SMELT (RETROPINNA RETROPINNA) POPULATION DYNAMICS AND PREDATION BY RAINBOW TROUT (SALMO GAIRDNERI) IN LAKE TAUPO

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ABSTRACT

This study examines smelt (*Retropinna retropinna*) population biology in Lake Taupo, New Zealand, and describes the development of a model which simulated their population dynamics and interactions with rainbow trout (*Salmo gairdneri*), their principal predator. The model was used to predict the effects of variation in habitat features on smelt population processes and on their consumption by trout. Implications for fisheries management are discussed.

The smelt population was comprised of three year classes. The juvenile 0+ year class occupied only the pelagic zone and fed exclusively on plankton whilst the adult 1+ year class also occupied the littoral zone and insects present there were included in their diet. A few smelt either failed to spawn at two years old or survived spawning. These grew rapidly, fed on larval bullies (*Gobiomophus cotidianus*) and spawned in late winter. Juvenile smelt reached 28-34mm FL after one year, 40-55mm FL after two years and 60-110mm FL when nearly 3 years old. Growth occurred all year but was most rapid between May and November.

Spawning commenced in October when adults first became abundant in the littoral zone and continued until April. Females often recovered and spawned a second time, 6 - 8 weeks after the first spawning. Males were sexually active for an extended period. Eggs were scattered over sandy areas along beaches in water less than 3.0m deep and in the lower reaches of tributary streams where water currents were sufficient to prevent formation of algal mats and deposition of silt or detritus. Egg mortalities were correlated with water temperature but not with their density, which reached $5000m^{-2}$ off Waihaha Beach and $40,000^{-2}$ in

the Waihora and Whanganui streams. Habitat perturbations caused by extreme weather conditions were thought to cause the most serious egg mortalities. Starvation was probably the principal source of larval mortality as there was little predation on 0+ smelt. Larger >30mm? (730mm) 1+ smelt were the most important item in the diet of rainbow trout, comprising over 80% by volume of items eaten. Trout tended to select the larger smelt available and the intensity of selection was correlated with measures of smelt abundance. Trout generally gathered in places where 1+ smelt densities were high.

Smelt population dynamics were simulated using length and density dependent models for movements between habitat zones, feeding, growth or starvation, breeding and predatory mortality. The form of simulated length frequency distributions largely determined the rates of these processes and was itself modified by the operation of each process. Modal groups occurred at lengths where food intake was equivalent to metabolic maintenance requirements and this was controlled by the interaction of diet breadth, the size structure and quantity of the food resource and the number of fishes sharing the same food particle size range. Growth of modal groups was controlled both by the duration of the spawning season and by seasonality in food resource quantity and size structure. Pelagic productivity and the ratio of littoral to pelagic habitat area were the most influential habitat features controlling smelt densities while densities of medium sized (30-55mm) smelt and water clarity were the most important factors controlling simulated quantities of smelt eaten by individual trout. Trout predation exerted little influence on simulated smelt population dynamics and consequently, the quantity eaten by individual trout was little affected by trout density. This result and comparison with trout stocking rates used in Canada suggest that a 1 - 2 order of magnitude increase in numbers of trout released annually into the larger Rotorua lakes would not significantly reduce their growth rates.

To Gloria

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I am particularly grateful for the encouragement, advice and helpful criticism given by my supervisors, Dr. Ann Chapman and Dr. John Green. I am indebted to the staff of the Wildlife Service, Department of Internal Affairs, who supported the project, giving help in the field and making facilities available for my use. Special recognition is given to Mr. Pat Burstall who initiated the project and to Mr. Dave Stack who arranged logistic support and whose continued committment ensured that the project reached this stage of development. Mr. Keith Hawkins and Mr. Rob McLay assisted with collection of smelt egg and nocturnal tow samples. Mr John Gibbs helped in the field work associated with estimating net avoidance and the prototype dropnet was developed by Dr. Peter Mylechreest. Mr. Trevor Thompson and Mr. Ken Short maintained communications and essential supplies for the field station, often in spite of particularly hostile weather. Special thanks are given to the anglers, whose help with sample collections and continued interest in the project is appreciated. Mr. Charles Sitwell and Mr. Bruce Davidson assisted in writing the computer programme and Mrs. Gaylene Quinton typed this thesis.

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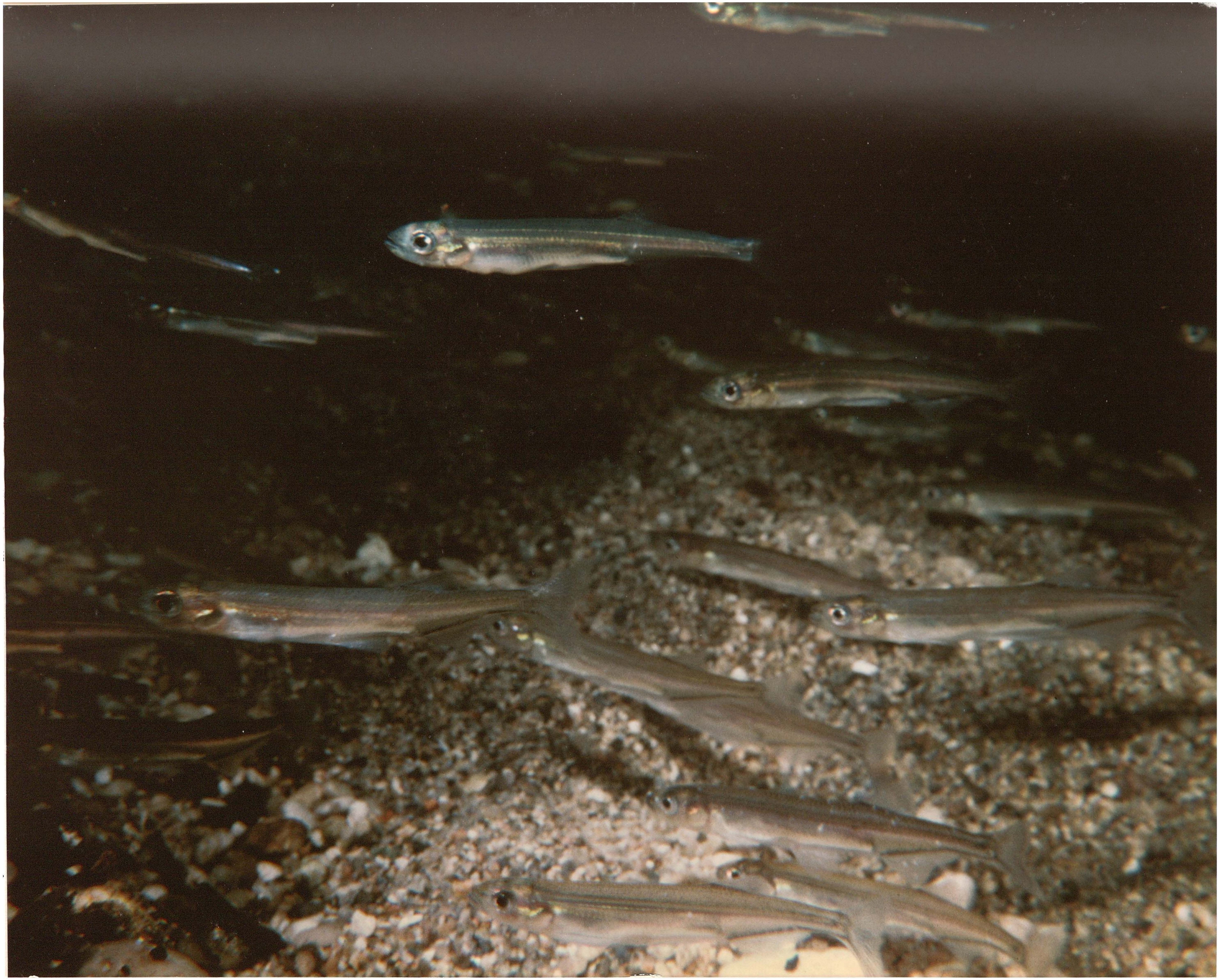
FRONTISPIECE

Ripe and part spent smelt in the Waihaha stream mouth.



CHAPTER 1 - INTRODUCTION

1. Trout and forage fish management in North Island lakes

New Zealand sportsfish management commenced on a trial and error basis when brown trout (*Salmo trutta*) and rainbow trout (*Salmo gairdneri*) were liberated in North Island lakes between 1883 and 1931 where indigenous forage fish species were koaro (*Galaxias brevipinnis*) and the common bully (*Gobiomorphus cotidianus*). The trout flourished, reaching exceptional sizes around the turn of the century but the koaro populations were decimated by rainbow trout predation (Phillipps 1924; McDowall 1978) and in the following five years, or thereabouts, the size and quality of the trout deteriorated dramatically (Burstall 1983). In response, the Tourist Department employed a man full time between 1906 and 1909 at Mercer, on the Waikato River, to catch small fishes for release in the Rotorua district to supplement available forage. These small fishes would have included anadromous smelt (*Retropinna retropinna*), bullies and may have included the galaxids *G. maculatus* and *G. fasciatus* as well as other species such as eels, mullet and the shrimps *Tenagomysis chiltoni* and *Paratya curvirostris* which would have been present amongst collections of small fishes if the fauna of the lower Waikato was similar to that found at present. However only the smelt and bullies became established in the Rotorua district. Phillipps (1926) recorded smelt from the Ohau Channel (the outlet to Lake Rotorua flowing into Lake Rotoiti) and it seems that a lake limited smelt population was firmly established by the early 1920's. However these fish were notably absent from the trout diet during 1918-19 when koaro and bullies were the most important forage species in these and other central North Island lakes (Phillipps 1924).

Little is known of smelt population dynamics, controlling environmental influences or the nature of the trout-smelt predator-prey relationship. Consequently fisheries management policy decisions regarding choice of management objectives, trout stocking, environmental protection or water use proposals cannot give full consideration to possible effects on smelt, the trout-smelt relationship and consequent ramifications for the fishery. It is suspected that current stocking practices make suboptimal use of available forage; concerns regarding habitat protection have been expressed and the consequences of further exotic fish liberations are periodically debated. Thus techniques for predictive assessment of forage management options and the information on which this could be based are required.

(a) Developments in forage fish management

Enhancement of production by predatory sportsfish has consisted largely of exotic fish introductions, either of predators to exploit resident forage or of prey to increase the supply of forage. This has been a haphazard trial and error process fraught with unforseen mistakes (as in examples described by Magnuson 1976) because techniques for predictive assessment of the direction and amount of change in population characteristics of resident species based on the interaction of major components of predator-prey population processes were not available. This approach is currently being developed and used as a basis for forage fish management policy in North America. In New Zealand this approach awaits development for application to the management of the major North Island rainbow trout fisheries where smelt are the principal forage species.

Swingle (1940, 1950, 1956; summarised and discussed by Hackney 1979) first demonstrated that there were complex interactions between forage fish growth, reproduction, survival and predator production which could be manipulated in pursuit of management objectives. Weatherly (1972) explored dynamic relationships between these population processes and considered growth to be of central importance in fish predator-prey systems. However, whilst he acknowledged the importance of competition for food, this was not considered in his simulations. Subsequent studies of fish growth have often demonstrated density dependence (e.g. Staples 1975; Craig et al. 1979) and this is generally recognised in the most sophisticated simulations of fish population dynamics. Fisheries managers have been aware of this and have attempted to control sportsfish growth by manipulating their population densities. However their management practices have been based on subjective considerations and experience, not on a knowledge of forage population dynamics. Optimum stocking rates designed to sustain maximum growth or, alternatively, to offer maximum catch rates might be achieved by an experimental trial and error approach but this offers little guidance in choosing suitable stocking practices in other systems. Techniques for predictive assessment based on the lake's productivity, morphometry, species composition and their interactions would seem potentially most useful.

Li and Moyle (1981) used loop analysis to predict the stability of systems following species introductions but this approach seems too general to be useful in assessing the consequences of less drastic management options. Stewart et al. (1981) used bioenergetic modelling simulations of alewife consumption by stocked salmonids in Lake Michigan but they failed to consider shifts in alewife population dynamics in response to increased stocking rates as they dealt with the prey side of the predator-prey system only in very general terms. Walters et al. (1980) developed a model simulating the dynamics of lake trout populations in Lake Superior in response to fishing and predation by lampreys. Considerable attention was paid to the dynamic interactions of lake trout and lampreys through models simulating density dependent and size selective predation but the lake trout forage species were treated as a fixed resource shared across trout year classes. Such treatment implies that interspecific competition is equally distributed throughout the population and that all population groups share the same prey resource. Nevertheless, Weatherly's (1972) and Walters' (1980) approach using interconnected models for growth, reproduction, survival and distribution seem to offer most potential for prediction of population characteristics under a variety of circumstances because the models for these processes are based on the functional components of the system (Holling 1966; Wright and O'Brien 1984) as opposed to descriptive correlation with observed (and possibly irrelevant) features of the system. Larkin (1979) pointed out that whilst multivariate analysis of time series records of predators, prey and their physical environment can provide descriptively satisfying results, this statistical approach may be useless for predictive purposes.

The accuracy of prediction using the functional components of the system depends on successful recognition and description of the key features and the operation of each component process. Verbal expression of system components and their interaction might offer useful qualitative predictions of changes in certain characteristics of the system but one cannot demonstrate whether the system is in fact understood in sufficient detail to predict quantitative changes in the behaviour of the system. This becomes possible when the functional relationships are expressed numerically because the results of system component interactions can be compared with analogous descriptive data for real systems. The numerical approach provides a precise statement of the author's perception of the system's structure and function so that the basis for predictions can be scrutinized to an extent which a verbal description will not allow. Furthermore, as more detail and understanding of components becomes available, the numerical expression can be updated and revised accordingly.

The first step in this approach to predictive assessment of management options is to describe the population processes for the species under consideration and to identify factors which influence these processes. Secondly, a series of interconnected numerical models based on the interaction between these influential factors and the population processes must be designed to simulate observed population characteristics. Finally the model will need to be fine tuned so that input data describing a particular system gives results similar to those observed for the fish population in that lake. This fine tuning violates generally accepted rules of model building and statistics but is nevertheless essential if the fisheries manager is to be persuaded that the model really captures the way the system works (Hilbourn et al. 1984). The consequences of certain management options can then be assessed by comparing outputs obtained before and after alteration of the habitat variable (e.g. trout stocking rate, limnetic productivity, spawning habitat enhancement etc) for which manipulation in pursuit of management objectives is contemplated.

Thus in this study, smelt movements, growth, reproduction and sources of mortality in Lake Taupo are described and factors influencing these examined. A conceptual simulation model based on the functional components of each population process is developed and fitted to features of Lake Taupo, the smelt population and its interactions with trout. The model is designed to simulate smelt population dynamics, trout feeding and movements in different lakes and is used to explore possible relationships between smelt population features, trout predation and environmental characteristics of lakes. Finally, factors controlling smelt population dynamics, trout predation on smelt and implications for management are discussed.

2. Lake Taupo

Lake Taupo (fig. 1) is suitable for a study of forage fish population dynamics and interactions with trout because it has a high smelt and trout population density (as indexed by angler catch rates) and so one would expect trout-smelt interactions to be readily detected. There is some background research: Jolly (1963, 1967) and Stephens (1983) have described smelt biology in Lake Taupo, and seasonal patterns in zooplankton (Jolly 1965, Forsyth and McCallum 1980), macroinvertebrates (Forsyth and McCallum 1981), water chemistry, phytoplankton (White et al. 1980; Vincent 1983) and nutrient loading (White and Downes 1977) have been examined. However there is no published information on rainbow trout biology in Lake Taupo.

Lake Taupo has not suffered any major biological perturbation since the introduction of smelt, and agricultural, forestry and hydro-electric developments have probably caused only a minor increase in the lake's productivity. Compared with other North Island lake fisheries, it seems relatively stable and predictable in its characteristics (Fish 1968).

The lake basin was formed by volcanic eruptions and subsidence between 300,000 and one million years ago (Suggate et al. 1978; Timperly 1983). The catchment (now 1300km^2) has recently been extended to include parts of the headwaters of the Rangitikei, Whangaehu and Wanganui rivers which lie to the south to increase the system's capacity for hydro-electric power generation. About half the water entering the lake does so at the southern end together with large quantities of sediment carried by the Tongariro river from the eroding slopes of the volcanoes to the south. The soils are recently derived from rhyolite pumice, soluble phosphorus concentrations in groundwater and springs are high and nitrogen is the limiting plant nutrient during summer stratification (White et al. 1980). Maximum phytoplankton biomass occurs in late winter when surface temperatures are 10-11°C (fig. 2) and Secchi disc readings may drop from ca. 18 to 10-12 metres at this time of year (Jolly 1968). Maximum crustacean zooplankton biomass occurs during early spring (Forsyth and McCallum 1980).

The shoreline is characterised by either cliffs (ca. 25% of shoreline) or the beaches which predominate along the eastern shore. Associated with these beaches are shallow benches below the wave zone ending in a steep slope down to the relatively flat bottom where mean and maximum depths are 110m and 165m respectively (Irwin 1972). Macrophytes colonise the less exposed beaches (ca. 37% of shoreline) but beds are not extensive except at the southern end of the lake (Howard-Williams 1983).

The water level has been controlled by gates at the outlet on the Waikato river since 1941. The lake level is manipulated for water storage and according to the demands of eight hydro-electric power stations down the Waikato river. The maximum extent of the drawdown zone is typically 1 to 1.5m but there is no statutory lower limit. However, lake level fluctuations in excess of 8cm per week are most unusual.

Smelt liberations from Lake Rotorua into Lake Taupo commenced with 10,000 fish in 1934, followed by 25,000 in 1935, 41,000 in 1936, 110,000 in 1938 and 70,000 in 1939 - some 45,000 in this final release coming from Lake Tarawera (Burstall 1983). The mean weight of rainbow trout caught by anglers (fig. 3) had declined dramatically prior to the introduction of smelt but between 1940 and 1948 a small increase was apparent. This decline continued for another decade before the mean weight stabilised at about 1.5kg. However, the extent of this latter decline is exaggerated because, prior to about 1950, angling was directed mainly at adult trout on their spawning run in the lake tributaries whereas latterly more trout have been taken trolling on the lake and smaller immature trout comprise a greater proportion of the catch.

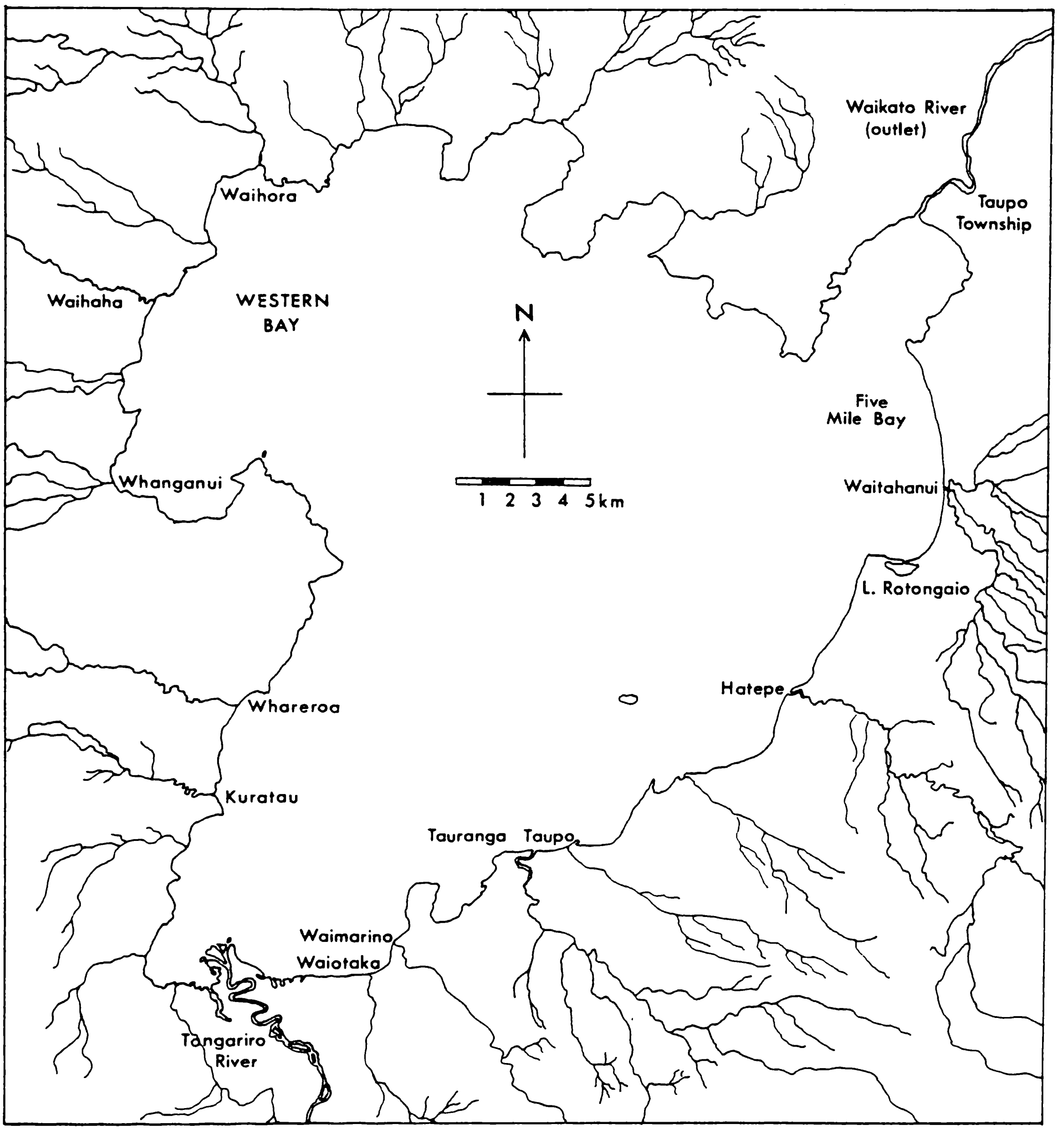


FIG. 1 Lake Taupo map showing major tributaries and place names mentioned in the text. Place names generally correspond to the name of the tributary entering the lake at that locality.

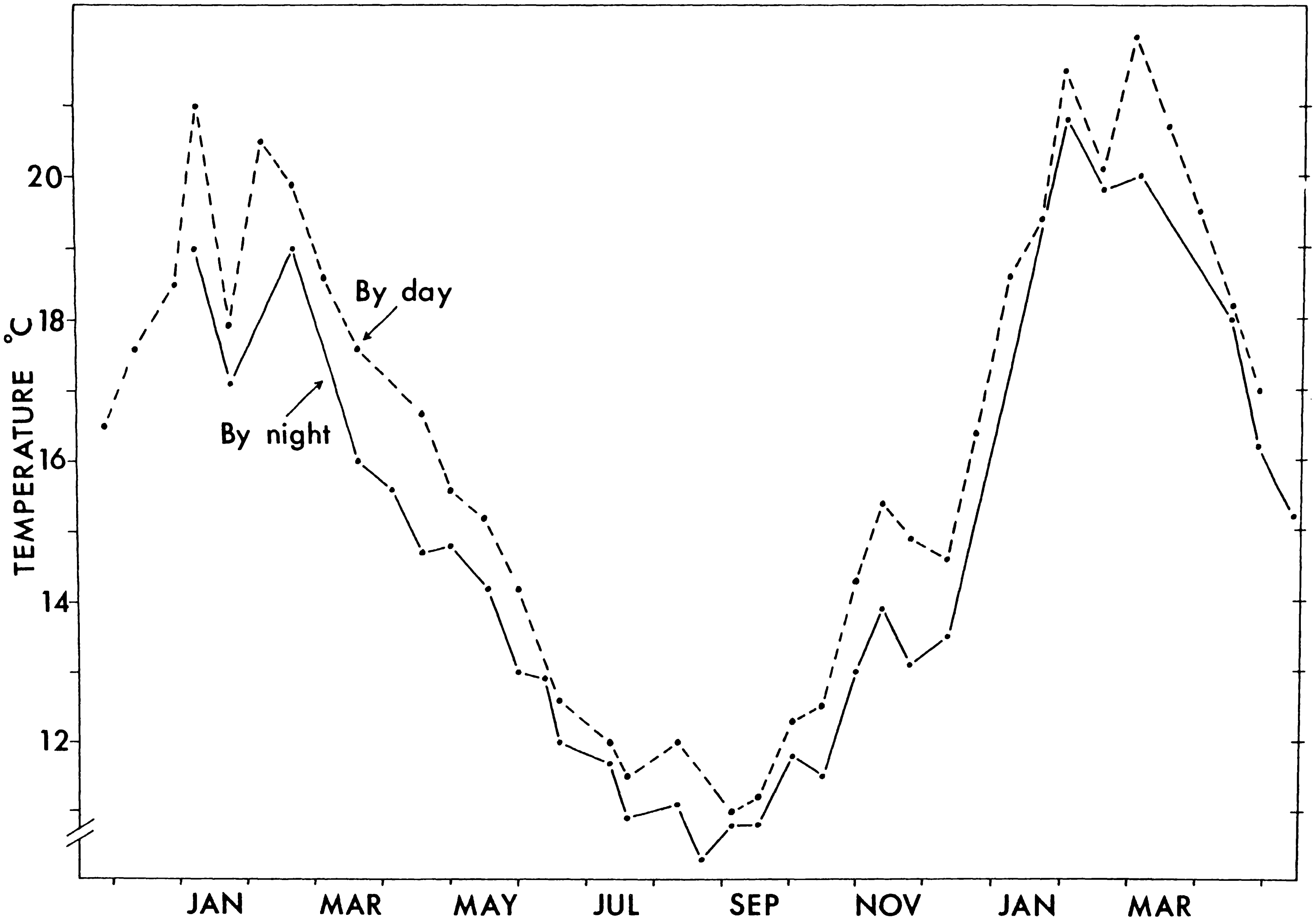


FIG. 2 Day and night surface temperatures at Waihaha Beach between December 1979 and April 1981.

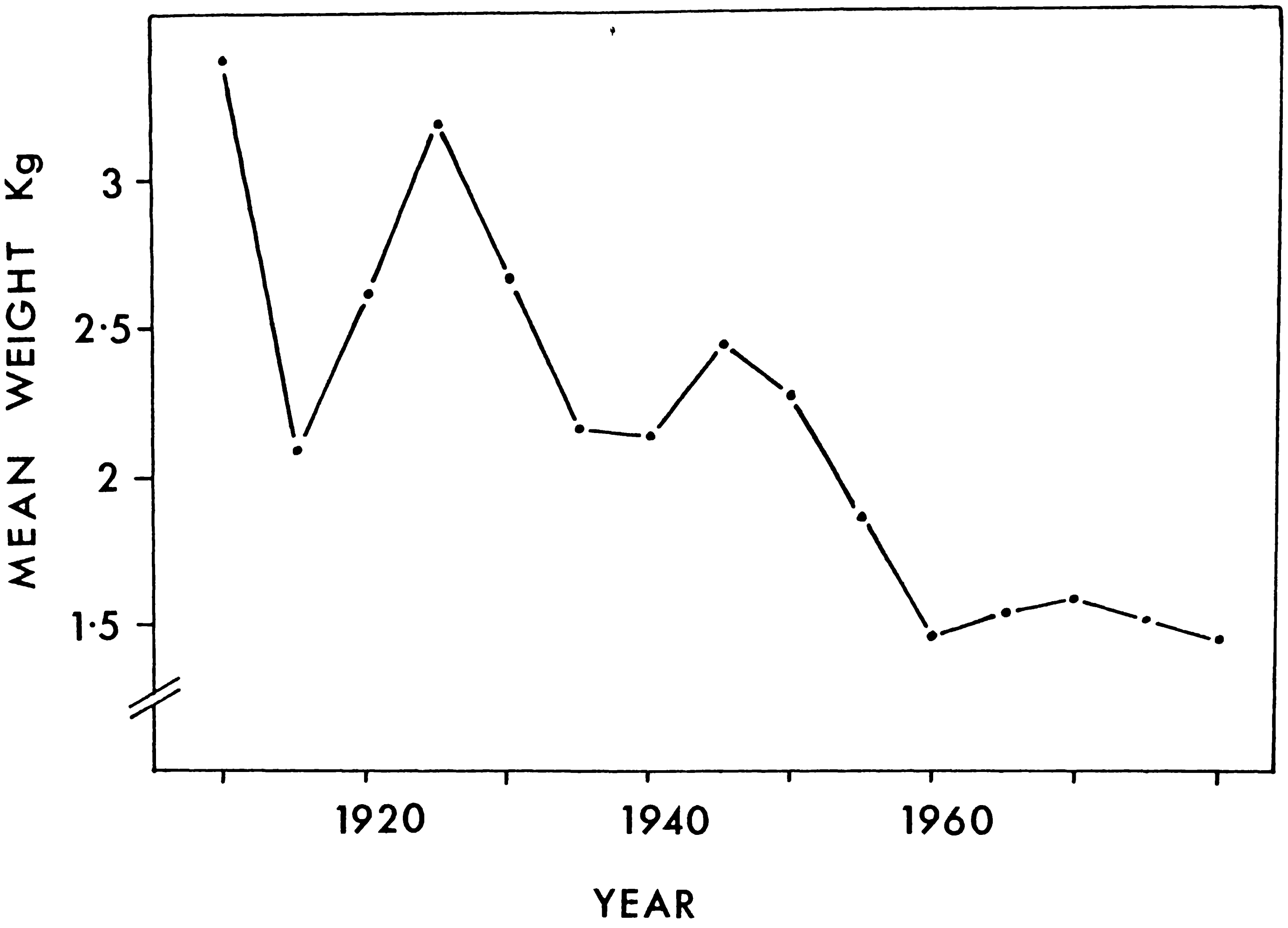


FIG.3 Mean weights, during five year intervals, of Taupo rainbow trout caught by anglers (Burstall 1983).

(a) Study area

The field base was at Waihaha in the Western Bay and so, for logistic reasons, routine sampling was confined to the Whanganui, Waihaha and Waihora bays although samples were also collected at intervals for comparative purposes at all localities shown in fig. 1.

The Western Bay area (fig. 4) is characterised by steep cliffs broken by relatively short beaches where major tributary streams enter the lake. The cliffs are as steep below the water as they are above (fig. 7) and littoral habitat is minimal. However each beach has a shallow bench below the wave zone extending 100m from the shore at Whanganui and to 350m offshore at Waihaha and Waihora. The streams are relatively stable, being predominantly spring fed with extensive areas of native forest or secondary scrub throughout their catchments which are broken by relatively small areas developed for pastoral grazing. The streams all have waterfalls a short distance upstream and these restrict further upstream migration of spawning trout. The Waihaha stream is the largest of the three major Western Bay tributaries (mean annual discharge $5.5m^3s^{-1}$) , the Whanganui the smallest ($1.2m^3s^{-1}$) and the Waihora ($1.9m^3s^{-1}$) the most stable with maximum peak flows being only $2.3m^3s^{-1}$ (Schouten et al.1981). Temperatures ranged from 9° to 16°C and the Waihora was slightly warmer than the Whanganui stream (fig. 6). The lower reaches of each stream are slow flowing ($0.1 - 0.3ms^{-1}$) with pumice and sand substrates and dense vegetation on the banks except over the lower 100-200m which are separated from the lake by sand bars formed by wave action. This zone was an important breeding area for smelt and regular collections of eggs and spawning adults were obtained from these portions of the Waihora and Whanganui streams. The site of the Waihaha stream mouth was quite changeable, being located near the willows (top left fig. 7) at the start of the project and returning there by early 1983, and so was considered unsuitable for routine monitoring of smelt spawning.

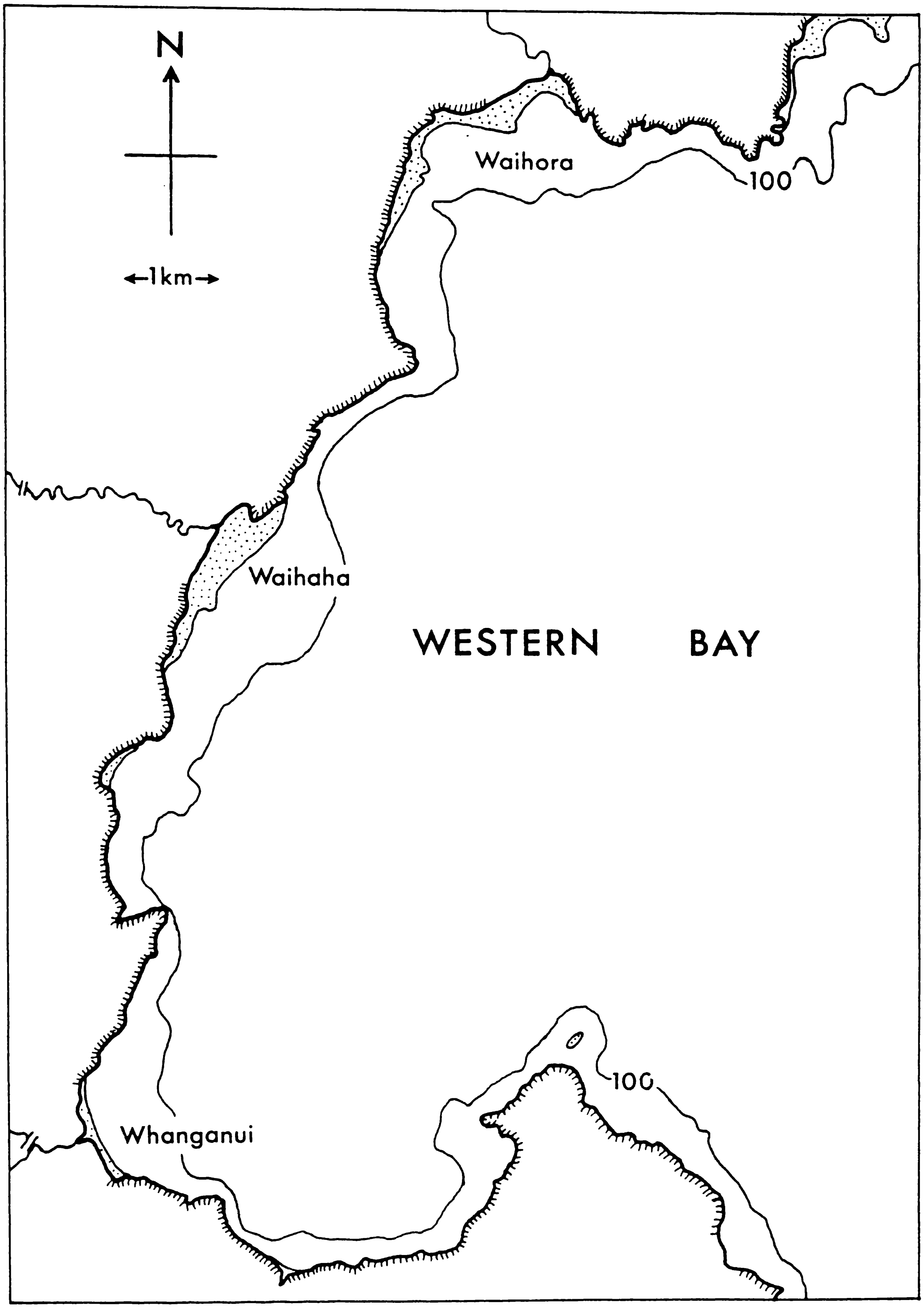


FIG. 4 The Westem Bay of Lake Taupo showing cliffs, beaches, areas less than 10m deep and the 100m isobath (from Irwin 1972).

FIG. 5

The Whanganui (above) and Waihora stream mouths.

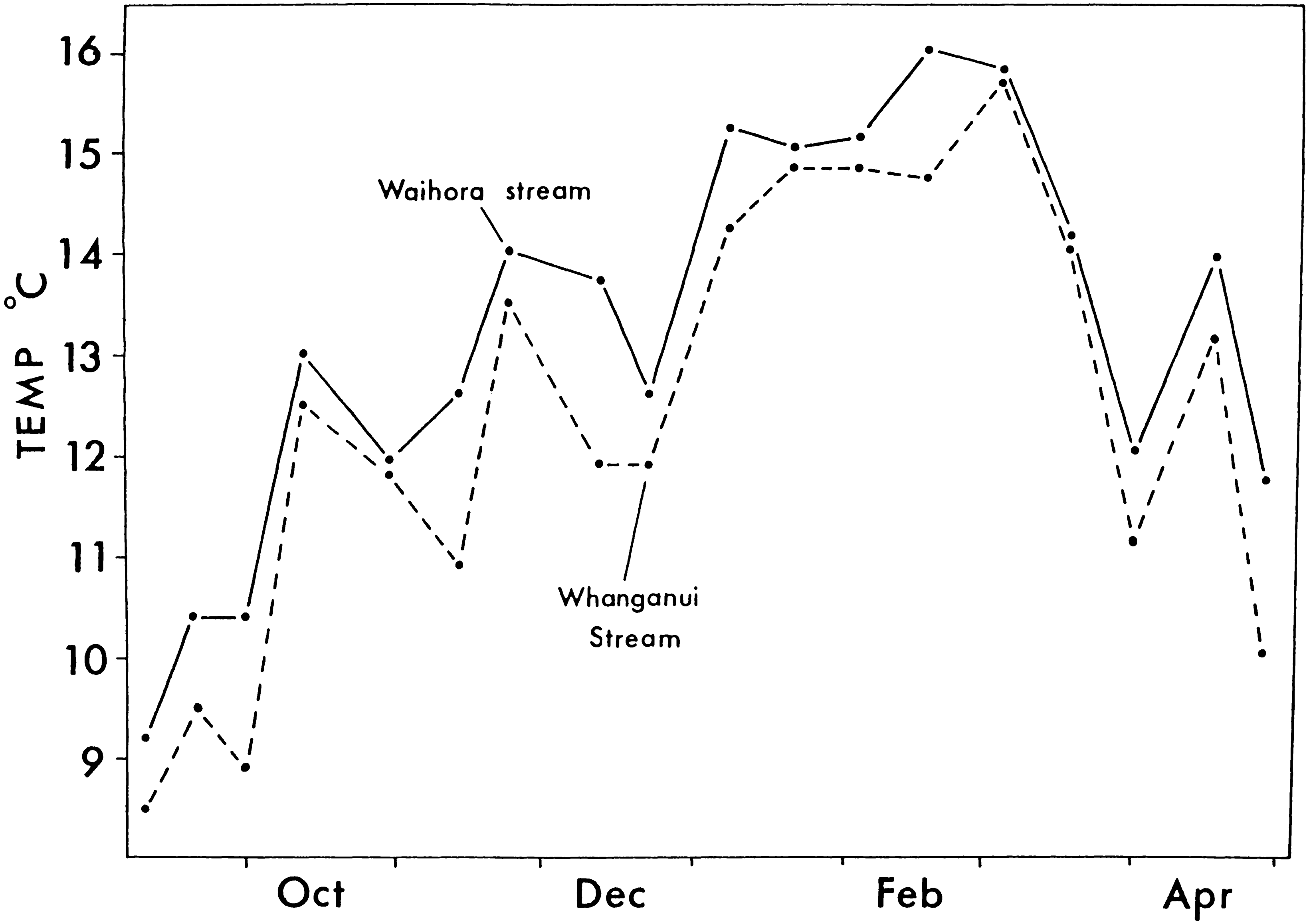


FIG. 6 Water temperatures in the Waihora and Whanganui streams between September 1980 and April 1981.

FIG. 7

ABOVE: Waihaha Beach littoral shelf and surrounding cliffs.

BELOW: Waihaha stream mouth. The location of the stream mouth was changeable, being near the willows (top left) at the start of the project and returning there by early 1983.

