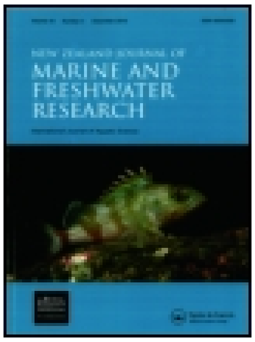

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Growth rates of five species of surf clams on a southern North Island beach, New Zealand

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Abstract Growth rates of five species of surf clam were estimated on the Kapiti Coast, southern North Island, New Zealand. Length-frequencies of sequential population samples were analysed by the computer program, MULTIFAN. Incremental growth of marked individuals was analysed by the computer program, GROTAG. The von Bertalanffy growth parameters k and L_∞ estimated by MULTIFAN for *Spisula aequilatera* (Deshayes in Reeve, 1854) were 0.80 yr^{-1} and 52.1 mm; for *Mactra murchisoni* Deshayes in Reeve, 1854 were 0.60 yr^{-1} and 72.3 mm; and for *M. discors* Gray, 1837 were 0.35 yr^{-1} and 60.1 mm. MULTIFAN could not model growth of *Paphies donacina* (Spengler, 1793) and *Dosinia anus* (Philippi, 1848) from the population samples. The growth parameters estimated by GROTAG for *D. anus* were 0.53 yr^{-1} and 53.0 mm and for *M. murchisoni* 1.84 yr^{-1} and 72.4 mm. The growth rates of *P. donacina*, *S. aequilatera*, and *M. discors* were estimated for the size range of their incremental growth data and the estimates are usable for this limited size range only. Growth rates of each species varied with depth in the surf zone in the same way in the North and the South Island. The growth rate of two species was faster in the South Island and asymptotic size of all species was greater in the South Island.

Keywords surf clams; Kapiti Coast; growth; recruitment; von Bertalanffy parameters; mark-recapture; length-frequency; *Paphies donacina*; *Spisula aequilatera*; *Mactra murchisoni*; *Mactra discors*; *Dosinia anus*; MULTIFAN; GROTAG

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INTRODUCTION

Large populations of seven species of surf clam have been found on New Zealand beaches (Cranfield et al. 1994a). Five of these species were harvested commercially in Cloudy Bay in the South Island and their growth rates have been estimated to determine a sustainable yield for this developing fishery (Cranfield et al. 1996). The maximum size attained by all surf clam species in the South Island is larger than in the North Island suggesting that growth rate of individual species may differ between islands (Cranfield et al. 1993). Maximum sizes attained by the five species of surf clams on the Kapiti Coast (Fig. 1) were representative of those from North Island beaches. We estimated growth in the same five species of surf clam on a Kapiti Coast beach using the same methods as Cranfield et al. (1996), so growth data would be available to estimate sustainable yields of surf clams in the North Island. Growth was estimated from analysis of sequential length-frequency samples using the computer program MULTIFAN (Fournier et al. 1990) and the analysis of incremental growth of marked surf clams using the computer program GROTAG (Francis 1988a).

METHODS

Area

We sampled surf clam populations at two sites along the Kapiti Coast, at Peka Peka and 10.4 km further north at Otaki (Fig. 1). Length-frequency distributions were measured at both sites; incremental growth was studied in a mark-recapture experiment at Peka Peka only.

The beach at each of these two sites slopes uniformly with a gentle gradient (1:110) from high water to a depth of 13 m. All depths relate to chart

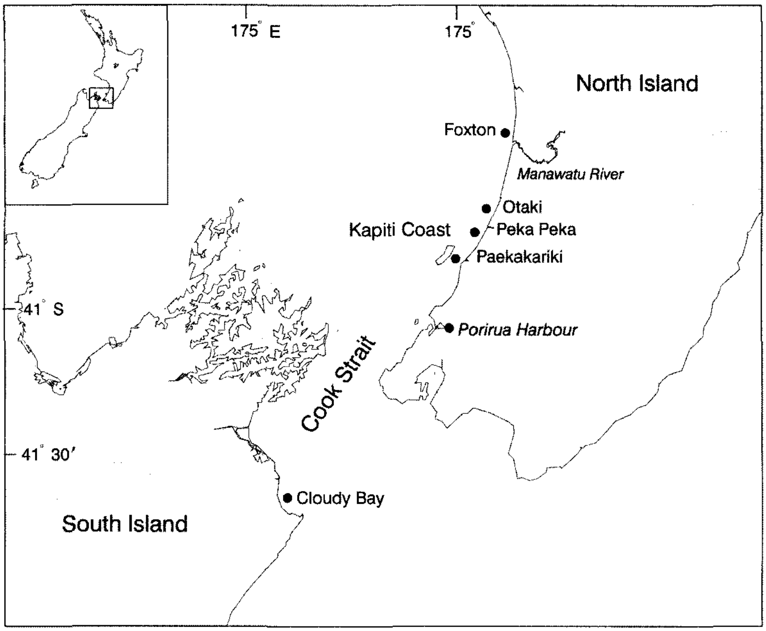


Fig. 1 Length-frequency samples were dredged from Peka Peka and Otaki on the Kapiti Coast, New Zealand between 1990 and 1991. Mark-recapture experiment was carried out off Peka Peka between 1992 and 1993. Growth of the same species was initially investigated in Cloudy Bay (Cranfield et al. 1996) in the South Island.

datum. In the categorisation of Short & Wright (1983), the beach is dissipative, with most of the wave energy being dissipated within the sediments of the seabed. The sediments are predominantly well-sorted, fine sand, which becomes finer offshore (Cranfield & Michael unpubl. data). Tidal range at spring tides is c. 2 m (Harris 1990). The predominant wind and wave direction is north-westerly. Farewell Spit on the north-western corner of the South Island shelters the Kapiti Coast from westerly swells and wind. Mean significant wave height decreases from 1.2 m at Wanganui in the north, to 1.1 m at Foxton Beach (Fig. 1) in the centre and 0.75 m at Paekakariki, south of the Kapiti Coast (Pickrill & Mitchell 1979; Harris 1990).

Surf clam species

We studied growth in five species of surf clam: the mesodesmatid, *Paphies donacina* (Spengler, 1793); the mactrids, *Spisula aequilatera* (Deshayes in Reeve, 1854), *Mactra murchisoni* Deshayes in Reeve, 1854, and *Mactra discors* Gray, 1837; and the venerid, *Dosinia anus* (Philippi, 1848). These species are zoned with increasing depth in this order and extend from just inshore of the wave break to outside the wave break at a depth of 10 m, however *D. anus* was found over the entire depth range (Cranfield et al. 1994a, 1996).

Collection of length-frequency data

Population samples for length-frequency analysis were dredged from six 1-m depth strata between mean low water and a depth of 6 m at each site. We sampled approximately every 2 months between February 1990 and September 1991. We collected eight length-frequency samples from the two sites using a small hydraulic dredge that retained all surf clams larger than 10 mm (the size of gaps in the filtration grill of the dredge). The dredge was towed parallel to the shore along the beach for c. 150 m in each depth stratum. Sampling sites were relocated in each period using landmarks. Sampling depths were measured by echo sounder and corrected for the state of the tide to a depth below chart datum. The corrections for tidal state were interpolated from the two nearest secondary ports giving mean sea level height data, Porirua Harbour and the Manawatu River Mouth (New Zealand Nautical Almanac 1989–90, 1990–91). The same correction was applied to both sites as they were relatively close to one another. As the mean sea levels differed between these two ports and the sea level heights are affected by weather and sea conditions, the precision of the corrected depths is uncertain.

