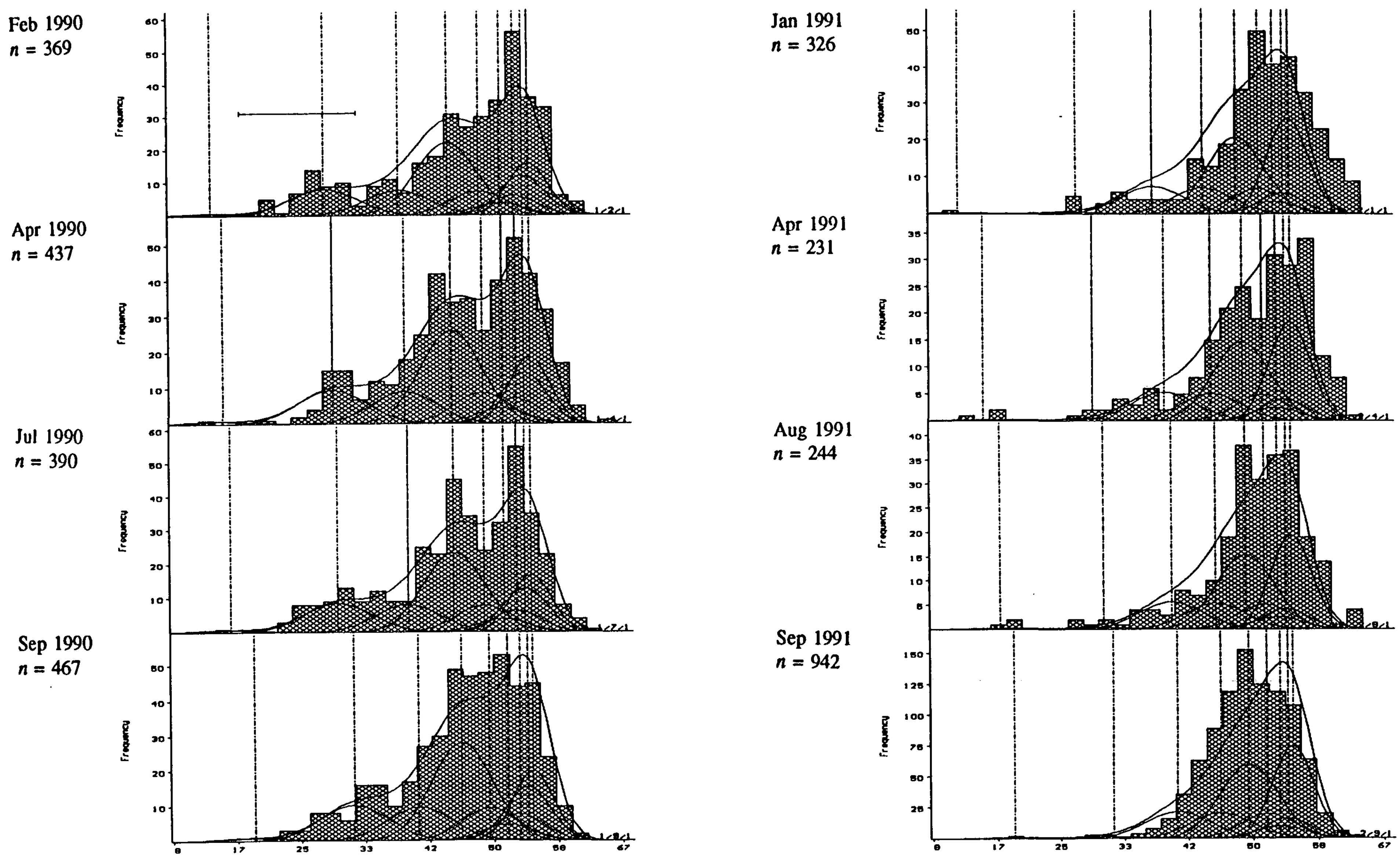


Figure 10: Length frequency histograms of *Mactra discors* from the Wellington west coast, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