PART ONE

FIELD STUDIES

CHAPTER 2 - MATERIALS AND METHODS

(a) Littoral and stream smelt samples

A 2.0mm mesh 8.0m x 0.9m seine net with a heavy basal chain was used to collect smelt from streams and beaches around the lake. Routine beach samples were collected at Waihaha Beach fortnightly between September 1979 and August 1981 but monthly thereafter until January 1982. On each occasion separate samples were taken by day and night. Additionally,on alternate months between September 1979 and November 1980, collections were made every four hours over a 24 hour diurnal cycle.These samples were intended to provide data on the length frequency distribution and abundance of smelt in the littoral zone. Comparison of length distributions of smelt taken during the diurnal sampling session of 19 & 20 September 1979 (see table below) indicated that there was significant variation in mean length ($F = 36.5$; $p \ll 0.001$) and in the size range of smelt caught by day and by night. It was therefore considered necessary to collect seine samples both by day and by night and to undertake regular diurnal sampling sessions to ensure that all sections of the smelt population which enter shoreline areas were represented in the samples collected.

Diurnal variation in the length distributions of smelt from four beach seine samples collected between noon on 19/9/79 and 1000 hrs on 20/9/79.

Collection time	Sample size	Mean Length (mm)	Standard deviation (mm)	Length range (mm)
19/9/79 at 1200 hrs	114	43.8	1.99	39 to 51
19/9/79 at 2000 hrs	62	48.5	5.49	40 to 82
20/9/79 at 0800 hrs	96	43.1	2.92	35 to 50
20/9/79 at 1000 hrs	72	43.5	3.32	35 to 50

A standard procedure was used to estimate fish densities. One end of the net was held 1.0m from the lake edge while the remainder was first hauled parallel to the beach until fully extended and then dragged in an almost semicircular arc until the whole net was brought up onto the beach; about 85m^2 of the littoral zone was effectively fished. This procedure was repeated until 200-500 smelt were caught. If the catch was more than about 2,000 smelt an appropriate proportion was taken and the others released. On the few occasions where this was necessary, smelt density data were based on estimates, made by eye, of the proportion retained.

Smelt tend to travel in shoals and consequently there is considerable variation in the number caught in replicate seine hauls (see table below).

Variation in the numbers of smelt caught in replicate samples taken at different times of the day and night.

	Number of samples	Mean number caught	Range	Standard error	SE as % of mean
Daytime samples					
27 & 28/11/79	5	185.6	36 to 400	63.4	34.2
23 & 24/1/80	4	1127.7	700 to 1663	283.2	25.1
20 & 21/3/80	3	1487.8	725 to 2784	478.6	32.2
30 & 31/5/80	4	284.3	4 to 503	112.4	39.5
Nocturnal samples					
27 & 28/11/79	3	53.3	12 to 95	24.0	45.0
23 & 24/1/80	3	22.8	3 to 54	15.8	69.3
20 & 21/3/80	3	10.3	6 to 15	2.6	25.2
30 & 31/5/80	3	2.7	1 to 5	2.1	77.8

Variation in the number of smelt caught in replicate samples taken by night was greater than variation in samples taken by day and the variances were proportional to the mean number caught, so that maximum variation in catches occurred when smelt were particularly abundant.

When smelt were particularly scarce a similarly constructed 15m x 2.0m seine net was set by boat about 100m offshore, generally by night, and hauled ashore using ropes attached at either end. These samples were used principally to obtain length frequency data. Smelt density estimates were based only on catches taken in the smaller net.

Smelt were collected monthly from the Waihora and Whanganui stream mouths between October 1980 and April 1981. Bi-monthly samples were taken from all major tributary streams named in fig. 2 between October 1981 and March 1982. These were not quantitative samples. The catch was usually first anaethetized in 5% urethane and always preserved intially in 10% neutralized buffered formalin and later, after washing and sorting, in 1% neutralized buffered formalin.

All smelt were measured and their reproductive status recorded. However they could only be sexed externally when mature. Males were recognised by their enlarged pelvic fins, prolific nuptial tubercles and relatively large head. Females were considered ripe when an enlarged ovary was clearly visible through the abdominal wall. Thus three categories were used: ripe males, ripe females and non-reproductive smelt. Morphological characteristics of juveniles, immature adults and spent fish overlapped somewhat and so it was not possible to confidently categorise them on the basis of external appearances.

(b) Pelagic smelt

Pelagic smelt were collected semi-quantitatively by dropnetting during the day and from ringnet tows samples collected by night. Modifications of a standard net were used in both methods. The net (fig. 8) consisted of a cylinder and truncated cone of 0.65m mesh aperture size attached to a canvas cylinder fastened to a heavy steel ring at the net mouth. As a dropnet there was a running throttle line spliced to the steel ring at the net mouth and this was threaded through about 20 "D" rings spaced around the circumference of the canvas in an elliptical fashion. The net fished from the lake surface as it descended until the throttle line was held fast; the weight of the steel ring then caused the throttle line to be drawn tight closing the net. Descent speed was 0.6m.s^{-1}.

The net was modified for towing by removal of the throttle line and attaching a bridle to the steel ring. This was most effective when towed by night at about 2.0m.s^{-1}on 100m of rope so the net fished at 10-25m depth. After a specified towing period the net was retrieved by hand but with the boat still under power to minimize escapement. The catch was preserved in 10% neutralized buffered formalin and fish lengths and reproductive status were subsequently recorded.

A series of trial drops (Table 1) indicated that at least 10 drops to 100 metres would be required to ensure that 95% confidence limits of any mean density estimate would be within ±50% of that estimate. This was not feasible without the aid of a winch. The absence in samples of larger smelt (35-40mm) which could be observed by night in open surface waters using a 100 watt spotlight, suggest that escapement was reducing the size range and number caught dropnetting. Comparison of catch frequency data from ten drops to 40, 60 and 100 metres and a 15 minute nocturnal tow (fig. 9) suggested that larger smelt, probably shoaling between 40 and 60m, were escaping whilst the net fished to 100m. However the nocturnal tow caught large smelt which consistently escaped the dropnet. Thus the nocturnal tow was regarded as the least selective and most practical sampling system and so was adopted for routine sampling. Later, when a boat fitted with a winch became available, the dropnet was developed into a potentially valuable

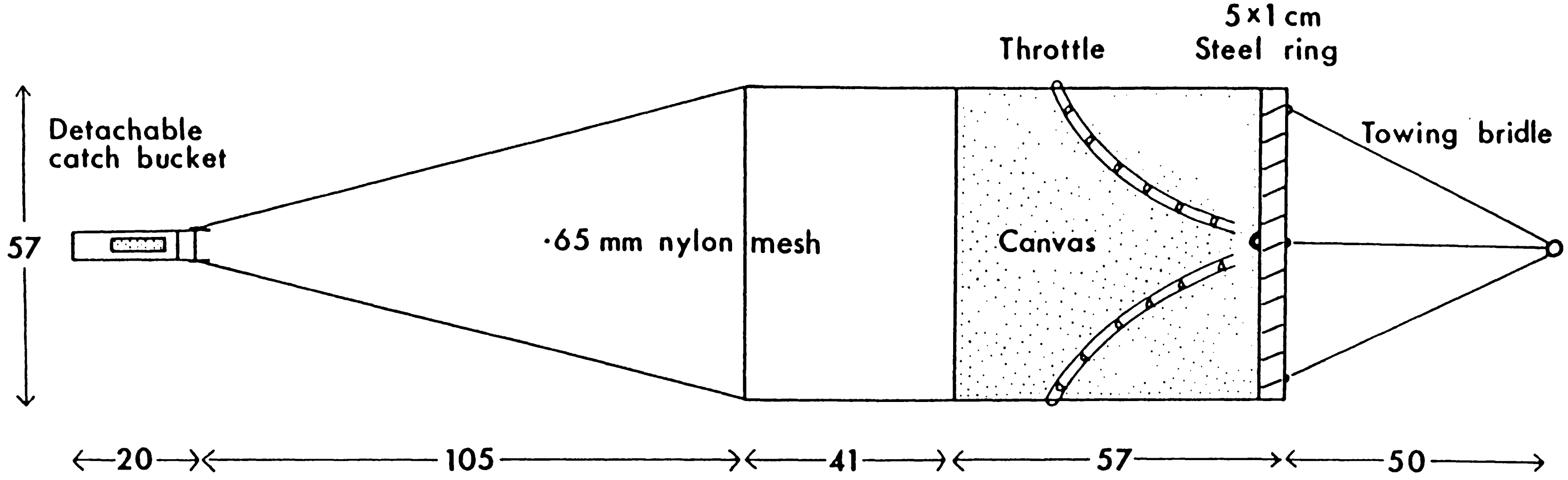


FIG. 8 Dropnet design showing the bridle used for towing as a ringnet. Unless otherwise specified, measurements are in centimetres.

TABLE 1.

Numbers of smelt caught in ten replicate dropnet catches between the surface and 40, 60 and 100 metres depth.

	DEPTH		
Drop No.	40m	60m	100m
1	2	2	7
2	5	18	7
3	5	8	9
4	3	6	6
5	5	18	11
6	4	10	1
7	5	26	7
8	4	2	7
9	5	7	5
10	6	4	2
Mean ± 95% CI	4.4 ± .84	10.1 ± 5.73	6.2 ± 2.12

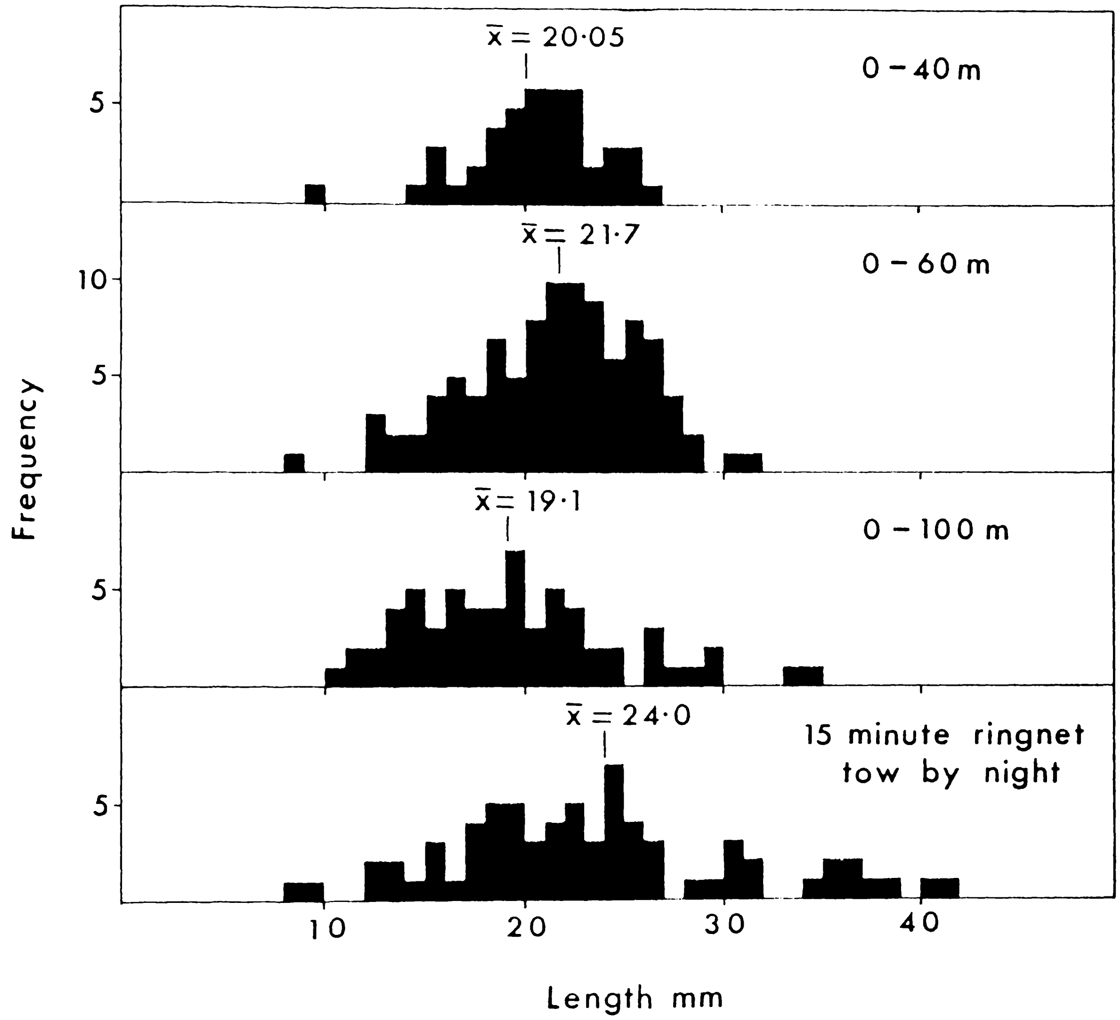


FIG. 9 Length frequencies of smelt caught in ten replicate dropnet catches from the surface to 40m, 60m, 100m and a 15 minute nocturnal ringnet tow. All samples were collected during the same twelve hour period from the Western Bay, Lake Taupo.

sampling device suitable for biomass estimates of small agile pelagic fishes (Appendix 1).

A Furuno FG 11 Mark 3 echo sounder was used to locate and follow the movements of pelagic scattering layers apparently caused by smelt.

(c) Zooplankton samples

A zooplankton sample was collected with each beach smelt sample. The net used was conical, 60cm long with a 15cm diameter mouth and 100cm mesh aperture size. Standard procedure was to throw the net to the full extent of a five metre line and retrieve the net slowly just above the bottom (depth about 1m) and rinse the catch bucket contents into a sample container. This was repeated three times; after the final throw the net was thoroughly rinsed into the sample container. Samples were preserved with formalin immediately. Subsamples (2 - 50% of total) were taken with a wide mouth pipette from a well mixed sample and counted in a 15ml chamber.

(d) Smelt egg samples

Smelt eggs were most easily found by stirring up the bottom, sweeping the area with a fine meshed handnet and sorting the sample in a white tray. Early work by Jolly (1967) and my own preliminary sampling indicated that eggs could be found on sandy or silty substrates but not amongst detritus, on mud, over algae coated sand or amongst macrophytes. Thus routine fortnightly quantitative sampling was conducted in preferred spawning areas off Waihaha Beach (September 1979 to January 1981) and in the lower reaches of the Waihora and Whanganui streams (September 1980 to May 1981). Eggs were collected with a corer and separated from the sandy substrate by density discrimination (Hellawell 1978).

A 56mm diameter corer was forced 10-15cm into the substrate, then pushed to one side so that one hand could retain the contents until rinsed into a 2.0 litre jar for temporary storage during transit to the field laboratory where samples were immediately processed. Here the lid on each jar was exchanged with one whose top had been cut out and replaced with 0.1mm gauze. The jar was then inverted and allowed to drain. The sand mixture was rinsed into a 15 litre bath containing about 5 litres of sugar syrup with specific gravity maintained at 1.12. The mixture was first stirred vigorously and then allowed to settle before pouring the syrup through a 0.2mm mesh sieve where suspended items collected. After reconcentrating the syrup it was again mixed with the sample and the process repeated once. Counts following repeated rinses indicated that two rinses were sufficient to collect over 95% of the eggs present (Table 2).

The sieve contents were washed into a 100ml sample container, preserved with formalin and stained with Rose Bengal stain to facilitate sorting (Hellawell 1978).

TABLE 2

Number of smelt eggs removed from sand and detritus by density separation after successive rinses.

Number of Rinses	SAMPLE A	B	C	D	E	Cumulative %
1	247	80	192	57	7	85.4
2	37	7	31	2	1	96.8
3	4	2	4	1	0	98.4
4	2	3	3	1	0	99.7
5	0	0	1	1	0	100
6	0	0	0	0	0	
7	0	0	0	0	0	

Waihaha Beach samples were collected along a transect down the littoral bench by diving. Five replicates were collected at six 0.5m depth intervals between 0.5m and 3.0m. From each stream ten cores, equally spaced along a transect across the channel about 200m upstream from their mouths, were collected. Temperature was recorded at each site.

(e) Trout stomachs

Rainbow trout stomachs were taken fresh (i.e. dead for less than about 3 hours) from consenting anglers between October 1980 and February 1982. Most trout were caught by anglers fishing the sublittoral zone with lead or wire lines which sink lures from 15 to 35m depth. A few were caught by stream mouth fly fishermen and these are included in November, December and March samples.

Stomachs were collected throughout each month but were grouped on a monthly basis. Each stomach (the region between the oesophagus and pyloric sphincter) was separated from the viscera and preserved in 20% formalin. Subsequently, after measuring the outside length of each stomach, the contents were removed, species were separated, counted and pressed volumes measured in a conical measuring cylinder. Lengths of all measurable smelt were recorded.

(f) Fecundity

The gonosomatic index and number of ova carried by ripe females was determined for about 30 smelt each month throughout the spawning season. Each smelt was blotted dry, weighed to the nearest milligram, then the ovary was removed and the fish reweighed to obtain the somatic weight.

$$\text{Gonad Weight} = \text{Total Weight} - \text{Somatic Weight}$$

$$\text{Gonosomatic Index} = \frac{\text{Gonad Weight}}{\text{Somatic Weight}} \times \frac{100}{1} \qquad (1)$$

The state of maturity, presence of atretic eggs and quantity of visceral fat deposits were recorded. The ovary was placed in a 10ml vial, shaken vigorously to separate the ova which were then rinsed into a 50ml measuring cylinder to be mixed by repeated inversion before a subsample was quickly withdrawn in a 10ml wide mouth pipette. Replicate subsamples from a known quantity of ova indicated that the subsample comprised about 23.2% of the total count. Thus

$$\text{Fecundity} = \frac{\text{No. in subsample}}{0.232} \qquad (2)$$

(g) Post-spawning mortality

A diamond-shaped netting enclosure 2.5m long, 1.5m wide and 1.0m deep was placed in the Waihaha River about 400m upstream from the river mouth (fig. 10). A number of smelt taken from the river were temporarily held in a seine net to permit a few at a time to be captured and individually examined in a glass jar so that they were never touched or taken out of water. 51 ripe female and 101 ripe male smelt were chosen and put into the enclosure. Dead smelt were removed daily, measured and their gonads examined to determine whether they had spawned. The enclosure was cleared of debris at least daily.

After 26 days all remaining smelt were captured, measured and their gonads examined.

Stomach analyses The stomach contents of a few smelt and bullies from selected samples were enumerated by microscopic dissection and counting. The number of each food item eaten and an index of stomach fullness were recorded. The fullness index is a five point scale where:

0 = Empty
1 = Food present but no stomach distention
2 = Stomach slightly distended
3 = Stomach moderately distended
4 = Stomach very distended

FIG. 10

Enclosure used to estimate smelt spawning mortality.

CHAPTER 3 - DISTRIBUTION, AGE STRUCTURE AND GROWTH

1. The catch

Beach seine hauls taken by day typically contained a majority of maturing and adult smelt, substantial numbers of juvenile bullies and occasional koaro. The largest catches were taken by day during spring and autumn (fig.11) when all species were most abundant along the shoreline. Seine samples collected by night generally contained fewer smelt but more bullies, many of which were full grown adults (up to 110mm). The largest smelt were taken during winter from nocturnal collections and this was the only period when differences between diurnal and nocturnal smelt sample length frequency distributions were apparent.

Dropnet and ringnet tow samples generally contained mostly larval and juvenile smelt with few adults, a few larval bullies (2 - 20mm) during summer and autumn and, occasionally during winter, juvenile koaro (30 - 50mm).

(a) Movements and distribution

Adult smelt were most abundant in daytime beach seine catches, being about one order of magnitude less abundant by night (Fig. 11). Seasonal patterns of abundance in beach seine catches were the same for hauls taken by day and by night, with winter catches being between 2 and 3 orders of magnitude less than summer catches. Thus there were both diurnal movements, in which adult smelt moved out of the shallow littoral zone at nightfall, returning at daybreak and seasonal movements whereby littoral smelt densities were high between November and June. It seems that there were continuous diurnal movements resulting in nett immigration during spring and nett emigration in early winter.

Larval smelt (<25mm FL) were never taken in beach seine samples but were common in nocturnal tow samples. Thus larval smelt were confined to the pelagic zone. Juvenile smelt (25 to 35mm FL) were frequently taken by both sampling methods, being almost continuously present in nocturnal tow samples and seasonally abundant in beach seine samples, in which they were most numerous from January until May. Outside this period, adult smelt usually dominated the catch. Thus it seems that juvenile smelt were continuously present in the pelagic zone and that they spread into the littoral zone between January and May. Adult smelt were almost always present in beach seine catches and were occasionally taken in nocturnal tow samples. Adults were were probably severely underrepresented in nocturnal tow samples because of the size selectivity of the sampling method (Appendix 1). However, the scarcity of adult smelt in the littoral zone between July and October compared with their abundance during spring and summer suggests that they must have moved out, presumably into the pelagic zone. Data from the pelagic sampling methods used were not adequate to determine which habitat(s) adult smelt occupied during winter. However, it is clear that they were making very little use of the littoral zone.

Thus a model which describes smelt movement between the littoral and pelagic zones must treat movement as a continuous size dependent process occuring at a rate which varies seasonally, such that there is always nett emigration from the littoral by larval smelt but with an increasing tendency for immigration by larger smelt, particularly from November until May.

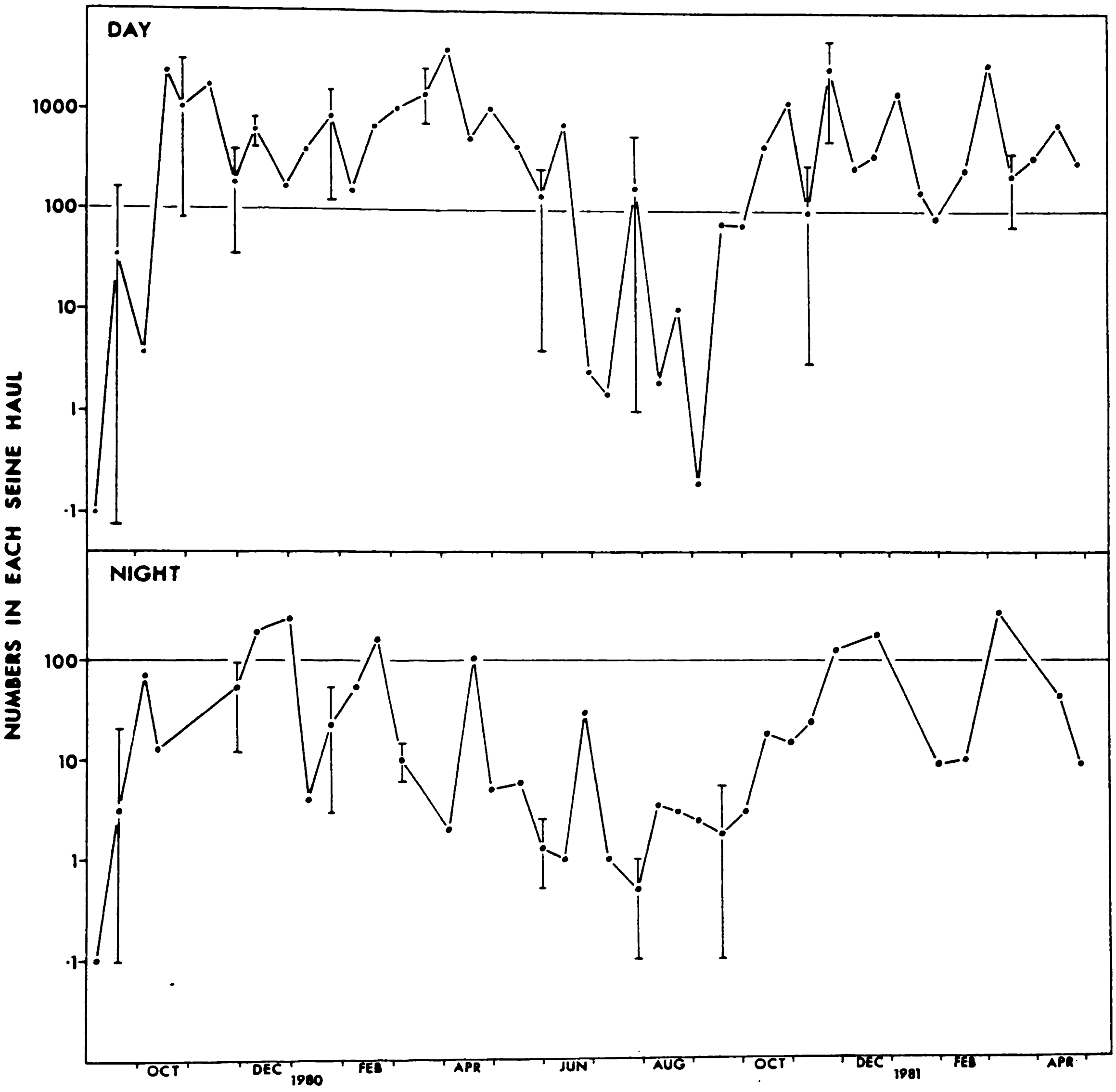


FIG. 11 Mean smelt abundance at Waihaha Beach as measured by standard seine hauls by day and by night. Vertical bars indicate the range where several samples were collected.

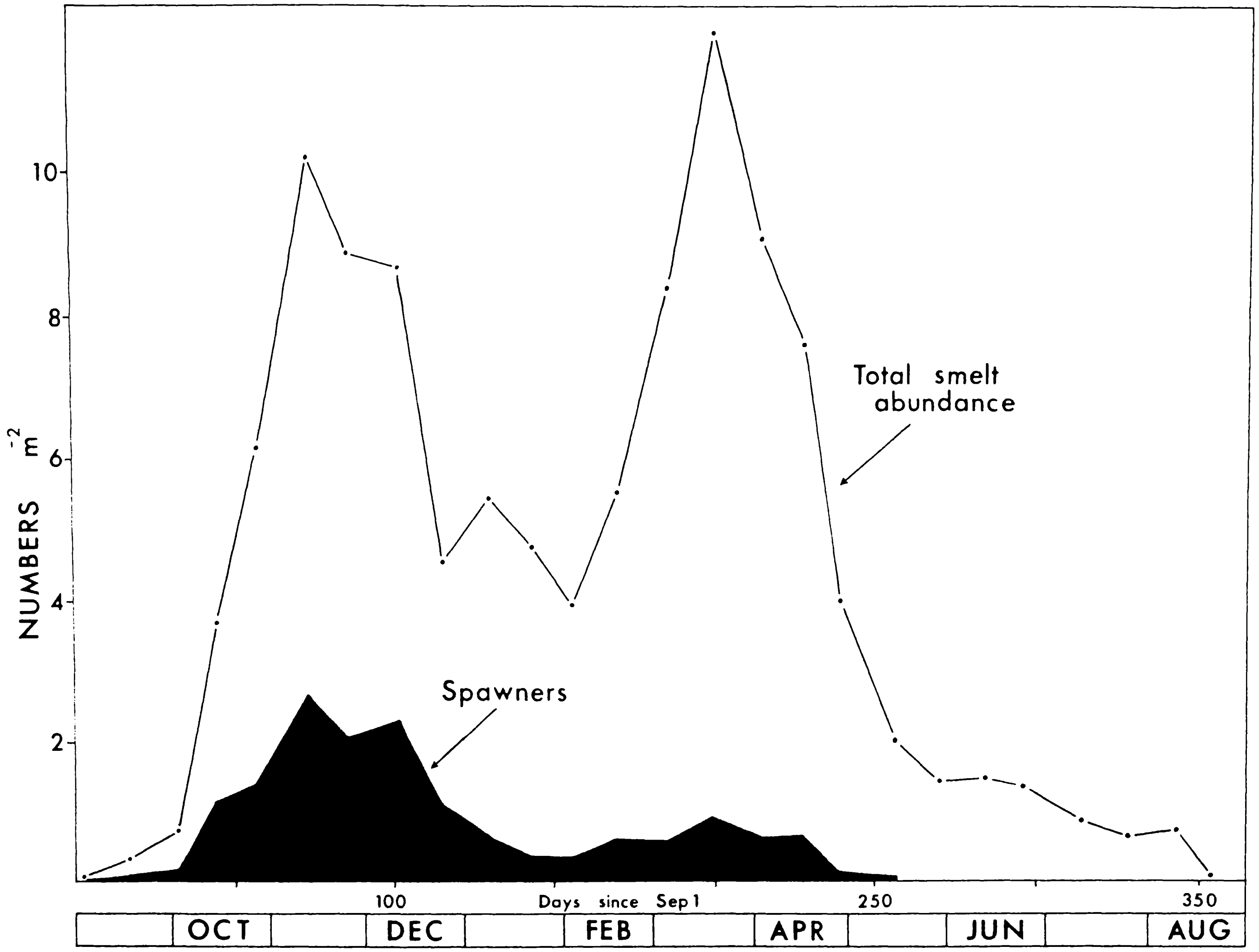


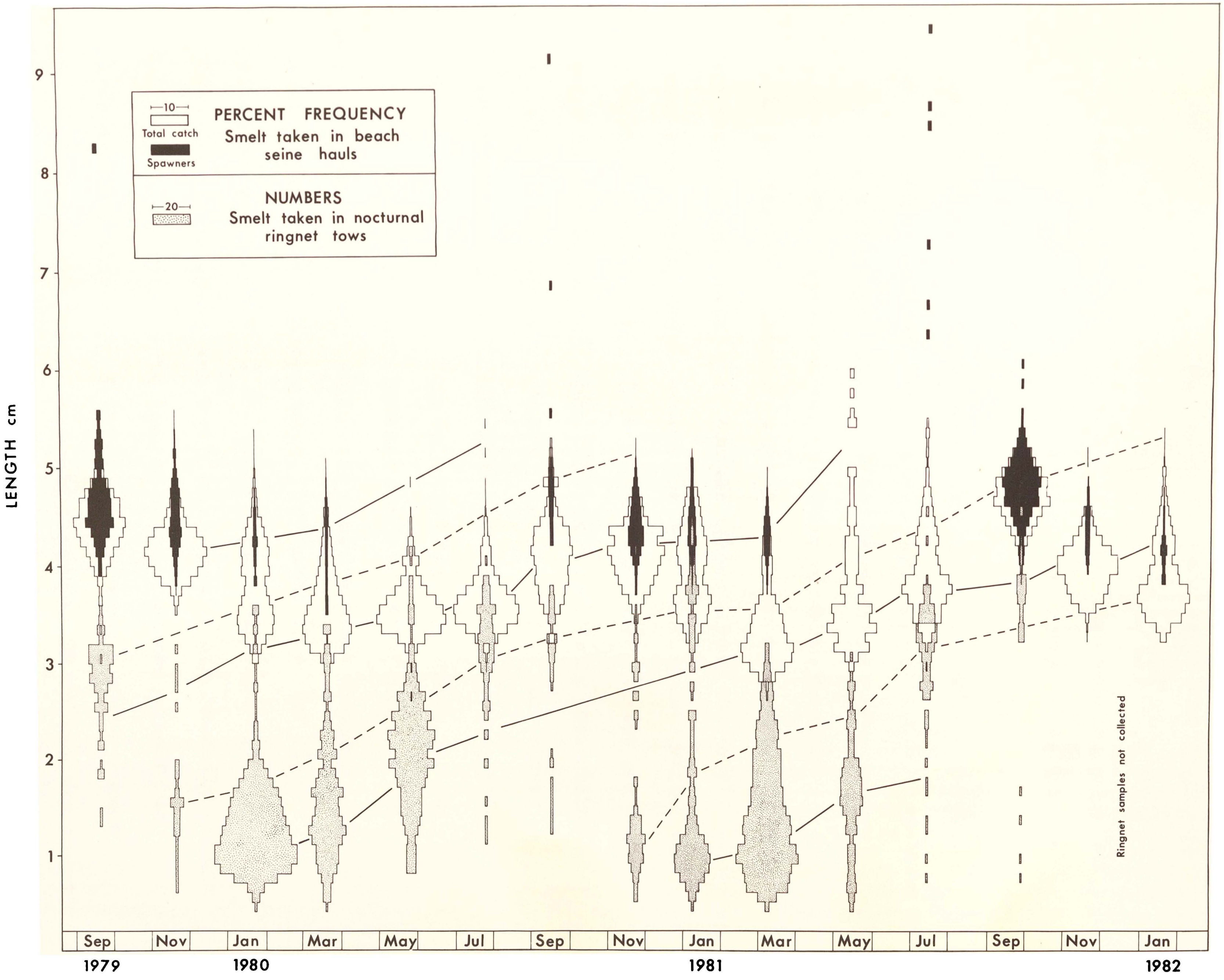
FIG. 12 Average smelt densities at Waihaha Beach. Data for the two years monitored were combined and smoothed using a triple point running mean.

FIG. 13

Smelt length frequency distributions during alternate months throughout the sampling period.

The data presented were collected during a single fortnightly sampling session and so represent only some of the dates sampled. The complete data set for each sample collected is given in Appendix 2.

Beach seine data are expressed as percent frequency distributions because variation in littoral smelt abundance was too great to present as absolute frequencies on a uniform scale. Thus these data show length frequency distributions and indicate variation in proportions (not abundances, which are given in Figs 11 and 12) of spawners and non-reproductive adults. Catch variation in nocturnal tows was not so great and therefore data could be expressed as absolute numerical frequencies on a uniform scale to provide some indication of the variation in numbers caught in nocturnal tows.



LENGTH cm
1
2
3
4
5
6
7
8
9
10
Total catch
Spawners
PERCENT FREQUENCY
Smelt taken in beach seine hauls
20
NUMBERS
Smelt taken in nocturnal ringnet tows
Ringnet samples not collected
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Jan
Mar
May
Jul
Sep
Nov
Jan
1979
1980
1981
1982

2. Age structure and distribution of age groups in the lake

Recently hatched larval smelt first appeared in nocturnal tow samples during November. These, and older smelt up to 30mm long, were unpigmented and had a distinctively elongate body form with a small head and limited fin development. Young of the year were most abundant in nocturnal tow samples during summer when they formed a distinctive modal group in sample length frequency data (fig. 13). The mode remained until June when larval smelt suddenly became scarce in tow samples, apparently because they were no longer migrating to or remaining near, the lake surface by night. Further dropnetting during October 1982 indicated the presence of high post-larval smelt densities (fig. 14) despite their absence in previous winter and spring nocturnal surface tow samples. Also, echo sounder traces (figs. 16 and 17) indicated a scattering layer between 85m by day during late winter which moved to the surface for the 15-20 minutes soon after sunset and then descended to 15-40m for the night. Juvenile smelt were seen whilst diving under cliffs and around reefs (fig. 18) but did not appear in beach seine samples until January when they were 25-36mm long and, it seems, about one year old. At this stage they were developing the adult body form: scales were forming; the head, trunk and fins were larger in relation to body length; the caudal fin was forked and the alimentary canal more differentiated. By March, this year class comprised the greater part of the beach seine catch; it was always well-represented in subsequent beach seine samples and generally present in nocturnal tow samples. The largest smelt commenced spawning in August-September, when most of the relatively small numbers present in the littoral at that time were ready to spawn. These spawners probably comprised a relatively small proportion of the total year class although their progeny were represented by a secondary mode in the length frequency distribution of each year class and this was intermittently identifiable until the year class was about two years old. Spawning continued until the following May by which time the adult year class, now a little more than two years old, was decimated by mortality associated with spawning. A few smelt (mostly male) survived, grew very rapidly and were taken during winter, by night, in the 15m seine net when it was hauled in from about 100m offshore. This procedure was used only when smelt were so scarce that adequate samples could not be taken with the 8.0m net. Such large smelt may have been able to evade capture in the smaller net if they were present within ten metres of the beach, although the only particularly large one taken in 1979 was caught in the smaller net. (The larger net was not used until the winter of 1980). Thus exceptionally large smelt may have been more abundant than the data in figure 13 indicated.

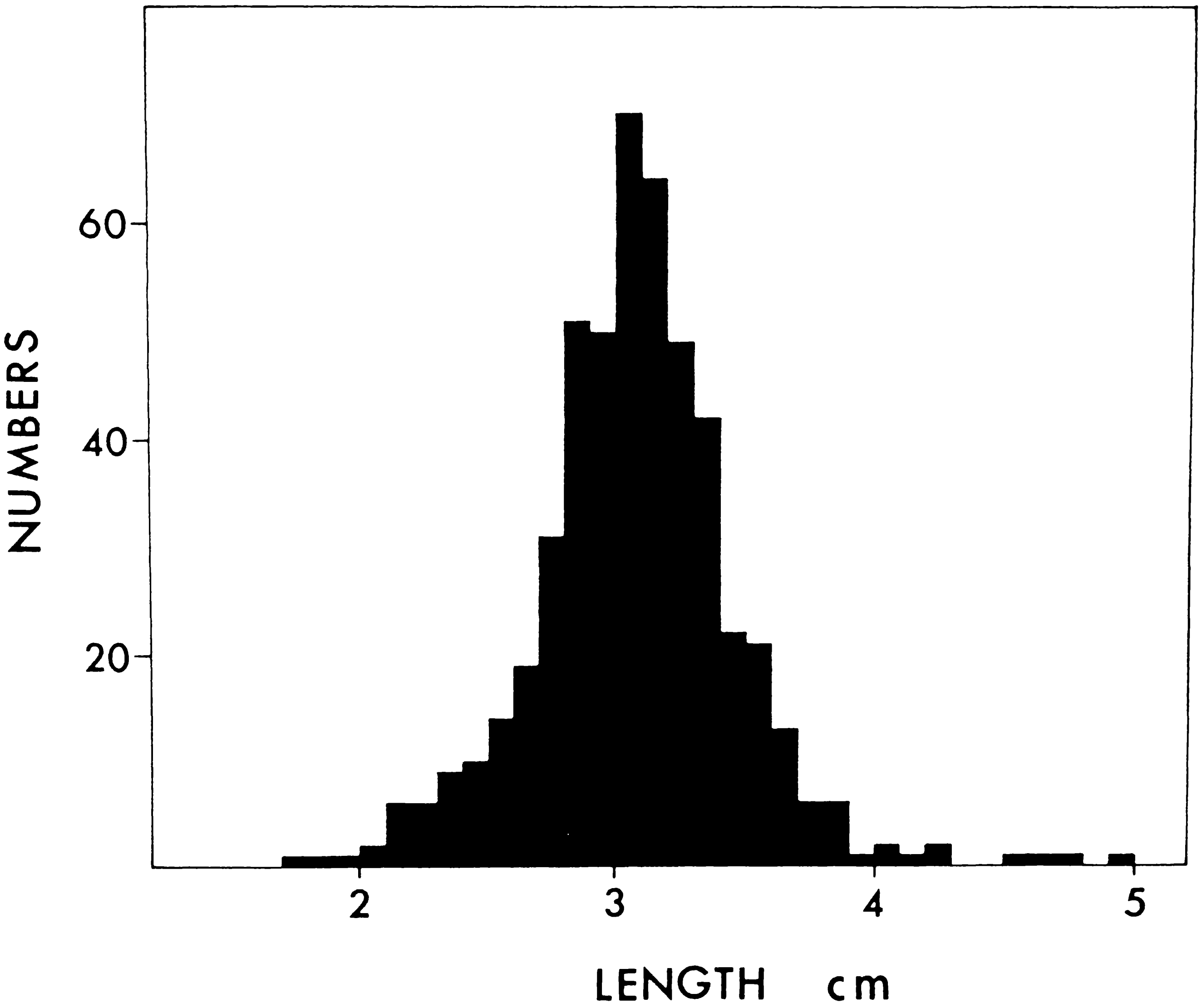


FIG. 14 The length frequency distribution of smelt taken dropnetting on 11-10-82 in 16 drops to 100m. The net mouth area was 0.49m^2 and it descended at 0.91m.s^{-1}.

FIG. 15

Echogram taken from a moving boat (ca. 3kn) during the early afternoon, 10 October 1983. The trace covers a path initially away from Waihaha Beach, into deep water and then back to the beach, taking 22 minutes.