Lengths of surf clams (the longest measurements along the anterior-posterior axis) were measured with an electronic measuring board to an accuracy of 0.1 mm, and the data captured electronically on a data logger.

Mark-recapture study

The surf clams to be marked were captured by hydraulic dredging at Peka Peka in October 1992. We marked 7158 surf clams of the five species by notching the anterior and posterior shell margins with high speed grinding bits and cutting a 8–20 mm line, up to 1 mm deep in the shell obliquely from the notches (Table 1). Marked clams were held in running seawater overnight so damaged clams could be identified. Divers reburied healthy marked surf clams in two plots at different depths offshore. We established the inshore plot within the depth range in which the distributions of *P. donacina*, *S. aequilatera*, and *D. anus* overlapped and the offshore plot within the depth range in which the distributions of *M. murchisoni*, *M. discors*, and *D. anus* overlapped. Due to uncertainties in the tidal corrections, it transpired that the inshore and offshore plots were further offshore than planned.

The inshore plot extended 65 m along the 3-m contour (intended depth was 2 m) and was 10 m wide. The offshore plot extended 54 m along the 7-m contour (intended depth was 5 m) and was also 10 m wide. The plots were established using differential GPS and HYDRO software that allowed dredging to be controlled precisely within the boundaries of both plots during recovery of marked surf clams (see Cranfield et al. 1996).

Marked surf clams were recaptured a year later by dredging (between October and November 1993). Recaptured surf clams were measured with vernier callipers to the nearest 0.1 mm. Length at recapture was measured from the anterior shell margin to the posterior shell margin. Length at marking was determined at recapture by measuring from the margins of the infilled anterior and posterior notches in the shell, or from the interruption ring produced by the marking. Cranfield et al. (1996) found that measurements made from the notches or from interruption rings produced length estimates that were on average 0.4 mm greater than the same measurement at release of tagged and notched surf clams. We corrected the data for the resultant downward bias of growth increment by adding 0.4 mm to all increments greater than 0.4 mm and doubling all increments from 0–0.3 mm (Cranfield et al. 1996).

Analyses of length-frequency data

The MULTIFAN model simultaneously analyses multiple sets of length-frequency samples using a robust likelihood method to estimate the proportion of clams in each age class, their size distribution, and the von Bertalanffy growth parameters. Francis & Francis (1992) used this model to analyse growth of rig, *Mustelus lenticulatus*, and Cranfield et al. (1996) used the model to analyse growth of surf clams from Cloudy Bay.

As the length-frequencies from both sites sampled were not different, the data were combined for analysis. Von Bertalanffy growth curves were fitted to length-frequency distributions for each species using the computer program MULTIFAN version 3.2 (Fournier et al. 1990). MULTIFAN makes three assumptions: (1) that the lengths of the shellfish in each age class are normally distributed around their mean length; (2) that the mean lengths at age lie on (or near) a von Bertalanffy curve; (3) that the standard deviation of the actual lengths about the mean length at age is a simple function of the mean length at age. The model estimates asymptotic size L_∞, the von Bertalanffy growth constant k, and the estimated age of the first appearance in the samples of age class 1 (a_1). Theoretical age at zero length (t_0) was estimated from the relationship $t_0 = T - a_1$ where a_1, the estimated age of the age class 1 in the month 1 sample, was calculated by the MULTIFAN model and T is the time in ages between the nominal birth

Table 1 Numbers of each species of surf clam notched and buried in the inshore and offshore mark-recapture plots on the Kapiti Coast, New Zealand in October 1992 and the numbers recaptured in and between plots in October 1992 and November 1993.

	Inshore plot		Between plots	Offshore plot	
Species	No. marked	No. recaptured	No. recaptured	No. marked	No. recaptured
Paphies donacina	593	140	1	362	0
Spisula aequilatera	1132	5	10	589	0
Mactra murchisoni	106	20	0	223	0
Mactra discors	385	2	15	771	2
Dosinia anus	854	266	24	2143	2
Total	3070	433	50	4088	4

date and the first sample containing individuals of the 0+ age class. Nominal birth dates were assigned as the second week in March for all species based on our knowledge of the reproductive cycles of two species (Cranfield & Michael unpubl. data). Standard errors estimated by a covariance matrix in MULTIFAN are presented for the von Bertalanffy growth parameters L_∞, k, and t_0. These errors are probably underestimated (see Fournier et al. 1990).

Four versions of the MULTIFAN model were fitted to these data: (1) the standard deviation of the lengths of all age classes was held constant; (2) the standard deviation was allowed to vary among age classes; (3) the standard deviation of age classes was held constant and growth was allowed to vary seasonally and; (4) both the standard deviation of age classes and growth was allowed to vary seasonally. The improvement of fit caused by addition of age classes within models was tested for significance at the level of 0.10 (Type 2 errors are more serious than Type 1 errors in estimating k (Fournier et al. 1990)). The improvement of fit between models was tested for significance at the 0.05 level.

Analysis of mark-recapture data

Francis (1988a) developed the computer program GROTAG to estimate growth rates from the incremental growth of recaptured marked fish. Francis (1988c) and Francis & Francis (1992) used the program to estimate growth of marked fish (*Rhombosolea plebeia* and *Mustelus lenticulatus*, respectively) that had been at liberty for variable periods after marking. Cranfield et al. (1996) used it to estimate growth in surf clams that had been recaptured a year after marking.

GROTAG fits growth of tagged individuals to a re-parameterised von Bertalanffy model in which parameters have near-linear properties (Francis 1988a). This model replaces the conventional parameters L_∞ and k, with g_α and g_β, the mean annual growth rates at sizes α and β, respectively, where α and β are chosen to cover the range of sizes of surf clams at marking. The parameters g_α and g_β are better descriptors of growth information in tagging data than the conventional von Bertalanffy parameters (Francis 1988a,b). The relationship between the two sets of parameters is given by:

$$L_\infty = (\beta\, g_\alpha - \alpha g_\beta)/(g_\alpha - g_\beta)$$
$$k = -\log_e[1 + (g_\alpha - g_\beta)/(\alpha - \beta)]$$

This model frequently did not fit incremental growth data from surf clams well because annual growth tended to zero asymptotically with increasing size rather than linearly as the von Bertalanffy model predicts. The model was modified to incorporate this asymptotic reduction in growth rate at a transitional length (L^*) (model 2, Cranfield et al. 1996).