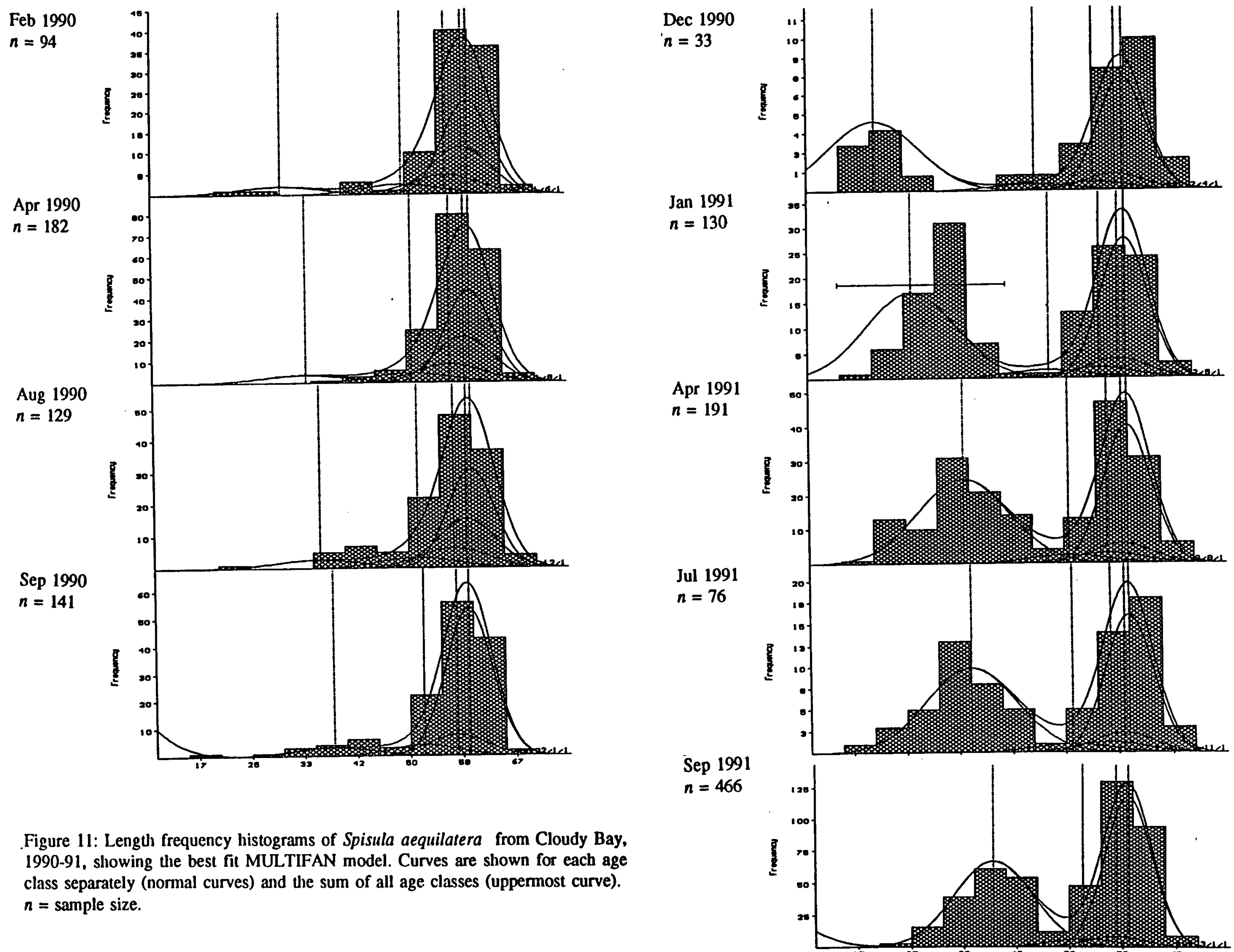


Figure 11: Length frequency histograms of *Spisula aequilatera* from Cloudy Bay, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). *n* = sample size.

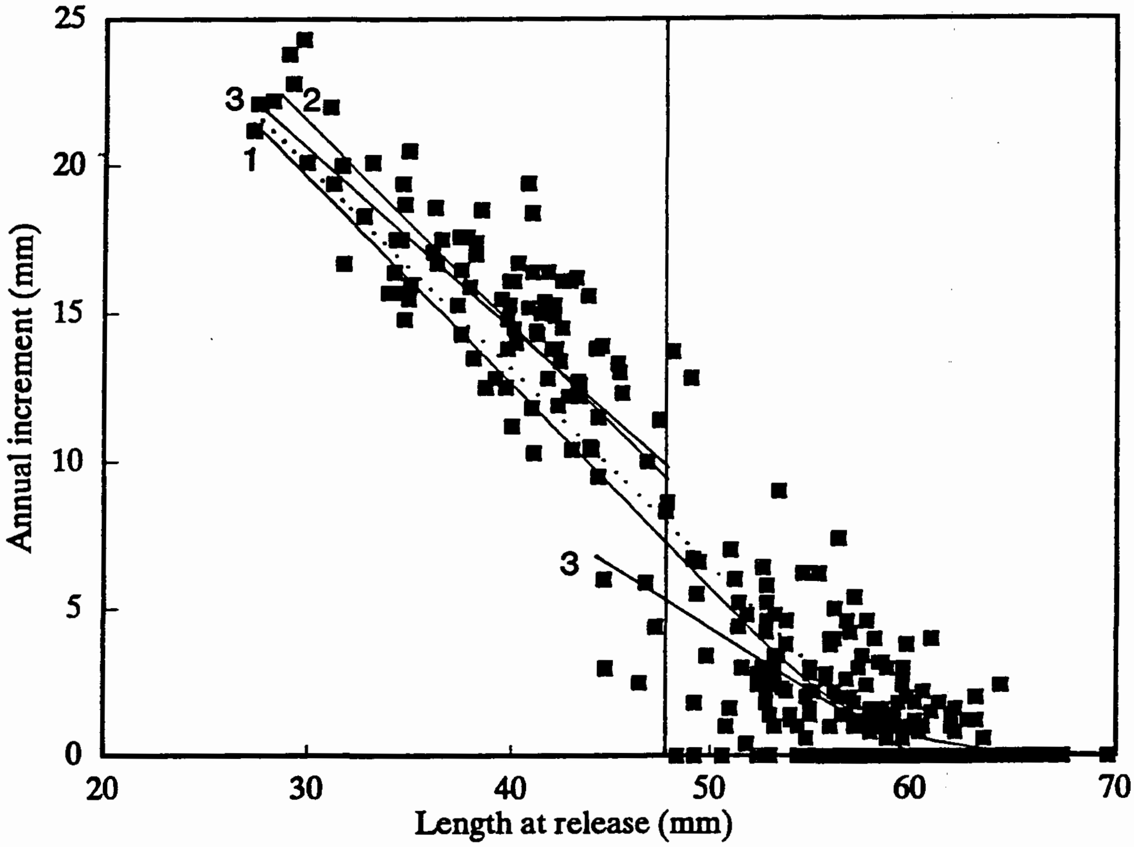


Figure 12: Length at release against growth increment for *Spisula aequilatera* from Cloudy Bay. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 48 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