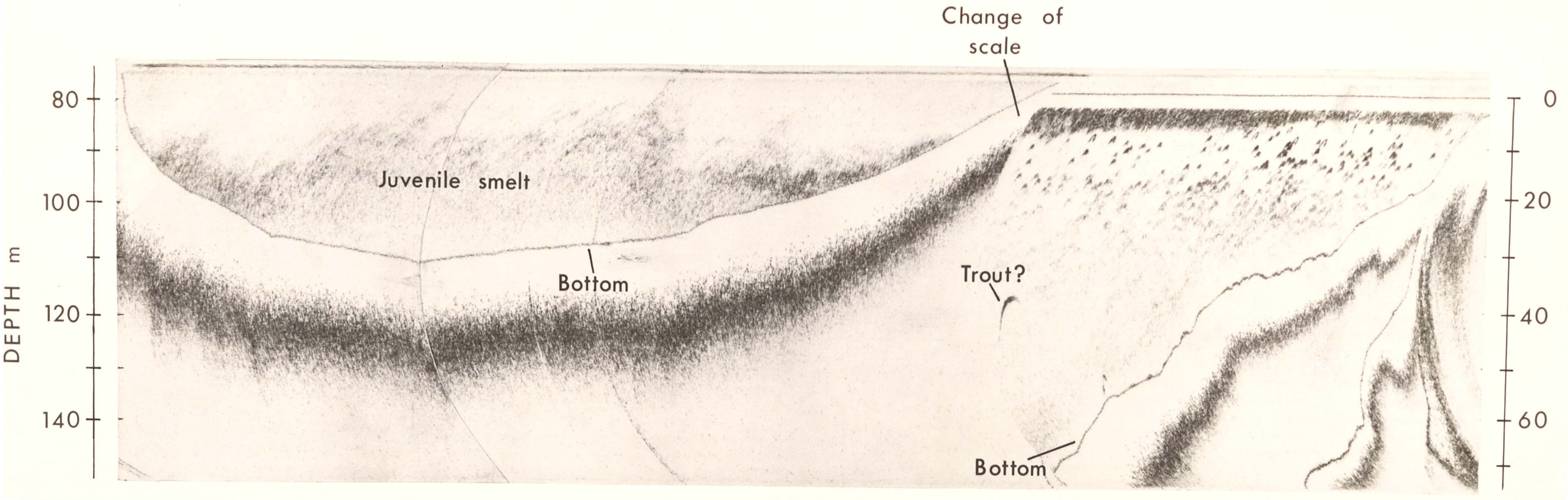
Change of scale
80
100
120
140
DEPTH m
0
20
40
60
Juvenile smelt
Bottom
Trout?
Bottom

FIG. 16

Echogram from a stationary boat before, during and after sunset.

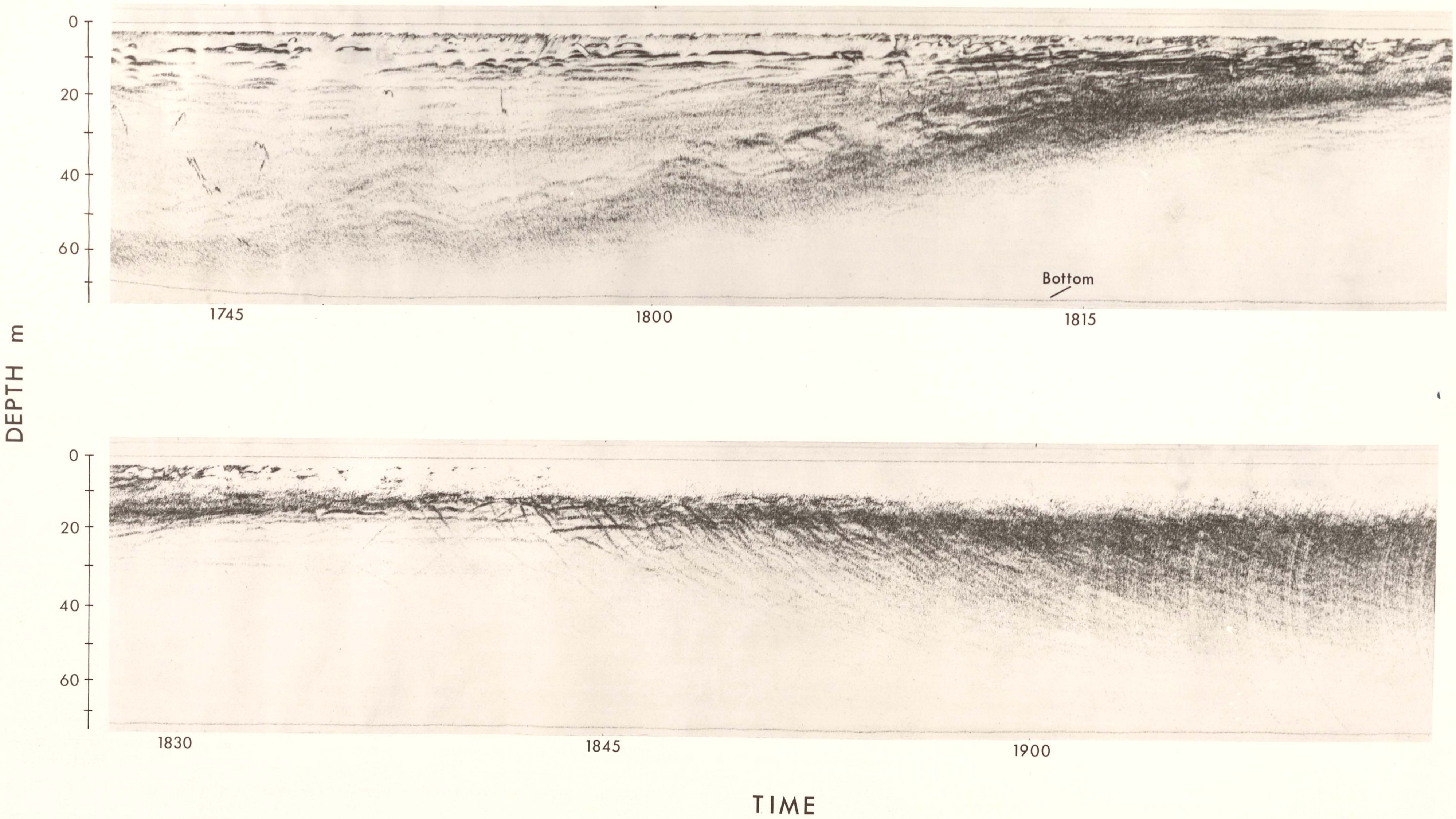
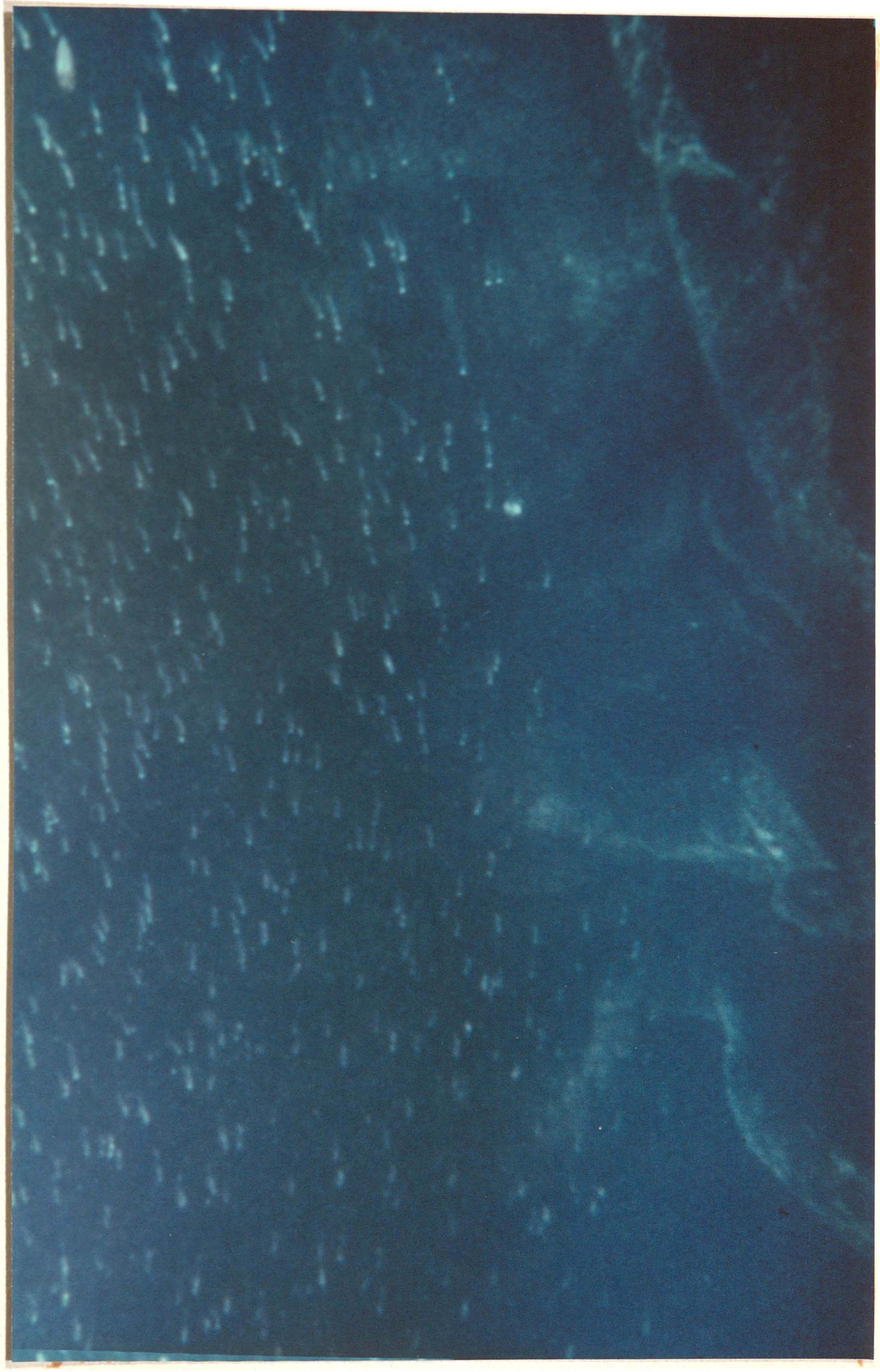

0
20
40
60
Bottom
1745
1800
1815
DEPTH m
0
20
40
60
1830
1845
1900
TIME

FIG. 17

Adult smelt in the littoral zone (ca. 2.0m) at Waihaha Beach, November 1981.

FIG 18

Juvenile smelt (ca. 25-30mm) near a cliff face at about 10 metres depth (December 1981).



3. Population structure

Four population groups were recognised in seine samples. These were ripe males, ripe females, non-reproductive adults and juveniles. Each group had a different mean length but their length ranges overlapped considerably (fig. 19), spawning smelt being amongst the largest present and ripe males being larger than ripe females. Non-reproductive adults and juveniles were not definitively separable on the basis of external morphological features so their respective length frequency distributions had to be determined indirectly. It was assumed that their length frequency distributions were both normal and that the mixture could therefore be approximated by the sum of two normal distributions (McDonald and Pitcher 1979):

$$f_i = \frac{n}{\sqrt{2\pi}} \left[\frac{P}{S_1} \, \mathrm{EXP} \, \frac{-(L_i - \bar{L}_1)^2}{2S_1{}^2} + \frac{1 - P}{S_2} \, \mathrm{EXP} \, \frac{-(L_i - \bar{L}_2)^2}{2S_2{}^2} \right] \qquad (3)$$

Where f_i = frequency at Length i (L_i)

n = sample size

P = proportion of juveniles

$\bar{L}_1$ = juvenile mean length

S_1 = standard deviation of juvenile length

$\bar{L}_2$ = non-reproductive adult mean length

S_2 = standard deviation of non-reproductive adult length

Best estimates of the five unknown parameters were calculated iteratively by Chi-square minimisation. Trial values for each were in turn incremented or decremented to improve the fit of the model as measured by the Chi square criterion. Iterations finished when mean and standard deviation estimates remained stable at two decimal places and proportion estimates at three places. They often converged rapidly without any parameter constraints but when the non-reproductive adult mode was not clearly apparent it became necessary to partially constrain the standard deviation ($S_{N/R}$) thus:

$$S_{N/R} \leqslant \frac{\bar{L} - 30}{3} \qquad (4)$$

If this was not sufficient to ensure that parameter estimates were biologically sensible in relation to previous and subsequent samples, the mean length ($L_{N/R}$) was defined and held constant. Parameter estimates and Chi-square measurements of fit are given in Table 3 and density functions fitted to percent frequency data are shown in figure 20. Skewness reduced the fit in some samples (e.g. 20.3.80; 17.3.81) and leptokurtosis was noticeable in others (e.g. 22.12.80; 23.1.80; 21.1.81; 16.2.81). However there was no indication that mean length estimates were significantly biased by these deviations from normality. McNew and Summerfelt (1978) demonstrated that means estimated by this technique are little affected by deviations from normality but proportion estimates are not so reliable and variance estimates could be seriously distorted.

The normality assumption was arbitrary and taken for convenience. There are no biological reasons why age group length frequency distributions should be normal, although the premise is almost universal in the literature. In the Lake Taupo population each year class comprised two unequal sized cohorts and ripe females and males are known to have differing mean lengths, the difference possibly originating early in their development. Consequently the length frequency of a given year class would be most correctly described by a mixture of density functions which may not be normal. However the difficulties in determining the functional form appropriate for each mixing component seem likely to outweigh any gains accrued from more precise parameter estimates.

Juvenile mean lengths were considered best estimates of their year class mean length but non-reproductive adult length frequencies were added to known spawner length frequency data to estimate the mean length of the senior year class.

TABLE 3 - Means, standard deviations and proportions estimated for juveniles and non-reproductive adults by Chi-square minimisation.

DATE	JUVENILES			NON-REPRODUCTIVE ADULTS				
	$\bar{L}$	S.dev	Prop.,	$\bar{L}$	S.dev	Prop.,	$\sum\chi^2$	Sample size (n)
10.1.80	34.4	1.20	.098	40.10	3.40	.902	2.86	358
23.1.80	33.97	2.28	.812	40.0**	3.33**	.188	3.66	3451
8.2.80	34.24	2.12	.642	40.0**	3.33**	.358	11.93	140
21.2.80	34.09	2.0	.584	40.23	3.41*	.416	2.15	730
5.3.80	33.33	2.14	.683	39.7	3.23*	.317	2.48	1014
21.3.80	33.68	2.45	.860	39.5**	3.17	.140	3.71	5733
5.4.80	34.22	2.07	.671	38.76	2.99	.329	1.38	3681
19.4.80	34.04	1.84	.507	38.4**	2.8**	.493	4.35	596
30.4.80	33.29	1.74	.614	38.03	2.83	.386	1.13	2095
17.5.80	34.30	2.21	.808	41.9**	3.1	.192	7.99	352
10.12.80	33.90	1.406	.137	41.66	3.62	.863	.493	259
23.12.80	32.97	2.0**	.117	42.36	3.13	.883	4.85	368
7.1.81	34.91	1.86	.301	39.69	3.23*	.699	2.04	1330
21.1.81	36.10	1.42	.459	40.77	3.667	.514	6.00	102
1.2.81	35.68	2.54	.368	43.08	3.9**	.632	11.18	147
16.2.81	32.74	2.41	.596	41.75	3.7**	.404	2.73	427
5.3.81	32.03	1.74	.938	38.69	4.0	.062	1.21	1495
17.3.81	34.46	2.09	.786	40.83	3.9	.214	2.24	399
30.3.81	34.06	2.60	.916	41.05	3.68	.084	5.66	324
15.4.81	32.56	2.07	.895	38.7**	3.00**	.105	2.33	784
27.4.81	35.18	2.48	.953	42.19	2.69	0.47	1.61	311

* denotes partial constraint

** denotes parameter held constant

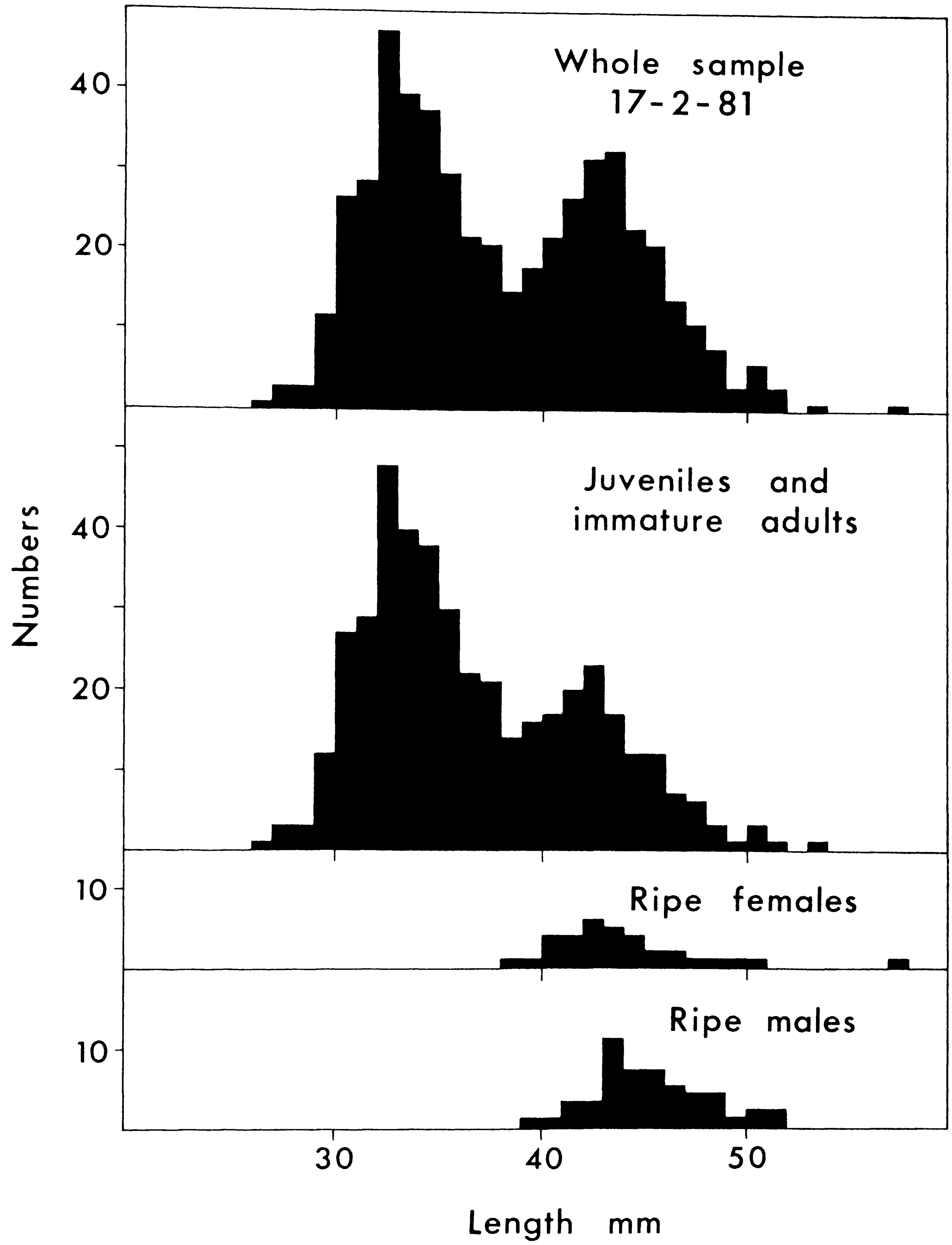
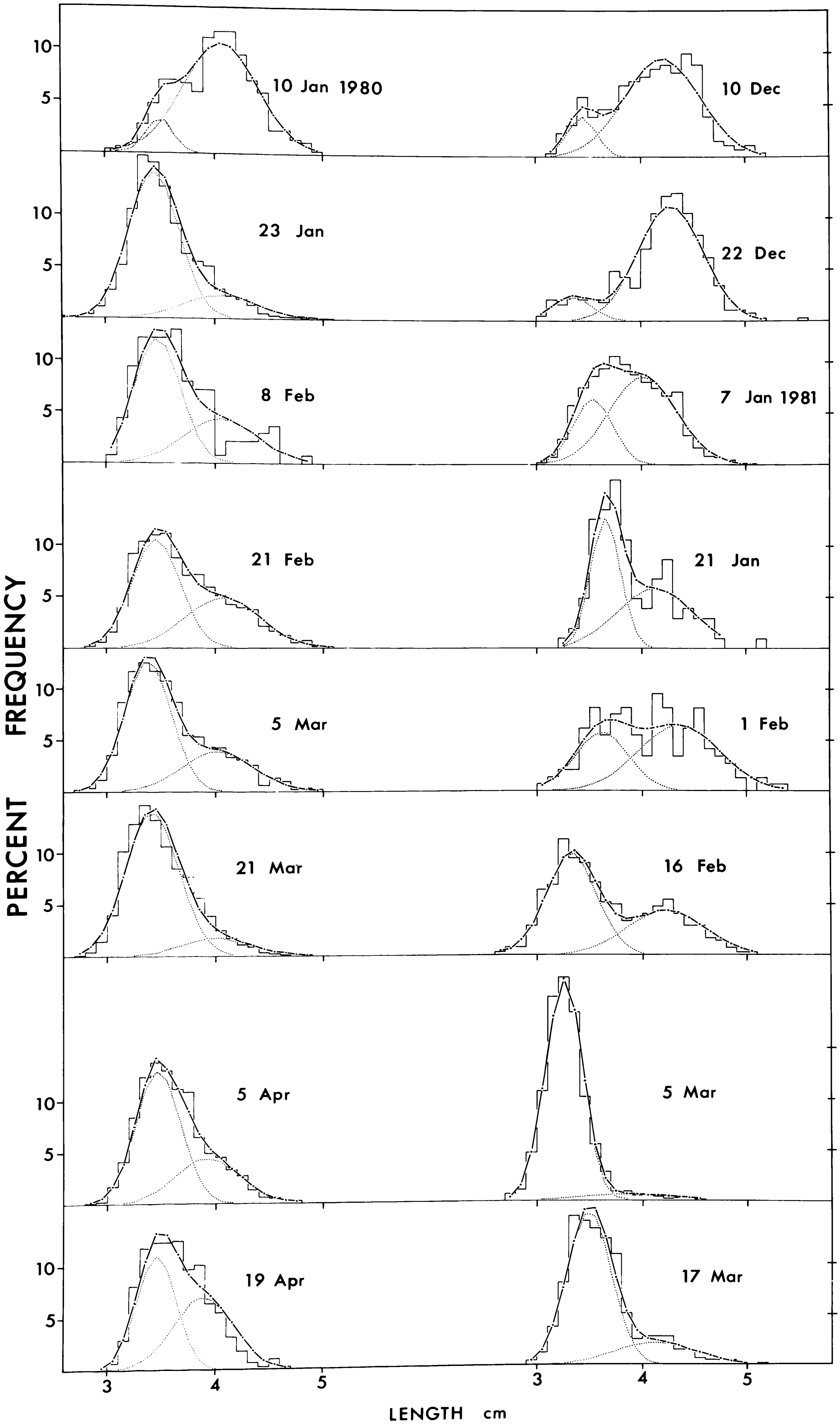


FIG. 19 Length frequency distribution of ripe males, ripe females, non-reproductive adults and juveniles in a typical summer smelt sample.

FIG. 20

Normal density functions fitted by Chi-square minimisation to juvenile and non-reproductive adult length frequency data (histograms). The dotted curves represent the functions describing the length frequency distributions of each population group and the sum of these is represented by the dashed line.


10 Jan 1980
10 Dec
23 Jan
22 Dec
8 Feb
7 Jan 1981
21 Feb
21 Jan
5 Mar
1 Feb
21 Mar
16 Feb
5 Apr
5 Mar
19 Apr
17 Mar
PERCENT FREQUENCY
10
5
3
4
5
LENGTH cm

4. Growth

Mean lengths of age groups present at each sampling date were used to examine seasonal and age related changes in length. Age groups used were generally whole year classes but wherever the smaller spring cohort and the dominant midsummer cohort were individually identifiable, they were treated separately. Birthdates used were October 1st and January 1st respectively. Ages were estimated from the time elapsed between the birthdate and the sampling date.

The spring cohort was apparent both in the adult year class from July until October and as their progeny taken in spring nocturnal tow samples. The first juveniles to appear in beach seine samples collected during December-January were also thought to belong to this group. Surviving adult spring cohort smelt (45-55mm in September) may have become the exceptionally large smelt (70-110mm) taken the following winter. However although this interpretation was used in the derivation of growth curves, such an inference was not implicit in the data. If, in fact, they originated from a more recent part of the year class then they were growing even faster than indicated by figs. 21, 22 and 23.

The population growth curves (figs 21, 22 & 23) are not equivalent to growth curves for individual fish because the mean lengths used are influenced by size related mortality and availability to the sampling gear as well as growth. The larger smelt were the first to spawn and so were subjected to a source of mortality which did not affect the immature ones. Also the smaller immature smelt appeared in the littoral later than the larger ones. Both factors cause the year class mean length to decrease with time. Separation of each year class into cohorts reduces this effect but the growth curves presented are nevertheless likely to underestimate the growth rate of individual smelt.

Length at age between 0.1 and 2.6 years of age (fig. 21) was found to be approximately described by a correction exponential function. Coefficients for the best fitting curve were found by iteration to be:

$$\text{Length (mm)} = a - b(c)^{\text{age}} \quad (5)$$

Where $a = 71.6$; $b = 62.3$; $c = 0.9989$

and age is expressed in days.

Whilst this function provided the best fit to the data, the predicted length at hatching (Age = 0) was 9.3mm whereas smelt are known to be 2 to 5mm long on hatching. When the coefficient "b" was partially constrained such that:

$$a - b = 3.0$$

the predicted length on hatching was 3.0mm and coefficients for the best fitting function were then found to be :

$a = 72.9$; $b = 69.9$; $c = .9988$

This underestimated length for much of the first year and so was not a useful description of the data.

The coefficient "a" is the maximum attainable length and is analogous to maximum attainable length in the Von Bertalanffy equation (Ricker 1973) but the data indicate that an asymptotic maximum is an inappropriate concept for the Lake Taupo smelt population because after about 2.6 years of age, the growth of large smelt (ca. 50mm) suddenly accelerated. However most smelt died before reaching this size and for these, length at age is usefully described by the curve. Nevertheless a descriptive growth model such as this is of little value for predictive assessment because growth is determined by the amount of food available per fish and by metabolic costs. A predictive model would require components relating fish numbers, food availability, allocation of this food to different fishes, varying in size and location as well as their individual metabolic requirements.

Mean lengths of age groups present at each sampling date (fig.22) and the data for each age group shown are combined in fig. 23 to emphasise seasonal growth patterns. Growth was slow during summer and autumn but faster during winter and so coincided with seasonal patterns of limnetic production which was maximal during midwinter (White et al. 1980). Littoral production, as indexed by Orthoclad chironomid densities (fig. 25) was maximal during midsummer and did not appear to influence smelt growth.

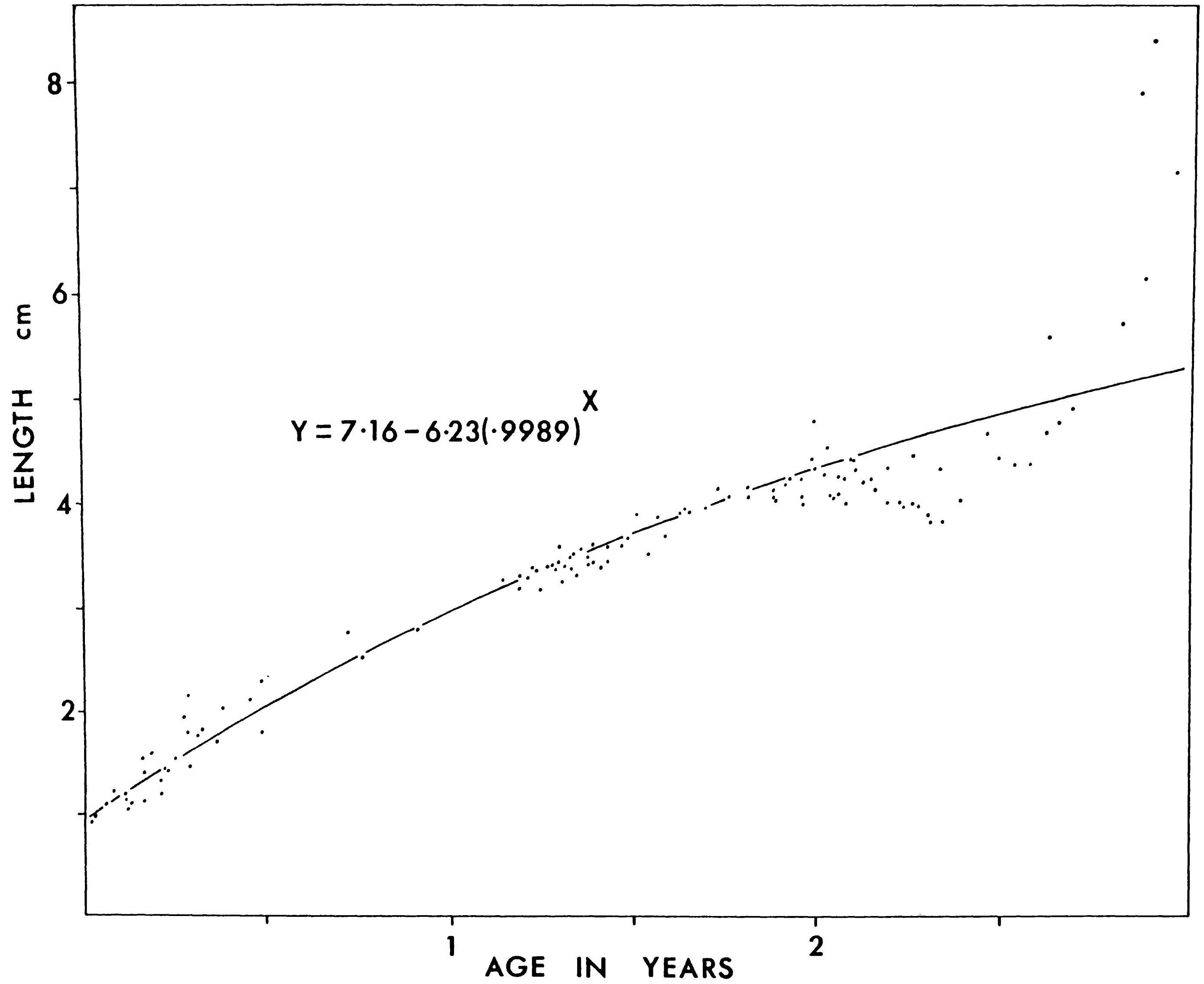


FIG. 21 Growth in Lake Taupo smelt. Mean lengths and the ages of modal groups were estimated from length frequency data. Note that growth of the largest smelt is not adequately described by the fitted curve.

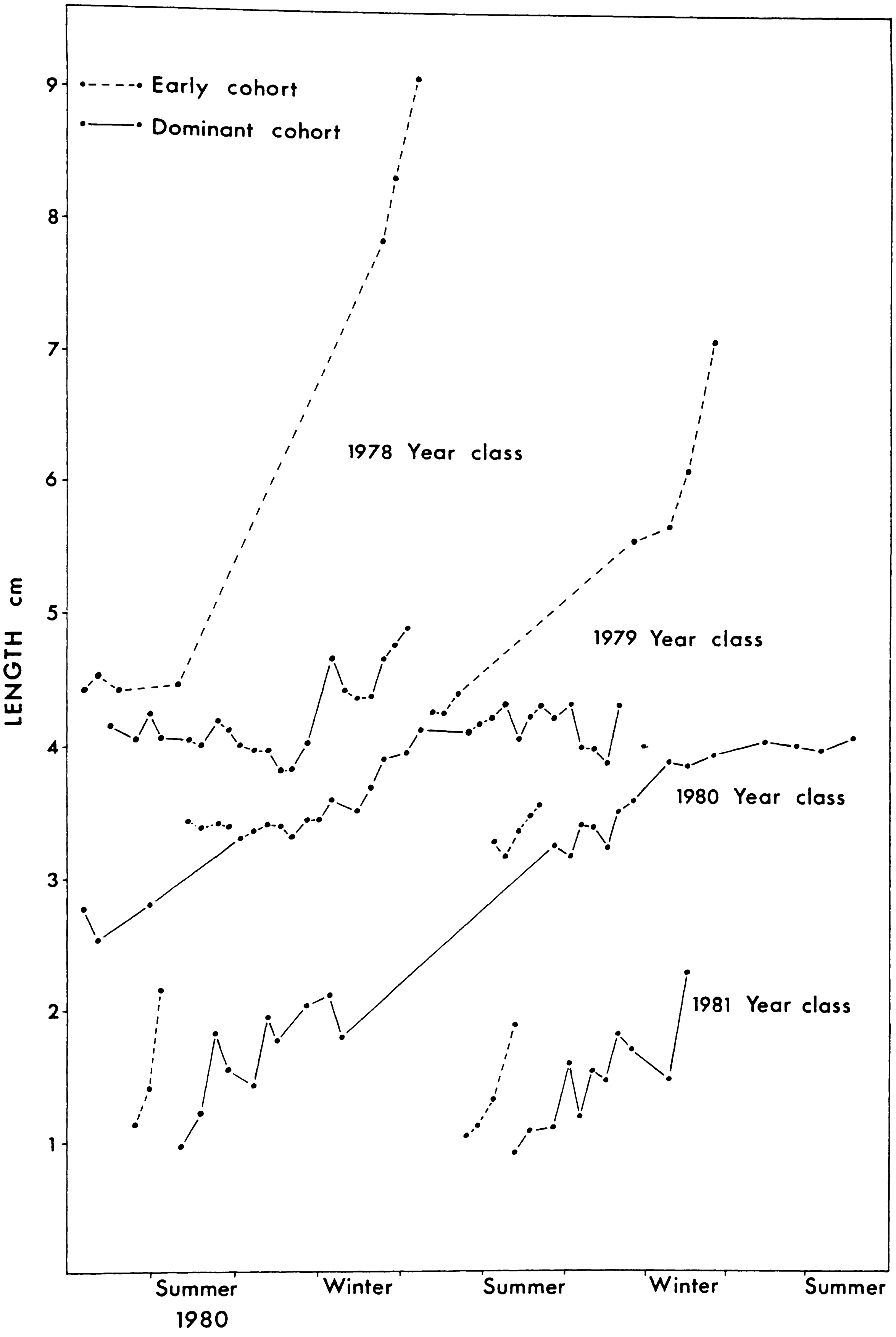


FIG. 22 Seasonal changes in the mean lengths of each age group.

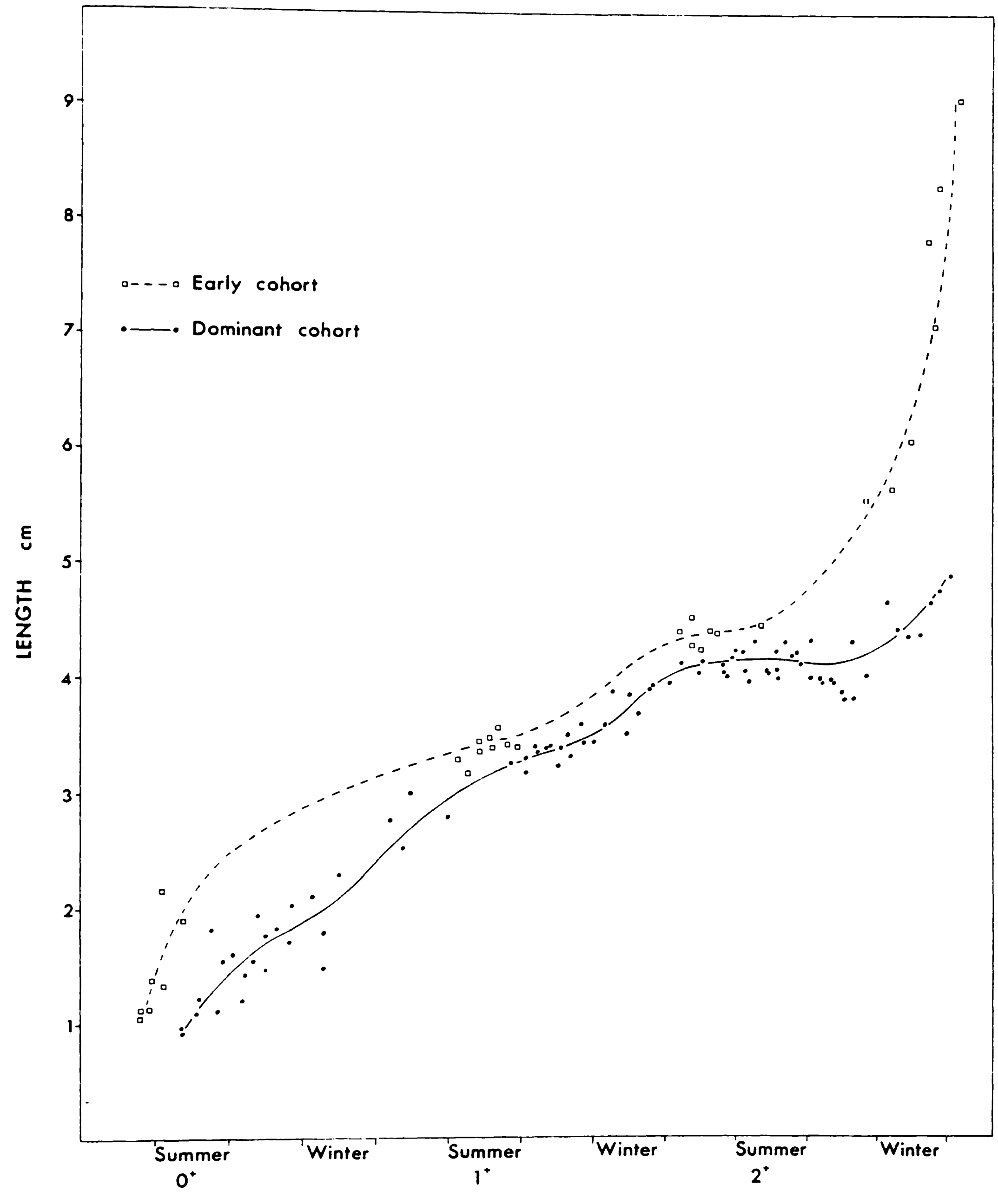


FIG. 23 Seasonal patterns of growth. Data for separate year classes presented in fig. 22 were combined to illustrate seasonal patterns.

5. Length-weight relationship

Smelt were found to have a complex length-weight relationship because their body form changed with development. Three overlapping stanzas were recognised (fig. 24): the elongate larval body form of pelagic smelt which persisted until they reached 30-40mm; the somewhat heavier juvenile body form typical of juvenile and immature adult smelt 31 - 50mm long; the more corpulent adult body form of ripe smelt.

Although separate power functions were fitted to each group, a single power function adequately predicted weight over most of the range of lengths encountered (5-110mm):

$$\text{Weight (g)} = a \text{ Length (mm)}^{b} \qquad (6)$$

Where $a = 1.316 \times 10^{-7}$; $b = 4.053$; $R^2 = .965$

The exponent "b" was large because smelt become substantially more corpulent with length. However this trend diminished beyond 45-50mm and consequently the above function overestimated weight for exceptionally large smelt (by 25-30% for smelt 90-110mm).

The three growth stanzas appear to be associated with feeding, breeding and possibly the predator avoidance requirements of each group. The elongate form of small larval smelt is probably important in maximising striking range per unit weight. Larval smelt feed by bending the trunk into an S-shape and then pushing forward to strike. Striking range is a function of length (Braum 1978) and consequently, if prey are mobile, feeding success is likely to be better for the most elongate larvae. However as they grow and are able to feed on larger items, the ability to pursue and capture evasive prey probably becomes more important. In addition, as smelt become larger they become more attractive to large predators and consequently, a disproportionate increase in escape ability with greater size is a useful adaptive characteristic. Feeding and predator evasion require the greater speed and manoeuverability obtained from well developed trunk muscles and fins and such development would cause smelt to become more corpulent with length. The raised elevation of the ripe adult length-weight relationship is a result of gonad development and accummulation of body tissue reserves.

The exponent was less than that for immature smelt presumably because the rate of increasing corpulence with length diminished after maturity.

FIG. 24

The weight-length relationship of Lake Taupo smelt.