RESULTS

Growth estimates from length-frequencies

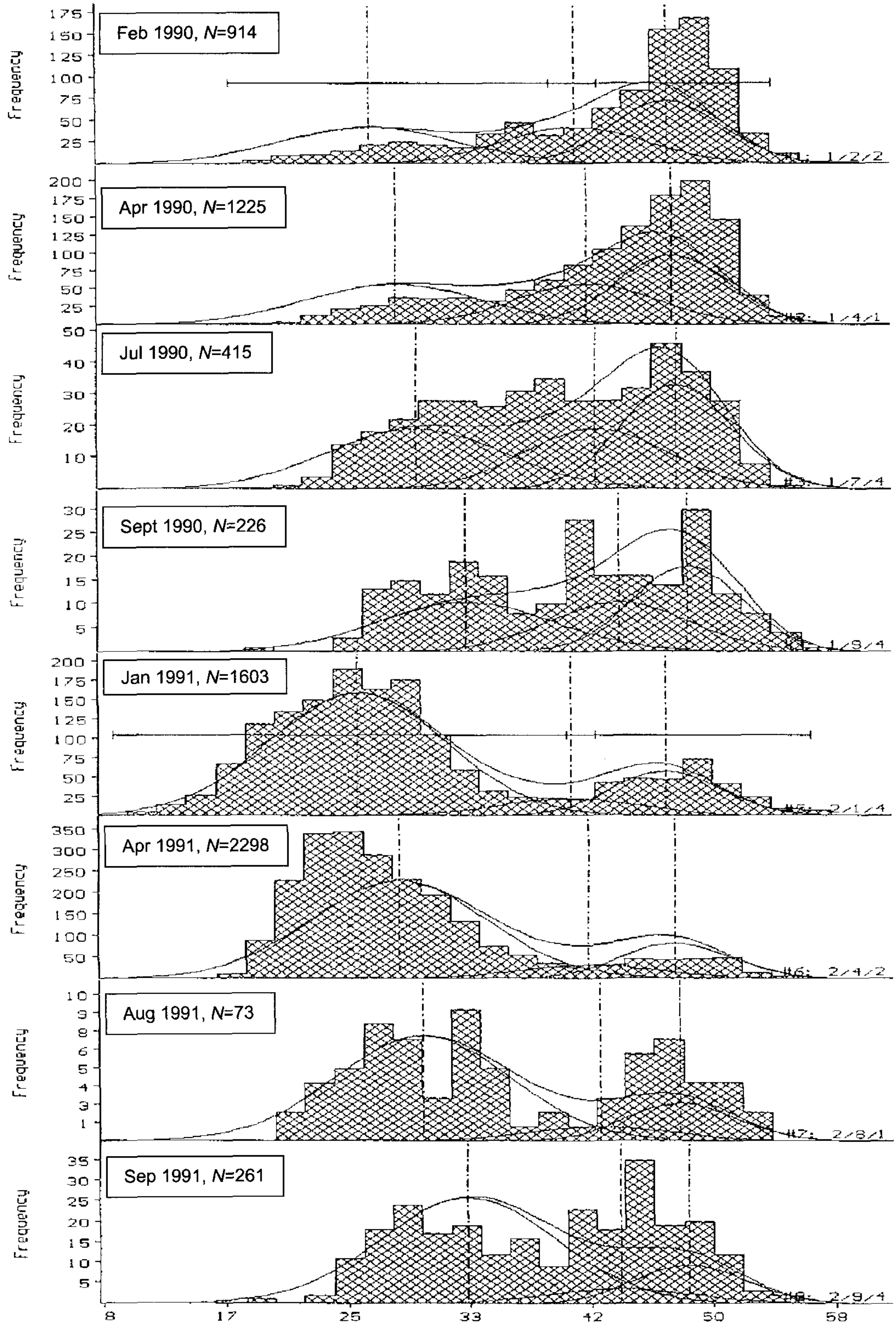
No samples were collected between the ends of September 1990 and January 1991 because of unfavourable sea conditions. Most surf clams sampled were caught in well-defined depth ranges that overlapped with other species: *P. donacina* (1–3 m); *S. aequilatera* (2–4 m); *M. murchisoni* (4–5 m); *M. discors* (3–5 m); and *D. anus* (2–5 m) overlapping with all the species. Length-frequency data from all depth strata and both sites were combined in the analysis for each species.

To estimate growth parameters, MULTIFAN requires length-frequency distributions in which it can trace clear age class modes through consecutive population samples. Surf clams grow rapidly in the first two ages of life and to estimate growth precisely, the first two age classes need to be well represented in length-frequency samples.

Juvenile age classes were generally well represented in length-frequencies of *S. aequilatera*, *M. murchisoni*, and *M. discors* (Fig. 2–4) in which they separated into clear modes that were traced through the samples. Length-frequencies of *S. aequilatera* and *M. murchisoni* had stronger juvenile age classes in 1991 than in 1990. These juveniles appeared in the January 1991 samples with modal lengths of 26 and 23 mm, respectively, as the 0+ age class progressed to 1+ in April 1991. The weak *M. murchisoni* 1+ age class in April 1990 samples was traced through the 1991 samples where it is an even weaker 2+ age class. *M. discors* had a weak 0+ age class in 1990 and 1991, and a weak 1+ age class in 1991. The 1+ age class in 1990 was traced through the 1991 samples as 2+ juveniles.

Fig. 2 Length-frequency histograms of the combined populations of *Spisula aequilatera* at the two sites on the Kapiti Coast, New Zealand. Normal curves derived from the best-fit MULTIFAN model are shown for each age class in each sample as well as the composite curve for the entire population. Vertical dash-dot lines represent mean length at age estimated by MULTIFAN and horizontal bars the extreme range of length at age to constrain the MULTIFAN model.

➤


Feb 1990, *N*=914
Apr 1990, *N*=1225
Jul 1990, *N*=415
Sept 1990, *N*=226
Jan 1991, *N*=1603
Apr 1991, *N*=2298
Aug 1991, *N*=73
Sep 1991, *N*=261
Frequency
#1: 1/2/2
#2: 1/4/1
#3: 1/7/4
#4: 1/9/4
#5: 2/1/4
#6: 2/4/2
#7: 2/8/1
#8: 2/9/4
8
17
25
33
42
50
58

Large numbers of *P. donacina* were caught in each length-frequency sample, but virtually no juveniles were caught. Length-frequency distributions from these samples represented a single mode with a modal length around 65 mm that did not progress in consecutive samples. We caught large numbers of *D. anus* and all samples had polymodal distributions, but these modes showed no systematic trend between consecutive samples. Von Bertalanffy growth parameters could not be estimated for these two species.

The von Bertalanffy growth parameters estimated by the best-fit models for *S. aequilatera*, *M. murchisoni*, and *M. discors* are shown in Table 2. Sample sizes, sampling dates, the number of age class modes that fitted the data best, and mean length at age are shown in Fig. 2–4. The von Bertalanffy growth curves with seasonal growth estimated by this model are shown in Fig. 5.

Length-at-age data were not available for any of the species and so constraints for the models were estimated from the population size structures in the length-frequency samples. The MULTIFAN model with variable standard deviation and seasonal growth gave the best fit for the *S. aequilatera* data. Three age classes were fitted to the data and the modes of length-at-age fitted the length-frequency data well (Fig. 2). The von Bertalanffy growth parameters k and L_∞ were estimated as 0.8 and 52.1 mm respectively. By age 3, most of these surf clams are close to asymptotic size and their length mode merged with a single length mode representing older age classes. Constant standard deviation and seasonal growth best-fitted the *M. murchisoni* data with six age classes fitted. The 2+ and 3+ age classes were not well represented in the length-frequency samples, but the 0+ age class that became 1+ in April 1991 showed clear progression through the samples allowing a good model fit to the data (Fig. 3). k was estimated as 0.6 and L_∞ as 72.3 mm. No length-at-age constraints were used in the analysis of the *M. discors* data as there was little structure in the length-frequency samples. The model with variable standard deviation and seasonal growth gave the best fit with eight age classes fitted (Fig. 4). Both 0+ and 1+ age classes were only apparent in the length-frequency data for 2–3 consecutive samples and although these modes were reasonably well defined, they were small compared with the length-frequency distributions of the other two species. k was estimated as 0.35 and L_∞ as 60.1 mm.