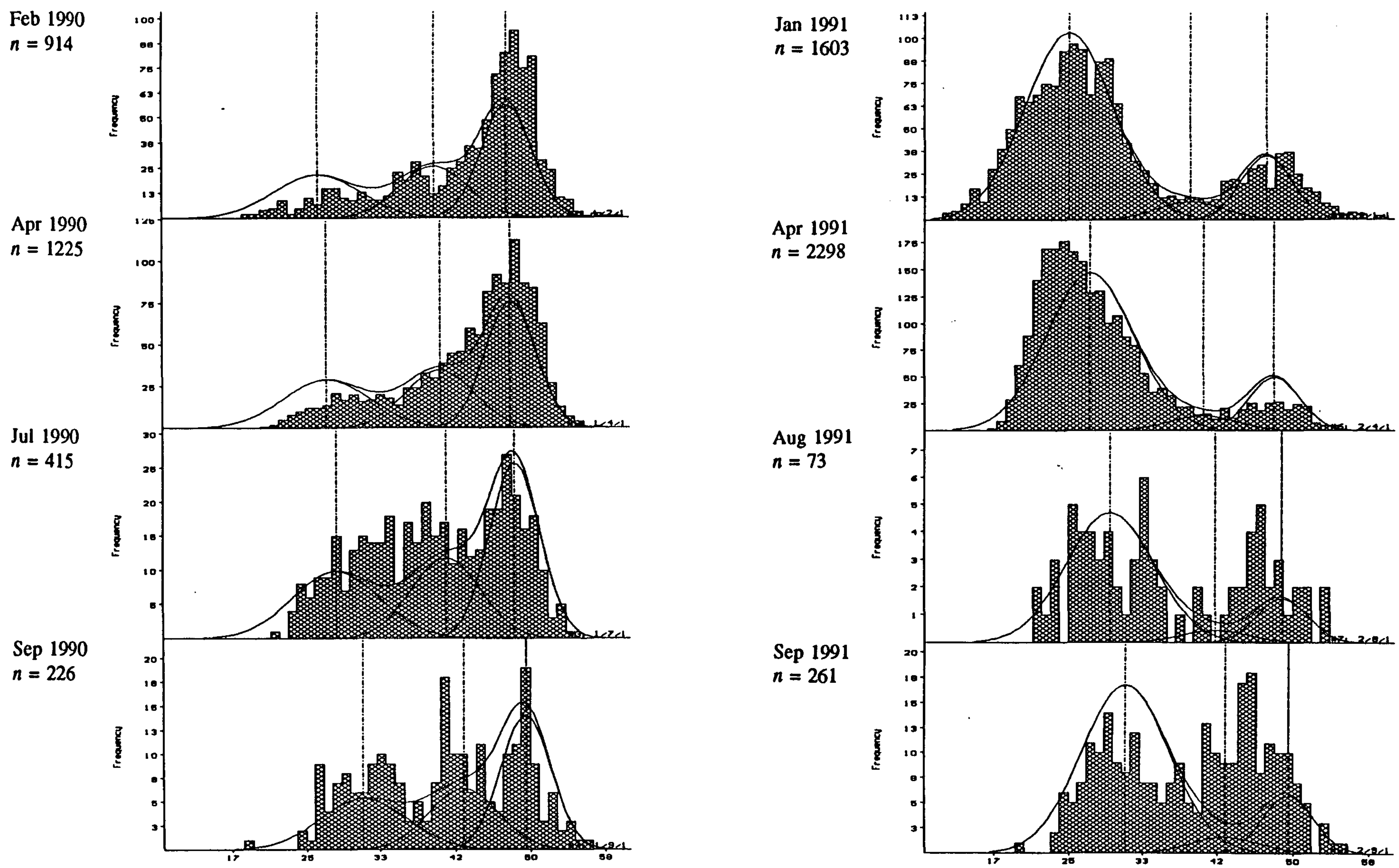


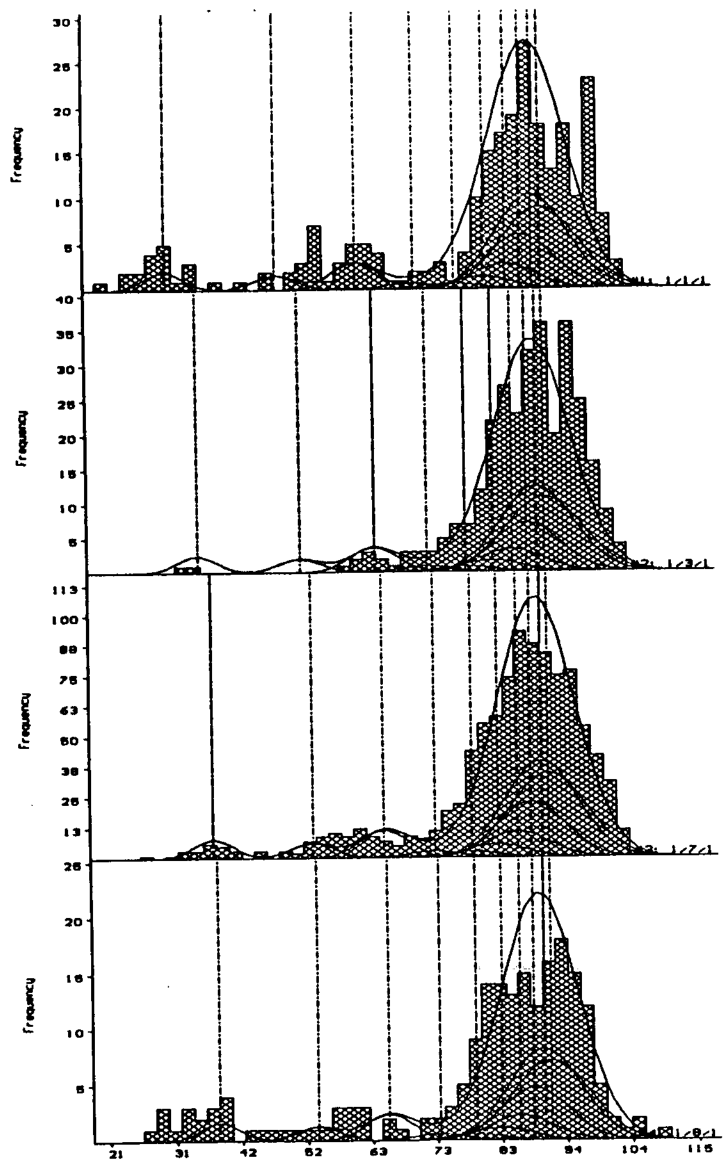
Figure 13: Length frequency histograms of *Spisula aequilatera* from the Wellington west coast, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