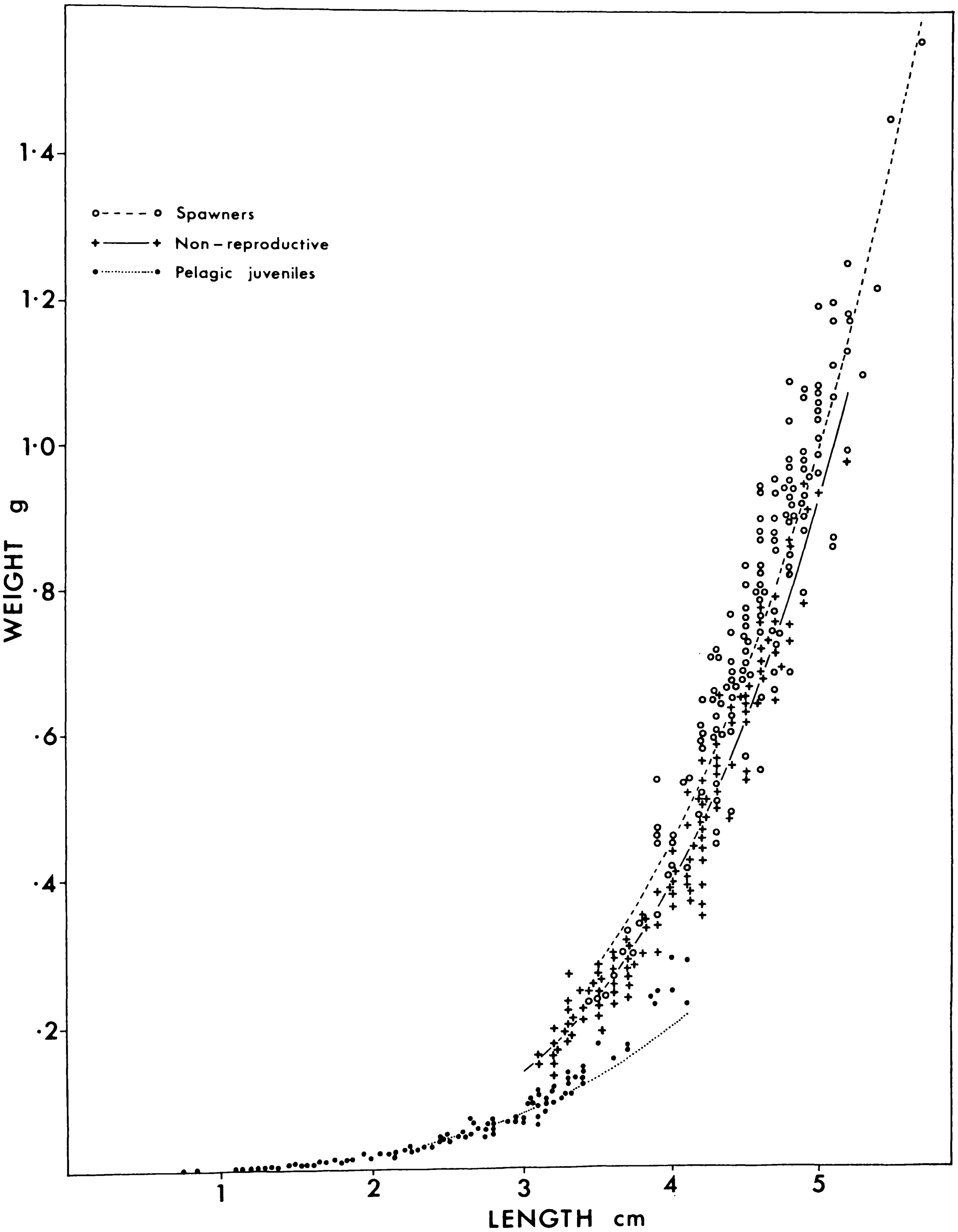
Pelagic juveniles : $W = 1.22 \times 10^{-6} L^{3.249}$; $R^2 = 0.98$

Juveniles and non-reproductive adults: $W = 3.16 \times 10^{-7} L^{3.807}$; $R^2 = 0.96$

Ripe adults : $W = 9.12 \times 10^{-7} L^{3.555}$; $R^2 = 0.91$

All data combined : $W = 1.316 \times 10^{-7} L^{4.053}$; $R^2 = 0.97$

Weight is expressed in grams and lengths are in millimetres.



WEIGHT g
1·4
1·2
1·0
·8
·6
·4
·2
o- - - - o Spawners
+——+ Non-reproductive
•·········• Pelagic juveniles
1
2
3
4
5
LENGTH cm

6. Feeding

Jolly (1963, 1967) found that smelt fed predominantly on zooplankton but insects and larval bullies were also included in the diet. The present study confirms this.

(a) 0+ larval smelt

Larval smelt up to 30mm long were exclusively planktivorous, apparently feeding on abundant species. Their stomachs were never very full and were often empty (Table 4a). Juvenile smelt (30-40mm) taken in summer beach seine hauls were also predominantly planktivorous, feeding largely on *Bosmina meridionalis* and *Ceriodaphnia dubia* (Table 4b) which were abundant at the time (fig. 26). Rotifers were also extremely numerous and may have been more widespread in the smelt diet than indicated as these were too small to be identified amongst other material under a dissection microscope. Stomachs from small larval smelt collected in a March nocturnal tow were examined at high magnification under a compound microscope and were found to contain both rotifer mastaxes and *Melosira* sp., although they contributed little to the stomach content volume. It seemed that rotifers were digested more quickly than crustacean zooplankters which were identifiable along much of the length of the intestine; *Melosira* appeared unaffected by digestive processes. Menninck (unpubl. data) found rotifers and dinoflagellates to be most important in the diet of small smelt in Lake Rotomanuka , near Hamilton.

(b) 1+ adult smelt

Adult smelt were also zooplanktivorous, but insects and smelt eggs were included in the diet and, although numerically less important than the zooplankters (Table 4b), these items comprised the greater food volume.

(c) 2+ adult smelt

The largest smelt taken in midwinter were mainly piscivorous, feeding on larval and juvenile bullies from 16-30mm in length. Their stomachs were generally full and several were stretched to near capacity. There were also extensive fat bodies surrounding the viscera, suggesting that food consumption had been considerable for some time previously.

(d) Competition for food

There was some dietary overlap between smelt of different age groups in that all fed on crustacean zooplankton. However only adult smelt were able to feed on insects and these smelt apparently did not feed on the smallest available zooplankton prey species. Competition between year classes was also reduced by spatial separation of adults in the littoral from young of the year in pelagic waters. It therefore seems likely that intraspecific competition for food operated more within than between year classes. There is some evidence for density dependent growth in that slow growth occurred during summer when three smelt year classes were abundant and faster growth occurred in late winter after spawning mortality had decimated the senior year class. However maximum pelagic production also occurred in late winter and was depressed in late summer (White et al. 1980). Thus seasonal cycles of food production and/or intraspecific competition could have caused these seasonal patterns of growth. Nevertheless, although the influence of each factor is largely inseparable, the difference between the winter growth rates of the 1+ and 2+ smelt (figs. 22 and 23) illustrated the influence of mortality on growth. The older group was decimated by mortalities associated with spawning which did not affect the younger immature group. The older year class was therefore much more severely reduced in number and growth of survivors was correspondingly greater. However this differential growth response was probably dependent on the existence of a large and unexploited food resource, such as larval bullies and could not have occurred if the diets of the two year classes had been the same.

TABLE 4a **Numbers of animals present in the stomachs of and fullness indices for (a) pelagic smelt and (b) littoral smelt.**

Pelagic Tow 20.9.79

SMELT LENGTh	*B. propinqua* Adults	*B. propinqua* Copepodites	Nauplii	*Ceriodaphnia dubia*	*Bosmina meridionalis*	Rotifers	Orthoclad Larvae	Chironomid Larvae	Terrestrial Insects	Smelt Eggs	Larval Bullies	FULLNESS
11			1									1
13.5												0
14				1								1
15		2	1									1
15				1								1
18												0
18		2	1									1
18			1	2								1
21												0
21												0
22	1											1
22												0
23												0
24	2											1
24	2			1								1
25												0
25												0
27	3	4										1
28												0
28		1		1								1
29	5	7		5								2
29	8	20										2
29												0
30												0
31	8	2		8								2
33	16	5		1								2
35	9	2	1	1								2

TABLE 4b **Littoral Smelt Stomach Contents**

	SMELT LENGTH	*B. propinqua* Adults	*B. propinqua* Copepodites	Nauplii	*Ceriodaphnia dubia*	*Bosmina meriodionalis*	Rotifers	Orthoclad Larvae	Chironomid Larvae	Terrestrial Insects	Smelt Eggs	Juvenile Bullies	FULLNESS
Waihaha Beach 19.9.79	40	17	1		19			1					2
	41	3	3		12					1			2
	42	4	1		4			2					1
	42												0
	42	23	7		31			1		1			3
	43	9	6	1	11								1
	46	37	19		23			2		1			3
	46	26	11		9			4		2			3
Waihaha Beach 23.1.80	30												0
	31		4		9	42							2
	32		1		5	120							2
	33		10		15	26							2
	33		51		17	7							2
	35		3		3	46							2
	37		1		9	181							2
	38		4		21	176							3
	38		8		4	84							2
	41				3	1							1
	42		2		8	286				1			3
	43				18	50				3			3
	44				26	147				1			2
	45		20										1
	46				1	4							1
	46		24		26	8				9			4
	47		2	4	30	260				1	4		3
	47		4	2	6	233				1	8		2
	47		1		2	41							1
	48		50		90	171				2			3
	49			2	3	121				9			4

TABLE 4b (cont'd **Littoral Smelt Stomach Contents**)

	SMELT	*B. propinqua* Adults	*B. propinqua* Copepodites	Nauplii	*Ceriodaphnia dubia*	*Bosmina meridionalis*	Rotifers	Orthoclad Larvae	Chironomid Larvae	Terrestrial Insects	Smelt Eggs	Larval Bullies	FULLNESS
Whanganui Stream 7.1.81	40							1		3	7		1
	42								4	3			1
	42							7	3	3	4		2
	43							1	1	1			1
	44									2	27		2
	44												0
	45								6	4	2		2
Waihaha Beach 10.8.80	64	21	6		17							2	2
	71											1	3
	72											2	4
	72	4										5	3
	84											11	4
	85								3			2	4
	91											3	4
	92								9			3	3
	94				9							2	2
	82											4	3

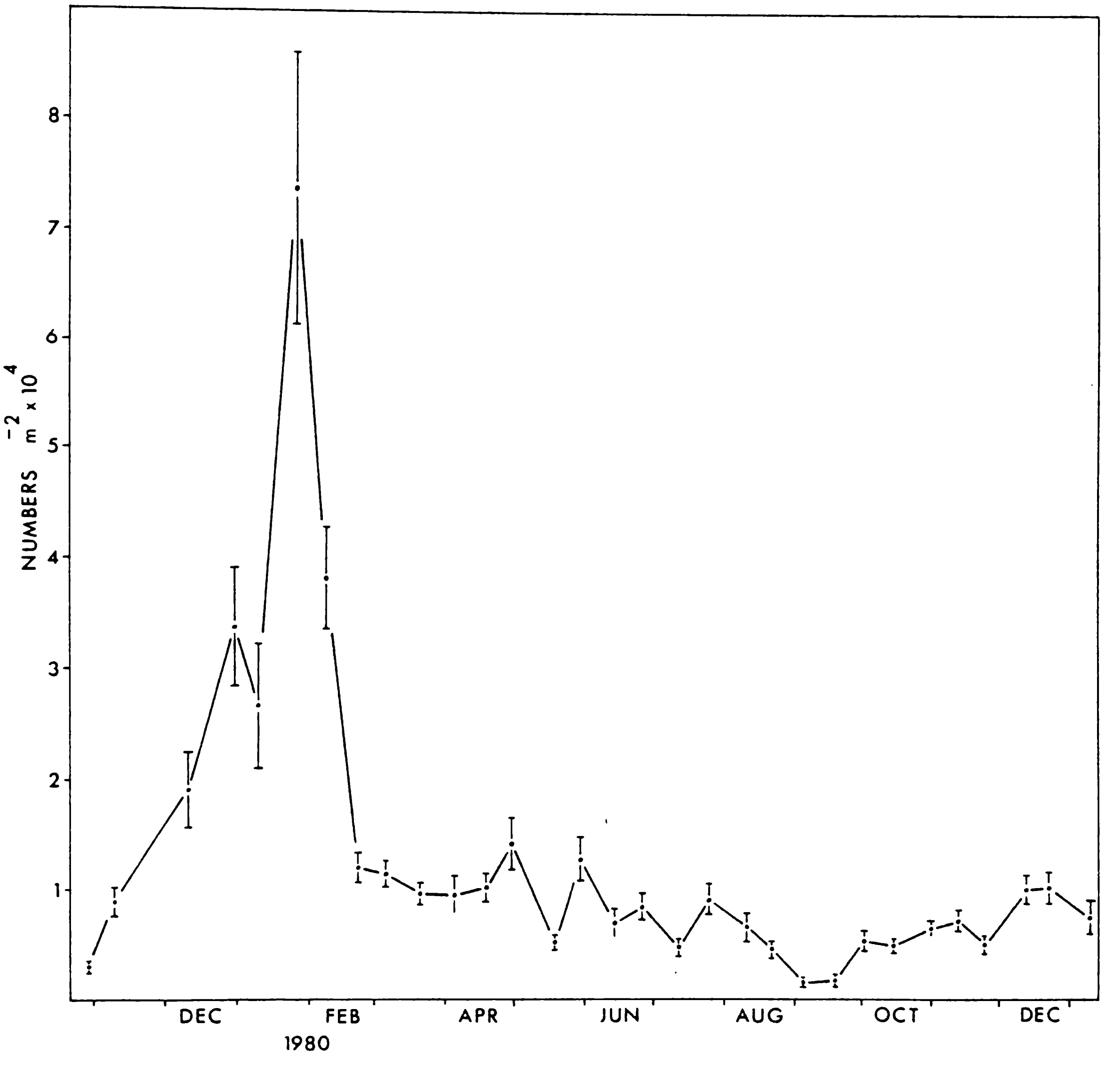


FIG. 25 Mean (± standard error) densities of Orthoclad chironomid midge larvae on the littoral bench at Waihaha Beach between 1.0m and 3.0m depth.

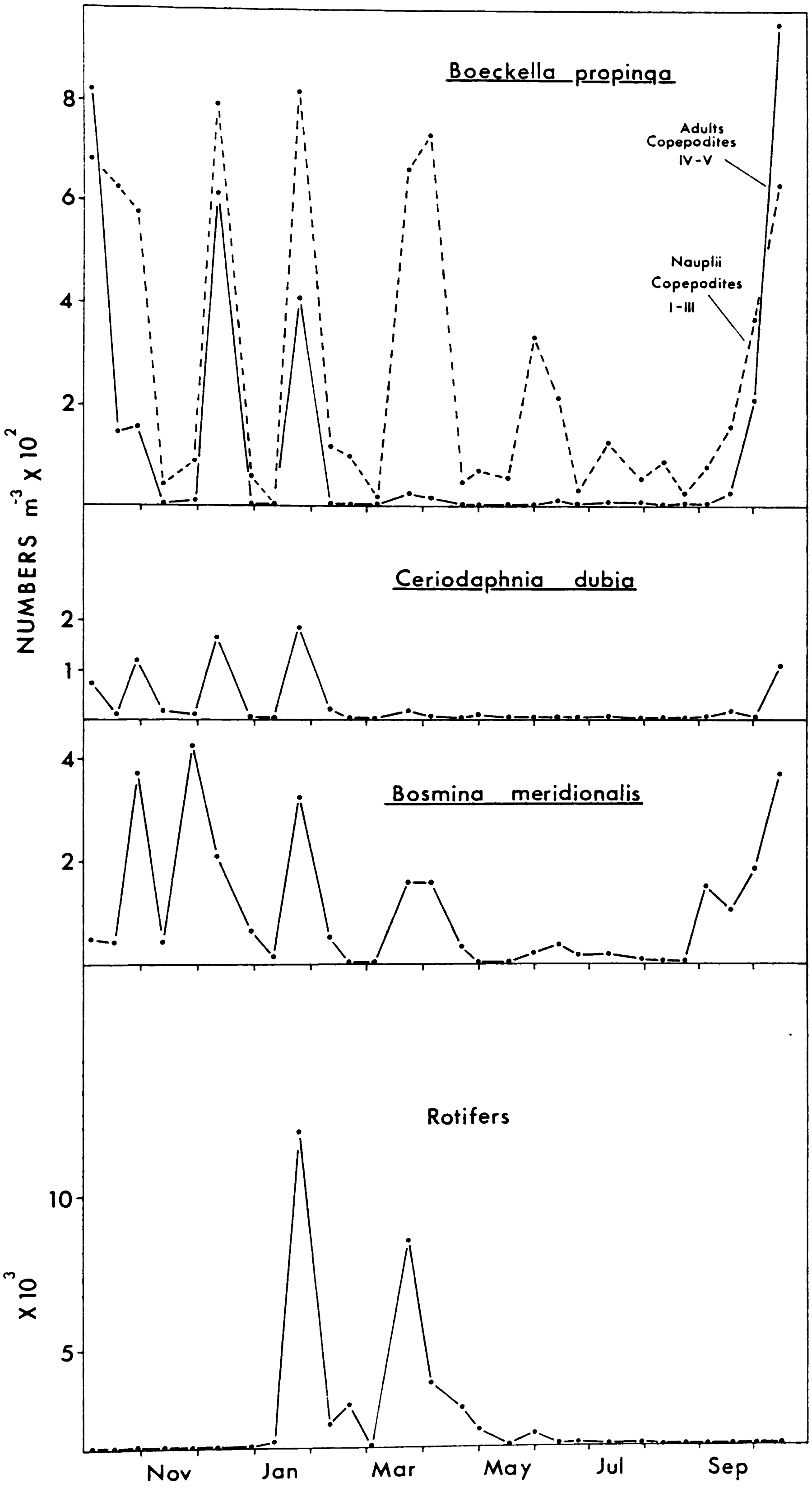


FIG. 26 Abundances of zooplankton species at Waihaha Beach.

CHAPTER 4 - **REPRODUCTION**

1. Spawning habitats and season

Ripe smelt were present for eight months of the year, between September and April. They became abundant in preferred spawning areas during October and by mid-December were numerous in most suitable localities. Maximum spawner densities (20 to 100 m^{-2}~~-100mm^{-2}~~) were found in the lower 100m of Western Bay tributary streams where the substrate was sandy and current velocity 0.1 to 0.3 m,~~-0.3m~~s^{-1} ; sufficient to transport pumice sand and prevent algal mats developing. Rainbow trout spawned further up these streams during winter but adults were scarce in streams during summer and absent in the open sandy reaches preferred by smelt. However they were almost continuously present and feeding actively around stream mouths throughout the smelt spawning season. Bullies and koaro were present in and around streams for most of the year.

Most smelt spawned within 200 metres of the lake and numbers typically diminished rapidly further upstream. Waterfalls (0.4 km up the Whanganui stream, 0.8km up the Waihora and 5km up the Waihaha) restricted upstream migration, but only a few reached the plungepools below these waterfalls.

Streams on the western side of the lake were used more intensively than those on the eastern side. Spawning smelt were almost absent from the Tokaanu, Tauranga-Taupo and Waitahanui streams throughout the spawning season, probably because the Tokaanu and Waitahanui streams were too swift near their mouths and the Tauranga-Taupo too variable in its flow and temperature characteristics (Schouten et al. 1981).

Limited numbers of spawning smelt were generally present in the Tongariro river mouth, the Waiotaka, Waimarino and Hatepe mouths and substantial numbers in the outlet to Lake Rotongaio. This was the only stable inflow on the eastern side of the lake which had especially suitable substrate and current velocity characteristics and was probably also a productive feeding area. (Catch data from these stream surveys are given in Appendix 2). Beach spawning habitat was most extensive along the eastern and northern lakeshores (fig. 27) and in these regions it seems likely that most smelt spawn on beaches. However in the Western Bay area, streams were most important.

Smelt egg densities reached 80,000m^{-2} in the Whanganui and Waihora streams but for most of the season were 20,000-40,000m^{-2} (fig. 28) and were most numerous near the centre of the main channel (fig. 29). At Waihaha beach, eggs were present over the whole littoral shelf (fig. 30) but tended to be scarce where organic detritus collected (2.0m during 1979-80) and where periphyton grew on the sand surface (3.0m and deeper). Maximum smelt egg densities were around 5000m^{-2} but egg densities normally averaged about 800m^{-2}. Relative proportions of beach and stream spawning habitat were estimated from aerial photographs by cutting out visible areas of sandy littoral habitat and the stream channels between the lake and the first waterfall and then measuring the surface area of the cutouts. The percentage of stream spawning habitat was calculated from:

$$\%\ \text{Stream area} = \frac{\text{Stream area}}{\text{Lake area} + \text{Stream area}} * \frac{100}{1}$$

Stream habitat provided about 4% of available spawning habitat in Waihora Bay, 7.5% in Waihaha Bay and 16% in Whanganui Bay. Assuming that egg densities at Whanganui and Waihora beaches were similar to those measured at Waihaha Beach, then the proportion of total spawning activity in stream and lake habitat can be estimated using the above percentages of stream spawning habitat and average smelt egg densities (800m^{-2} along the lakeshore and 30,000m^{-2} in streams):

$$\begin{array}{l}\text{Proportion of}\\ \text{total spawning}\\ \text{in streams}\end{array} = \frac{\%\ \text{stream habitat} * 30{,}000}{(\%\ \text{stream habitat} * 30{,}000) + (\%\ \text{beach habitat} * 800)}$$

Thus from 60% of total spawning activity in Waihora Bay to 90% in Whanganui Bay took place in streams. It seems, therefore, that in the Western Bay area, stream spawning habitat is of major importance to the smelt population. **{Cont'd on Pg.73.}**

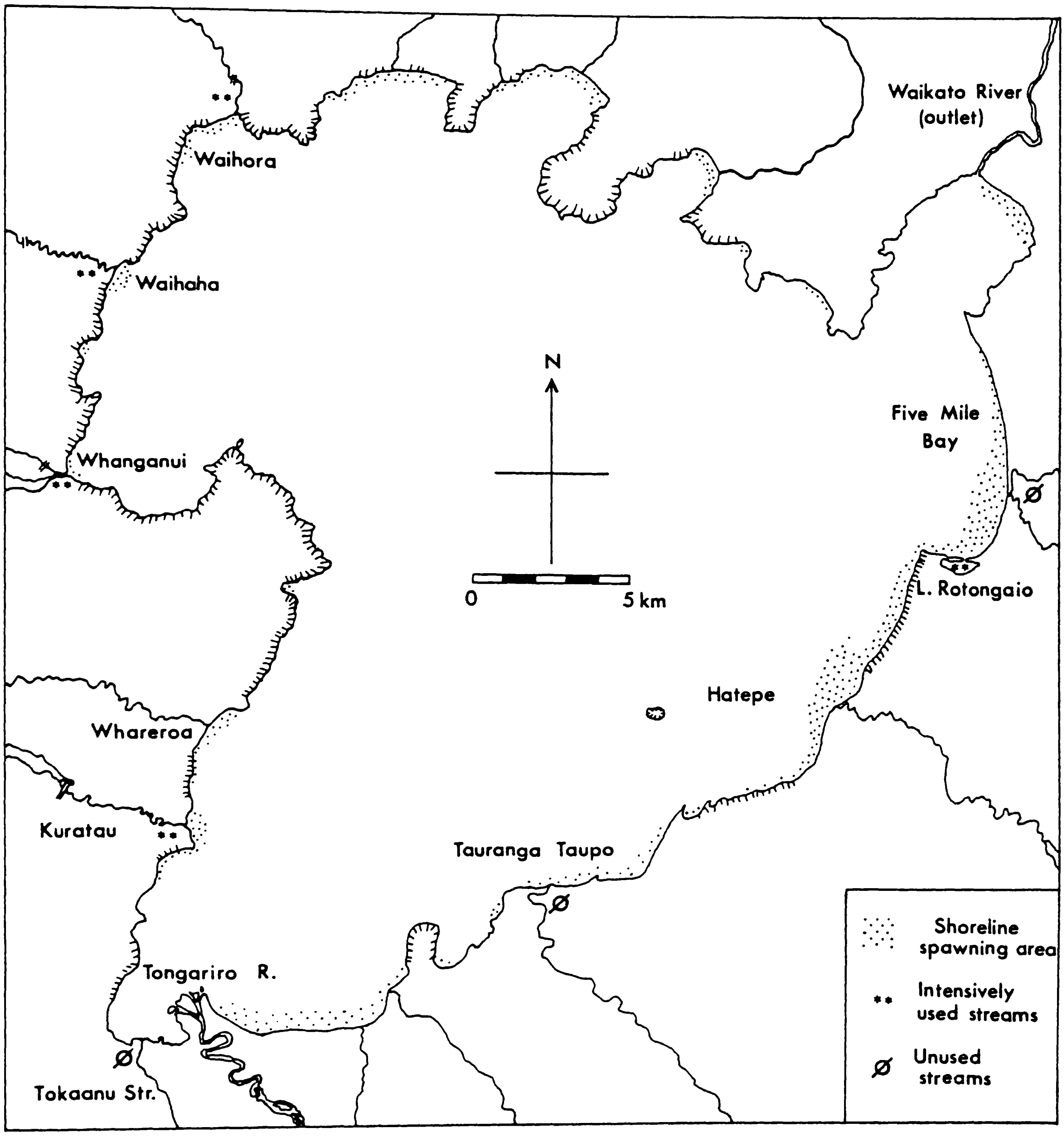


FIG. 27 Smelt spawning areas in Lake Taupo.

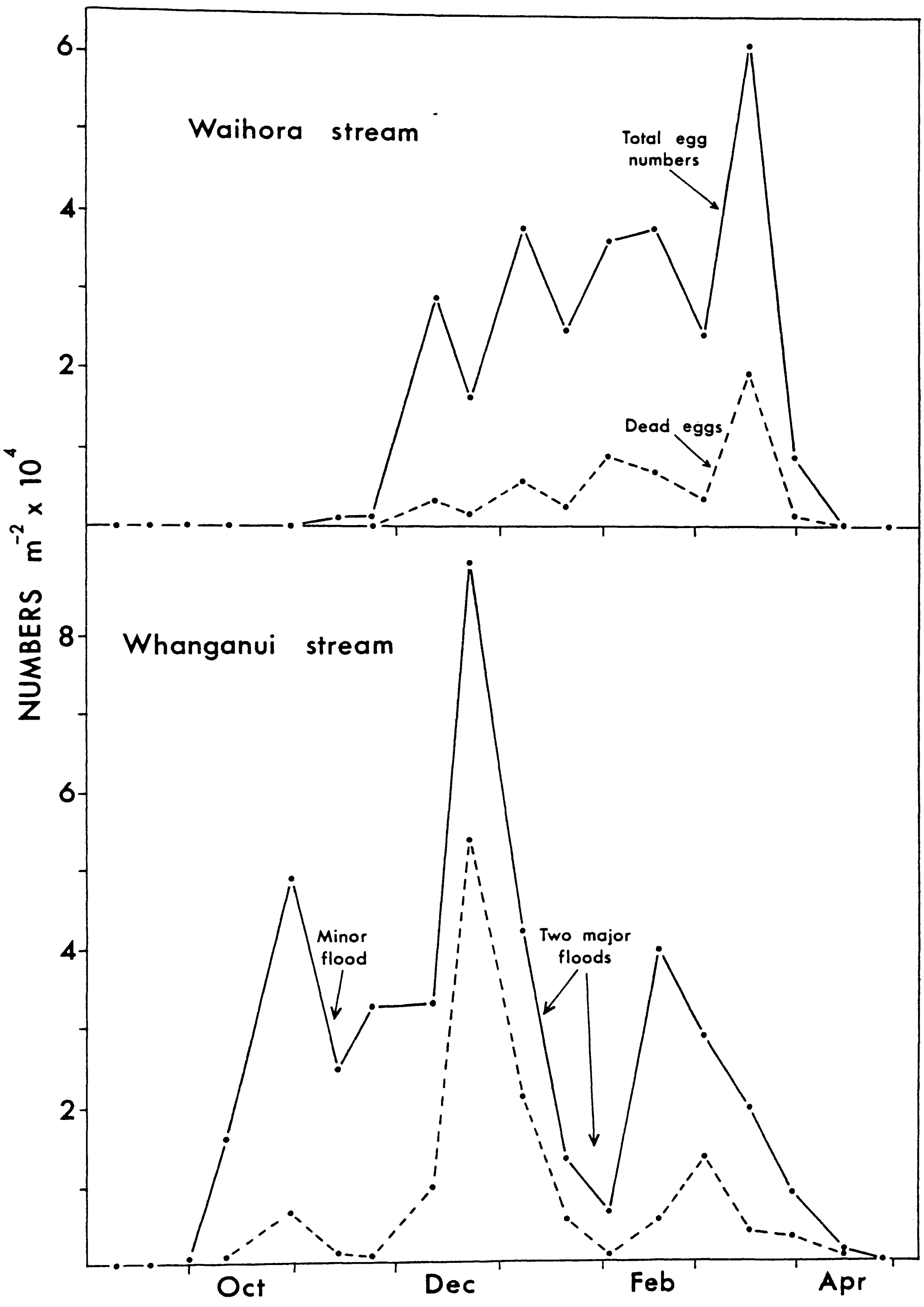
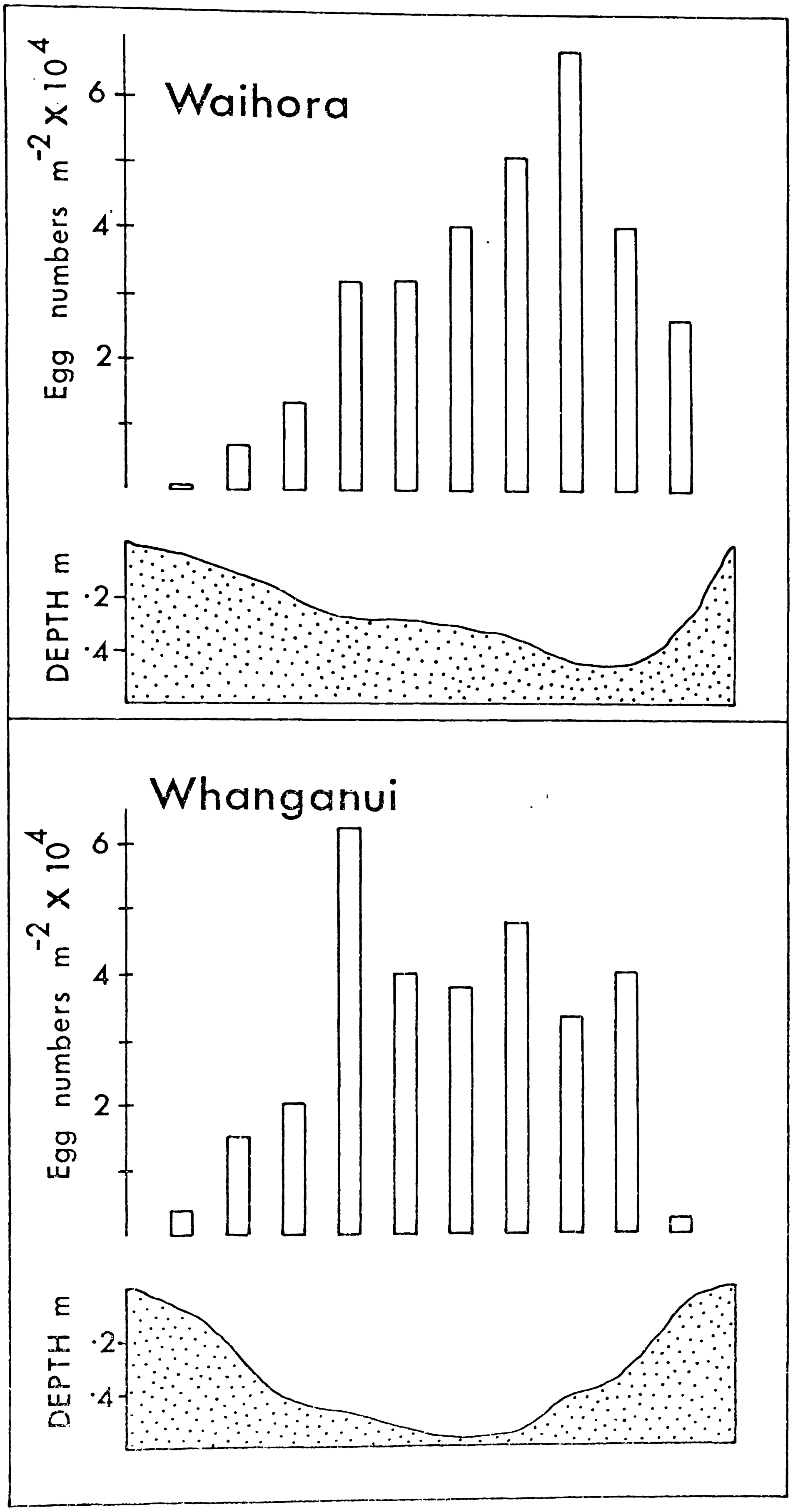


FIG. 28 Smelt egg densities in the Whanganui and Waihora streams between September 1980 and April 1981.

FIG. 29

Distribution of smelt eggs along transects across the channels of the Whanganui and Waihora streams. Data are mean estimates for all samples collected between October 1980 and March 1981.


Waihora
Egg numbers m^{-2} X 10^{4}
6
4
2
DEPTH m
·2
·4
Whanganui
Egg numbers m^{-2} X 10^{4}
6
4
2
DEPTH m
·2
·4

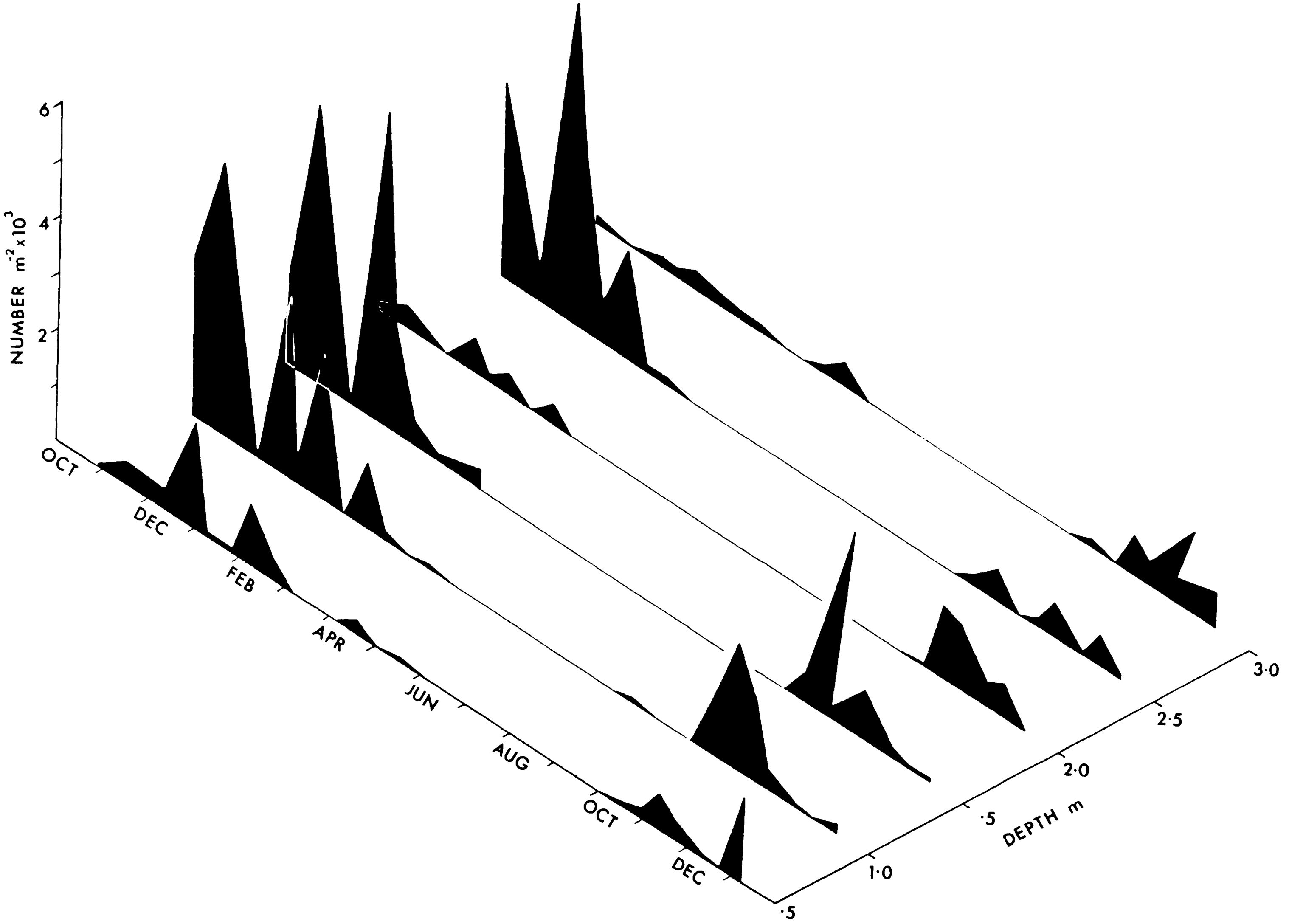


FIG. 30 Distribution of smelt eggs down the Waihaha littoral bench between October 1980 and December 1981.

However these were the most extensively used of all the lake's tributaries and so extrapolation of these results to describe reproductive habitat utilization for the whole lake is misleading. If the Whareroa stream, Kuratau river and the Lake Rotongaio outlet were used as extensively as the Western Bay streams and the Tongariro river, Waimarino, Waiotaka and Hatepe streams used half as much, while all suitable beach spawning areas were equivalent to Waihaha Beach, then only 5-10% of total spawning would take place in streams.

(a) Spawner population structure and processes

Spawners comprised from 10-30% of adults in samples collected at Waihaha Beach and 30-90% in stream samples (fig. 31). The proportion increased whilst mean and minimum length decreased as the season progressed. It seems that maturing smelt did not grow; that larger smelt matured before smaller ones; that post-spawning survival was negligible, but possibly better for smaller smelt as only these remained at the end of the season. The diminishing mean diameter of eggs laid as the season progressed (fig. 32) was perhaps a reflection of this size decrease in spawners.