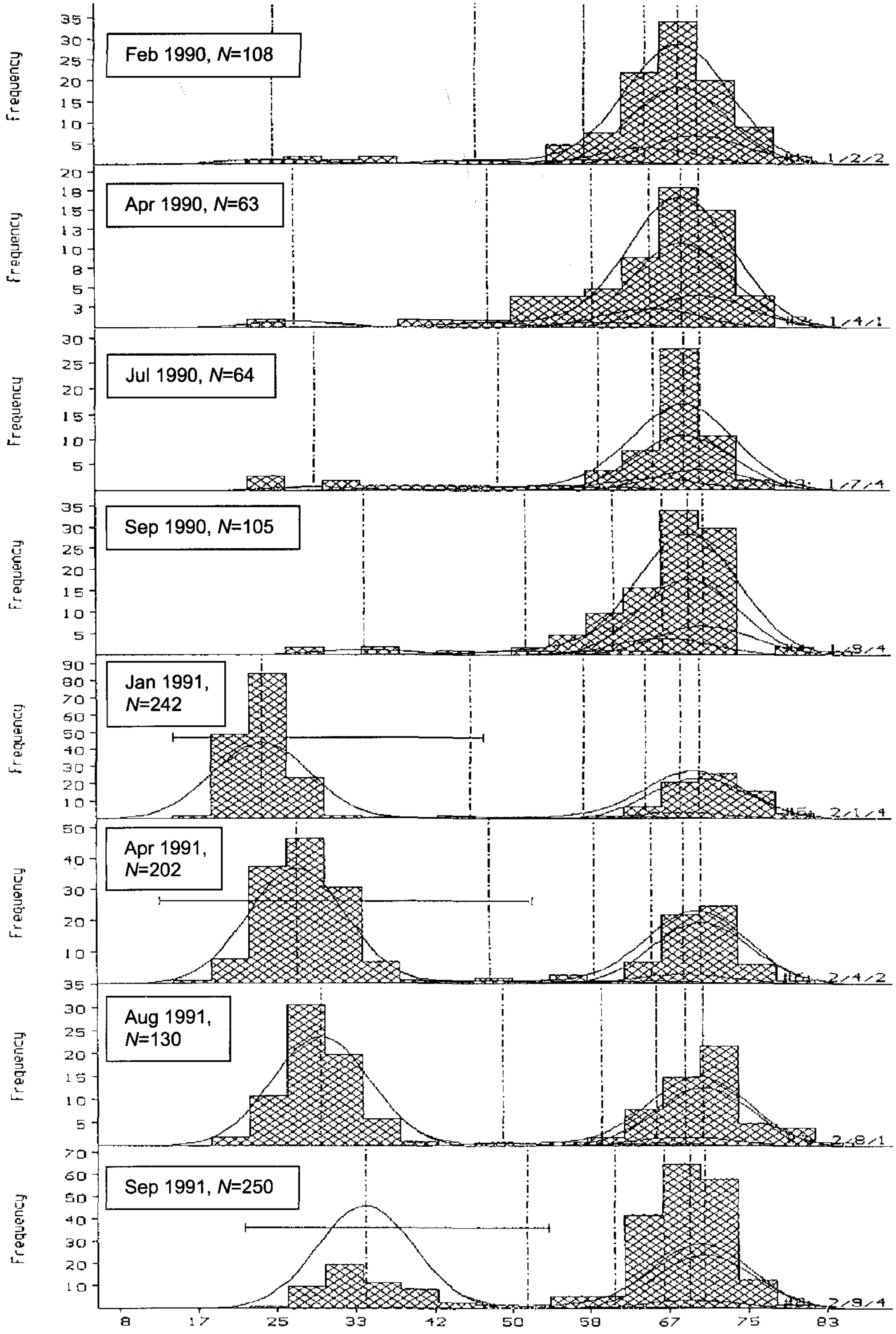
All three species showed strong seasonally oscillating growth with amplitude of 0.95 and seasonal phases between 0.7 and 0.9. As the nominal birth date was set as 1 March, most of the growth took place in late spring and summer with almost no growth during winter. The seasonal growth curves shown in Fig. 5 show the pattern of growth synchronised between species.

Growth estimates from mark-recapture data

We made 41 dredge tows through the inshore plot to recapture marked surf clams and catches of marked and unmarked clams declined by 47% and 42% respectively between the first and last tow. These tows recaptured 433 marked clams, 14% of the 3070 marked (Table 1). Seven tows in the offshore plot (400 m offshore from the inner plot) recaptured four live marked surf clams and the shells of 18 that had died *in situ*. The position of the plot was found to be deeper than planned and outside the depth that these clam species are normally most abundant. The small number of live clams recovered and small number of clams that had died *in situ* (especially when no such evidence of death was found in the inshore plot), suggested that although some had died at this deeper than normal habitat, others may have moved inshore. Four tows within 50 m of the plot found no marked clams nearby. We therefore towed the dredge 150 m along the depth contours at about 50 m intervals between the plots to see whether the marked clams from the outer plot (or inner plot) had migrated out of the plots. The greatest density (c. 4 marked clams per tow) was found half way between the two plots. A further 11 tows in this area and the nine exploratory tows recaptured 50 marked clams. It was not possible to determine which plot these clams originated from because the same method of tagging was used for both inshore and offshore plots.

The precision of growth estimates from the GROTAG model depends on the marking and recapture of adequate numbers of marked individuals spread over the entire size range of the population,

Fig. 3 Length-frequency histograms of the combined populations of *Mactra murchisoni* at the two sites on the Kapiti Coast, New Zealand. Normal curves derived from the best-fit MULTIFAN model are shown for each age class in each sample as well as the composite curve for the entire population. Vertical dash-dot lines represent mean length-at-age estimated by MULTIFAN and horizontal bars the extreme range of length at age to constrain the MULTIFAN model. ➤