Feb 1990
n = 247

Apr 1990
n = 301

Aug 1990
n = 955

Sep 1990
n = 197



Dec 1990
n = 272

Jan 1991
n = 309

Apr 1991
n = 363

Jul 1991
n = 376

Sep 1991
n = 744

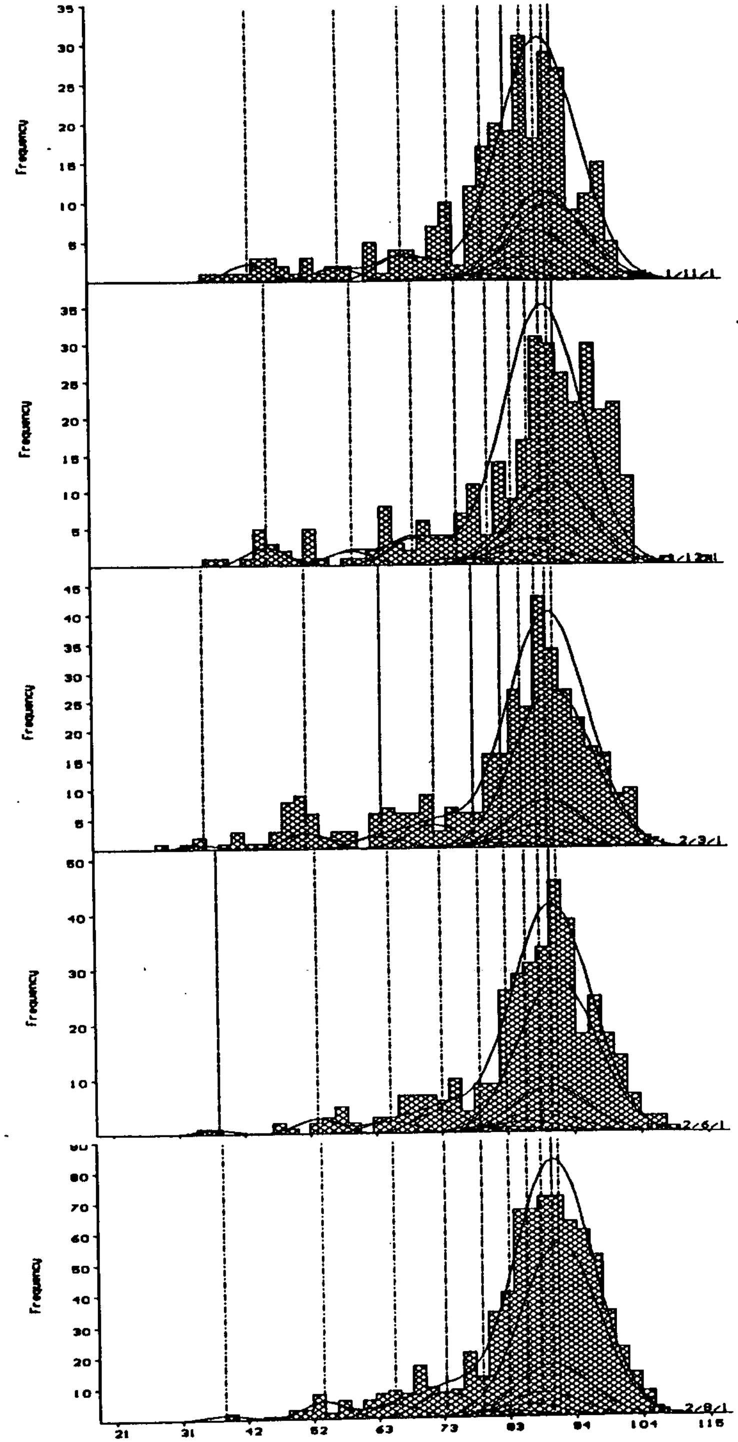


Figure 14: Length frequency histograms of *Paphies donacina* from Cloudy Bay, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

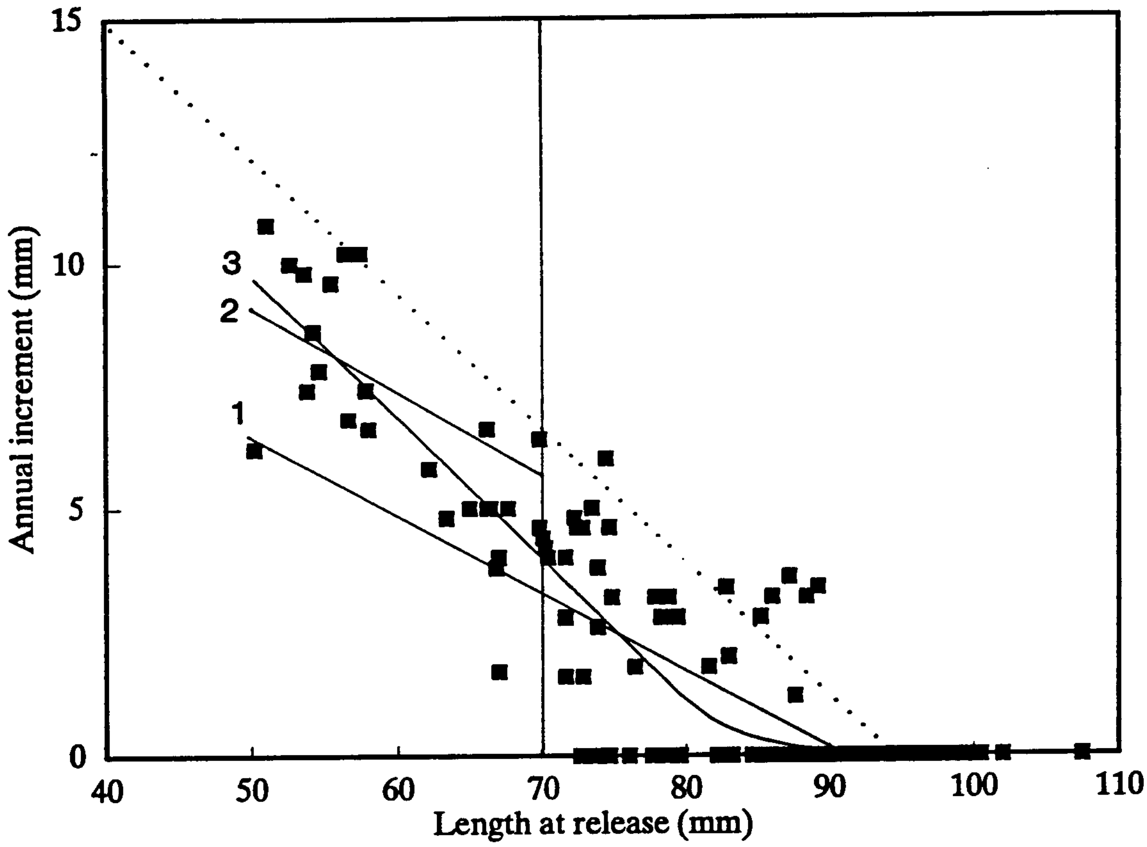


Figure 15: Length at release against growth increment for *Paphies donacina* from Cloudy Bay. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 70 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