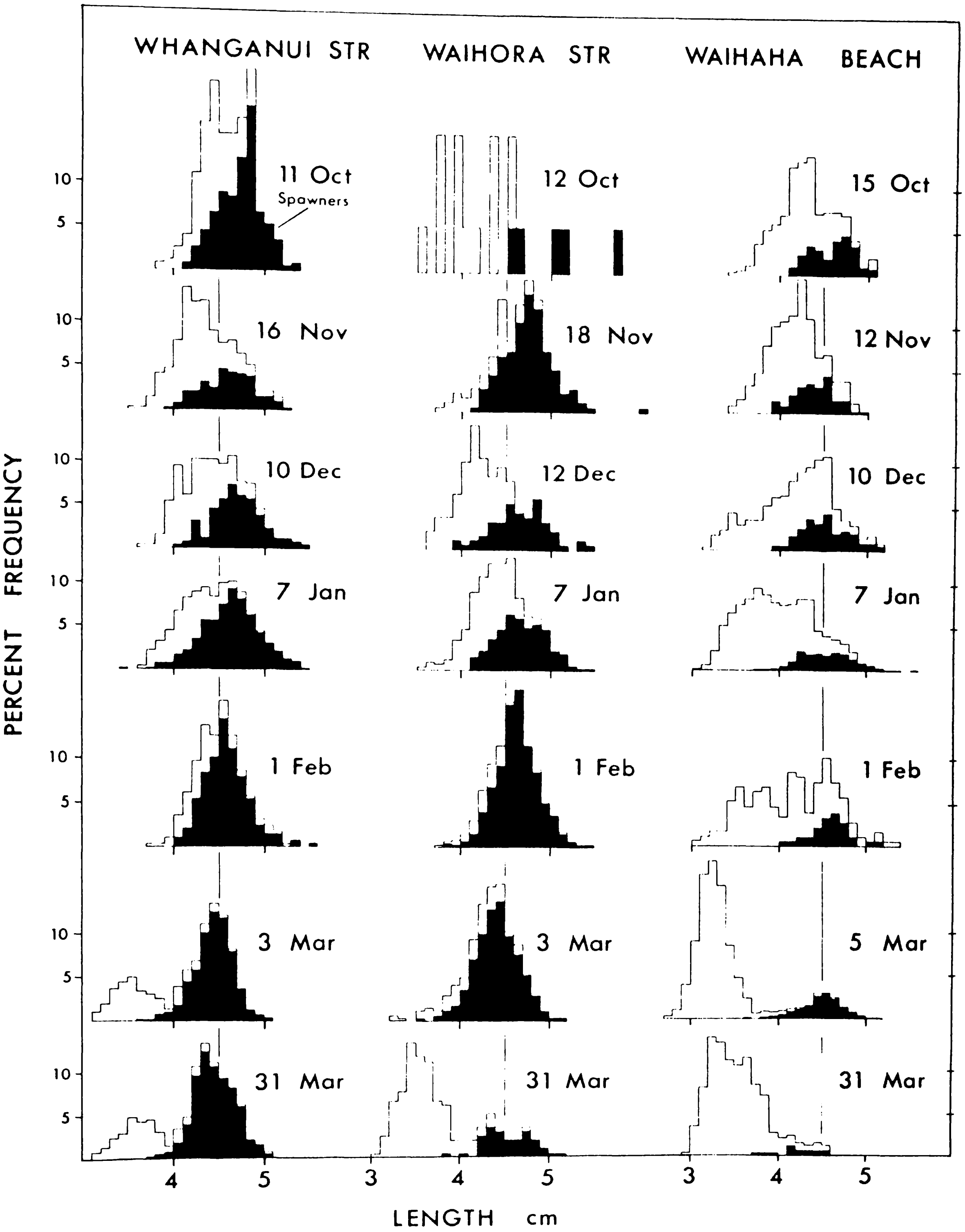


FIG. 31 Length frequency distributions of smelt taken at Waihaha Beach, the Whanganui and Waihora streams throughout the October 1980 to March 1981 spawning season. The black areas in each histogram indicate the length frequency distributions of ripe smelt.

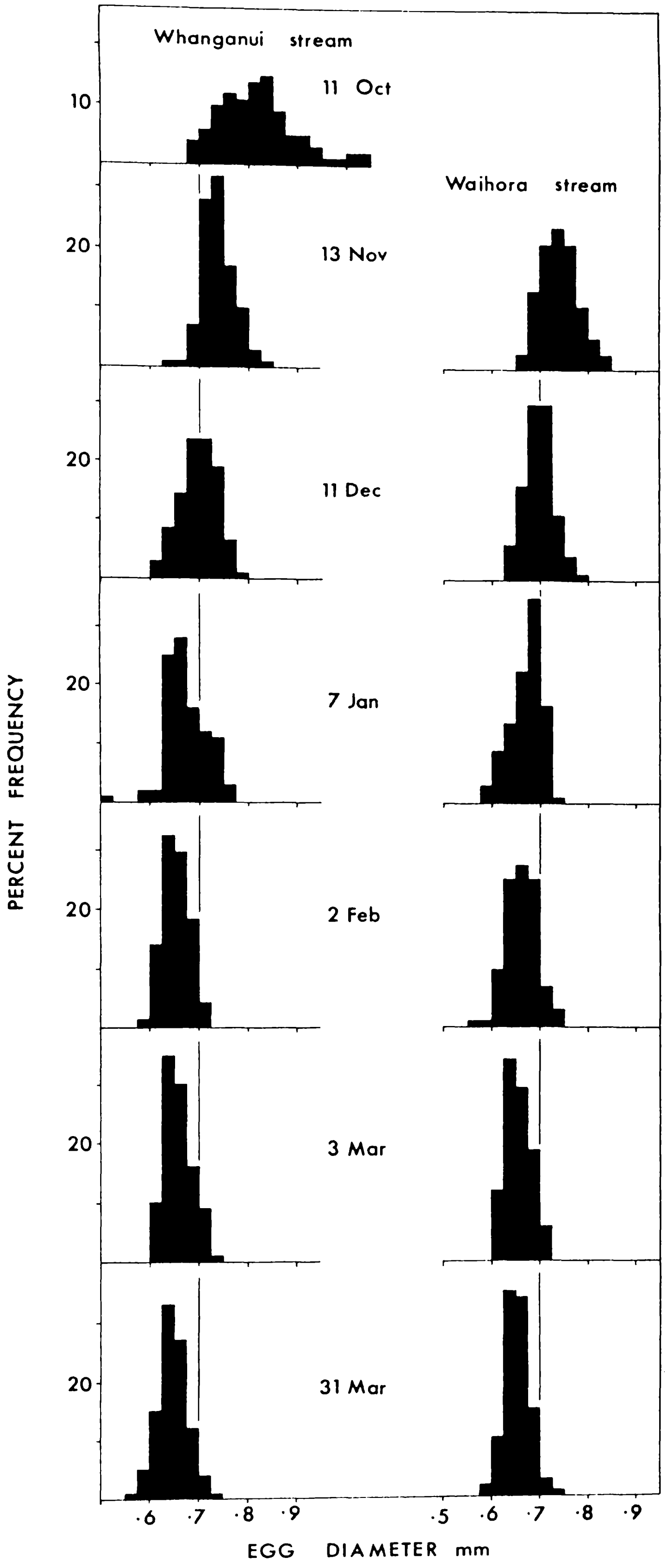


FIG. 32 Diameters of smelt eggs collected from the Whanganui and Waihora streams between October 1980 and March 1981.

2. Smelt gonad development

(a) Females

Only one gonad develops in *R. retropinna* and for females taken early in the season the ovary typically contained two ova size classes (fig. 33). The smaller group was a mixture of primary oocytes and small vacuolated, but not yolked, developing ova. The larger group consisted entirely of maturing yolky ova. Extensive firm yellow fat bodies attached to the viscera were typical in these fish. The ovary in running ripe females was usually 20-30% (max. 42%) of somatic weight and they contained three ova size classes. The smallest were primary oocytes; the intermediate group were vacuolated and often yolky; the largest were fully developed spherical golden ova with 3-5 oil droplets. Numbers present in the intermediate and mature groups were similar but highly variable (150-1500) and correlated with length (fig. 34). Mature and intermediate size groups were segregated within the ovary of running ripe females; mature ova were loose in the ovary whilst the intermediate group remained bound by ovarian tissue in the anterior lobe and dorsal region of the ovary. Visceral fat bodies in running ripe females were less extensive and not so cohesive as in less mature smelt.

(b) Evidence for repeat spawning

Recently spawned females were in visibly depressed condition, but after dissection it was clear that their ovaries were redeveloping prior to spawning a second time. The size frequency distribution of their ova was similar to that of maiden females except that large atretic ova were often present amongst the posterior developing ova. Visceral fat bodies, if present, were small, pale and inclined to disintegrate in these smelt. Running ripe females thought to be about to spawn for the second time were still in poor condition, having no visceral fat, and mature ova were paler than in maiden spawners. However atretic ova from the previous spawning were rarely found in these fish. Fully spent smelt were severely emaciated and condition factors of 0.6 - 0.7 were typical; many had finrot and whitespot infections and it seemed that smelt were probably not capable of spawning more than twice in a season.

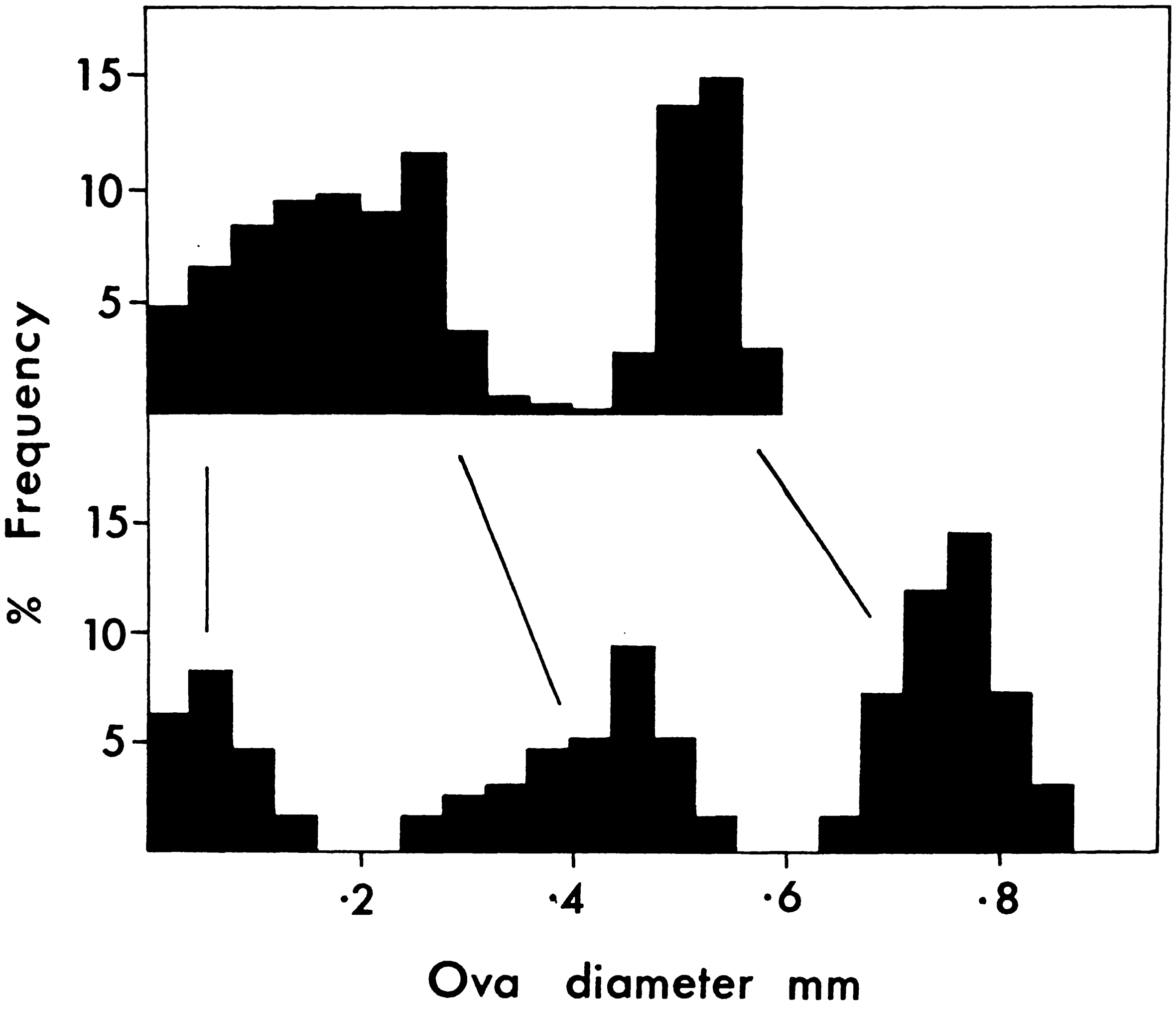


FIG. 33 Ova size frequency distributions from a maturing ovary (top) and from a running ripe smelt.

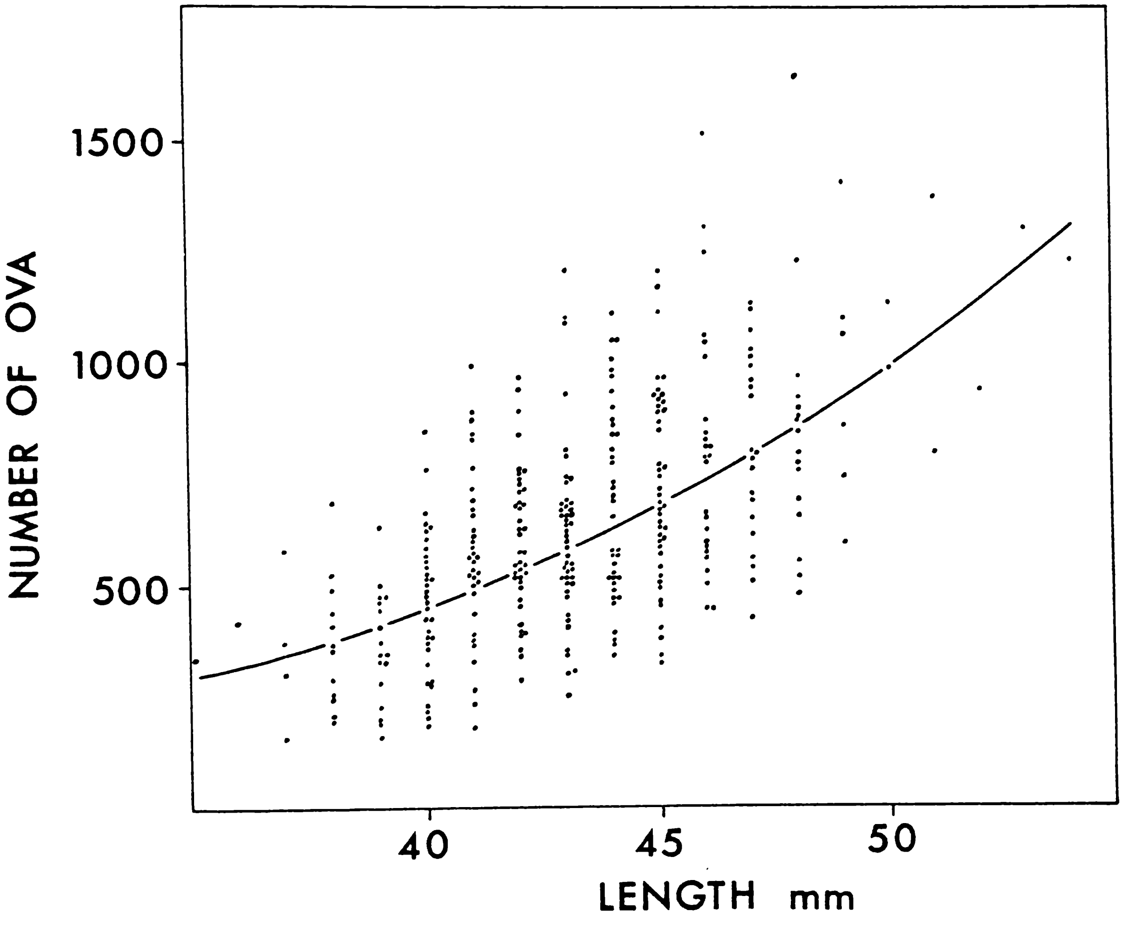


FIG. 34 The relationship between body length and the number of maturing ova in the ovary. All data from Waihaha Beach, the Waihora and Whanganui streams are included.

$y = 7.84 \times 10^{-4} x^{3.59}$ $R^2 = 0.43$

FIG. 35

Proportions of maiden and repeat spawners (black) throughout the 1980-81 spawning season at Waihaha Beach, the Whanganui and Waihora streams. The number of females examined in each sample is indicated beneath each column.

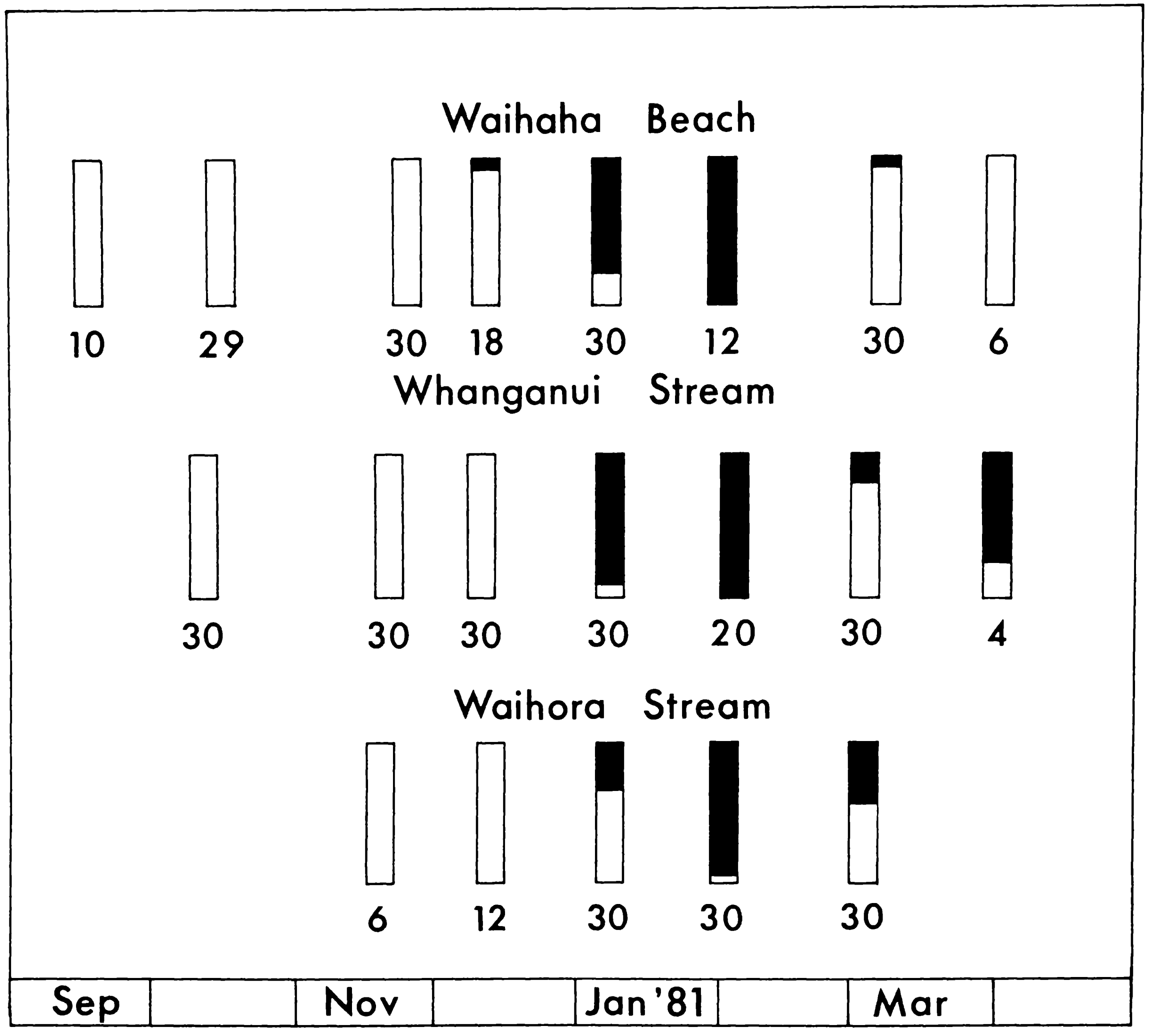

Waihaha Beach
10
29
30
18
30
12
30
6
Whanganui Stream
30
30
30
30
20
30
4
Waihora Stream
6
12
30
30
30
Sep
Nov
Jan '81
Mar

FIG. 36

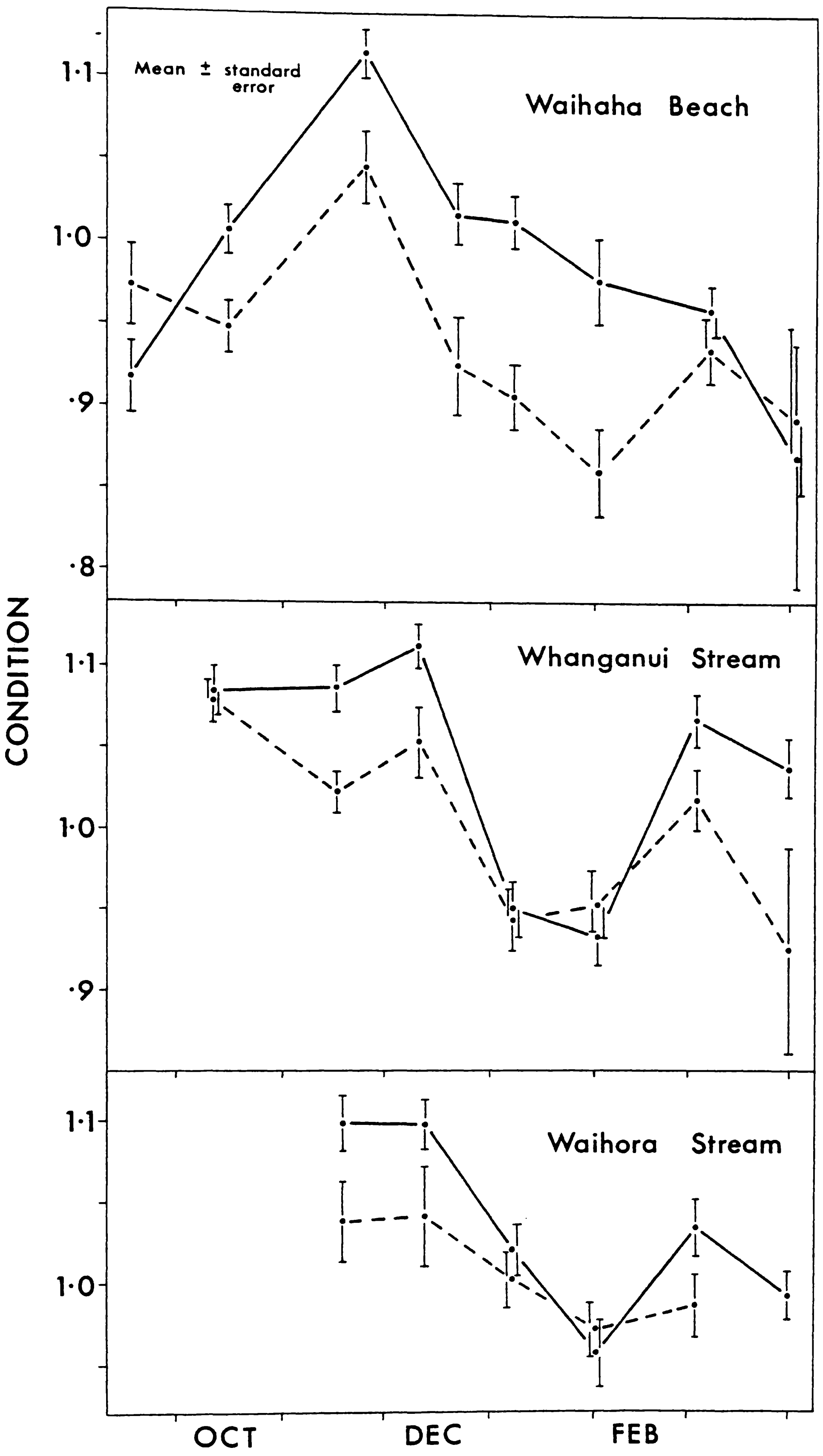
Condition factors of ripe male (continuous line) and female (broken line) smelt at Waihaha beach, the Whanganui and Waihora streams between October 1980 and March 1981.

$$\text{Condition factor} = \frac{\text{Weight}}{\text{a Length}^{\,b}}$$

where a and b are coefficients for the weight-length relationship (fig.24), weight expressed in grams and length in millimetres.

$a = 1.316\text{ E-07}$

$b = 4.053$


Mean ± standard error
Waihaha Beach
Whanganui Stream
Waihora Stream
CONDITION
1·1
1·0
·9
·8
OCT
DEC
FEB

(c) Male gonad development

The reproductive cycle of males was less complex. The testis ran the whole length of the body cavity but was never as bulky as a ripe ovary although visceral fat was often more extensive. Spent males were in very poor condition and often diseased although the anterior lobe and dorsal parts of the testis still contained milt.

Some large males taken near the end of the season which had no distinguishing secondary sex characteristics but had little visceral fat, may have been recovering post-spawners. It seems that males became ripe and remained sexually active for an extended period whereas females spawned in pulses. Both sexes lost considerable condition, suffered infections and presumably intense mortality was associated with these. It seems likely that after spawning for the second time most, and perhaps all, repeat spawners died.

(d) Maiden and repeat spawners

The proportion of maiden and repeat spawning ripe females was estimated monthly from Waihaha Beach, Whanganui and Waihora stream samples (fig. 35). The first arrivals were all maiden spawners; repeat spawners were not detected until December at Waihaha Beach and not until January in the two streams. Most ripe females present during January and February were repeat spawners but during March a major run of maiden smelt arrived at each site. Mean condition factors of both ripe males and females (fig. 36) are consistent with such a sequence of events.

3. Post-spawning survival

The time lag between maiden spawners first becoming abundant and the first appearance of repeat spawners was 50-60 days and it seems likely that this represented the recovery period between the first and second spawning. Mortality attributable to spawning alone was estimated by observing post-spawning mortalities amongst ripe smelt recently arrived in the Waihaha stream that were held in an enclosure. Pre-spawning mortality was recognised in dead females if significant numbers of mature ova were present in the ovary and in dead males if milt was present throughout the testis. The first smelt to die were still ripe and so probably succumbed to handling stress. Twenty of the twenty-four pre-spawning deaths occurred during the first nine days of confinement and were probably amongst the most mature fish which are more sensitive to handling.

After 22-25 days of confinement when the number of post-spawning mortalities became negligible, all remaining smelt were removed. Two males and four females could not be accounted for, perhaps because they were taken by kingfishers *(Halcyon sanctus)*. The remaining smelt were all spent and some males had lost their secondary external sex characteristics and no milt was present in their testis. However most males were still recognisable externally and the anterior portions of their testis contained milt. All females had residual ova in their ovaries and these seemed to be redeveloping in some. The condition of surviving smelt appeared to the eye to range from normal to moderately depressed; none were severely emaciated and there was no reason to expect many more to die.

Thus all surviving smelt spawned within 20-25 days of capture and 50-60% died after spawning. There was also a tendency for larger smelt to die before the smaller ones (fig. 37) and this accounted for much of the difference between the survival of males and females and also the size difference between dead and surviving post-spawners.

TABLE 5 Mean lengths (mm) ± standard deviation of dead and surviving male and female smelt after 26 days of confinement.

	MALES	FEMALES
Dead Smelt	47.4 ± 2.9	43.0 ± 2.2
Survivors	44.3 ± 2.3	40.4 ± 2.3

A reciprocal equation which predicts the proportion of a sample of ripe smelt surviving spawning in terms of both length and time was fitted (fig. 37) thus:

$$\text{Spawning Survival} = \frac{1}{1 + bT\,(L_i - 33)}$$

$$b = .00525 \qquad (7)$$

where T is time (days) elapsed since sample collection and length (L_i) is expressed in millimetres.

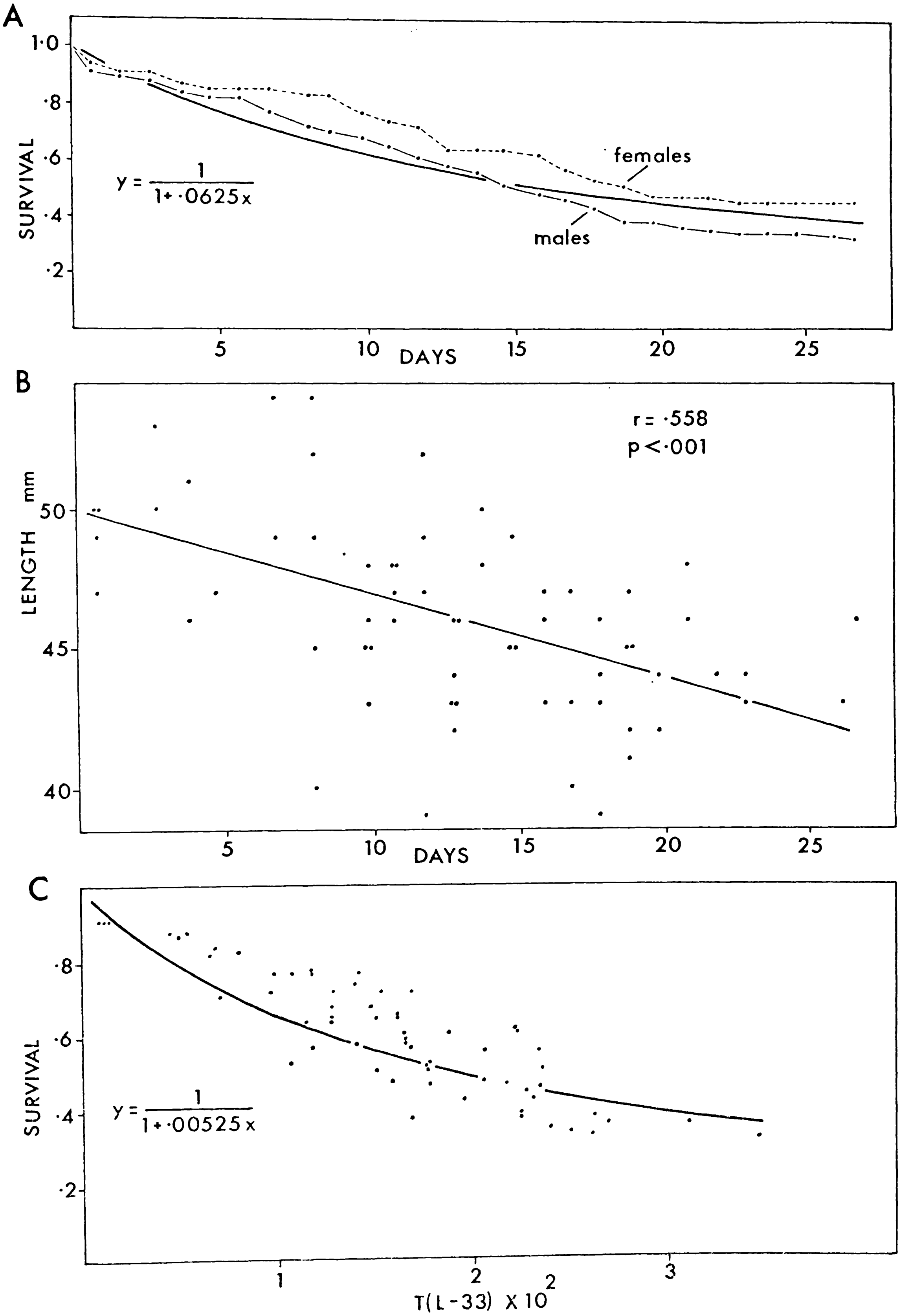
FIG. 37

Survival of ripe smelt confined in an enclosure.

A. Total survival, including pre-spawning mortalities.

B. The relationship between smelt length and the number of days the fish remained alive in the enclosure.

C. Length dependent survival in the enclosure.


A
1·0
·8
·6
·4
·2
SURVIVAL
y = 1 / 1+·0625x
females
males
5
10
DAYS
15
20
25
B
r= ·558
p<·001
LENGTH mm
50
45
40
5
10
DAYS
15
20
25
C
·8
·6
·4
·2
SURVIVAL
y = 1 / 1+·00525x
1
2
3
T(L-33) X 10^2

The length term was constrained so that L_i-33 was always greater than or equal to zero. This provided additional realism because smelt smaller than 34mm did not spawn and so their theoretical spawning survival was complete.

Spawning survival in an enclosure may be equivalent to total post-spawning survival in streams where predators are scarce, but along the lakeshore where rainbow trout were numerous and feeding actively, it seems likely that post-spawning survival would be lower. Spent smelt which recover successfully in a stream might be unable to avoid trout predation if they were living in the lake.

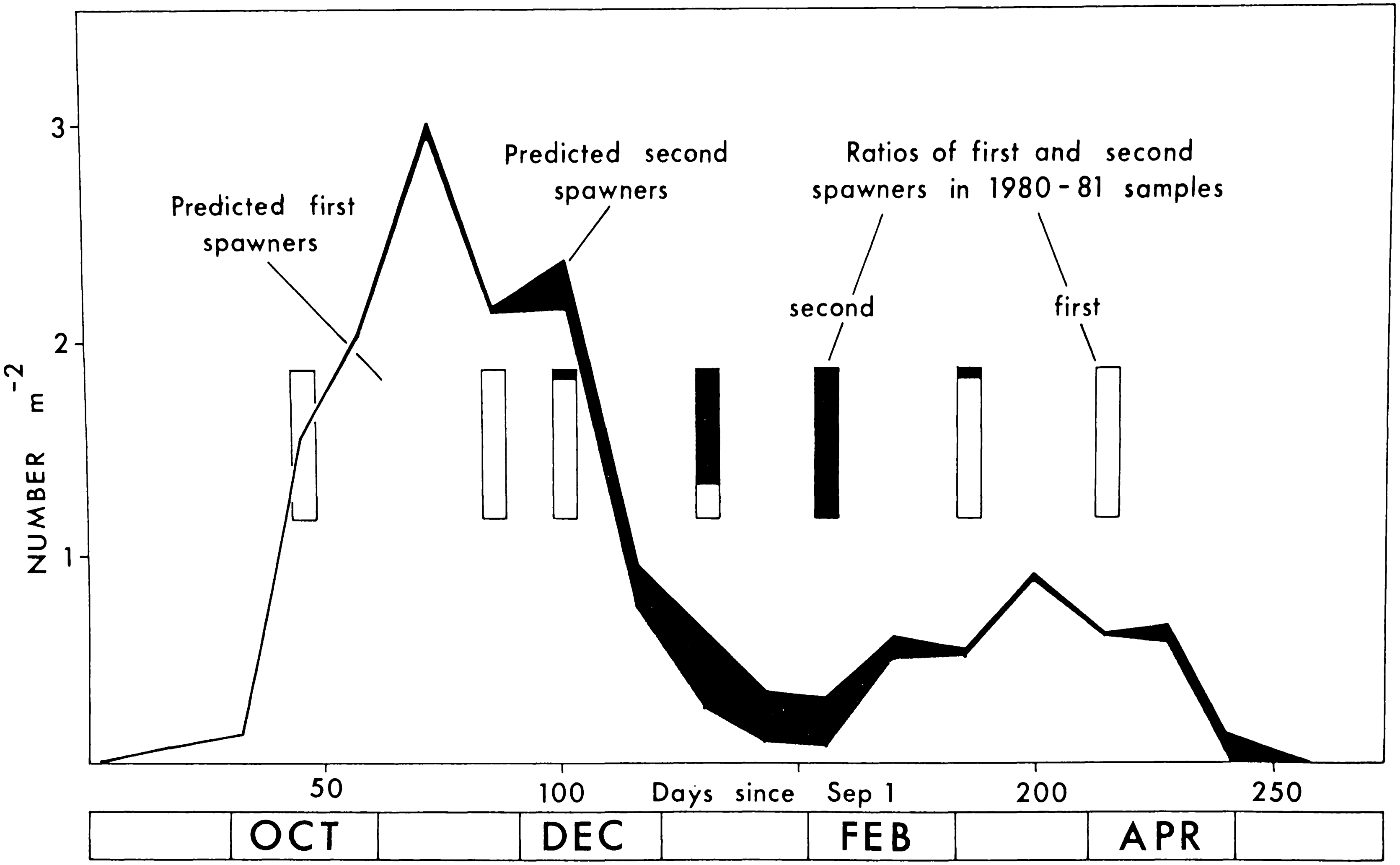
Total post-spawning survival at Waihaha Beach was estimated using fortnightly abundances of ripe smelt (fig. 38) and ratios of maiden to repeat spawners. Trial survival rates over a varied recovery period were applied to maiden spawner abundances to predict the number of repeat spawners present after the recovery period. The best fit to observed ratios of maiden to repeat spawners was found with 16% post-spawning survival over a 50 day recovery period. (Calculations are given in Table 6).

TABLE 6 Estimation of numbers of smelt spawning for the second time based on a 16% survival rate over a 50 day recovery period.

	A	B	C	D
DAYS SINCE SEPT. 1st	TOTAL SPAWNERS PER SEINE HAUL	FIRST SPAWNERS AT T-50 DAYS (linear extrapolation from D)	SECOND SPAWNERS (.16 x B)	FIRST (MAIDEN) SPAWNERS (A - C)
3	2.3	0	0	2.3
17.2	7.1	0	0	7.1
32.1	12.3	0	0	12.3
44.8	132.6	0	0	132.6
57.2	174	3.8	.6	173.4
72.2	256.7	8.4	1.3	255.4
85.6	183.7	43	6.9	176.8
100.6	202.2	52	8.3	193.9
115.5	81.7	220	35.2	46.5
130	56.5	208	33.3	23.2
143.8	29.7	186	29.8	-.1(0)
155.8	27.7	150	24.0	3.7
170	51.7	39	6.2	45.5
185	46.5	14	2.2	44.3
199.3	77.1	2.0	.3	76.8
214	53.4	27	4.3	49.1
227.5	56.1	44.6	7.1	49.0
239.5	11.9	55	8.8	3.1
257	.5	62	9.9	-9.4(0)

FIG. 38

Abundances of spawning smelt at Waihaha Beach between September 1980 and May 1981 and predicted numbers of maiden spawners (open areas) and repeat spawners (black areas) given 16% survival after a 50 day recovery period. Ratios of maiden and repeat spawners estimated from catch subsamples (vertical bars) are included for comparison.


Predicted first spawners
Predicted second spawners
Ratios of first and second spawners in 1980-81 samples
second
first
NUMBER m^{-2}
3
2
1
50
100
Days since Sep 1
200
250
OCT
DEC
FEB
APR

This approach assumes that spawners and spent smelt do not emigrate, and their absence in ringnet tow samples, despite the presence of maiden adults, supports the assumption. The spawning survival model predicts survival after 50 days to be .24 (for 45mm smelt) whilst total post-spawning survival was estimated to be 0.16. The proportion of a sample of ripe smelt which survive spawning and also survive predation for 50 days might therefore be:

$$SP_{tot} = \frac{\text{Total survival after 50 days}}{\text{Spawning survival after 50 days}} = \frac{.16}{.24} = .67$$

Since spawning survival in the enclosure was probably underestimated because of stress associated with handling and confinement it follows that predator survival would be overestimated. Thus it seems that at least a third, probably more, of the smelt which survived spawning were taken by predators. Predators and scavengers also must have taken almost all of those which died after spawning because spent smelt carcases were scarce and rarely found.

4. Summary and discussion

The total number of eggs likely to be laid by a female smelt is greater than the number of maturing ova in her ovary (fig.33) because she may survive to spawn again later in the season. Post-spawning survival for stream spawning smelt may have been higher than for beach spawners which were exposed to more intense predation by trout and large bullies which were scarce in favoured spawning streams. Thus one might expect stream spawners to produce more eggs per fish because of increased post-spawning survival in streams. However smelt densities in streams were substantially greater than was usual along the lakeshore and presumably competition for available food resources was correspondingly more intense in streams and so reduced their potential as feeding areas. The low proportion of juvenile and non-reproductive adult smelt in streams compared with the lakeshore (fig. 31) may be a consequence of the relatively low value of stream habitats for smelt feeding. Extrapolation of smelt density estimates in stream mouths and along the lakeshore suggested that only 5-10% of the population breed in streams. Thus it seems that gains in egg production obtained by spawning in areas of lower predation risk are smaller than those accrued from spawning in places where feeding success is better. This situation could reverse if shoreline predation increased substantially, if feeding opportunities in streams were enhanced relative to the shoreline or if smelt densities in streams were considerably lower.