Feb 1990, *N*=108
Apr 1990, *N*=63
Jul 1990, *N*=64
Sep 1990, *N*=105
Jan 1991, *N*=242
Apr 1991, *N*=202
Aug 1991, *N*=130
Sep 1991, *N*=250
Frequency
1/2/2
1/4/1
1/7/4
1/8/4
2/1/4
2/4/2
2/8/1
2/9/4
8
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33
42
50
58
67
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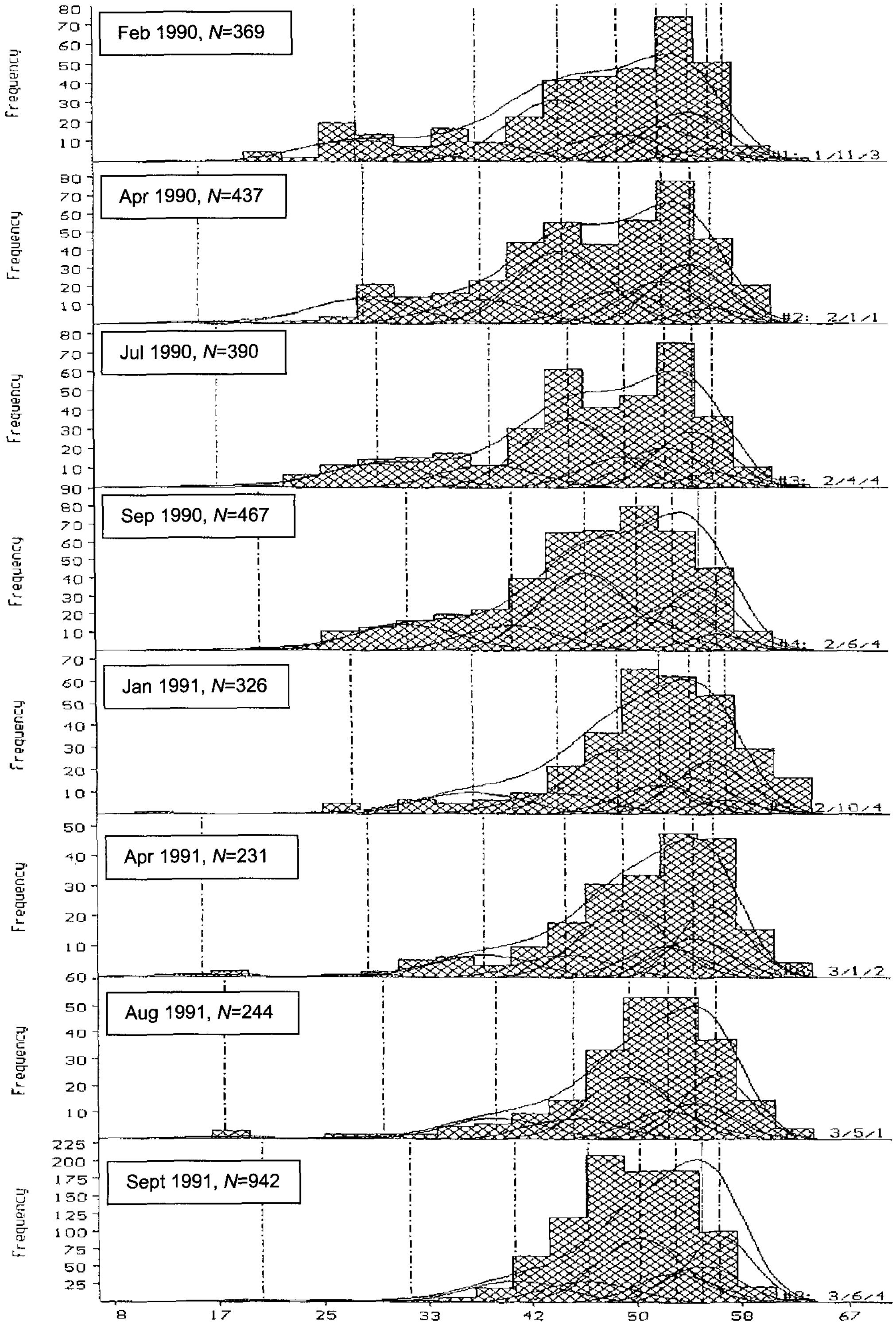
83


Feb 1990, N=369
Frequency
80
70
60
50
40
30
20
10
#1: 1/11/3
Apr 1990, N=437
Frequency
80
70
60
50
40
30
20
10
#2: 2/1/1
Jul 1990, N=390
Frequency
80
70
60
50
40
30
20
10
#3: 2/4/4
Sep 1990, N=467
Frequency
90
80
70
60
50
40
30
20
10
#4: 2/6/4
Jan 1991, N=326
Frequency
70
60
50
40
30
20
10
2/10/4
Apr 1991, N=231
Frequency
50
40
30
20
10
3/1/2
Aug 1991, N=244
Frequency
60
50
40
30
20
10
3/5/1
Sept 1991, N=942
Frequency
225
200
175
150
125
100
75
50
25
3/6/4
8
17
25
33
42
50
58
67

◄ **Fig. 4** Length-frequency histograms of the combined populations of *Mactra discors* at the two sites on the Kapiti Coast, New Zealand. Normal curves derived from the best-fit MULTIFAN model are shown for each age class in each sample as well as the composite curve for the entire population. Vertical dash-dot lines represent mean length at age estimated by MULTIFAN and horizontal bars the extreme range of length-at-age to constrain the MULTIFAN model.

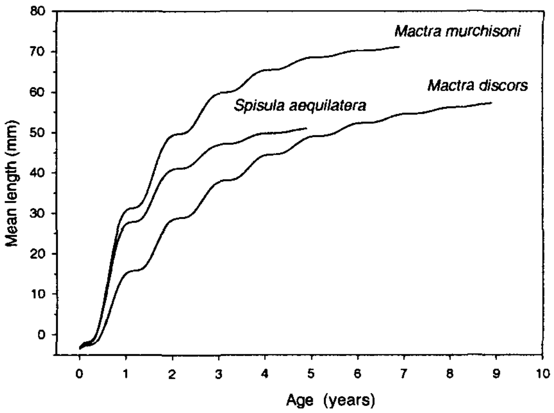


Fig. 5 Seasonal growth curves for *Spisula aequilatera*, *Mactra murchisoni*, and *M. discors* predicted from growth parameters estimated by MULTIFAN.

and preferably at liberty over a variable period. All marked clams of each species were grouped together regardless of depth of recovery to provide sufficient data to analyse with GROTAG. As all marked clams were recovered at the same time 1 year later, we could not estimate seasonal growth parameters from these data. Cranfield et al. (1996) found the error structure used in the original model (Francis 1988a) did not fit surf clam data from Cloudy Bay well. Variability in growth was not proportional to expected growth and measured growth increments could never be negative. As this was also the case with these data, growth variability, measurement bias, and the proportion of outliers (Francis 1988a) were set to zero. Residual error (*m*) was estimated (Table 3).

We recaptured large numbers of marked *P. donacina* (141) and all but two individuals were between 55 and 79 mm in length at release (Fig. 6). As this group was not representative of the size range of the population, we used model 1 to estimate annual growth in larger individuals only and omitted the two smaller individuals from the data. The mean annual growth at 58 mm (α) was 2.31 mm and at 77 mm (β) 1.97 mm.

A small number of *S. aequilatera* (15) were caught and their lengths were uniformly spread between 30 and 47 mm (Fig. 6). The size range of recaptured clams did not cover small or large individuals near asymptotic size, but they were spread well enough to estimate growth parameters using model 1 (Table 3). The mean annual growth at 30 mm (α) was 18.74 mm and at 50 mm (β) 3.50 mm. Although the sample number was small, Model 1 fitted the data well (Fig. 6).

Recaptured *M. murchisoni* (20) covered a length range of 30–79 mm, but only five individuals were smaller than 65 mm (Fig. 6). We used Model 2 to estimate growth parameters and the transitional length of each model to allow the asymptotic reduction in growth rate zero (Table 3). The mean annual growth at 30 mm (α) was 35.70 mm and at 70 mm (β and the transitional length) 2.03 mm (Fig. 6).

Similar numbers of *M. discors* (19) were recaptured. Apart from one 38 mm individual, all the

Table 2 Estimates of von Bertalanffy parameters (with standard errors) for MULTIFAN best-fit models for three surf clam species from the Kapiti Coast, New Zealand 1990–91. Age classes are the number of age classes fitted by the models; not age at asymptotic size. Amplitude and phase parameters describe seasonal growth, SD, standard deviation; c, constant; v, variable.