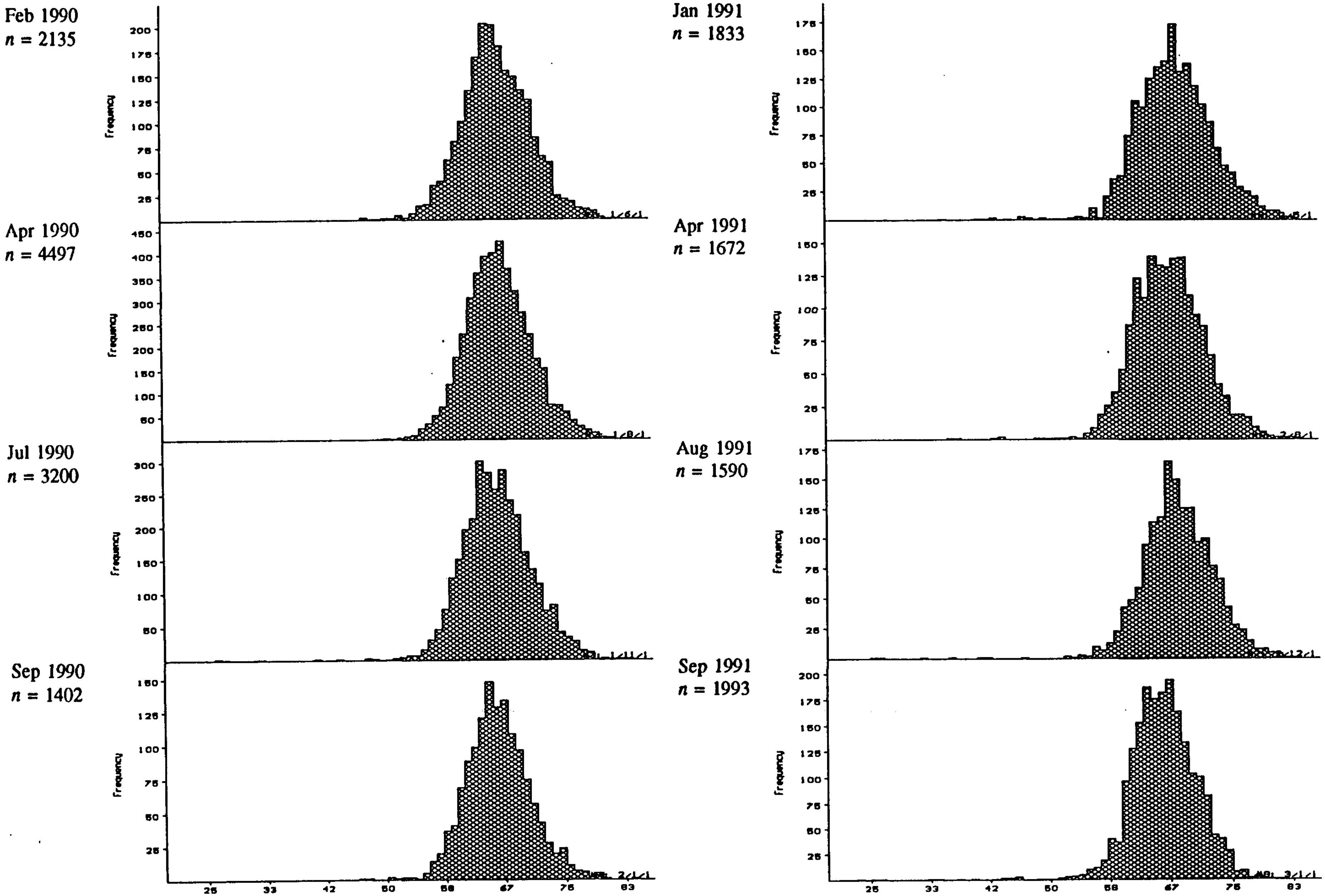


Figure 16: Length frequency histograms of *Paphies donacina* from the Wellington west coast, 1990-91.

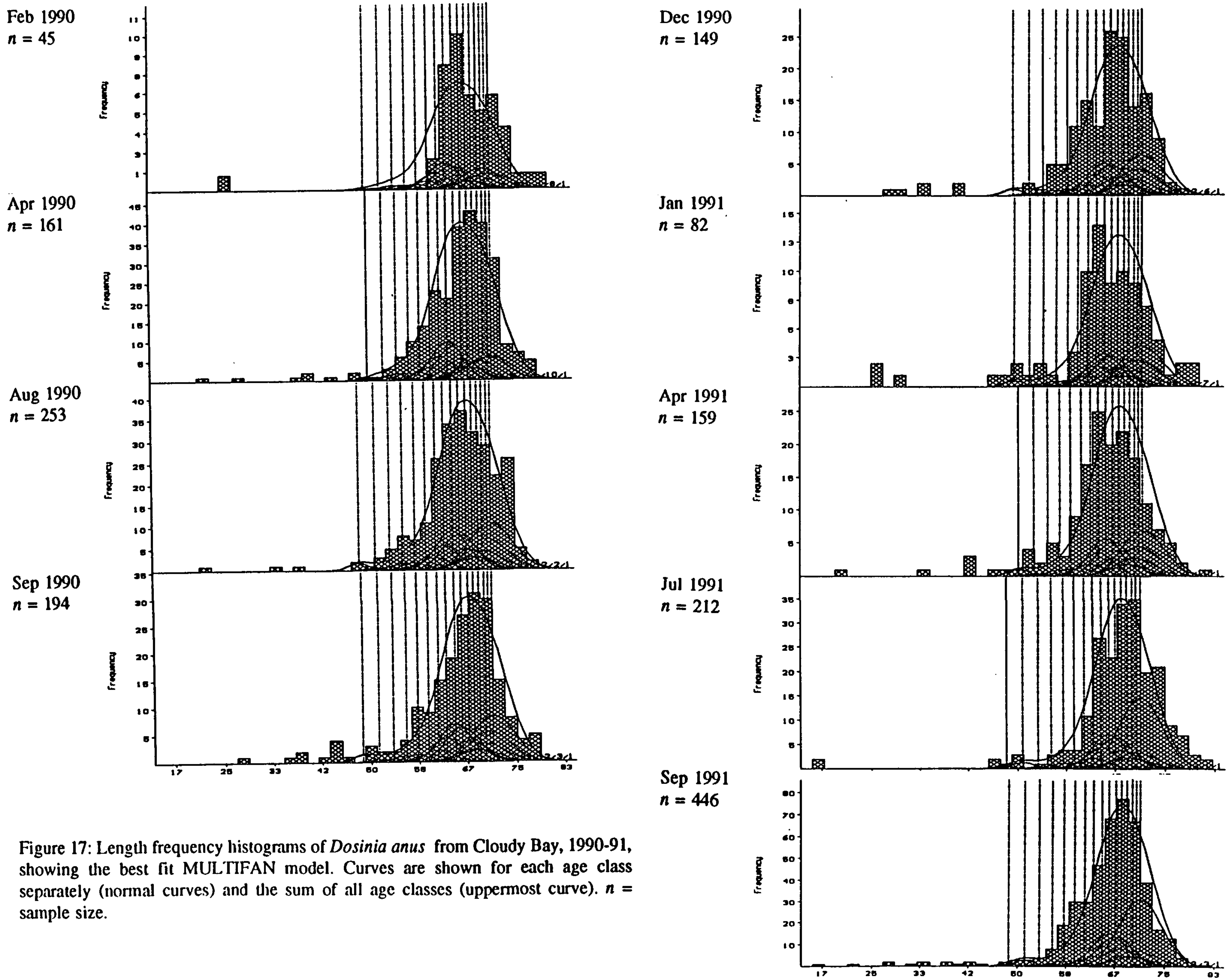


Figure 17: Length frequency histograms of *Dosinia anus* from Cloudy Bay, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