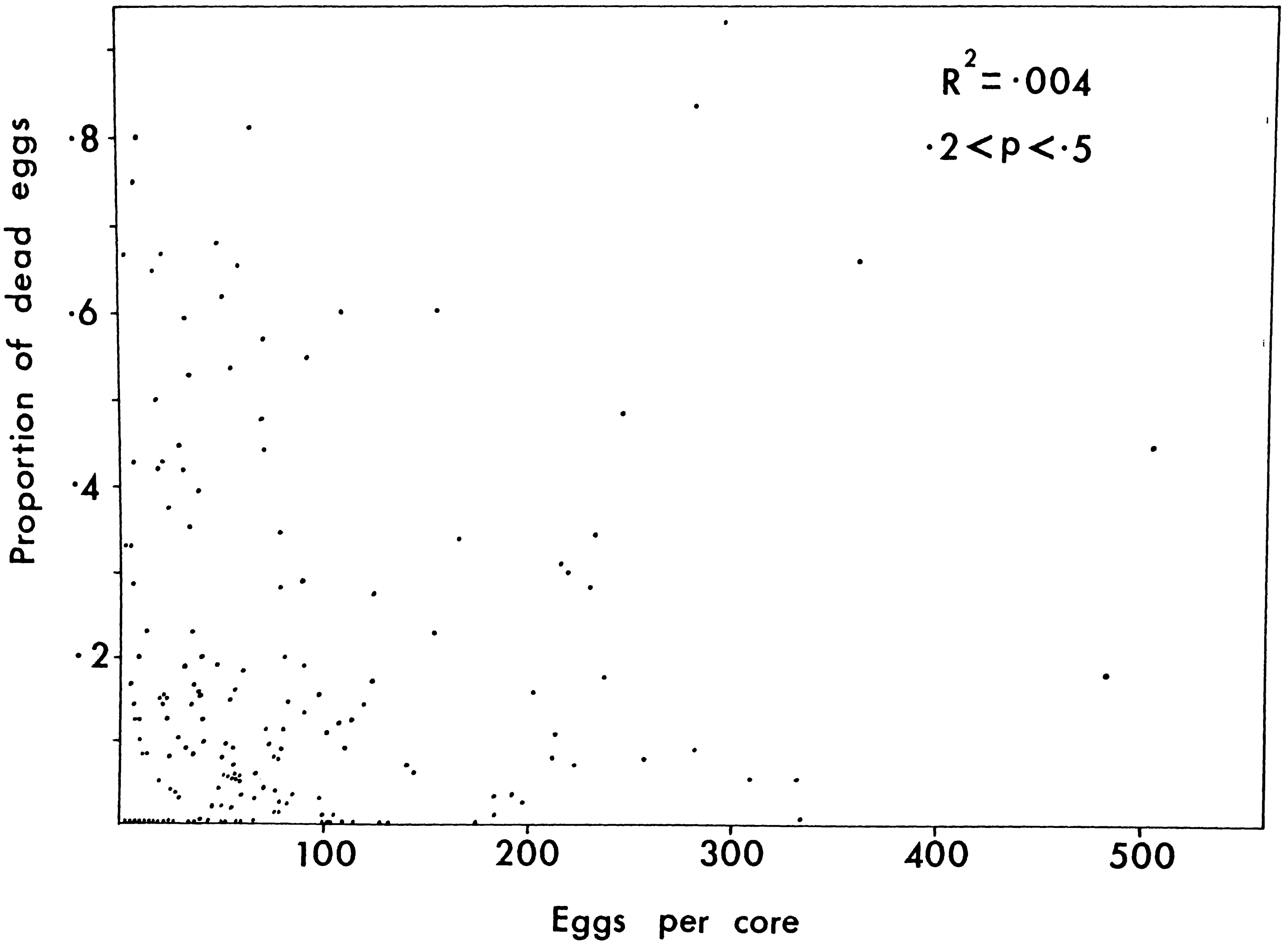
CHAPTER 5 - SURVIVAL

1. Sources of egg mortality

Smelt egg samples generally contained a few infertile eggs and a greater number which had died after fertilisation. Infertile eggs comprised only 2.4% of the samples and so this would have little influence on reproductive output. Eggs which died after fertilisation comprised 18% of those collected in the Waihora stream, 28% in the Whanganui stream and 46% on Waihaha Beach. These were infected by a fungus but it is not clear whether the fungus was the cause of death or merely a saprophyte. Infected eggs were found to be in all stages of development but most seemed to have died soon after fertilisation. There was no siginificant correlation between egg numbers per core and the proportion of dead eggs present (fig. 39). Thus the source of mortality was not density dependent and so it would seem that spawning success is unlikely to be restricted by the amount of suitable habitat available. Therefore, from this and because smelt are not territorial in their breeding habits, it seems unlikely that population numbers would easily be limited by the extent of suitable spawning areas. The correlation between water temperature and the proportion of dead eggs present at each sampling date (fig. 40) was significant and although this accounted for much of the difference between stream and beach samples, the difference between the two streams remained anomolous as the Waihora was slightly warmer than the Whanganui stream (fig. 6). There were, it seems, additional but unidentified physical or chemical factors influencing egg survival.

FIG. 39

Correlation between smelt egg numbers per core and the proportion of dead eggs in each sample. Data from all cores collected from Waihaha Beach, the Whanganui and Waihora streams between October 1980 and March 1980 are presented.


R^2 = ·004
·2<p<·5
Proportion of dead eggs
·8
·6
·4
·2
100
200
300
400
500
Eggs per core

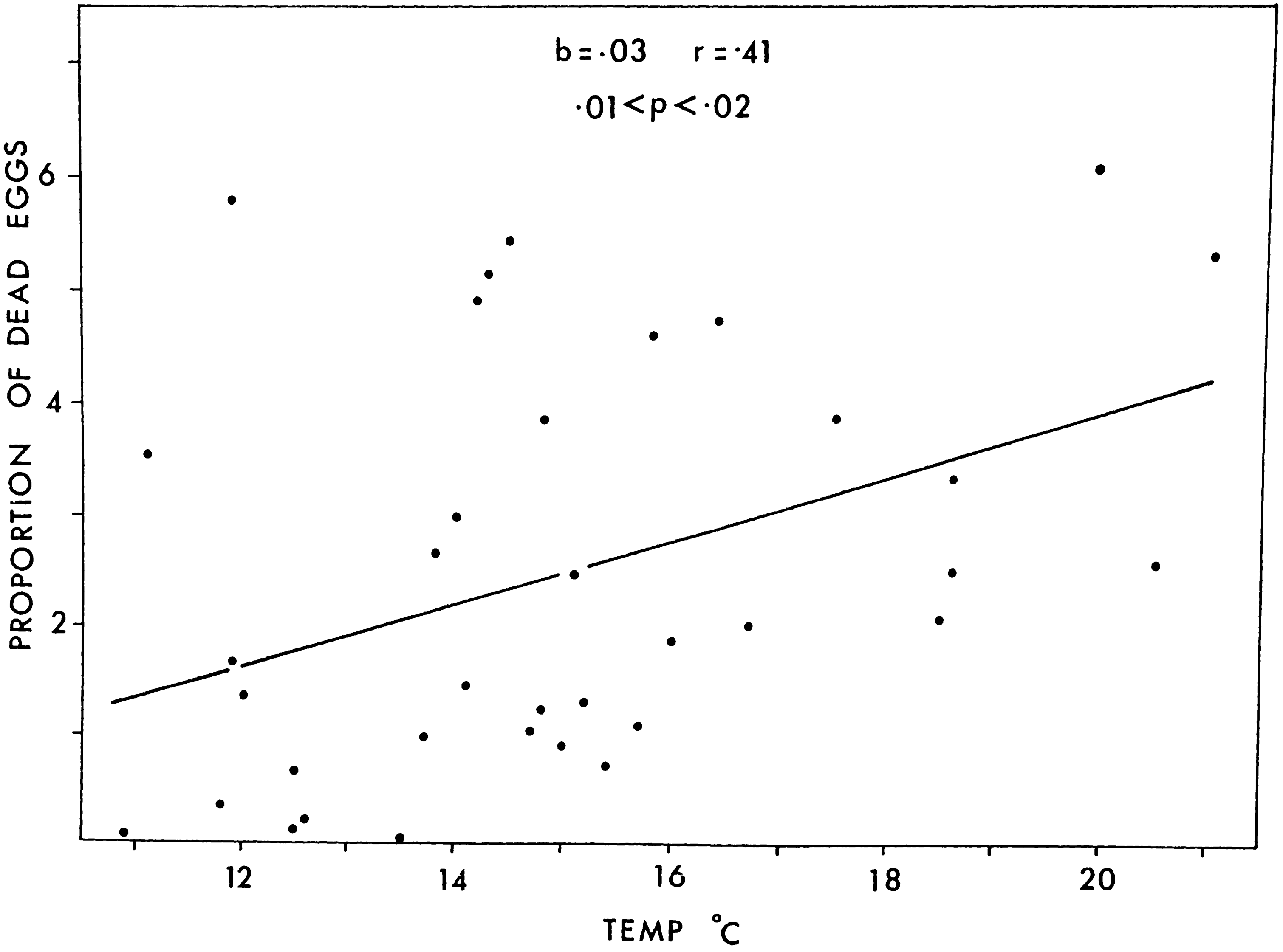


FIG. 40 Correlation between water temperature and the proportion of dead smelt eggs present in core samples.

Weather conditions had a profound effect on egg densities. Freshes after heavy rain severely reduced densities in the Whanganui stream but not in the more stable Waihora stream (fig. 28) whose flow is little affected by heavy rainfall. Presumably intense egg mortality was associated with these events as eggs carried by the flow would have been redeposited in the lake amongst fine silt and organic detritus also being carried by the stream. Low flows during extended summer drought conditions which occurred in 1982 and the 1982-83 summers permitted growth of thick algal mats (*Melosira sp.* and *Oscillatoria sp.*) over almost all of the stream channel. Smelt eggs could not be found amongst these growths, despite the presence of numerous spawners and it seemed that smelt avoided spawning in these areas. There was little, if any, adequate spawning habitat between late January 1982 and early March 1983 in the Waihaha stream, and the Waihora and Whanganui streams were almost as severely affected. Streams on the eastern side of the lake have more variable flow regimes (Schouten et al. 1981) so that extreme conditions probably occurred sufficiently frequently to make them comparatively unsuitable for smelt spawning.

Wave action during strong onshore winds reduced egg densities at Waihaha Beach (fig. 41) and presumably the eggs were carried away to be redeposited in deep water where conditions may not be adequate for survival. During periods of calm weather periphyton accumulated on the sand surface and few eggs were found amongst this. However calm spells were not long enough to permit much periphyton development in less than 2.0m depth and consequently there were always substantial areas available for spawning. Low lake level conditions probably increased susceptibility to mortality associated with wave action but this wave action also inhibited periphyton growth and so extended suitable spawning habitat.

Stream spawning may be restricted by both summer floods and summer droughts but these do not affect beach spawning. Extended dry, windy summer conditions associated with a low lake level would constitute the least favourable spawning conditions and would be likely to cause low year class strength, but as smelt were able to spawn over more than half the year, suitable weather conditions would be encountered at least intermittently. Lake level fluctuations of up to 10cm in a week can occur in Lake Taupo but these are unlikely to influence smelt egg survival as few eggs were present along beaches at depths less than 0.5m and egg development time is relatively brief, being about ten days (Jolly 1967).

Egg mortality due to predation was probably very low. Whilst both bullies and smelt eat smelt eggs (Tables 4 and 7), their densities and the number of eggs present in their stomachs were small in comparison to measured egg densities. Predation by larval Tanypodinae, a group of carnivorous chironomids, may have occurred in streams where they were abundant, but this was not investigated. Predation by large bullies and trout on spawning and recovering smelt was probably of much greater significance.

TABLE 7 Bully Stomach Contents. Data are numbers of each taxa per stomach.

DATE	LENGTH of Bully	Chironomid Larvae	Oligochaetes	Littoral Crustaceans	Smelt	Smelt eggs
6.9.79	76	1			1	1
	32	48	1			
	30.5	11				
	50	2				2
23.1.80	34	1				5
	31			6		
	30	37				11
	29	2				2
	28	4				
	27	2				
	25	8				1
	25	6		6		
	50	11			1	
	56				3	
	57	9	2			7
	65	72			1	
	68				1	
	72	3	1		1	

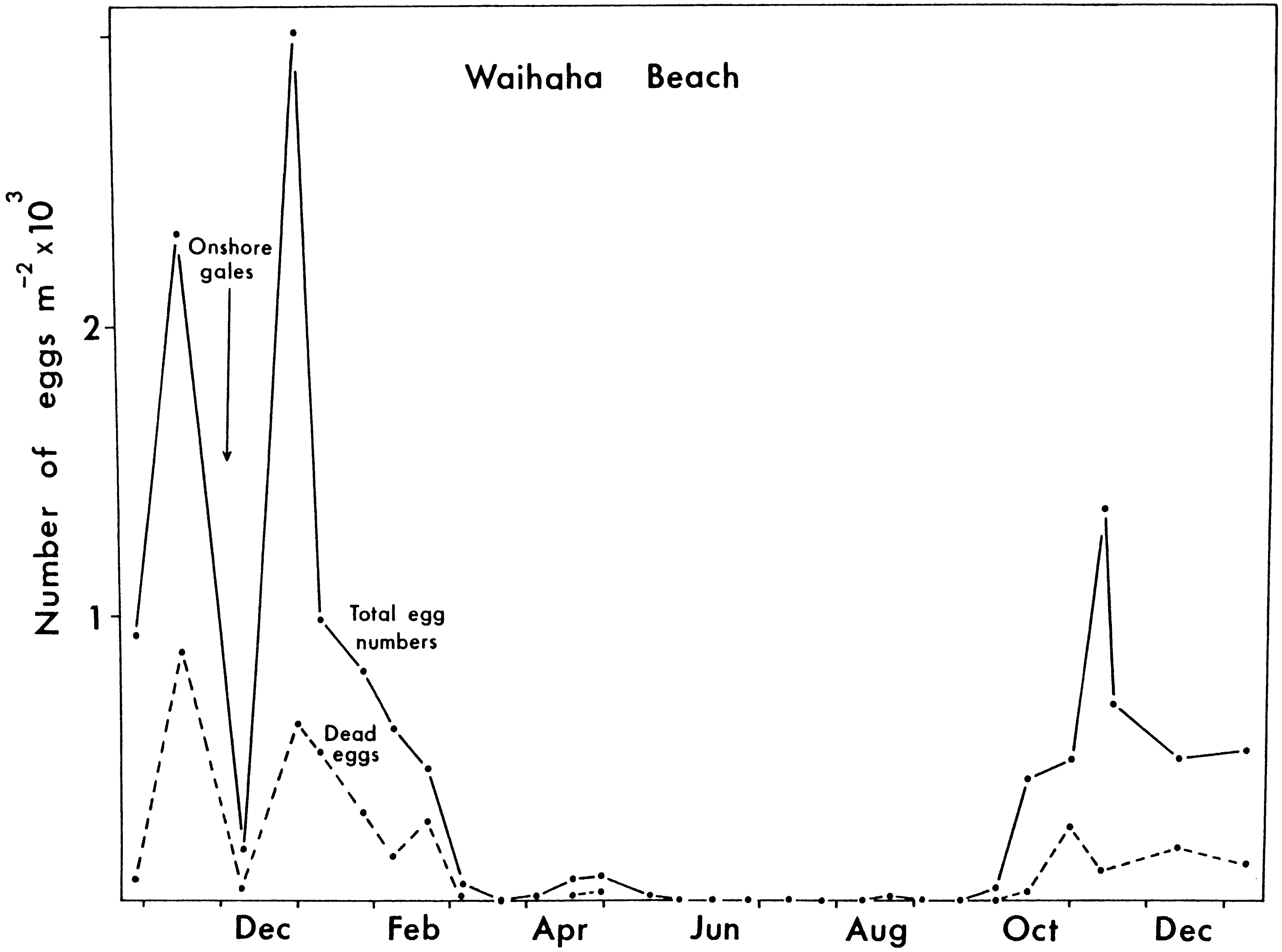


FIG. 41 Mean smelt egg densities on the littoral bench at Waihaha Beach between October 1979 and January 1981.

2. Early larval survival

Bullies caught along the beach and in streams occasionally were found to have eaten freshly hatched smelt (Table 7) but recently hatched larvae never comprised a significant proportion of the food volume. Freshly hatched larvae apparently moved into the pelagic waters immediately after emergence as they were never taken in either zooplankton samples or ringnet tows along the beach. In pelagic waters smelt are almost free from predation; they are largely unavailable to the benthic bullies and were never found in either adult smelt or trout stomachs. Predatory cyclopoids were scarce although *Macrocyclops albidus* was occasionally present in nocturnal ringnet tow samples. It would seem that starvation due to inability to find sufficient food was the principal source of mortality but, as it was not possible to estimate larval mortality rates, the extent of larval mortality remains unknown. Mortality estimates made from nocturnal tow catches (fig. 42) were confounded by recruitment until the end of the spawning season and then by changing patterns of vertical migration which reduced catchability thereafter (pg ~~35~~ 22 and fig 13). Lower abundances and/or increased escapement was indicated by the difference between catches per unit effort on moonlit and dark nights. However the slopes of the exponential functions fitted to the data were not significantly different ($P = 0.5$) and the overall daily mortality rate was 1.25% per day ($b = .0206$), which seems too high to be realistic because if a pair of smelt produced 500 offspring then, according to this, only 1.5×10^{-4} of these would remain two years later. In view of the absence of predators on larval smelt, the mortality rate estimate must be grossly overestimated.

Catch data, corrected for escapement (as in Appendix 1), from a regular dropnetting programme would have yielded useful larval mortality estimates, but unfortunately the equipment required did not become available until the final stages of the project.

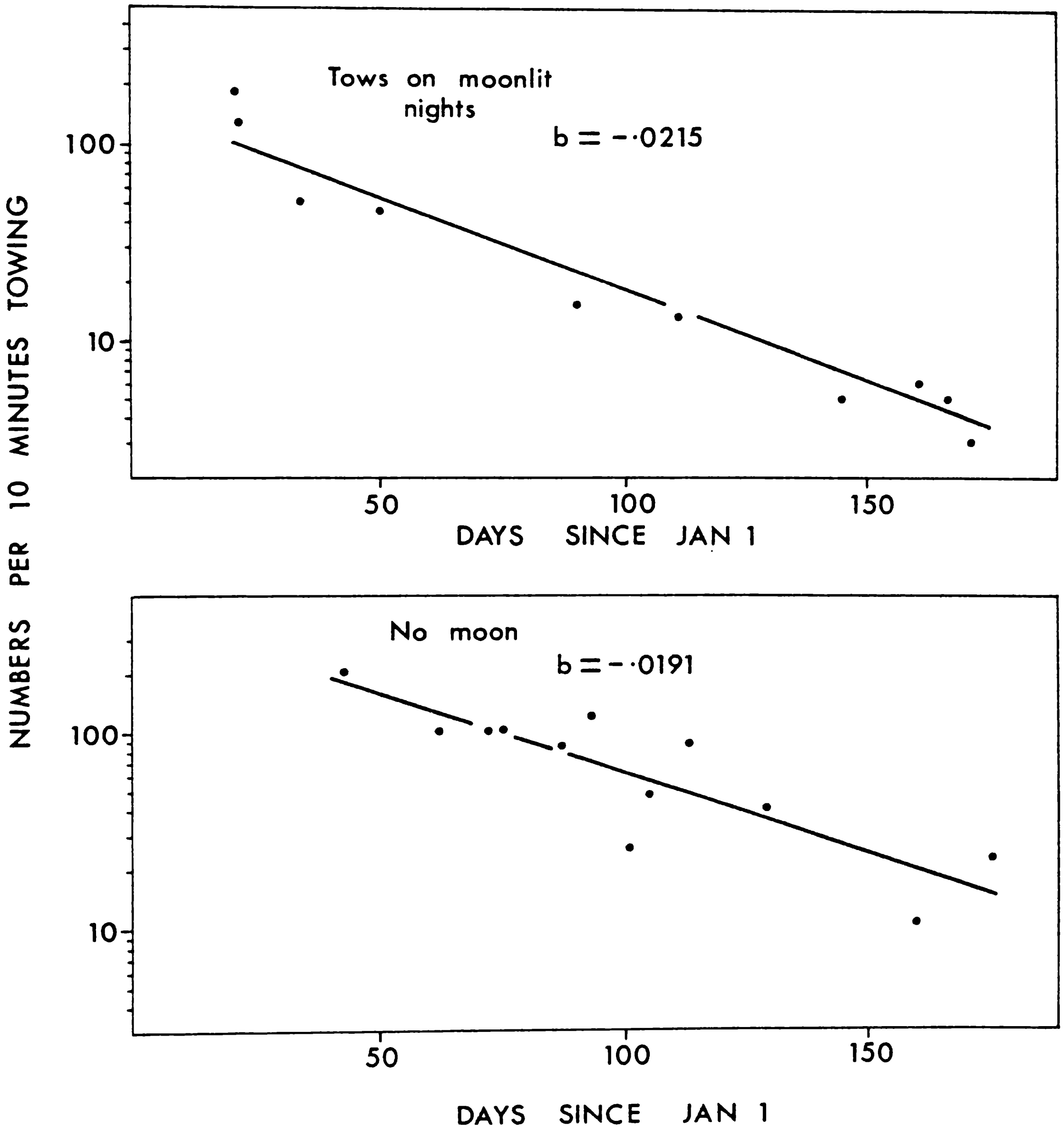


FIG. 42 Numbers of larval smelt per unit towing time taken in nocturnal ringnet samples.

Predation by Rainbow trout

Rainbow trout stomachs taken from angler-caught fish were examined to determine how important smelt were in their diet and which sectors of the smelt population were preyed on by trout. There is no published information on the biology of trout in L.Taupo and little is known of their feeding habits, juvenile life history or seasonal and size/age related patterns of distribution. Trapping operations have been conducted on several tributary streams, but results have never been published. Clearly, the scope of the work required to remedy this is beyond this study and consequently there is considerable reliance on field observations where measurement was not possible.

The trout were caught mainly by anglers trolling on the lake, using sinking fly, lead or wire lines which, judging by the depths at which snagged lines were found whilst diving, do not appear to carry lures much below about 30m. Anglers troll near the shoreline so that their lures fish near cliff faces or near the bottom. Midwater trolling in the deep open waters is unpopular and seems quite unproductive. Trollers usually work within 50m of cliff faces but are often several hundred metres from beach shorelines where shallows extend a considerable distance offshore, particularly along southern and eastern shores where the sublittoral shelf can extent over a kilometre into the lake (Irwin 1972). Thus anglers take most of their catch from the lower littoral zone of the lake and consequently trout feeding in surface, pelagic or profundal areas of the lake are likely to be under-represented in the anglers catch.

The trout ranged from 35cm (minimum legal size) to 72cm but most were 45-60cm. Stomach fullness and volume measurements (figs. 44 & 45) underestimate true values because trout often regurgitated some and occasionally all of their stomach contents and this was probably a major source of variation in estimates of quantities eaten. However it seems unlikely that the proportion regurgitated would change seasonally or that prey species would be differentially regurgitated. Size related diet differences were minor, being restricted to the inclusion of adult bullies and crayfish in the diet of large trout (Addendum fig. 1 ~~greater than 60cm~~) which were rarely eaten by small ones (~~less than 50cm~~). The size ranges of smelt eaten by large and small trout were indistinguishable. (Addendum fig. 2). ~~However the diet of trout less than 35cm long was not examined~~.

Smelt were the most important species in the diet except during August when bullies and crayfish became more important (fig. 43). The high proportion of crayfish during February 1981 is misleading as only four stomachs were examined, and one trout was exceptionally large and had eaten several crayfish. Large numbers of green beetles (*Pyronota sp*) were eaten during December when they were briefly extremely abundant. Dense windrows several hundred metres long and piles of moribund beetles along the shoreline occur every December, but despite their superabundance, smelt were still the most important species in the trout diet at that time. Inanimate items such as pumice, sticks, leaves, pebbles and paper were also commonly eaten, particularly by trout with little food in their stomachs.

Stomach fullness indices ranged from 0 (empty) to 17.8 (stretched tight containing 125cm^3 (fig. 44)) but were relatively empty during the winter when they contained only 2-6cm^3 (fig. 45A). Low average fullness during times of maximum littoral smelt abundance suggest that these densities were insufficient to saturate the capacity for predation by trout.

Seasonal patterns in the number of smelt present in trout stomachs (fig. 45 below) suggested that individual trout caught more smelt during summer than in winter. However, because the number of trout present in the lake probably varies seasonally, as adult trout emigrate to tributary streams to spawn in winter, returning in spring and early summer, numbers of smelt eaten by individual trout cannot be considered a useful index of smelt mortality due to trout predation. Variation in the size of the trout population must also be considered. Whilst no attempt was made to measure trout abundance, general observations indicated that the number of trout feeding in the littoral was maximal in early summer when smelt were particularly abundant. These trout were feeding on the maturing smelt which had gathered in the littoral zone for breeding. During autumn, trout numbers in the lake were probably still high, but they were feeding on the smaller one year old smelt (fig. 46). Thus although the numbers eaten were similar to numbers of adult smelt eaten, the volume consumed by each trout (fig. 45 above) was somewhat less in autumn. Both numbers and the volume eaten were minimal in winter.

The proportion of the smelt population eaten by trout must have varied seasonally as the year class preyed upon, the number of smelt eaten by individual trout and the number of foraging trout all varied seasonally. Predation mortality was probably most intense for adult smelt concentrated in the littoral zone during early summer. It seemed that numbers of feeding trout were maximal at that time and each trout was consuming near maximum numbers of smelt. Large numbers of smelt were also eaten during autumn but these belonged to a younger year class which was probably numerically larger and so the proportion of this junior year class eaten would have been smaller than that of the adult year class which almost dissappeared in autumn. During winter before the new maturing adult year class was ready to breed, they were dispersed throughout the lake and their year class population numbers were higher than later in the year (after motality during the intervening period). Trout numbers were probably low as many adults would have been away spawning, and those present were not catching many smelt. Thus mortality caused by trout predation was probably minimal in winter. Shoaling and dispersion of these probably further reduced predation mortality by reducing the encounter rate of foraging trout (Hobson 1979; Stein 1979; Radovich 1979; Brock and Rittenburgh 1960). It seems likely that lack of space suitable for spawning in the littoral zone and consequent congregation for breeding would exacerbate predation mortality by increasing the encounter rate of foraging trout.

(a) Size selection by trout

Smelt present in stomachs ranged from 25mm to 75mm in length and were predominantly members of the senior year class present. Percent frequency distributions for smelt taken in beach seine samples and from trout stomachs are compared in fig. 46. Positive size selection was evident from November 1980 until April 1981 and again from October 1981 until December. Apparent negative size selection during October 1980, July and September 1981 was probably not real because the larger members of the year class were more inclined to enter shallow water during winter and spring and consequently these dominated beach seine catches during this period. The whole year class was probably fully represented during and after November 1980 and again in October 1981.

Post-larval and juvenile smelt belonging to the juvenile year class were seen whilst diving during the spring and summer. They were abundant around cliffs, reefs and below the littoral bench (fig. 18), although they did not appear in beach seine samples until late summer. They were relatively more abundant at 15-30m depth where anglers caught the trout than near the beach where smelt were sampled with the net seine. Thus if the trout had been feeding mainly in the sublittoral then positive size selection was even more intense than the data indicate.

The preference ratio:

$$\frac{\%\text{ in trout stomach}}{\%\text{ in seine haul}}$$

was calculated for each smelt length interval present in trout stomachs and in seine samples. Seine haul length frequency data for September 1981 was discarded and data from August and October seine catches were combined and used to calculate preference ratios. These generally increased with length (fig. 47) and exponential functions were fitted to the data for each month although data for smelt length intervals known to be under-represented in beach seine samples were excluded (crosses in fig. 47). The exponent "b" was used as a measure of the intensity of size selectivity.

FIG. 43

The diet of Taupo rainbow trout. Data are percentages, by volume, of each food item present in stomachs collected during the month indicated.

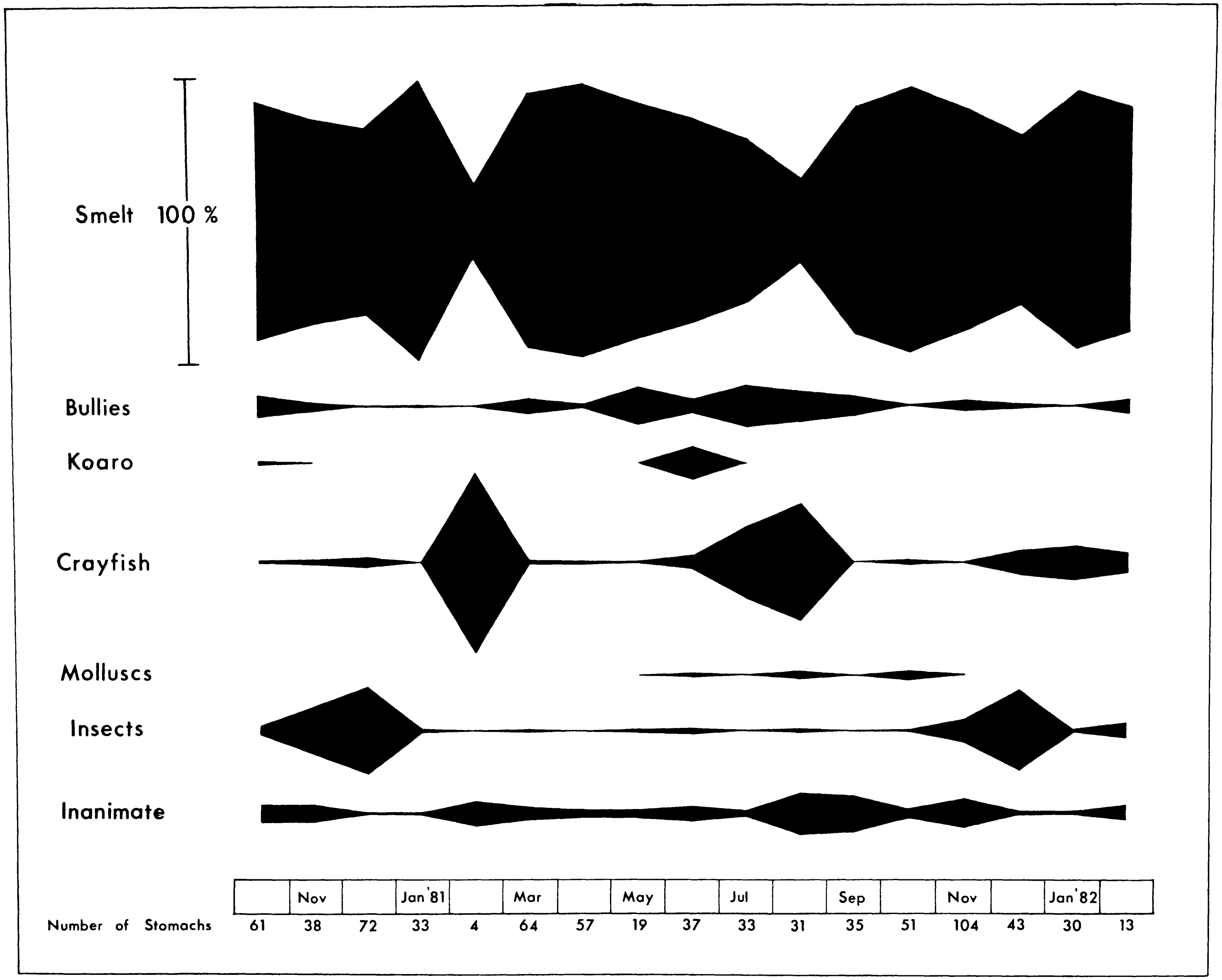
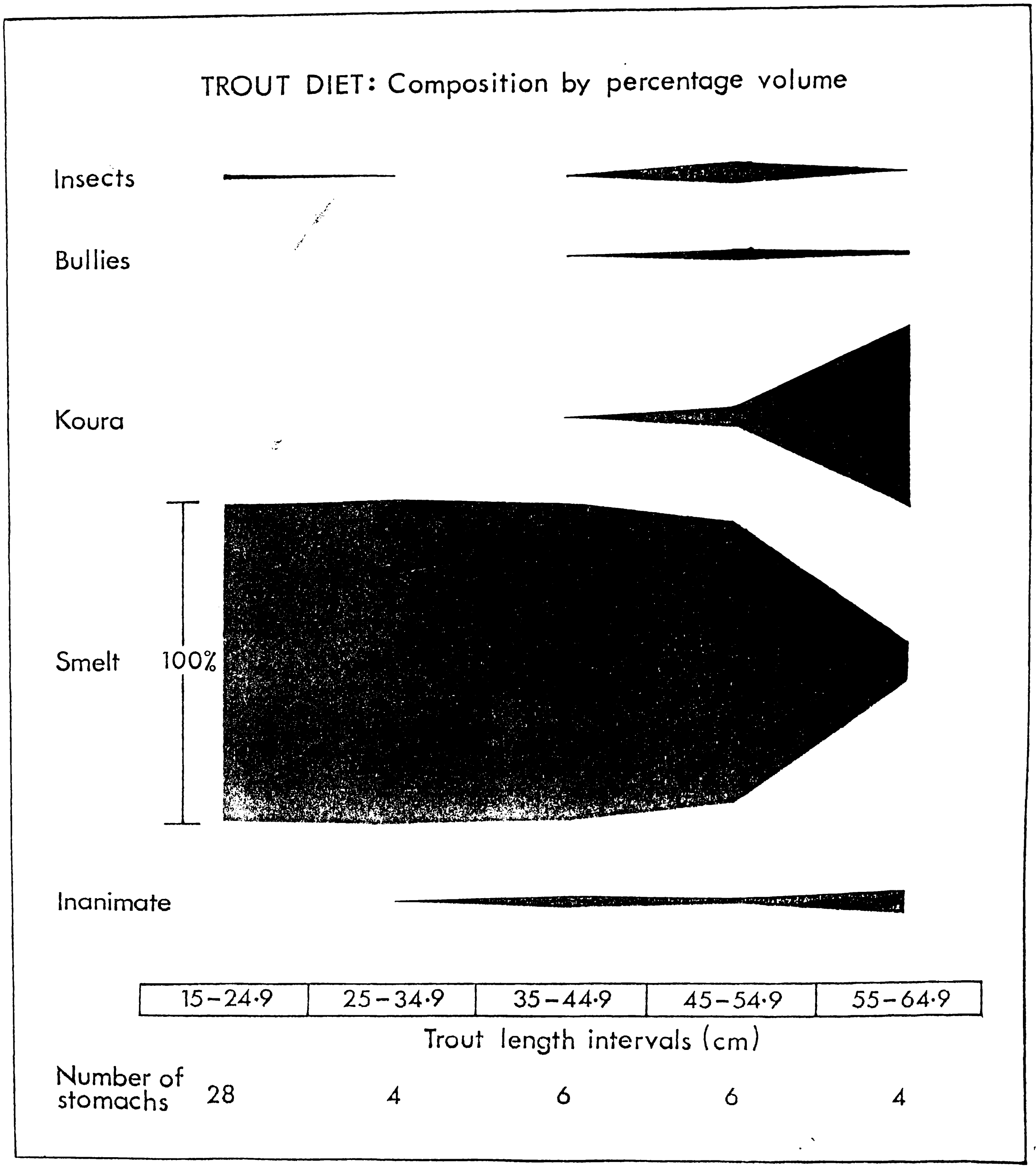

Smelt
100 %
Bullies
Koaro
Crayfish
Molluscs
Insects
Inanimate
Nov
Jan'81
Mar
May
Jul
Sep
Nov
Jan'82
Number of Stomachs
61
38
72
33
4
64
57
19
37
33
31
35
51
104
43
30
13

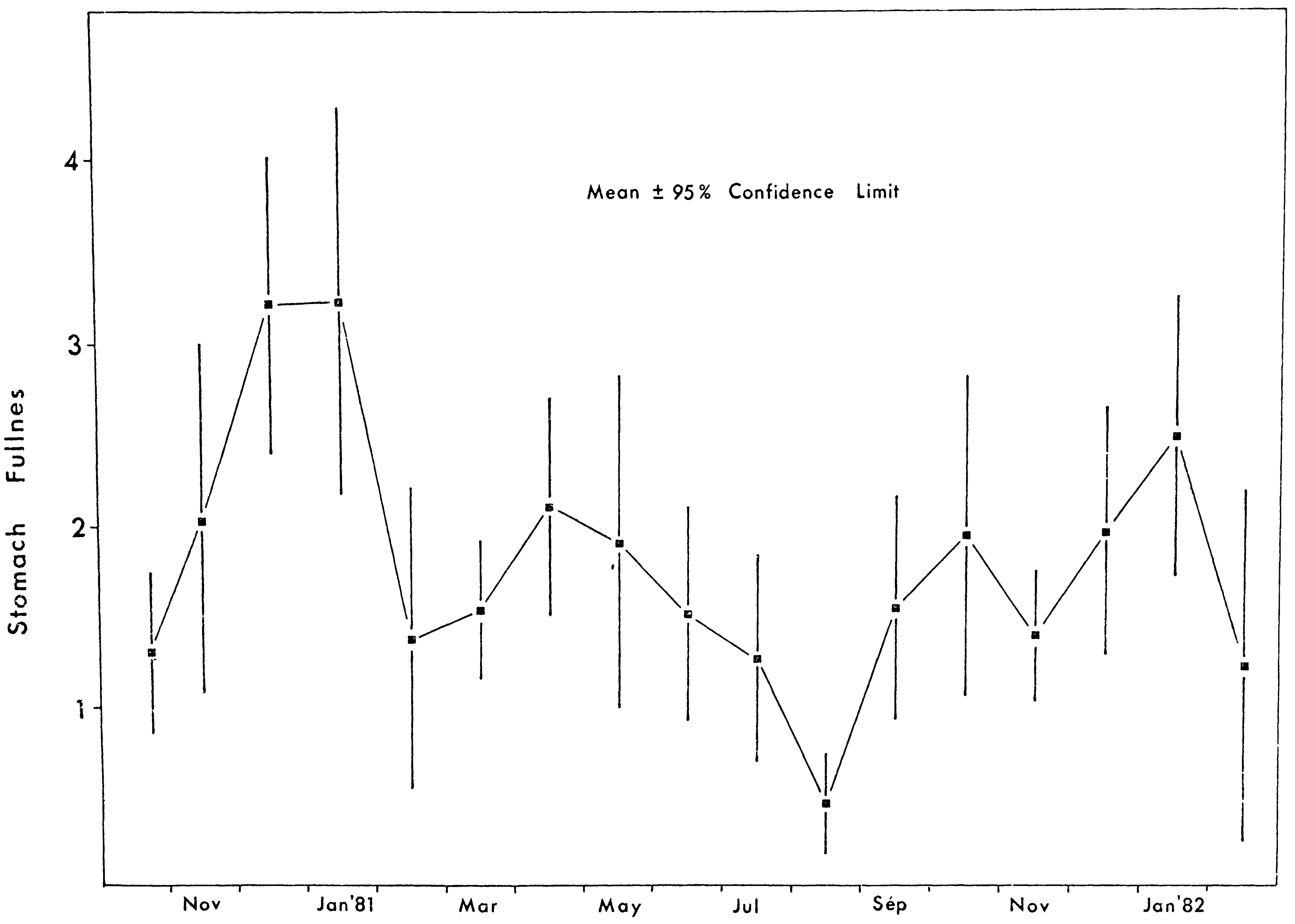
FIG. 44

Trout stomach fullness indices

$$\text{Fullness} = \frac{\text{Food Volume} \times 10^3}{(\text{stomach length})^3}$$



Addendum Fig. 1 Size related variation in the diet of rainbow trout caught in Lake Taupo using gill nets set on the bottom from 18 to 55m depth on 6 February 1986.