Species	*Spisula aequilatera*		*Mactra murchisoni*		*M. discors*	
SD	v		c		v	
Age classes	3		6		8	
k (yr^{-1})	0.80	(0.03)	0.60	(0.02)	0.35	(0.10)
L_∞ (mm)	52.1	(0.3)	72.3	(0.4)	60.1	(0.9)
t_0 (yrs)	0.2	(0.3)	0.4	(0.02)	0.3	(0.13)
Amplitude ϕ	0.95	(0.01)	0.95	(0.01)	0.95	(0.01)
Phase ϕ_2 (yr)	0.94	(0.01)	0.93	(0.02)	0.66	(0.03)
Average SD (mm)	4.90	(0.20)	5.12	(0.26)	3.61	(1.67)
Ratio SD	0.62	(0.01)	1.00		0.58	(0.08)

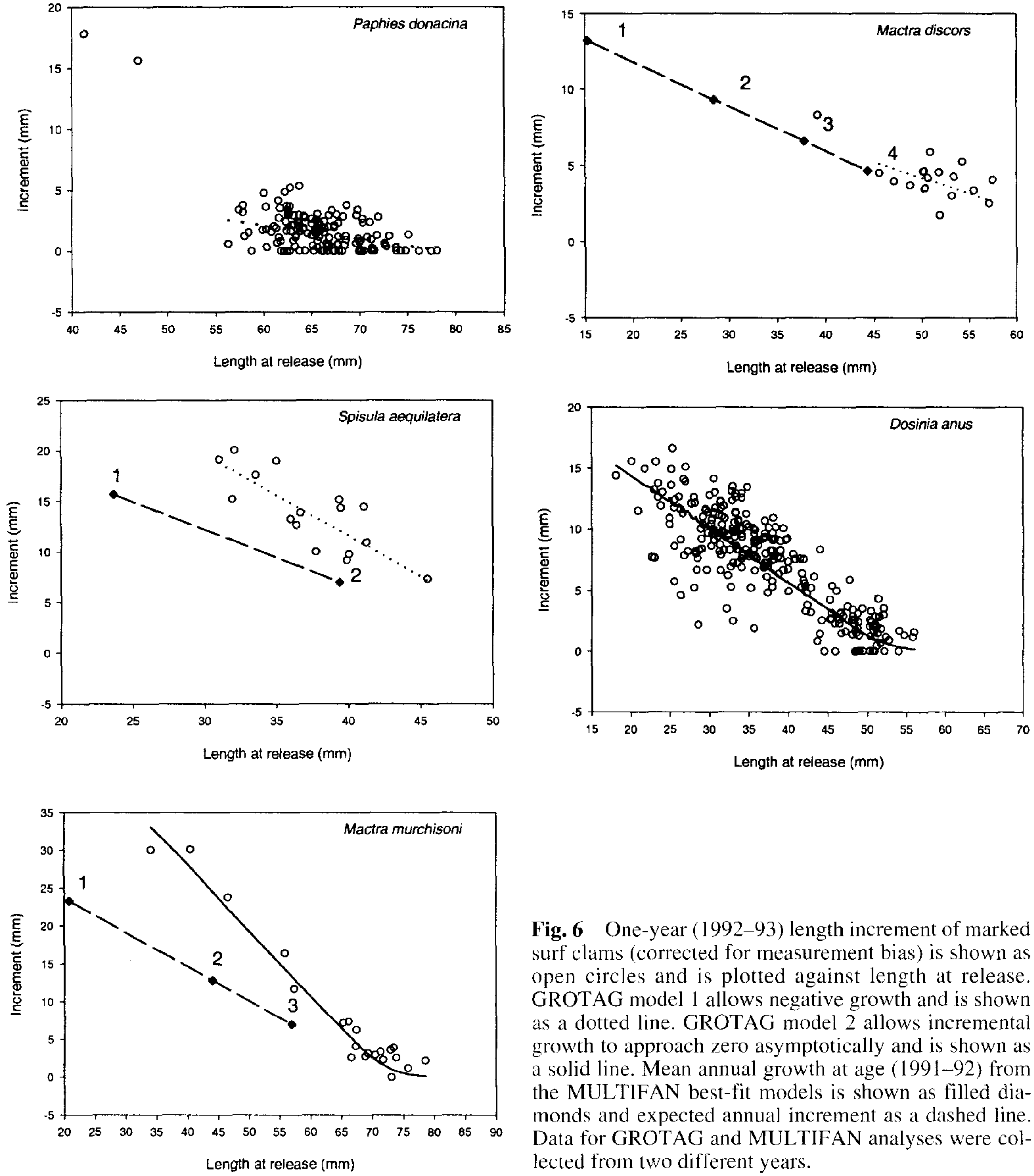


Fig. 6 One-year (1992–93) length increment of marked surf clams (corrected for measurement bias) is shown as open circles and is plotted against length at release. GROTAG model 1 allows negative growth and is shown as a dotted line. GROTAG model 2 allows incremental growth to approach zero asymptotically and is shown as a solid line. Mean annual growth at age (1991–92) from the MULTIFAN best-fit models is shown as filled diamonds and expected annual increment as a dashed line. Data for GROTAG and MULTIFAN analyses were collected from two different years.

other *M. discors* were between 45 and 57 mm in length representing the portion of the population approaching asymptotic size (Fig. 6). Model 1 was used to estimate mean annual growth at 40 mm (α) 5.27 mm and at 65 mm (β) 1.30 mm (Table 3).

Large numbers of *D. anus* (292) covering the entire length range of the population that could be sampled by the dredge were recaptured (Fig. 6). Model 2 with a transitional length (L^*) of 50 mm estimated the mean annual growth at 20 mm (α) as 13.52 mm and at 48 mm (β) 2.05 mm (Table 3).

The von Bertalanffy growth parameters *k* and L_∞ were calculated for species where the length range of recaptured clams represented a significant portion

Table 3 Growth parameters estimated by GROTAG analyses. Von Bertalanffy growth parameters k and L_∞ were calculated for species where the length range of recaptured clams represented a significant portion of the population size range. These parameters were calculated for *S. aequilatera*, *M. murchisoni*, and *D. anus* only. (CI, confidence interval; L^*, transitional length; –, no data; na, not applicable.)

Species	α (mm)	$g\alpha$ (mm yr^{-1})	95% CIs	β (mm)	$g\beta$ (mm yr^{-1})	95% CIs	L^* (mm)	L_∞ (mm)	k (mm yr^{-1})	Residual error
Paphies donacina	58	2.31	(2.16–5.00)	77	1.97	(0.19–2.0)	na	–	–	1.19
Spisula aequilatera	30	18.74	(16.4–20.8)	50	3.50	(0.9–6.0)	na	54.6	1.44	2.31
Mactra murchisoni	30	35.70	(33.2–38.0)	70	2.03	(1.2–2.6)	70	72.4	1.84	2.00
Mactra discors	40	5.27	(3.9–6.3)	65	1.30	(0.0–2.7)	na	–	–	1.25
Dosinia anus	20	13.52	(13.3–14.0)	48	2.05	(1.7–2.5)	50	53.0	0.53	2.49

of the population size range. These parameters were calculated for *S. aequilatera*, *M. murchisoni*, and *D. anus* only (Table 3).