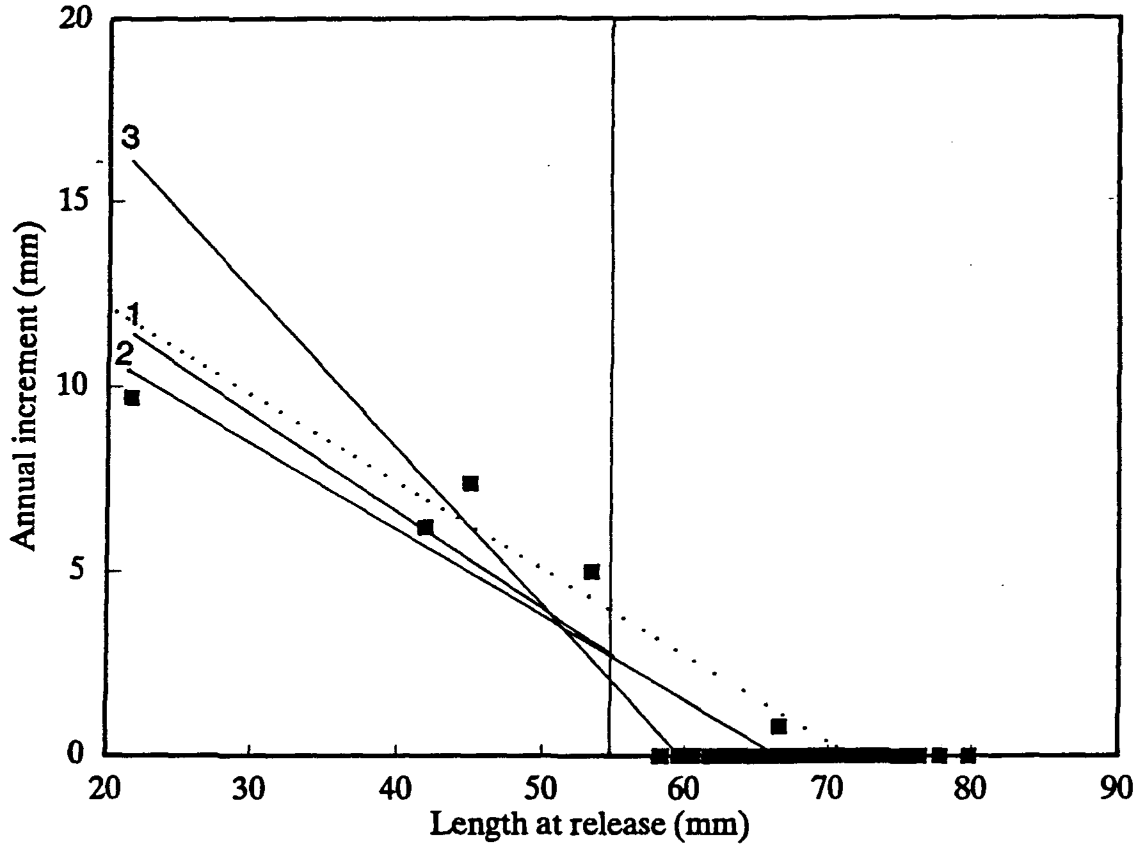


Figure 18: Length at release against growth increment for *Dosinia anus* from Cloudy Bay. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 70 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