Mean ± 95% Confidence Limit
Stomach Fullnes
4
3
2
1
Nov
Jan'81
Mar
May
Jul
Sép
Nov
Jan'82

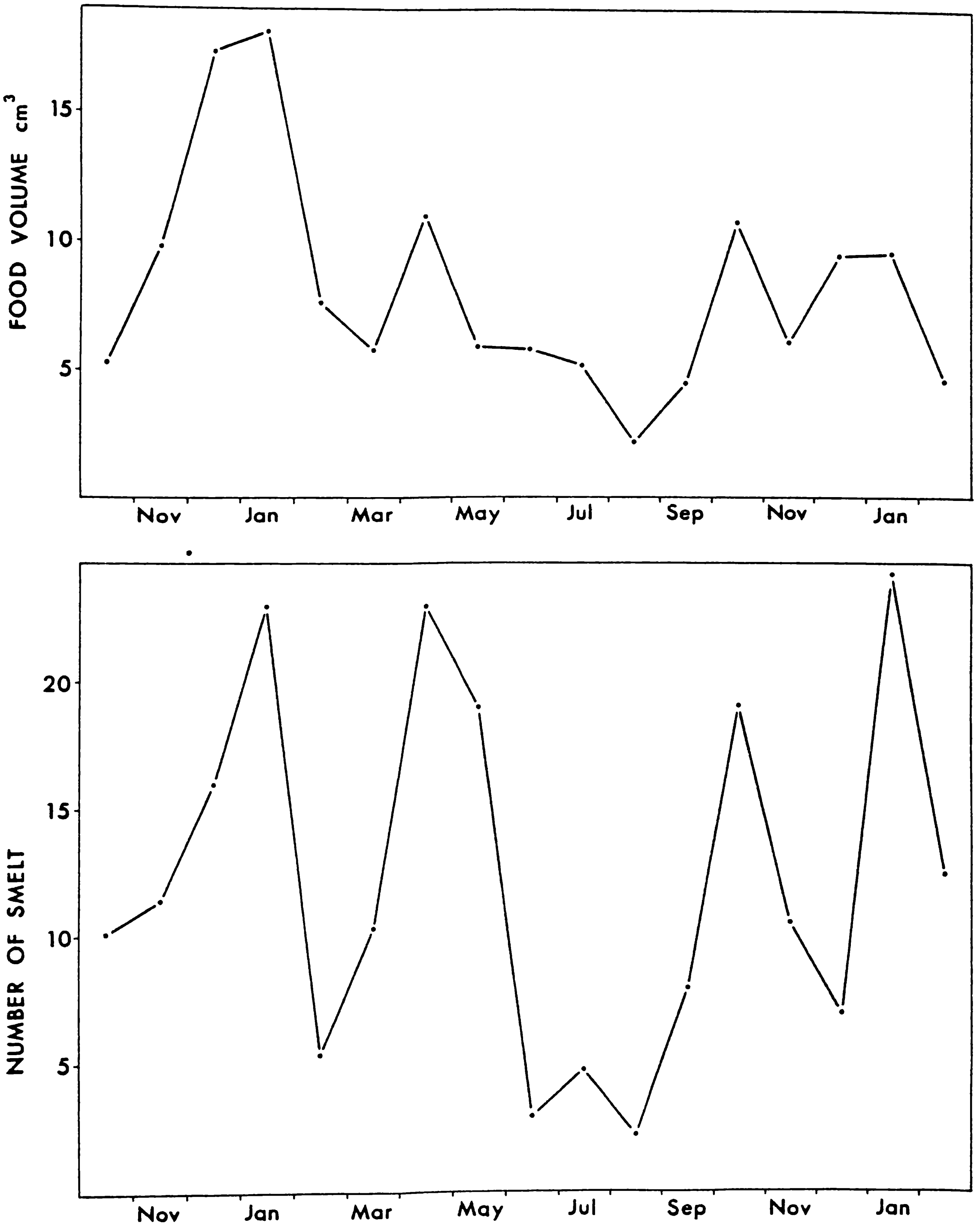


FIG. 45 Quantities of food in the stomachs of each trout taken by anglers between October 1980 and February 1982.

Above - The mean volume of the contents of each trout stomach

Below - Mean numbers of smelt in each trout stomach.

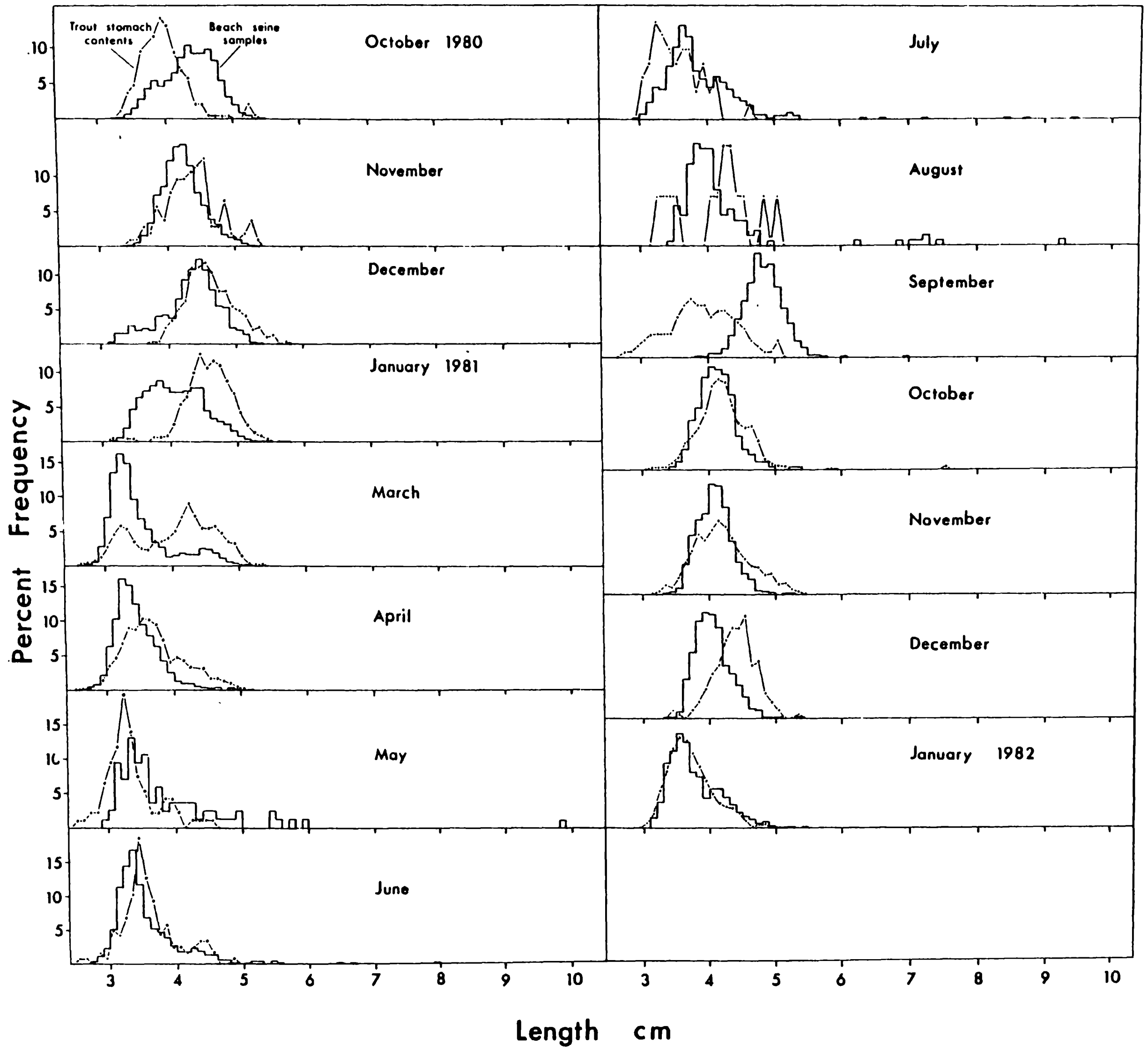


FIG. 46 Percent frequency length distributions of smelt taken in beach seine samples and from trout stomachs.

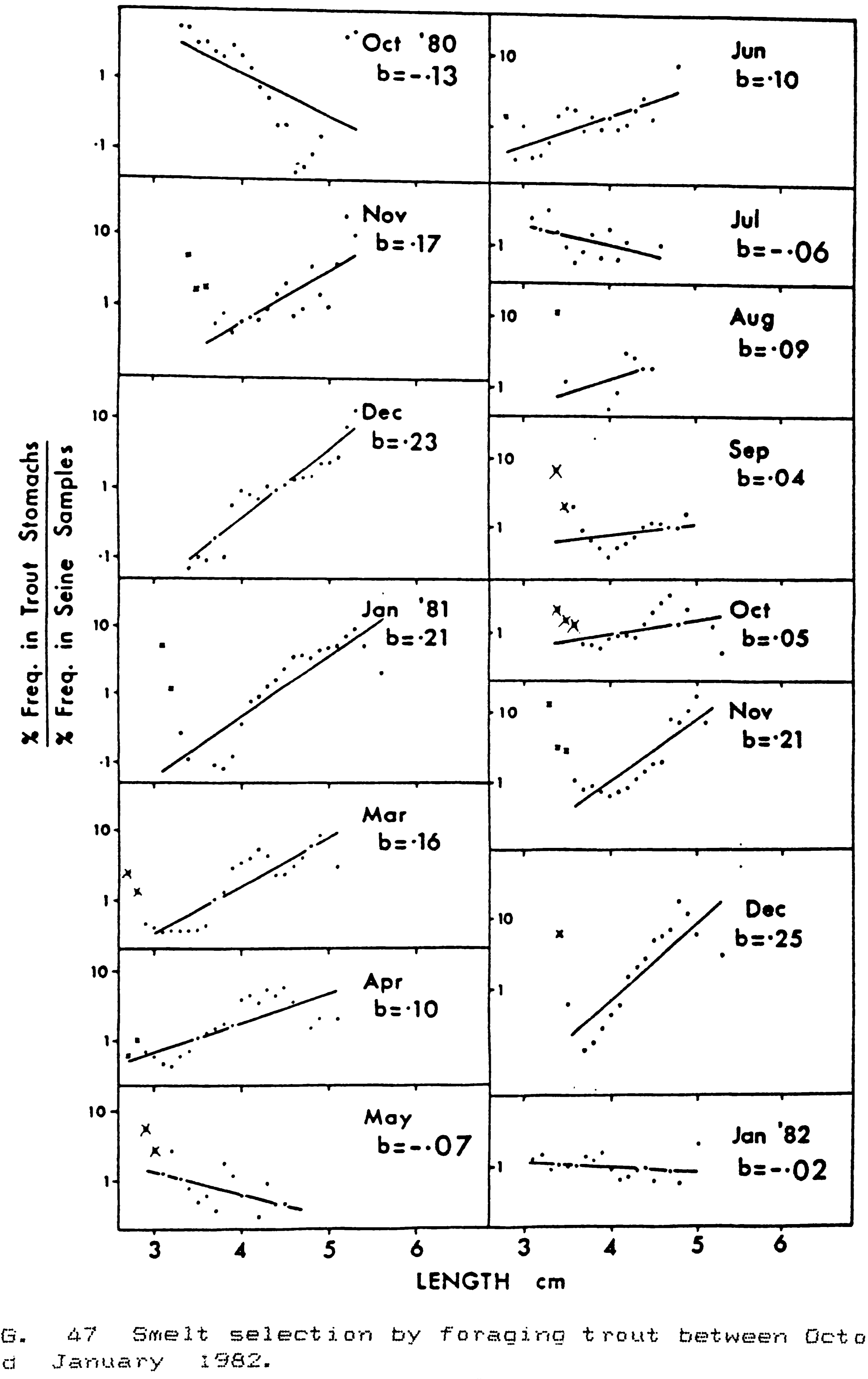
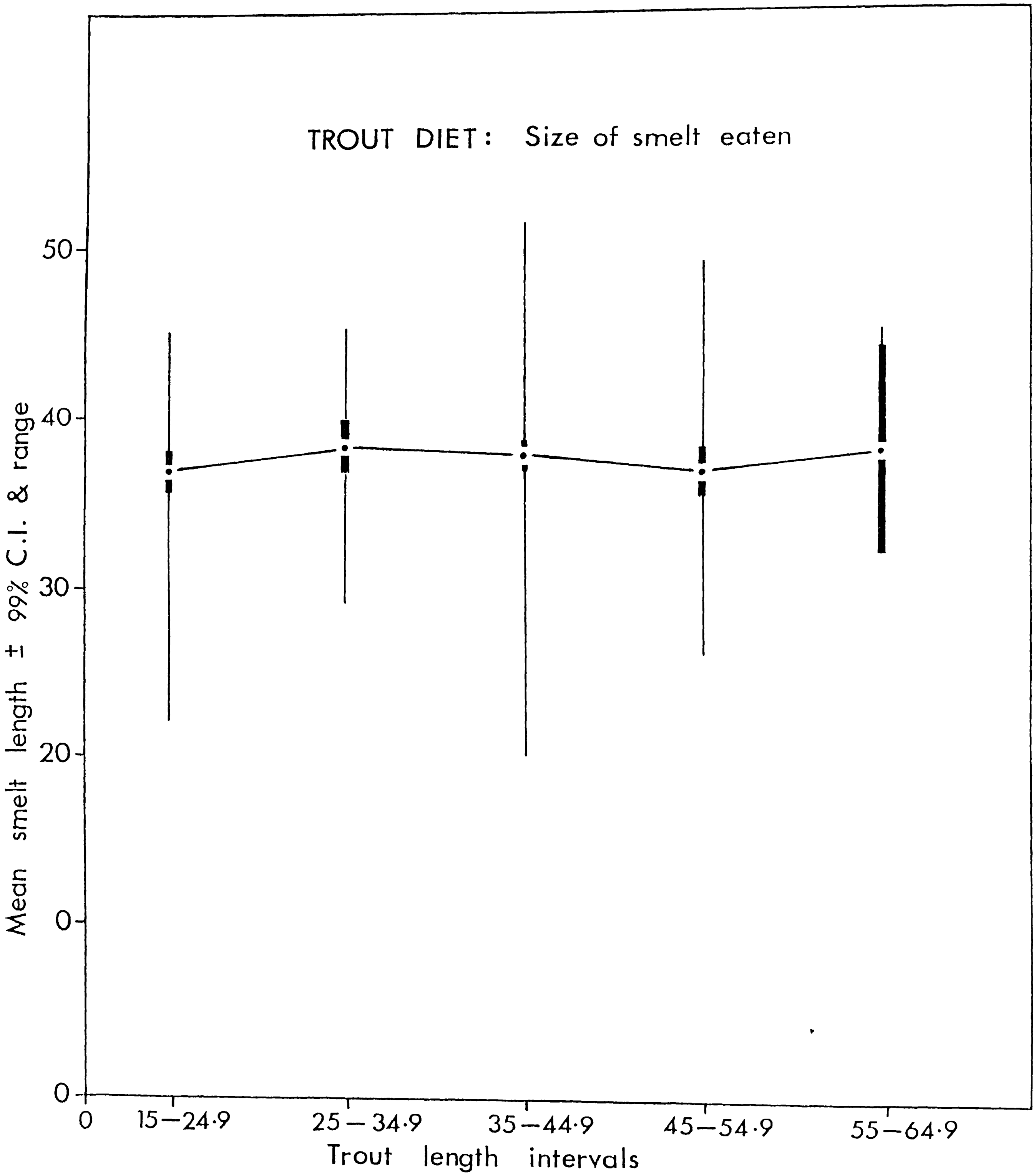


FIG. 47 Smelt selection by foraging trout between October 1980 and January 1982.

Each data point is the preference ratio described on Pg. 104 and the slope (b) of the regressions is treated as a measure of the intensity of size selection which was then used in the correlations presented in Fig. 48. No data are shown where smelt frequencies were zero in either trout stomachs or in beach seine samples because the logarithmic scale used does not allow for either zero or infinite values. Data not included in regression calculations, because the length intervals concerned were thought to be underrepresented in beach seine samples, are indicated by crosses.



Addendum Fig. 2 Variation in the lengths (mm) of smelt eaten by different sized rainbow trout from Lake Taupo. The trout were caught in gill nets set on the bottom from 18 to 55m depth on 6 February 1986.

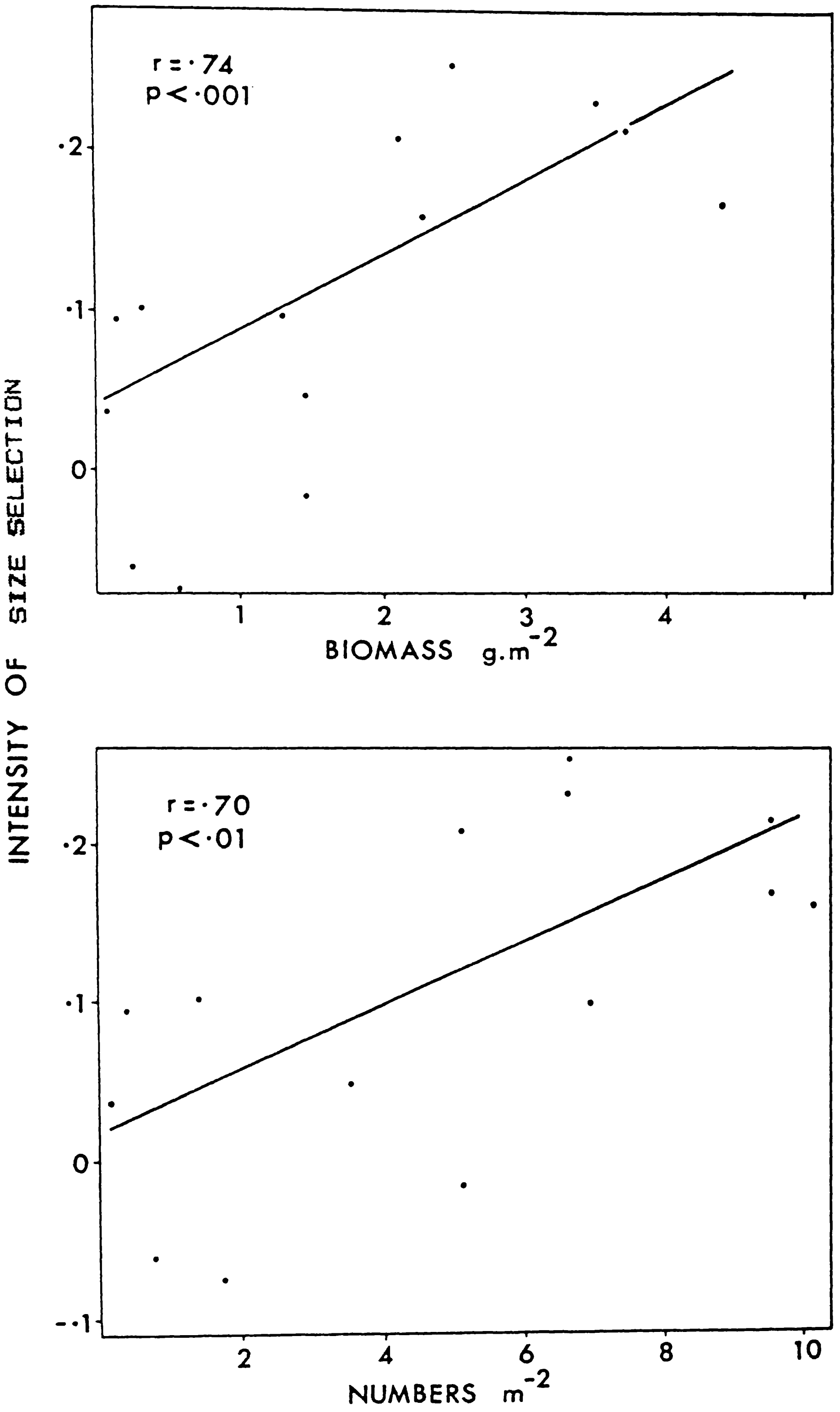


FIG. 48 The relationship between the intensity of size selectivity by trout and smelt biomass (above) and smelt density (below) along Waihaha Beach, between October 1980 and January 1982.

Whilst the relationship between the size preference ratios and smelt length was adequately described by an exponential function, (with the exponent 'b' providing a measure of the intensity of size selection), often ratios were maximal for smelt 48 to 50mm FL and lower for larger smelt. Very few smelt larger than 55mm FL were found in trout stomachs despite their regular occurrence in beach seine samples. The ordinate scale used in Fig. 47 does not permit presentation of data for zero frequencies in either trout stomachs or in beach seine samples. Thus Fig. 47 understates the declining preference trout have for smelt larger than about 50mm FL. Large smelt eaten by trout often appeared spent and emaciated, suggesting that they were eaten because they were easily caught. Conversely, it seems likely that particularly large smelt were often able to evade capture and so were not often eaten. Mean monthly smelt biomass and mean monthly smelt density estimates were both found to be significantly correlated with the intensity of selection (Fig. 48), probably because these measurements index availability of and choice between different food items. Thus the most intense size selection occurred when smelt availability and potential for choice were both maximal.

In summary, trout predation on smelt was most intense during summer when trout numbers in the lake were probably maximal, individual trout were eating most and were feeding most selectively. At this time they were feeding preferentially on large adult smelt congregating in the littoral to breed but it seemed that the largest smelt present avoided predation by trout. It appears that smelt spawning habitat requirements and the very small ratio of littoral to pelagic habitat which characterize particularly the western and northern parts of Lake Taupo are of profound importance in causing the adult smelt concentrations which provide the most intensively used forage resource for angler caught trout.

4. Other sources of predatory mortality

Inclusion of smelt mortality due to bully and bird predation are required to provide a complete account of predatory mortality. Smelt eaten by bullies were generally smaller than those taken by trout as the bullies caught mainly juveniles and only a few adults that strayed close to the bottom. Bully predation did not appear to be density dependent as the abundance of bullies in the littoral was more influenced by their territoriality and breeding habits (Stephens 1982) than by smelt abundance. However white-faced herons *(Ardea novaehollandiae)* were obviously more numerous during the summer months and they could be seen along the shoreline feeding on spawning smelt. Herons were therefore another source of size selective and density dependent predation. Shags *(Phalacrocorax carbo and P. sulcirostris)* could be seen feeding throughout the year though seasonal changes in their abundance were not obvious and the smelt size range eaten, and whether the number caught was dependent on smelt density remains unknown.

PART TWO

SIMULATION STUDIES

CHAPTER 6 - MODELLING OF SMELT POPULATION DYNAMICS

Studies such as this which endeavour to identify and describe the processes characterizing a predator-prey system offer no basis for management policies unless the results provide some means of predicting the consequences of management options and changes to the environs of the system. Objective predictions can be based on experience gained from trial and error experimentation (e.g. Swingle 1950) and some insight might be obtained from surveys of similar systems in diverse environs (e.g. Fish 1968, Mylechreest unpubl. data) but models based on correlation fail to capture the mechanics of the system (Larkin 1979). Both approaches can be expected to indicate associations between certain habitat features and specific characteristics of predator or prey populations, but only rigorous experimentation would be likely to demonstrate whether or how these habitat conditions control a given feature of the predator-prey system. Even this will fail if the features under consideration are moulded by the interaction of several interdependent processes (e.g. smelt length frequency distributions). Modelling, using the functional components of the system, seems likely to be both the best guide to how certain habitat features could influence the trout-smelt predator-prey relationship and the best way to predict consequences of certain management options. Field surveys of smelt populations and trout feeding in diverse lakes would then be required to identify prediction deficiencies and indicate where improvements are required. An experimental approach would probably be necessary to effectively improve deficient component sub-models.

The usefulness of a model based on the functional components of the system depends first on successful identification of these components and then on formulation of submodels which adequately describe them and their interactions in numerical terms (Walters et al. 1980). The principal processes of population dynamics are reproduction, growth, mortality and migration. However, they cannot be considered in isolation because the outcome of each is dependent on the others (Weatherly 1972); all four processes are interrelated and, to further complicate matters, each is influenced by a host of habitat variables. Many studies demonstrate how one or more of the population processes are affected by specific influences such as competition (Staples 1975), predator abundance (Swingle 1950, Hackney 1979, Craig et al. 1979), physical and chemical conditions, (Brett 1971), food intake (Elliott 1976), activity rhythms, movements and distribution (Harden-Jones 1968, Northcote 1969, Staples 1978). Together, these studies illustrate the multiplicity and complexity of influential processes and environmental variables. However, because of the desire for simplicity and arithmetic convenience, population processes are rarely based on these functional components. Consequently realism, generality and predictive value are compromised (Larkin 1979).

Mortality is typically treated as a single process which can be subdivided into "natural" and "fishing" (cf. predation) mortality. This seems a gross simplification on consideration fo the sources of mortality and the way they can operate. There are at least five important causes, these being starvation, disease, predation, reproduction and misadventure. Each source is likely to be of particular importance for only part of the population size range, may be restricted to specific habitat locations and its intensity may be modified by the density of other, not necessarily conspecific, individuals in the vicinity. For instance, losses due to predation will be confined to those size classes lying within the diet size range of their predators. The number eaten will be influenced by the density and physical fitness of both predator and prey as well as by habitat features such as water clarity, illumination and availability of cover, either for ambush or escape. Similarly, mortality caused by starvation or disease can be size and density dependent. Contagious diseases will kill more if densities are high and the rates of infection and subsequent mortality expectations may be size dependent (e.g. whirling disease, Hewitt and Little 1972). Starvation might be most intense amongst post-larval fishes which can feed only on a very restricted prey size range, and this will be exacerbated by high densities and consequent competition. Loss of condition and other stresses associated with spawning are often a major source of mortality and since maturity is size and/or age dependent, so is post-spawning survival. Thus mortality is in part dependent on the presence and nature of causative agents and in part dependent on factors which influence size frequency distributions and abundance; one such factor being previous mortality!

Growth occurs when food intake exceeds maintenance requirements and the amount of food eaten by a fish depends on the quantity available, the proportion lying within its diet breadth size range, the number of individuals competing for all or part of this size range and the vigour with which the individual under consideration feeds.

A large fish has a greater diet breadth and so, depending on the distribution of productivity over the prey size range might (or might not) be able to utilize a greater proportion of the food resource and this may (or may not) compensate for increased maintenance requirements associated with larger size. Thus growth is not only dependent on the abundance and size range of the food resource available, but also on factors which influence the frequency distribution and abundance of competing fishes. Among these are reproduction, past growth, mortality and patterns of movement between habitat zones. A predictive growth model should therefore be based on food production, feeding habits, competition, metabolic maintenance requirements and set within the context of models for distribution, reproduction and mortality.

Migration between habitat zones is typically a seasonal size and/or age dependent process and results in changes in abundance and population size frequency distributions in two or more habitat zones. Consequently,other size and density dependent population processes are affected. Reproductive output depends on the abundance and size of parents as these determine the number of eggs laid. This quantity results from all other population processes and is the initial abundance which will influence subsequent patterns of growth, mortality and distribution. Thus the population processes of fish are best regarded as being inseparable and interdependent because all are size and density dependent and each process modifies at least one of the variables on which the others depend. The population size frequency structure must therefore be of central importance as this as this expresses the final resultant of all population processes.

The model described in the following pages simulates this interdependence and each population process is comprised of what seems to be its functional components. Interdependence is obtained by modelling each process sequentially over brief periods of time for a predetermined number of consecutive time intervals. The sequence of execution within each time interval is indicated as a flow chart in fig.49. Output data for both littoral and pelagic habitats include length frequency distributions of live smelt and those eaten by trout (numbers under $100m^2$), smelt biomass, weight eaten per trout and trout densities. A listing of the programme is given in Appendix 4.

1. Modelling smelt movements and distribution

Movements of smelt which result in observed patterns of abundance in littoral and pelagic habitats are an important aspect of population processes as these influence the size frequency structure and abundances of smelt in each habitat zone and consequently affect the course of subsequent growth, mortality and reproduction.

Distribution is the result or expression of movement and therefore development of a model simulating movement must be based on comparison of observed with predicted patterns of distribution. Beach seine catch data provided a detailed description of distribution with respect to length and season but corresponding data for pelagic waters was confounded by seasonal and length dependent patterns of catchability which caused significant sample bias (fig. 13 vs. fig. 14). Furthermore as movement is a size dependent process, the length frequency of the whole population must influence smelt abundance in the littoral and pelagic zones. The complexities and uncertainties of correction

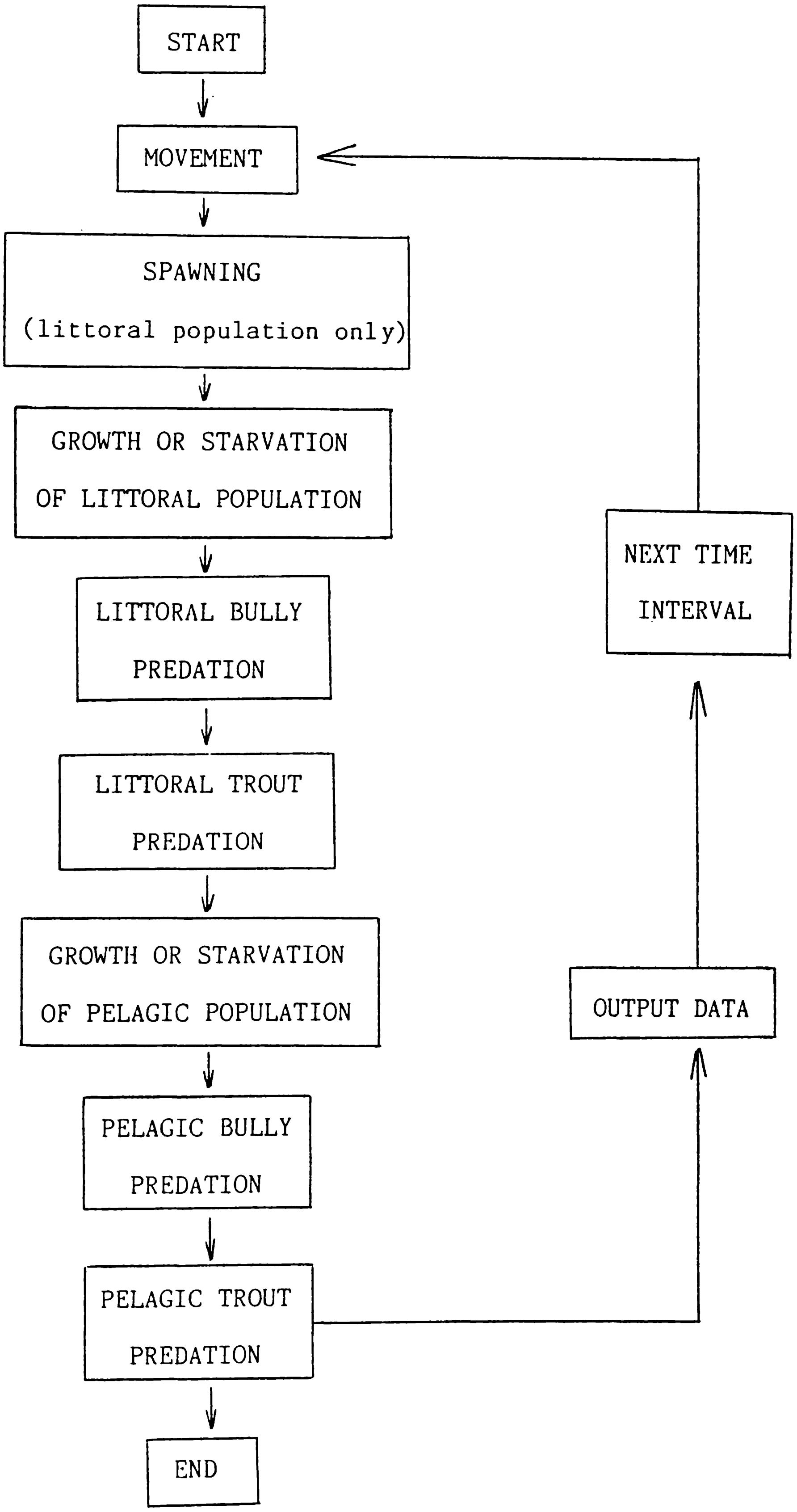


FIG. 49 Flow diagram showing the sequence of processes used to simulate smelt population dynamics.

for seasonal changes in smelt population length frequencies precluded directly fitting a model describing movement to catch data. A suitable model was developed by simulating movement between the littoral and pelagic zones for a hypothetical population with fixed (constant) frequencies at each length interval.

The proportion of smelt of a given length currently located in the littoral zone which move into the pelagic (LITTOPEL) at a specified date during a specified time interval (TIMEINTERVAL) was defined by:

$$\text{LITTOPEL} = \text{EXP}\ (\text{b} * \text{TIMEINTERVAL} * \text{L} * \text{S}) \qquad (8)$$

where "b" is a scale constant (ca. -0.00004), L and S are length dependent and seasonal components. The proportion emigrating from the pelagic to the littoral zone was defined by:

$$\text{PELTOLITT} = 1 - \text{LITTOPEL} \qquad (9)$$

The seasonal component was defined by the exponential sine function:

$$\text{S} = [\text{SIN}\ (\text{T}-60) + 1.2]^{2.5} \qquad (10)$$

where T is the number of days since October 1st. This provides for maximum littoral immigration on March 1st, peak emigration on September 1st and the power term gives an appropriate degree of seasonal variation to the rate of movement.

FIG. 50

Simulated patterns of smelt distribution.

The diagrams illustrate quarterly length frequency distributions for a hypothetical smelt population Data are proportions of each smelt length interval distributed between littoral and pelagic (shaded) habitats (of equal area) on four days during an annual cycle. When a littoral to pelagic habitat area ratio appropriate for Lake Taupo (ca. 1:20) was used, it became apparent that a steeper length depended component (as in Equ 11) was required. In this example, movement from the littoral zone into the pelagic was defined by:

$$\mathrm{LITTOPEL} = \mathrm{EXP}\ [b * \mathrm{TIMEINTERVAL} * L * S]$$

where $b = -0.00004$

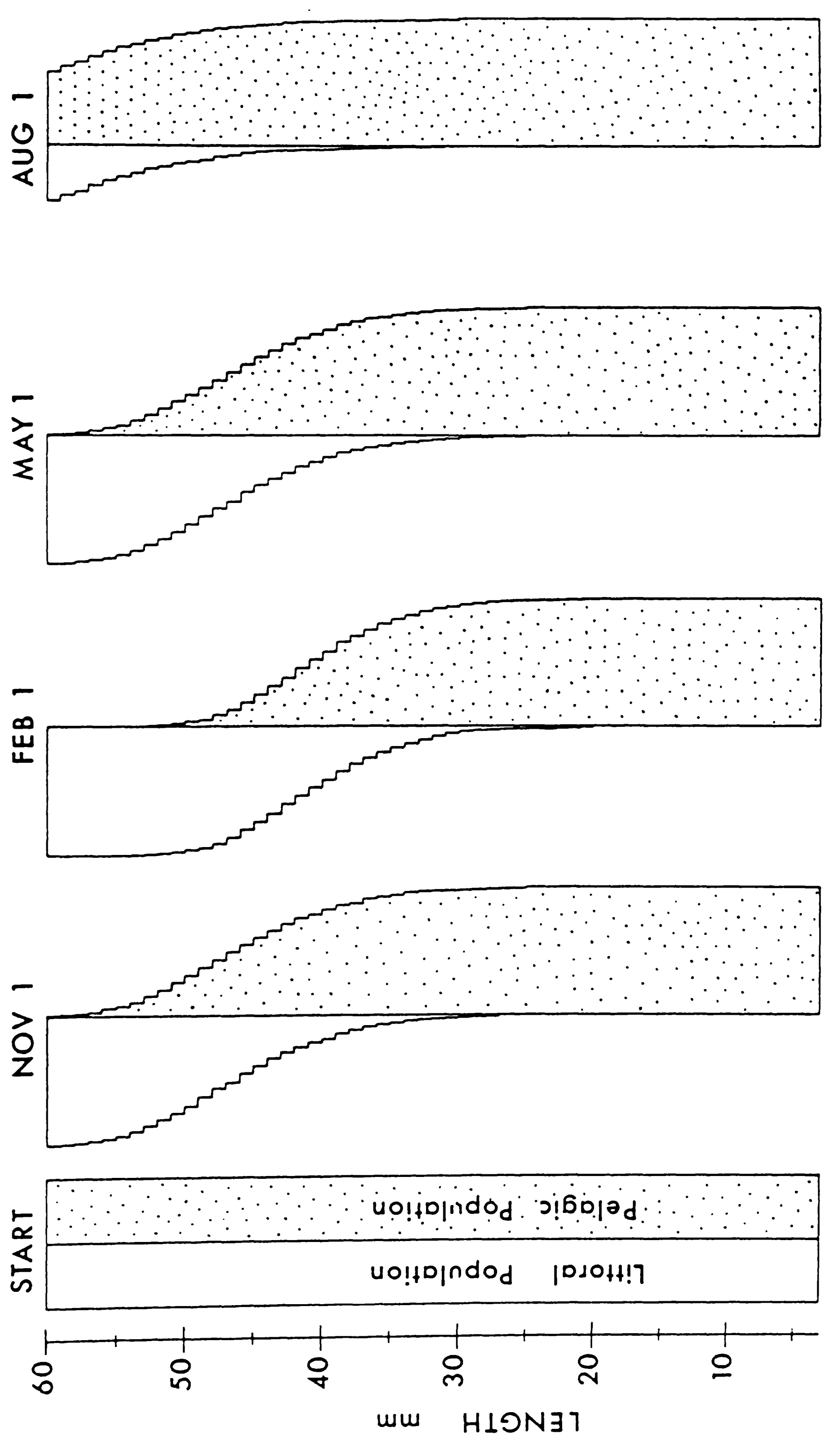
$\mathrm{TIMEINTERVAL} = 0$

$L = [0.05 * \mathrm{LENGTH}]^{8}$

$S = [\mathrm{SIN}\ (T-60) + 1.2]^{2.5}$

and movement from the pelagic zone into the littoral by:

$$\mathrm{PELTOLITT} = 1-\mathrm{LITTOPEL}.$$


START
NOV 1
FEB 1
MAY 1
AUG 1
Littoral Population
Pelagic Population
LENGTH mm
60
50
40
30
20
10

The length dependent component was defined by the power function:

$$L_i = \left[0.036 * \text{LENGTH}\right]^{12} \qquad (11)$$

in which length is expressed in millimetres. This provides for almost complete emigration from the littoral by smelt smaller than 25mm but the proportion emigrating decreases rapidly with increasing length after 30mm and the proportion larger than 60mm which leave the littoral is small. Thus seasonal and size dependent aspects of smelt movement are treated as being genetically fixed and are not modified by habitat variations. This may be a simplistic view as feeding success in different locations is likely to influence distribution and movements between them.

An hypothetical smelt population in which each length interval contained equal numbers equally distributed between littoral and pelagic habitats was generated and smelt were "moved" according to the model described above. Numbers of smelt in each size interval in the littoral zone (LITFREQ) during the next time interval (t_1) were defined by:

$$\text{LITFREQ}_{i,t_1} =$$

$$\text{LITFREQ}_{i,t_0} + \left[\text{PELTOLITT}_i * \text{PELFREQ}_{i,t_0}/\text{L:P}\right] - \left[\text{LITTOPEL}_i * \text{LITFREQ}_{i,t_0} * \text{L:P}\right] \qquad (12)$$

and numbers in the pelagic zone (PELFREQ) by:

$$\text{PELFREQ}_{i,t_1} =$$

$$\text{PELFREQ}_{i,t_0} + \left[\text{LITTOPEL} * \text{LITFREQ}_{i,t_0} * \text{L:P}\right] - \left[\text{PELTOLITT} * \text{PELFREQ}_{i,t_0}/\text{L:P}\right] \qquad (13)$$

where t_0 is the present time interval and L:P is the ratio:

$$\text{LITTORAL HABITAT AREA / PELAGIC HABITAT AREA} \qquad (14)$$

A ten day time interval was used for simulation of movement and coefficients for the model were adjusted until seasonal and length dependent patterns were similar to those observed in Lake Taupo. Quarterly length frequency distributions are given in fig. 50 and model coefficients used are given in the caption.

2. Modelling smelt reproduction

The components of reproduction which modify the population length frequency structure are maturation, parental post-spawning survival, fecundity and egg survival. The model used to describe movement from the pelagic zone to the littoral was adapted to describe length dependent and seasonally variable maturation. The proportion of smelt at length interval $_i$ which were ready to spawn (RIPE_i) was defined by:

$$\text{RIPE}_i = \left[\text{EXP} \left(b * \text{TIMEINTERVAL} * L_i * S\right)\right] \qquad (15)$$

where b is a scale constant (ca. -0.0003), L and S are length dependent and seasonal components:

$$S = 2 + \text{SIN } (T-70) \qquad (16)$$

where T is the number of days since October 1st. This provides for maximum proportions of ripe smelt on March 10th. The length dependent component was defined by:

$$L_i = 0.026 \text{ LENGTH}_i^{\ 12} \tag{17}$$

where length is expressed in millimetres. This provides for low proportions of smelt less than 35mm to ripen but high proportions for smelt over 50mm (fig. 51 cf. figs. 13 and 31).