DISCUSSION

Growth estimates from length-frequency data

Normal curves derived by the best-fit MULTIFAN models for each age class fit the length-frequency distributions for *S. aequilatera*, *M. murchisoni*, and *M. discors* well (Fig. 2–4). Estimates of L_∞ for *S. aequilatera* and *M. discors* were also well estimated, but underestimated for *M. murchisoni*. If the real value of L_∞ is higher for *M. murchisoni*, the estimate of k is likely to be lower as the von Bertalanffy parameters k and L_∞ are strongly negatively correlated.

The size selectivity of the hydraulic dredge probably under sampled 0+ and 1+ age class clams and 0+ clams were probably not retained by the dredge until the end of their first year's growth. Efficient sampling of these first two age classes by airlift or water venturi samplers may allow k to be estimated more precisely.

Variation in recruitment of surf clams

The absence of juvenile *P. donacina* in our length-frequency samples is probably due to *P. donacina* spat recruiting in the mid tide region of the beach (Cranfield & Michael pers. obs.) and then migrating offshore as they grow (Cranfield et al. 1994b). It probably does not reflect variation in recruitment or mortality of juvenile *P. donacina* in the surf zone.

The general shape and dimensions of shells of the small mactrids *S. aequilatera*, *M. murchisoni*, and *M. discors* are similar and juveniles of these species are likely to be fully selected by the dredge at the same size. The retrieval of the dredge was controlled precisely by winching it back to the vessel for 25 min at 6 m per min. Tow length was thus consistently maintained at 150 m so changes in numbers of surf clams caught between sampling periods therefore reflect real changes in relative abundance. The relative abundance of juveniles of the inshore species *S. aequilatera* and *M. murchisoni* was c. 10 times greater in 1990 than in 1989, whereas relative abundance of the more offshore species *M. discors* was greater in 1988 than in 1989 or 1990 (see Conroy et al. 1993). Relative abundance of juveniles in length-frequencies of the same species in Cloudy Bay on the north-east coast of the South Island showed the same pattern over the same period of time (Cranfield et al. 1996) and may reflect inter-annual differences in recruitment. The pattern must be the result of factors that vary over a wide scale and affect the species differently in different years. Differential predation of spat results in among-age variation in recruitment of the North American surf clam, *Spisula solidissima* (MacKenzie et al. 1985). Such predation is unlikely to be localised enough to cause the variation found among species on the Kapiti Coast, especially as the range of *S. aequilatera*, *M. murchisoni*, and *M. discors* overlaps and the centre of abundance of each species is along contours between 50 and 150 m apart (Cranfield et al. 1994b).

Variation in recruitment of individual surf clam species will probably have a marked impact on changes in population size and the dynamics of species composition over time. The rate of such changes could be reinforced by high post-settlement mortality during storms accompanied by low temperatures and salinity conditions (Eggleston & Hickman 1972; Bremner 1994), as a result of accumulation of parasites (Michael 1987) or toxic algal blooms (Chang 1998, 1999; Wear & Gardiner 2001).

Growth estimates from mark-recapture data

The low numbers of *S. aequilatera*, *M. murchisoni*, and *M. discors* recaptured in the inshore plot and low numbers of all species recaptured in the offshore plot are probably the result of these surf clams being buried outside their preferred depth range.

To estimate growth reliably with the GROTAG model, marked animals should be recaptured over a wide range of time, and increment data should cover the entire size and age range of the population. All recaptured clams in this investigation were at liberty for c. 1 year. Estimates of growth from these increment data are for clams recaptured in the period October 1992 and November 1993 only, and give no information on seasonal growth or inter-annual variability of growth. Of the species marked, large numbers of *D. anus* only were recaptured with increment data that encompassed the size range of the population. With the proviso that these data estimate growth in only 1 year, growth estimates for this species can be used in management. Increment data from recaptured *M. murchisoni* also covered the size range of the population, but the small numbers of marked clams recaptured suggests the growth estimate should be used cautiously in management. Increment data for the other three species were from a small size-range of the population and with the exception of *P. donacina*, only small numbers of individuals were recaptured. Growth estimates for *P. donacina*, *S. aequilatera*, and *M. discors* are only indicative.

Comparison of growth estimates from both methods

Age-based growth rate estimates from MULTIFAN and length-based estimates from GROTAG are not directly comparable and the data can be biased in different directions (Cranfield et al. 1996). The expected mean annual length increment for the five surf clam species estimated by MULTIFAN and GROTAG are compared graphically in (Fig. 6) following Francis (1988b).

The expected length increment for *S. aequilatera*, and *M. murchisoni* from GROTAG were greater than those estimated from MULTIFAN. Expected increments for *M. discors* by these two methods did not overlap sufficiently for comparison (Fig. 6), but appeared similar.

The MULTIFAN model estimated growth of surf clams between February 1990 and September 1991, whereas the GROTAG model estimated growth between October 1992 and November 1993. The growth estimates from neither model were good enough to establish whether inter-annual variation in growth was likely to be important.

If size selective mortality resulted in death of larger or smaller individuals preferentially, growth estimated by MULTIFAN would be biased. GROTAG estimates growth rate only from surviving surf clams and could give unbiased estimates of growth, providing individuals from the entire size range are recaptured.

Variation in growth among species

We compare relative growth rate among species from the speed, *k*, each species grows to asymptotic size, following the method recommended by Francis (1996) (Table 4). This method does not compare absolute growth rates (mm per year). Furthermore, it is not an appropriate method of comparing absolute growth rates between populations of a species unless L_∞ is the same. On the Kapiti Coast, *k* estimated from MULTIFAN showed *S. aequilatera* grew the fastest, then *M. murchisoni*, and *M. discors* was the slowest. Estimates of *k* from GROTAG showed *M. murchisoni* grew faster than *S. aequilatera*, but the estimate of *k* for *M. murchisoni* is largely driven by the incremental growth of five small individuals and is therefore likely to be high. It is much higher than the other three estimates in Table 4.

In the South Island, the five species of surf clam grew at different rates but followed the same order; *S. aequilatera* was the fastest, followed in descending order by *M. murchisoni*, *M. discors*, *D. anus*, and *P. donacina*. The interspecific differences in growth rates correlated with the mean depth of distribution of each species. *Spisula aequilatera* occurs within the primary wave break area and grows the fastest. *Mactra murchisoni*, *M. discors*, and *D. anus* occur increasingly further offshore and grow progressively more slowly. *Paphies donacina*, occurs inshore of the wave break region and grows at about the same rate as *D. anus* (Cranfield et al. 1996). Cranfield et al. (1996) discuss factors affecting the growth rates of bivalves in general and New Zealand surf clams in particular. They concluded that the most likely cause of the different growth rates of New Zealand surf clams was that individual species occur and feed within a gradient of surf diatom density. The gradient is the result of the interaction of diurnal changes in the physiology of surf diatoms and wave action that can result in low concentrations of surf diatoms of 10^2 cells ml^{-1} outside the breaker zone but high concentrations, 10^5–10^6 cells ml^{-1}, within the breaker zone (Talbot & Bate 1988; Talbot et al. 1990). The three species of surf diatoms, *Gonioceros armatus*, *Asterionella glacialis*, and *Aulacodiscus kittoni*, that occur on New Zealand beaches show regional difference in abundance (Cassie-Cooper 1996). These species have different shapes and sizes of colony (*A. kittoni* alone, remains a solitary disc) that might result in wave action concentrating each species in different parts of the surf zone and further diversifying feeding conditions for New Zealand surf clams.