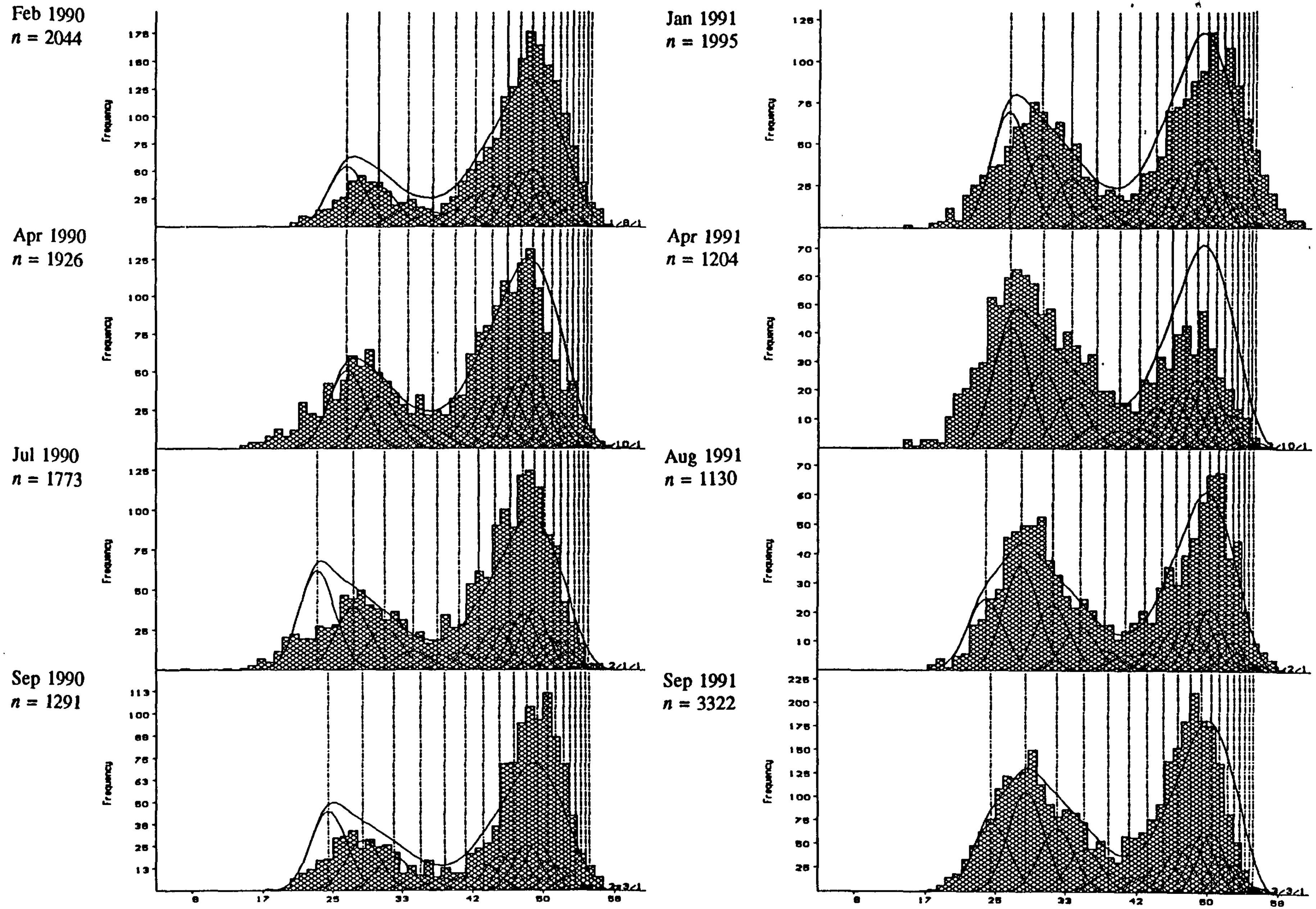


Figure 19: Length frequency histograms of *Dosinia anus* from the Wellington west coast, 1990-91, showing the best fit MULTIFAN model. Curves are shown for each age class separately (normal curves) and the sum of all age classes (uppermost curve). n = sample size.

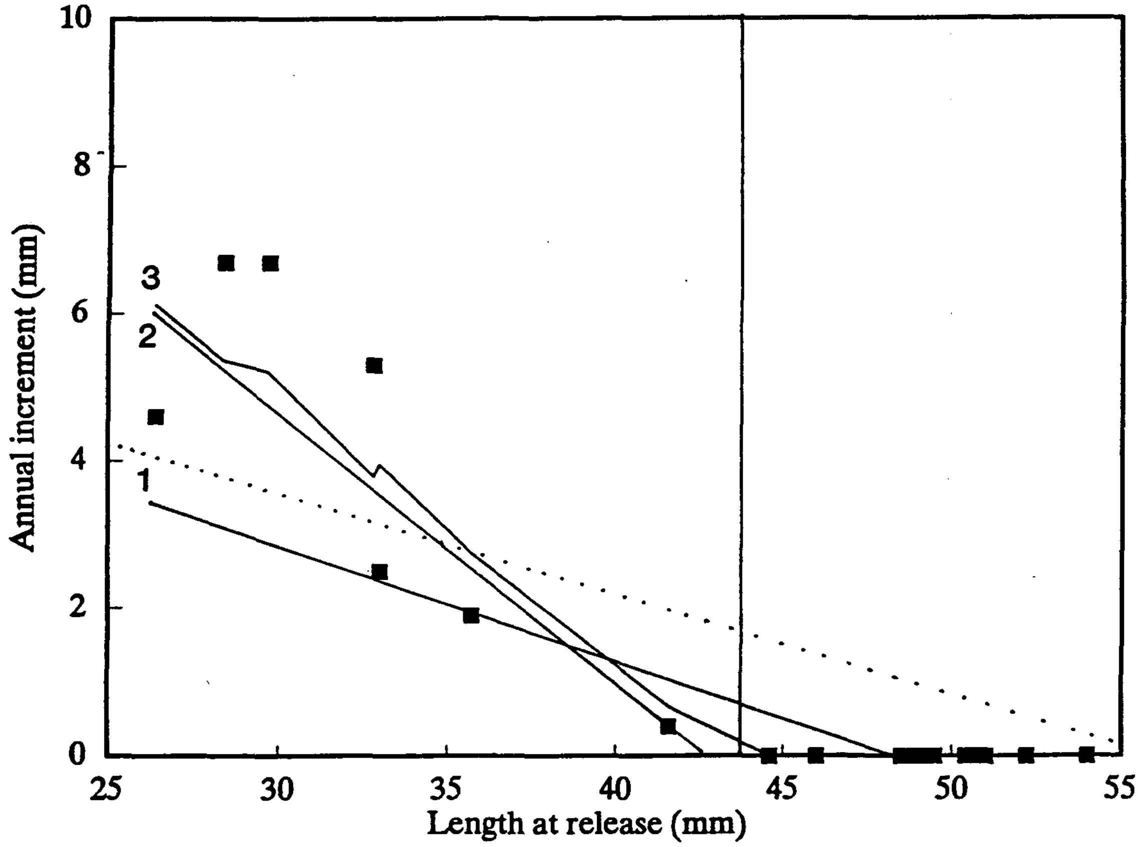


Figure 20: Length at release against growth increment for *Dosinia anus* from Wellington west coast. Solid squares represent observed growth increments from recaptured marked clams. Solid lines 1-3 are expected growth from GROTAG methods 1, 2 and 3 respectively. The vertical line at 70 mm is the length at which the data was truncated to contain only individuals which grew over the time at liberty (method 2). Dotted line is expected growth from the MULTIFAN model.