Variation in growth between North Island and South Island sites

Expected increments of growth of the five species of surf clams from the Kapiti Coast and Cloudy Bay estimated from MULTIFAN and GROTAG are shown in Fig. 7. Expected increments of growth from GROTAG show no consistent pattern between locations, but MULTIFAN data show that surf clams in Cloudy Bay have a greater expected increment than the same species from the Kapiti Coast. Estimates of *k* as a measure of relative growth and L_∞ from MULTIFAN and GROTAG are compared from the Kapiti Coast and Cloudy Bay in Table 4. MULTIFAN estimates of *k* showed *S. aequilatera* and *M. discors* grew to asymptotic size faster in Cloudy Bay, while *M. murchisoni* grew at relatively similar rates. However, asymptotic sizes (L_∞) of all species were larger in the South Island (Table 4). Estimates of *k* from GROTAG for *M. murchisoni* and *D. anus* were higher from the Kapiti Coast, but asymptotic sizes (L_∞) of the species were larger in the South Island.

Length-frequency samples were collected from both locations over the same period whereas mark-recapture samples over different years, hence growth increment data from GROTAG could be confounded by inter-annual variation in growth. MULTIFAN growth increment data are therefore probably more reliable indicators of differences in growth between locations. These data show that two, of the three species whose growth can be compared, (*S. aequilatera*, *M. murchisoni*, and *M.* discors) do grow faster and that all five species reach a greater asymptotic size in the South Island (Table 4). The causes of this difference may be environmental. The generally 2–3° cooler temperatures of the South Island coastal waters (Uddstrom & Oien 1999) may delay the onset of sexual maturity of surf clams so growth rate remains more typical of juveniles for much longer. Lower temperatures in the South Island could also affect which species of surf diatoms dominate the surf zone. We have no evidence on development of sexual maturity of surf clams, nor of surf diatom composition in the South Island surf

Table 4 Estimates of von Bertalanffy parameters *k and* L_∞ for five species of surf clams on the Kapiti Coast, North Island and Cloudy Bay, South Island, New Zealand (Cranfield et al. 1996). –, no data. Note that comparisons in this table should be made between species; comparisons between data types are not appropriate (see Francis 1988a).

	P. donacina		*S. aequilatera*		*M. murchisoni*		*M. discors*		*D. anus*	
Length frequency	*k*	L_∞	*k*	L_∞	*k*	L_∞	*k*	L_∞	*k*	L_∞
Kapiti Coast	–	–	0.80	52.1	0.60	72.3	0.35	60.1	–	–
Cloudy Bay	0.33	94.1	1.01	60.3	0.57	88.0	0.41	68.0	–	–
Mark-recapture										
Kapiti Coast	–	–	1.44	54.6	1.84	72.4	–	–	0.53	53.0
Cloudy Bay	0.35	84.8	1.74	57.6	0.58	80.6	0.54	61.5	0.36	61.6

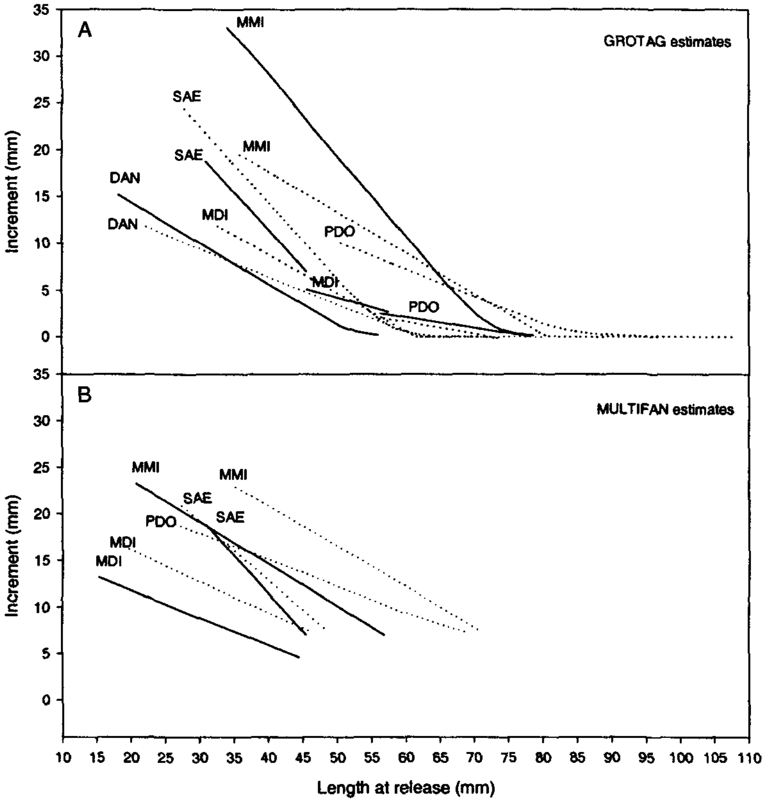


Fig. 7 Graphical comparison of growth rates estimated by, **A**, GROTAG and **B**, MULTIFAN for the five species of surf clam: *Paphies donacina* (PDO); *Spisula aequilatera* (SAE); *Mactra murchisoni* (MMI); *M. discors* (MDI); and *Dosinia anus* (DAN) on the Kapiti Coast, North Island (solid lines) and Cloudy Bay, South Island (dotted lines), New Zealand. **A** gives the expected mean annual length increment of surf clams plotted against length at release from GROTAG models. **B** gives expected mean annual growth at age from the MULTIFAN best-fit models plotted against the mean length at each age. GROTAG estimates describe growth in the size range of marked clams recaptured for the year October 1992 and November 1993, at liberty only. Caution should be used when inferring population growth parameters from these data.

zone with which to test these hypotheses. On the other hand, the differences in growth rate between populations may be genetic. Although differences in growth between populations of the North American venerid, *Mercenaria mercenaria*, have been attributed to environmental effects (e.g., Grizzle & Lutz 1989) they could also be the result of genetic effects that can be seen in the growth data of a reciprocal transfer experiment with Canadian populations of *M. mercenaria* (Landry et al. 1993). Similar differences in growth rates of different stocks of shellfish have been shown in reciprocal transfers of Scottish populations of mussels (*Mytilus edulis*) (Stirling & Okumuş 1994). Growth differences between North Island and South Island populations of New Zealand surf clams could also have a genetic basis. The Tasman Front and Subtropical Front current systems around New Zealand are likely to restrict gene flow between the North Island and South Island and within central New Zealand for marine species with larval phases. Tasman Front water flows south down the west and east coasts of the North Island in the West Auckland and East Auckland and East Cape currents, subtropical water flows north up the west and east coasts of the South Island in the Westland Current and Southland Front, and the west coast water then flows out to the east through Cook Strait (Uddstrom & Oien 1999). Genetic differences have been found between North Island and South Island populations of an inshore surf clam species, *Paphies subtriangulata* (Smith et al. 1989), which is solely harvested recreationally. Similar genetic differentiation between North Island and South Island populations has been found in the green-lipped mussel, *Perna canaliculus* (Smith 1988), and the coastal teleost, *Chrysophrys auratus* (Smith et al. 1978). Genetic variation has not been investigated in populations of any of the five species of surf clam whose growth was studied here.

Growth data from the mark-recapture experiments at both North Island and South Island sites show that individual growth is highly variable and may change with depth. Limiting growth experiments to more precise depth zones may reduce variation in growth and make among-site comparisons more meaningful.

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