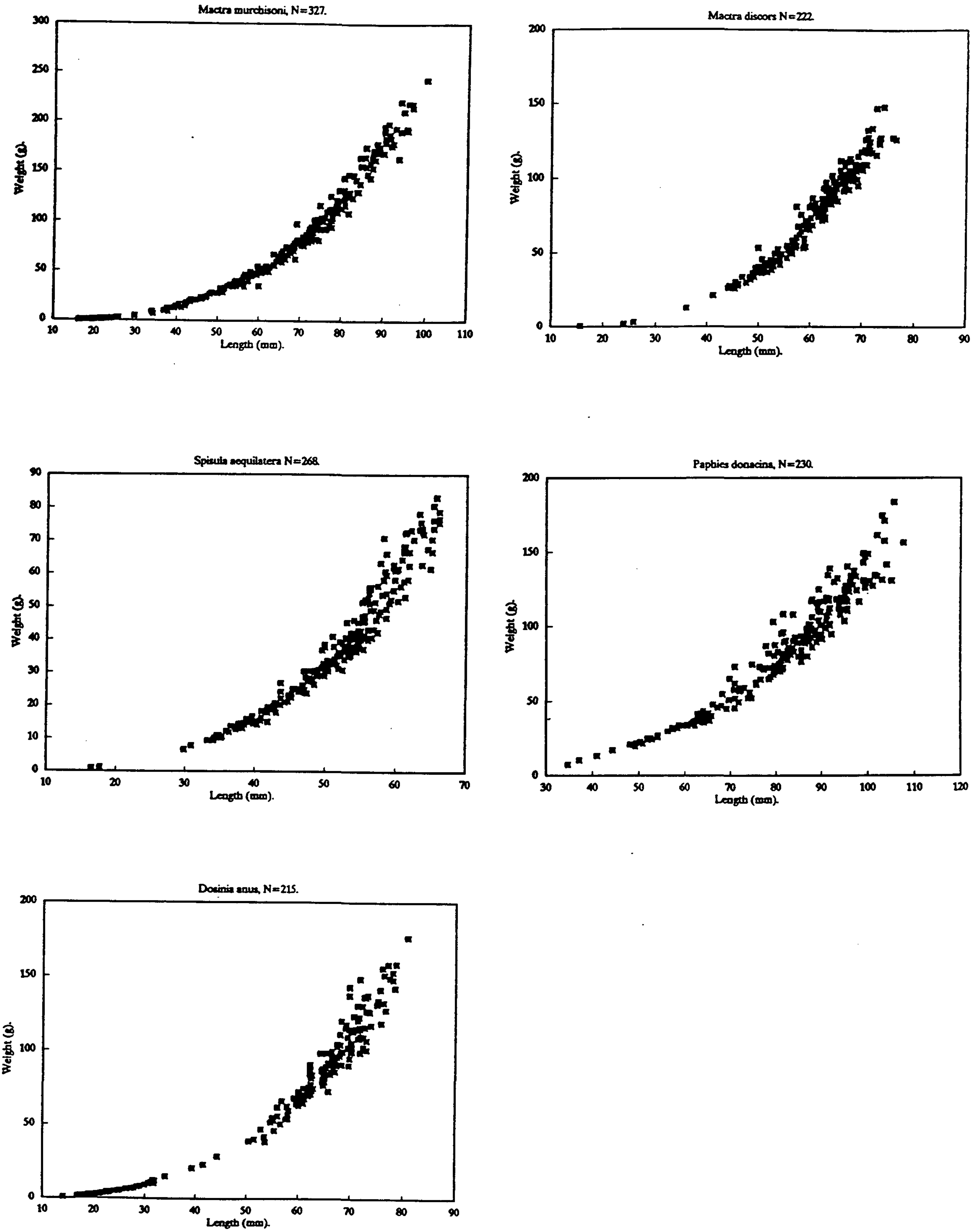


Figure 21: Plots of length against weight for surf clams from Cloudy Bay.

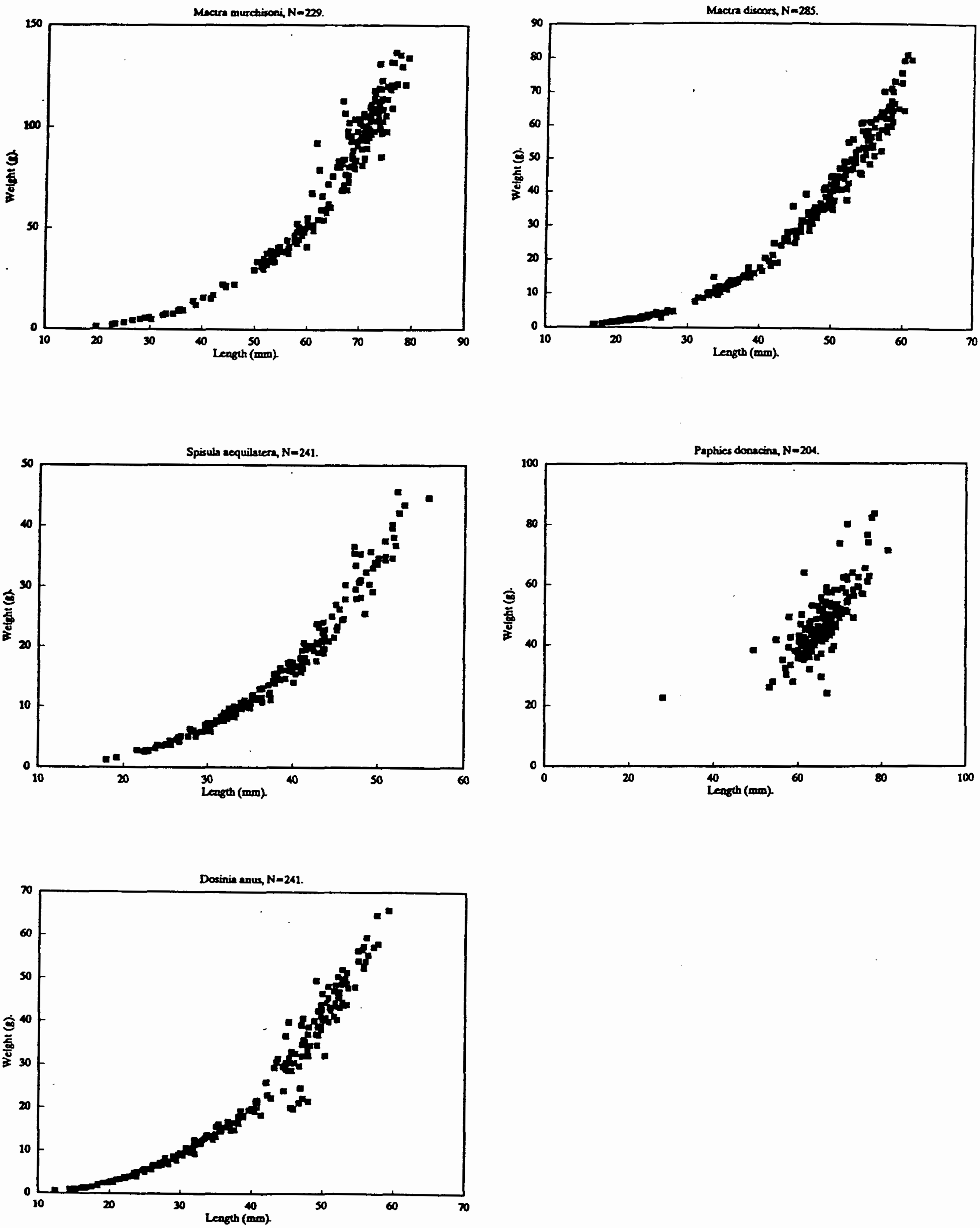


Figure 22: Plots of length against weight for surf clams from the Wellington west coast.