The number of survivors (SURVIVORS) after spawning was predicted using the model describing post-spawning mortality in an enclosure (fig.37) thus:

$$\text{SPAWNMORT}_i = 1 - \left[1 \Big/ (1{+}0.00525 * \text{TIMEINTERVAL} * (\text{LENGTH}_i{-}33))\right] \tag{18}$$

where LENGTH_i-33 was constrained to be greater than or equal to zero.

The number of survivors can then be determined from:

$$\text{SURVIVORS}_i = \text{FREQ}_i - \left[\text{FREQ}_i * \text{RIPE}_i * \text{SPAWNMORT}_i\right] \tag{19}$$

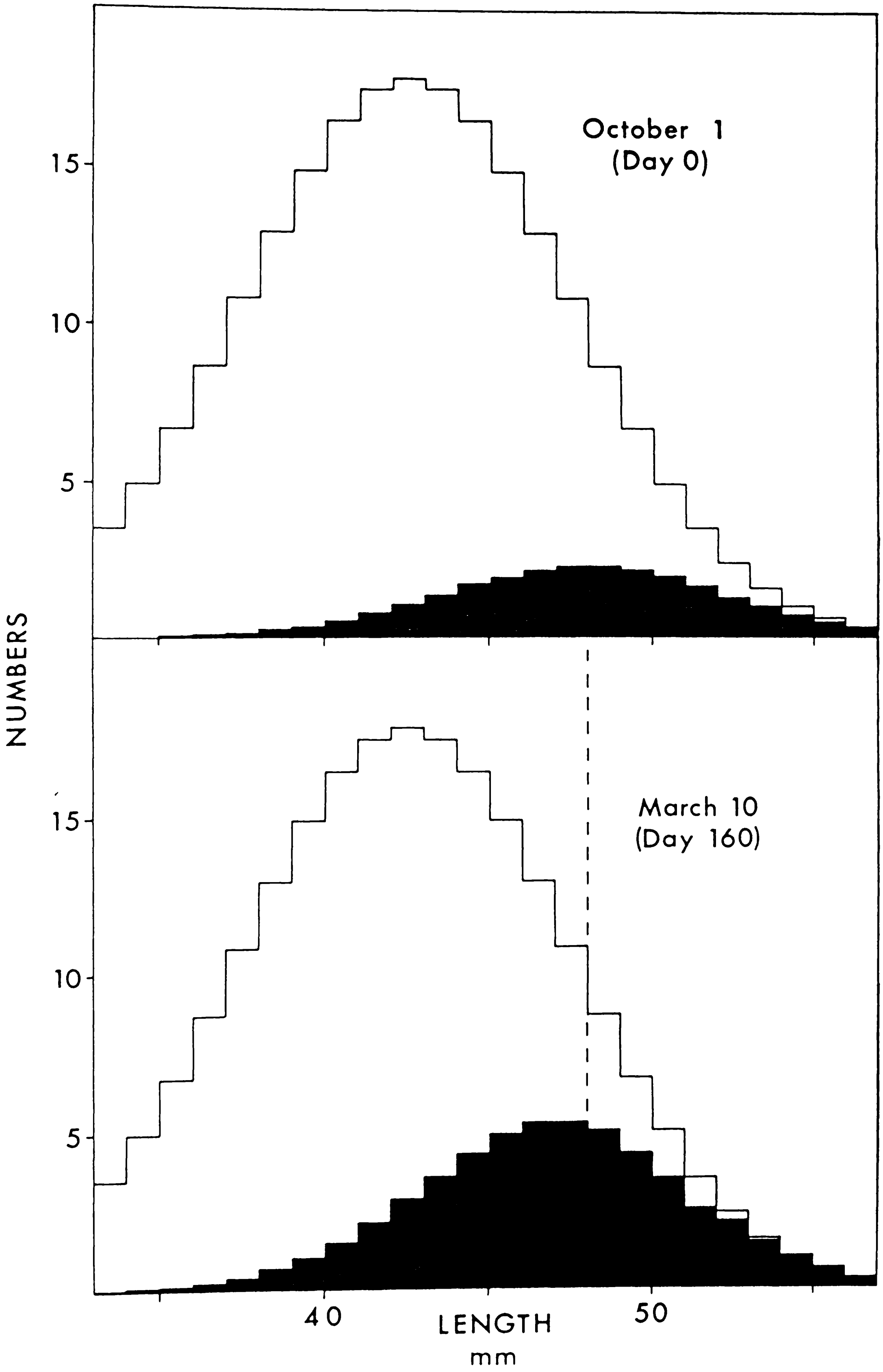
The number of eggs laid by each smelt was predicted using the power function relating the number of mature eggs in the ovary to length (fig. 34) and the total number of eggs laid during the time interval under consideration was defined by the summation:

$$\text{EGGS} = \sum_{n}^{i=34} \text{FREQ}_i * \text{RIPE}_i * 0.000784 * \text{LENGTH}_i^{3.59} \tag{20}$$

Egg survival was considered constant as it was not found to be density dependent. Egg development time used was ten days (Jolly 1967) and after this period smelt of 2, 3 and 4mm were added to the pelagic population in the ratios 0.3: 0.4: 0.3.

FIG. 51

Simulated numbers of smelt reaching maturity (black histogram) during a ten day time interval early in the spawning season (October) and in March when the maturity rate was thought to be maximal (cf. fig. 31).


October 1
(Day 0)
March 10
(Day 160)
NUMBERS
15
10
5
15
10
5
40
50
LENGTH
mm

3. Modelling growth

A predictive model for growth which takes density and size dependent aspects into account seems best based on the components of feeding and maintenance requirements. The major components of feeding which determine food intake per fish are food resource partitioning (i.e. the proportion of the total food resource available to a fish of a given size in the habitat zone under consideration) and allocation per fish (i.e. the actual proportion eaten). Food resource partitioning was defined using a description of the distribution of productivity over the prey size range and the diet breadth size limits of the fish concerned. Allocation per fish would depend on the quantity of food present within the food resource partition and on the number of organisms sharing any part of that partition. An upper limit to the amount eaten during a given time interval was required because there is an upper limit to feeding rate, stomach capacity and digestion time; a maximum of about 25% body weight per day seemed a plausible upper limit for smelt. There must also be variation in the food intake of otherwise identical fish; predators and prey are not regularly distributed in a given habitat and some individuals will feed more actively and successfully than others.

In summary the important factors controlling food intake per fish would seem to be:

1. Daily food production.
2. The distribution of daily food production over the prey size range.
3. The fishes' diet breadth.
4. The amount of diet overlap with competing individuals.
5. The number of competing individuals.

(a) Seasonal patterns of food production

The species eaten by smelt were predominantly primary consumers (i.e. grazing zooplankters) but some detritus feeding chironomid larvae and some of the smaller secondary consumers (*Asplanchna sp.*, *Macrocyclops albidus*, Tanypodinae and larval bullies) were also eaten as were certain primary producers (*Melosira sp.*, *Botryococcus sp.*) and terrestrial insects. However throughout the following discussion, the species eaten by smelt will be termed smelt "food" or "prey" and treated, for convenience, as though all were primary consumers.

Zooplankton species exhibited asynchronous cycles of abundance (Forsyth and McCallum 1980) and consequently, in the absence of turnover estimates, neither the timing nor the amplitude of seasonal cycles of pelagic smelt food production are obvious from their data. However the littoral zooplankton was dominated by pelagic species (fig.25) and if patterns of abundances in these samples represented similar patterns occurring the pelagic zone then it would seem that maximum zooplankton biomass occurred in October when large *Boeckella propinqua* were particularly abundant. Presumably maximum productivity preceeded this. Primary production was maximal during winter (White et al. 1980) and it seems likely that maximum productivity of pelagic primary consumers would occur soon afterwards. Crustacean zooplankters were scarce during autumn when only rotifers were abundant and it seems that production by crustacean zooplankters was minimal, but whether or not total zooplankton production was also minimal at this time is uncertain.

There was a distinct seasonal cycle in the modal size and size range of pelagic food species. During spring the zooplankton was dominated by large calanoids (1-2mm) but the largest species present were *Daphnia carinata* (2-3mm) and post-larval bullies (15-20mm). As the summer progressed all these species became scarce and were replaced by freshly hatched larval bullies (2-15mm), small cladocerans (0.2-1.0mm) and rotifers (0.04-0.2mm) which became particularly abundant. The modal size at which production was concentrated thus fell from around 0.8mm (the size of the larger copepodites) in spring to around 0.08 (ca. average size of rotifers) during the autumn. The largest prey were still present, albeit scarce, during the summer and it would therefore seem that production was spread over the most extensive size range during summer.

Production by littoral consumers was clearly maximal during midsummer. The benthic fauna was dominated by orthoclad chironomid larvae and these became especially abundant for a brief time during midsummer (fig. 25). Around the same time, small oligochaete worms, nematodes, tardigrades and harpacticoid copepods also became abundant. However during winter only late instar larvae of the chironomid groups Tanypodinae, Orthocladiinae and Chironominae were present and these were not numerous. The modal size at which production was concentrated was probably around 0.4mm (the size of early instar orthoclad larvae and the oligochaete worms) ranging perhaps up to 8-10mm (the size of the largest Chironomidae and terrestrial insects) during summer. During winter the modal size must have been much larger, perhaps 3mm (the size of final instar orthoclad larvae) but there was no obvious change in maximum size.

In summary, it seems that production by pelagic prey species was maximal during spring, minimal during autumn but the magnitude of seasonal variation was not great. Pelagic production was apparently concentrated amongst larger species during spring and was most widely spread over the prey size range during autumn. In the littoral zone invertebrate production was clearly maximal during midsummer, the peak lasting 4-6 weeks and the difference between seasonal maxima and minima was considerable, possibly in excess of one order of magnitude. Littoral production seemed most widely distributed over the prey size range during summer but was restricted to larger organisms during winter.

(b) Modelling seasonal patterns of daily food production

Seasonal patterns of daily food production can be described by a modified cosine function and a density function can be used to describe the distribution of daily production over the prey size range. The chosen density function may be skewed, must have an explicit integral (because the food partition is defined as the quantity lying between diet breadth size limits) and the position of the mode, direction of skewness and extent of the spread must be able to be easily manipulated to accommodate seasonal patterns. The Weibull function (Johnson and Kotz 1970) satisfies these criteria and has the form:

$$y = \frac{c}{a} \left[\frac{x-b}{a}\right]^{c-1} \quad \mathrm{EXP} - \left[\frac{x-b}{a}\right]^{c} \qquad (21)$$

the integral is:

$$1 - \left[\mathrm{EXP} - \left[\frac{x-b}{a}\right]^{c}\right] \qquad (22)$$

The mode is defined by:

$$\text{Mode} = a\left[\frac{c-1}{c}\right]^{\frac{1}{c}} + b \qquad (23)$$

The "c" term controls the direction and extent of skewness. When 1<c<3.6 the distribution is skewed to the right, and it is skewed to the left when c>3.6. The "b" term is the x value at which $y = 0$. The "a" term is a scale constant and can be defined in terms of b, c and the mode,

$$a = \frac{\text{Mode} - b}{\left[\frac{c-1}{c}\right]^{\frac{1}{c}}} \qquad (24)$$

Thus three values, the minimum prey size, the modal prey size and the "c" term are required to define this density function. A minimum size for primary consumers of 1 micron seems plausible but this would vary seasonally and, perhaps, between habitats. The modal value, the spread term "c", and the total amount of daily food production can be varied according to the time of year using a cosine wave describing unimodal seasonal fluctuations over a 360 day year (Batschelet 1981):

$$x = x_{\text{min}} + \left[\frac{x_{\text{max}} - x_{\text{min}}}{2}^{\,1/K} \left[1 + \text{COS}\ (\text{T}-\text{T}_{\text{max}})\right] \right]^{K} \qquad (25)$$

where x_{min} is the minimum value

x_{max} is the peak value

T is the number of days since October 1st

T_{max} is the number of days between October 1st and the date on which the peak value occurs.

The κ term defines the length of time that x exceeds the median x value. When $0<\kappa<1$, values exceed the median value for more than half the year and for less than half the year when $\kappa>1$.

Whilst seasonal cycles of smelt food production and modal prey size in the littoral and pelagic zones were described by unimodal functions it must be pointed out that both the seasonal cycles and the size distribution of production may be polymodal in form. There may be spring and autumn peaks in productivity (Stephens 1978, Boubée 1983) and the distribution of this productivity over the prey organism size range will depend on the sizes of the species present and so may not necessarily be best described by a smooth unimodal curve with respect to size. However these complications can be accommodated by summation of two or more cosine or Weibull functions to generate bimodal or polymodal distributions.

(c) Modelling diet breadth size limits, food resource partitioning and allocation

The upper limit for the size range of smelt prey species (USL) seems to be determined principally by gape and so can be defined in terms of length by the relationship between gape and body length (fig. 52):

$$\text{Gape or USL} = 0.00742L^{1.69} \qquad (26)$$

$$(r^2 = 0.95)$$

The lower size limit (LSL) of prey items eaten was determined from stomach analyses. Minute prey species such as dinoflagellates, small rotifers and copepod nauplii were eaten by smelt up to 35mm long.

The smallest cladocerans were eaten by smelt up to 50mm long but only the largest zooplankters were present in the stomachs of smelt over 60mm long. Thus the minimum prey size increased with body length at a rate substantially slower than that for gape. The coefficients for the power curve

$$\mathrm{LDL} = 0.001\ L^{1.6} \tag{27}$$

were chosen to provide an appropriate description of the relation between smelt length and the lower size limit of prey items eaten (LDL). The relationship between body length and the distance separating gill rakers would have provided an alternative estimate of the relationship between the minimum prey size and body length, but difficulties in obtaining useful measurements for smelt less than about 25mm long and in choosing precisely where the measurement should be taken rendered this approach inadequate. Furthermore, Wright et al. (1983) demonstrated that retention probabilities determined from distances between gill rakers substantially underestimate measured retention by white crappies (*Pomoxis annularis*).

Diet breadth size limits and the Weibull function describing the distribution of production over the prey size range were used to define the resource partition available to smelt of a given size :

$$\begin{matrix}\text{Food Resource} \\ \text{Partition}\end{matrix} = \left[1 - \left(\mathrm{EXP} - \left(\frac{\mathrm{UDL} - b}{a} \right)^{c} \right) \right] - \left[1 \ \left(\mathrm{EXP} - \left(\frac{\mathrm{LDL} - b}{a} \right)^{c} \right) \right] \tag{28}$$

where the coefficients are as defined for equations 21 to 23.

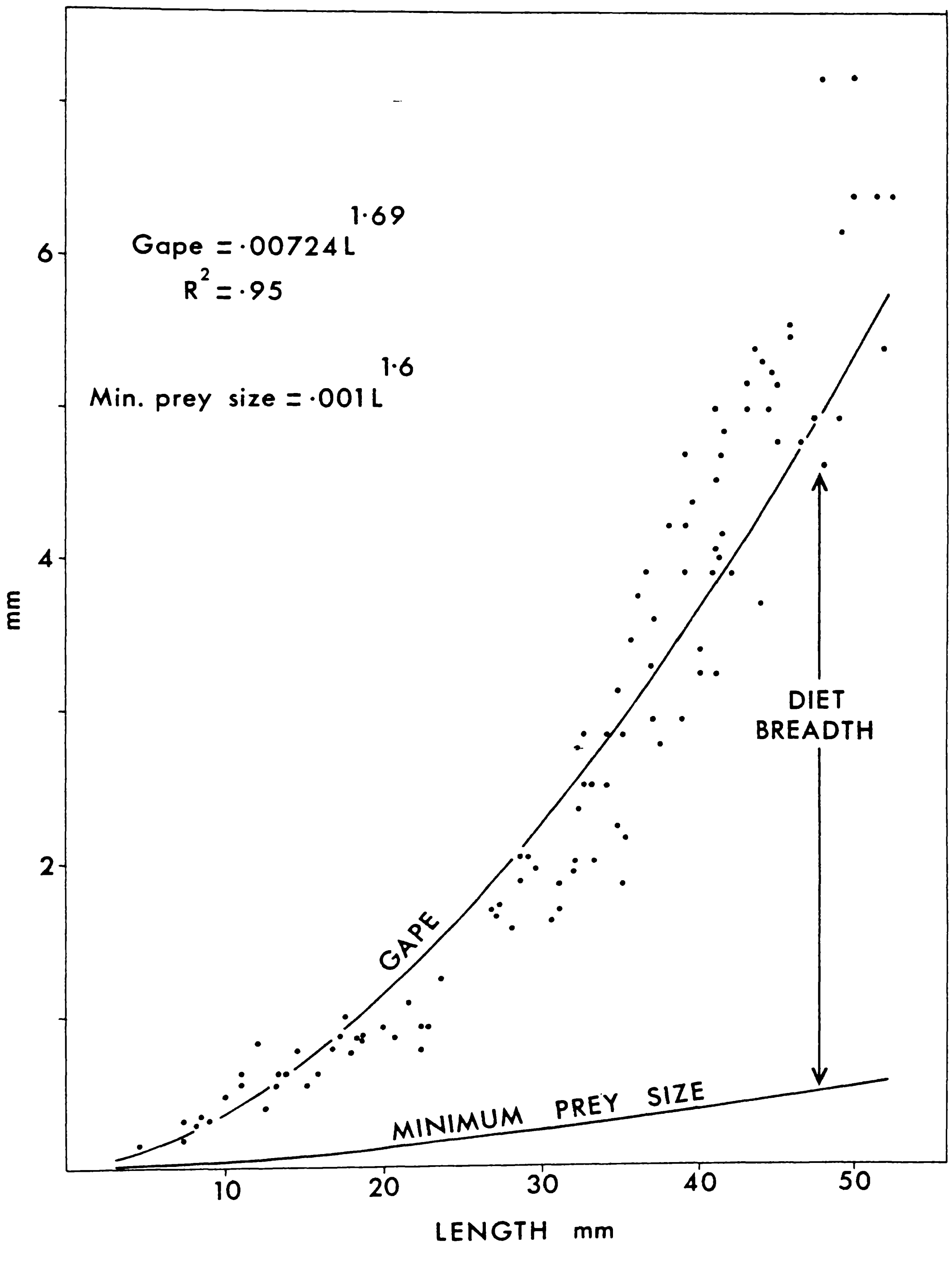


FIG. 52 The relationship between smelt length and smelt diet breadth. The upper prey size limit was defined by gape and the lower limit by the minimum size of prey species found in smelt stomachs.

The proportion allocated to a single smelt of this given size is a fraction of this quantity, the size of the fraction diminishing with increasing diet overlap and abundance of competing organisms, and is defined by the summation:

$$\text{FOOD ALLOCATION} = \sum_{\text{UDL}}^{i=\text{LDL}} \frac{\int \text{UPPA} - \int \text{LOWA}}{\sum_{\text{UPPA}}^{i=\text{LOWA}} \text{COMPETITORS}} \qquad (29)$$

where LDL is the lower diet size limit for smelt Lmm long.

UDL is the upper diet size limit for smelt Lmm long.

UPPA and LOWA are consecutive diet limits in a ranked series ranging from LDL through all lower size limits for fish larger than smelt L and through all upper size limits for fish smaller than smelt L whose diet limits lie within the range LDL to UDL.

$\int$UPPA and $\int$LOWA are the integrals of each diet limit, calculated as in Equation 22 and their difference is the proportion of the area under the density function enclosed by these limits (Equ 28).

The minimum size of a conspecific competitor is defined by:

$$\left[\frac{L}{0.001}\right]^{1/1.6} \qquad (30)\text{: cf. Equ 27}$$

The maximum length is:

$$\left(\frac{L}{0.00742}\right)^{1/1.69} \qquad (31)\text{: cf. Equ 26}$$

The actual food intake by fish of length L_i during the time interval under consideration is:

$$\text{FOODINTAKE}_i = P * \text{FOOD ALLOCATION}_i \qquad (32)$$

P is total food production during the time interval. These calculations (Equ 29 to Equ 31) are illustrated in figure 53.

FIG. 53

Division of a Food Resource Amongst Competing Fishes.

The curve, defined by a Weibull function, indicates the size frequency structure of the food resource and the horizontal bars represent diet breadths of six fish, ranging in size from L_1, (top left) to L_5 (lower right). Since the total area beneath the curve is unity, the proportions of the food resource (D) available to each fish size interval are:

$$D_1 = A_1 + \frac{A_2}{3} + \frac{A_3}{4}$$

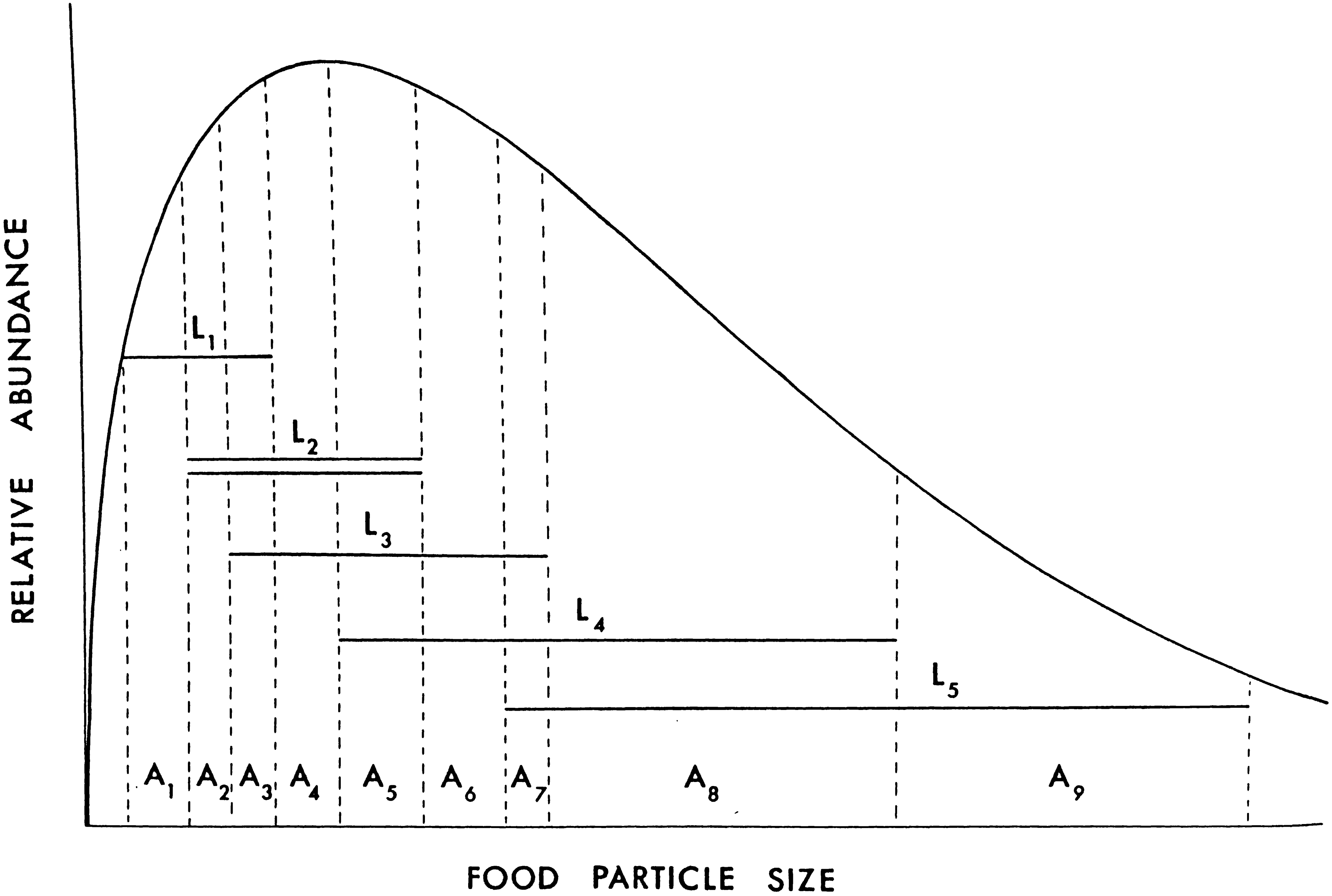
$$D_2 = \frac{A_2}{3} + \frac{A_3}{4} + \frac{A_4}{3} + \frac{A_5}{4}$$

$$D_3 = \frac{A_3}{4} + \frac{A_4}{3} + \frac{A_5}{4} + \frac{A_6}{2} + \frac{A_7}{3}$$

$$D_4 = \frac{A_5}{4} + \frac{A_6}{2} + \frac{A_7}{3} + \frac{A_8}{2}$$

$$D_5 = \frac{A_7}{3} + \frac{A_2}{2} + \frac{A_9}{9}$$

where A_i is the area under the curve between the food size limits of fishes with overlapping diet breadths and the denominators are the number of fishes competing for the prey size range, defined by the limits of A_i (dashed lines).


RELATIVE ABUNDANCE
L1
L2
L3
L4
L5
A1
A2
A3
A4
A5
A6
A7
A8
A9
FOOD PARTICLE SIZE

(d) Maintenance, growth and starvation

Food intake requirements of fish for maintenance alone are usually equivalent to 5-10% of wet body weight per day for fishes feeding on other animals and are dependent on temperature (Brett 1971). Since water temperatures vary seasonally in a sinusoidal fashion (fig. 2) it seems reasonable to expect smelt maintenance requirements to behave similarly. Thus the seasonal cycle model (Equ 25) was used to describe this seasonal variation:

$$\text{MAINTENANCE} = \text{WEIGHT}\left[x_{\text{min}} + \left[\frac{x_{\text{max}} - x_{\text{min}}}{2}\left[1 + \text{COS}\left(\text{T}-\text{T}_{\text{max}}\right)\right]\right]\right] \tag{33}$$

where $x_{\text{max}} = 0.1$

$x_{\text{min}} = 0.05$

$\text{T}_{\text{max}} = 140$

The growth increment is the difference between food intake and maintenance:

$$\text{GROWTH} = \text{FOODINTAKE} - \text{MAINTENANCE} \tag{34}$$

When positive, weight increases thus:

$$\text{NEW WEIGHT} = \text{OLD WEIGHT} + \text{GROWTH} \tag{35}$$

and the new length interval becomes:

$$\text{NEW LENGTH} = \text{INTEGER}\left[\left(\frac{\text{NEW WEIGHT}}{1.316\text{E-}07}\right)^{1/4.053} + 0.5\right] \tag{36}$$

Individual variation in foodintake per fish and subsequent growth is conveniently expressed by an unequal distribution of growth amongst the smelt in the length interval under consideration.

Weight loss and mortality occur when maintenance requirements exceed food intake. In this model smelt size is measured in terms of length and shrinkage is deemed not to occur. Thus zero growth and some starvation mortality are the consequences of negative growth. Starvation survival is related to the size of the growth deficit and so might be defined by:

$$\mathrm{STARVSURV} = \mathrm{EXP}\ [\mathrm{GROWTH} * \kappa/\mathrm{WEIGHT}]$$

Daily minimum starvation survival occurs when FOODINTAKE = 0 and if $\kappa=1$ then minimum daily survival ranges from 0.951 during winter (when maintenance requirements are depressed) to 0.905 during summer.

4. Modelling survival from predation by small predators

Bully predation appeared to be the most important source of predator mortality for juvenile smelt. Bullies were probably selective for smaller smelt which were within the size range that bullies can catch and swallow but the predation rate was apparently little influenced by smelt densities. Daily survival from predators such as bullies and insects (eg. *Anisops* sp. and certain Odonata) which could prey on small smelt is most simply described by :

$$\text{BULLYSURV} = 1 - c\,(0.9)^{L}; \qquad 0 < c < 1 \qquad (37)$$

where c is a scaling term which determines the rate of predation, increasing with predator abundance.

5. Modelling trout predation and smelt mortality

Smelt mortality due to trout predation seemed to be principally dependent on the number and size of feeding trout. Trout feeding activity would be determined largely by their hunger, their feeding success depending on the smelts' size range and abundance as well as the distance over which foraging trout can see them. (Cover is not important as both species are pelagic). When trout are hungry, smelt mortality will be increased by factors causing persistent localized smelt concentrations in places where trout can feed on them. Mortality will be reduced if the smelt are too large and agile to be caught, if their density is sufficient to satiate trout hunger or if the water is so dark or turbid that trout cannot see them. A model describing smelt predation by trout must therefore consist of components describing trout and smelt distribution in the principal habitat zones, trout hunger, vision and selectivity as well as smelt escape ability.

(a) Trout densities and distribution

Total trout numbers in Lake Taupo vary seasonally as adults emigrate to tributary streams to spawn during winter and their progeny enter the lake during the following summer and autumn. There are no useful trout density or population size estimates for Lake Taupo and so estimates used hereafter are merely intuitive guesses. However it seems likely that the lake population is at a minimum during winter, when 2-3 of the 4-5 year classes normally present are away spawning, and that maximum densities occur during summer when almost all adult trout and the early juvenile immigrants are present in the lake. It seems reasonable to use the "seasonal cycle model"

(Equ 25) to describe seasonal trout densities for the lake. Thus if average trout density (n.Ha) is described by:

$$\mathrm{TROUTDENSITY} = x_{min} + \left[\frac{x_{max} - x_{min}}{2} \left[1 + \mathrm{COST}\ T - T_{max} \right] \right] \qquad (38)$$

where x is areal trout density for the whole lake, T is days since October 1st and T_{max} is the number of days after October 1st that trout population numbers are maximal. The total number of trout present is proportional to TOTALTROUT which is defined by:

$$\mathrm{TROUTDENSITY} * \left[1 + \frac{1}{L:P} \right] \qquad (39)$$

where L:P is the ratio of littoral to pelagic habitat area.

It seems reasonable to expect trout distribution between littoral and pelagic feeding habitats to be dependent both on relative feeding success (Dill 1983) and on temperature in each habitat zone. The preferred temperature range for rainbow trout is 10-21°C (Bovee 1978) and temperatures either near freezing or above about 23°C are avoided. Littoral water temperatures ranged from 10.5°C during August to 22°C during March. Pelagic temperatures vary with depth and a maximum of 15°C also during March was arbitrarily chosen for the pelagic zone. The seasonal cycle model (Equ 25) was used to describe seasonal water temperatures. Probabilities of habitat use in relation to temperature are given by Bovee (1978) and temperature preference for the littoral zone (LITTEMPREF) was described by:

$$\mathrm{EXP} - \left[\frac{(\mathrm{LITTEMP}^2 - 225)^2}{10{,}000} \right] \qquad (40)$$

where LITTEMP is the temperature (°C) in the littoral and preference for the pelagic zone (PELTEMPREF) was described by:

$$\mathrm{EXP} - \frac{(\mathrm{PELTEMP}^2 - 225)^2}{10{,}000} \qquad (41)$$

The algorithm used to predict trout distribution between littoral and pelagic habitats on the basis of temperature preference and recent feeding success (CONSUMPTION) whilst allowing for an arbitrary proportion (i.e. 1%) straying was as follows:

LITPREF = (LITCONSUMPTION * LITTEMPREF) + (0.01 * PELCONSUMPTION)

PELPREF = (PELCONSUMPTION * PELTEMPREF) + (0.01 * LITCONSUMPTION)

TOTALPREF = LITPREF + (PELPREF/L:P)

LITTROUT = TOTALTROUT * LITPREF/TOTALPREF

PELTROUT = TOTALTROUT * PELPREF/TOTALPREF

The prefixes LIT and PEL refer to littoral and pelagic zones respectively. The total preference value was weighted by the ratio of littoral to pelagic habitat area (L:P) and trout density (n. Ha^{-1}) in each zone was determined by multiplying the total trout density by the weighted preference for each zone.

Ideally additional physical factors such as depth, cover and disturbance should be considered as these probably influence trout distribution and movements. However inclusion of these factors must await further understanding of their operation and effects before adequate numerical models can be developed to describe their influence.

(b) Modelling smelt size selection by foraging trout

When a foraging fish encounters several prey it must choose which to attack first. Experimental work (O'Brien et al. 1976) suggests that they select prey which appear largest, either because of their actual size or because of their proximity to the predator. However this choice is likely to be modified both by the degree of contrast between a given prey and its background and by learning after previous experiences (Gibson 1980). Nevertheless, in general, as the predator's choice becomes more complex, the probability of attack on a given prey individual diminishes even though net feeding success increases with the number of prey instantaneously encountered.

The apparent size of the prey is a measure of its visible surface area which, for smelt could be modelled by the rectangular approximation:

$$\text{VISIBLE AREA} = \text{POST-PECTORAL BODY DEPTH} * \text{LENGTH}$$

Post-pectoral depth is not a constant fraction of length because smelt become more heavily bodied as they grow; thus this measurement must be predicted from the relationship with body length (fig. 54) which is best approximated by the power curve:

$$\text{POST-PECTORAL BODY DEPTH} = 0.0119 * \text{LENGTH}^{1.59} \qquad (43)$$

The range at which a trout might see a smelt probably depends on the contrast of the smelt against its background and on the trout's visual acuity, and therefore water clarity, light intensity and depth (Allen et al. 1973; Muntz and Wainwright 1978). Acuity can be defined as the ratio of prey "size" and distance to the eye (i.e. tangent of subtended angle).

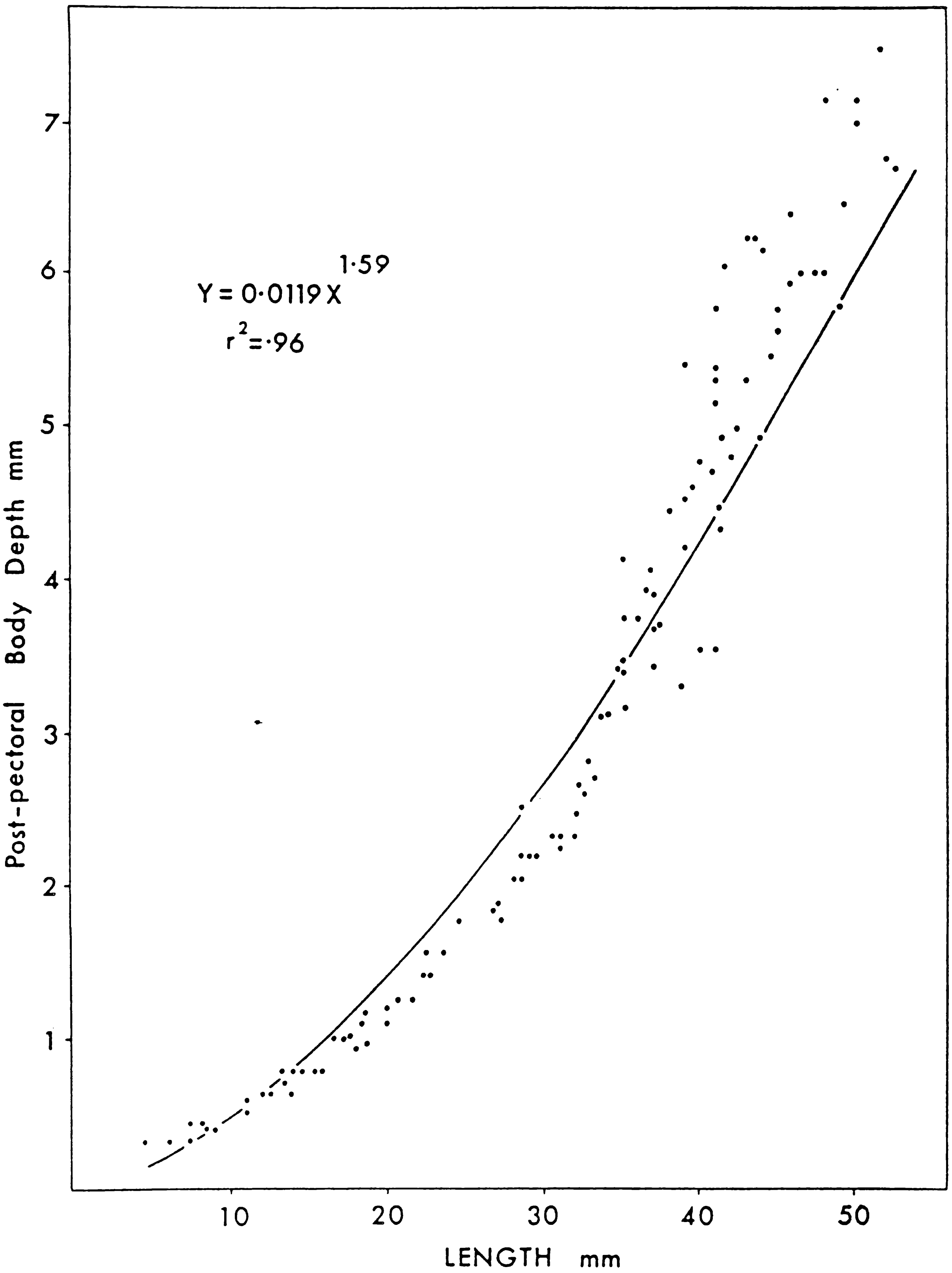


FIG. 54 The relationship between post-pectoral body depth and body length (FL) in smelt.

However this requries some standard definition of "size" which recognises that the eye sees surface area and not just a single dimension. One approach is to define the apparent size of a prey item as the diameter of a circle whose area equals the visible area of the prey:

$$\text{APPARENT SIZE} = 2 * \sqrt{\frac{\text{VISIBLE AREA}}{\pi}} \qquad (44)$$

Ware (1972) determined the distance at which rainbow trout respond to prey items and found a strong correlation with prey size. His data were used to define an appropriate value for acuity associated with feeding:

$$\text{ACUITY} = \frac{\text{PREY SIZE}}{\text{REACTIVE DISTANCE}} = 0.023 \qquad (45)$$

The range at which a given object might be seen will be limited either by acuity or by water clarity (Ware 1973) and so can be defined as the lesser of:

$$\text{RANGEVISIBLE} = \begin{matrix} \text{Either} & 0.001 * \text{APPARENTSIZE/ACUITY} \\ \text{or} & \text{SECCHI DEPTH} \end{matrix}$$

where secchi depth is regarded as including all factors influencing the range of visibility.

The volume of water instantaneously scanned for a given smelt size class will be limited either by the maximum range at which it is visible (as defined above) or by depth. If depth is not limiting then the volume of water instantaneously scanned might be defined as that of a cone or sphere of radius RANGEVISIBLE. If depth is less than double the water clarity then the volume of water searched seems most simply defined by the volume of a cylinder thus:

$$\text{VOLSEARCHED}_i = (4/3) * \pi * \text{RANGEVISIBLE}^3 \qquad \text{IF RANGEVISIBLE} < (0.5 * \text{DEPTH})$$

$$\text{VOLSEARCHED}_i = \text{DEPTH} * \pi * \text{RANGEVISIBLE}^2 \qquad \text{IF RANGEVISIBLE} > (0.5 * \text{DEPTH})$$

The "proportion" of a given smelt size class likely to be seen by a foraging trout can now be defined:

$$\text{PROPSEEN}_i = \text{VOLSEARCHED}_i * \text{TROUT} * 0.01/\text{STUDYVOLUME} \qquad (48)$$

where STUDYVOLUME is the water volume below the surface area under consideration (i.e. $100m^2$) and TROUT is trout density (n. Ha) under this area. Note that this quantity can exceed unity if trout and/or any smelt size class is especially abundant or conspicuous. Thus the model predicts that trout see (and will be likely to attack) many more large than small equally abundant smelt but both this difference and the proportion seen diminish with increasing turbidity. However this proportion is likely to vary with the choice of smelt sizes available and with trout hunger. If there are only a few smelt size classes present, then the probability of attack on one of these groups is much greater than if many size classes are present or if the trout are not particularly hungry.

(c) Modelling choice and the size range visible

The total number of smelt instantaneously visible to a foraging trout was defined by:

$$\mathrm{CHOICE} = \sum_{n}^{i=1} \mathrm{VOLSEARCHED}_i * \mathrm{FREQ}_i \tag{49}$$

and the proportion of this quantity which the size class under consideration comprises ($\mathrm{UNIFORMITY}_i$) was defined by:

$$\mathrm{VOLSEARCHED}_i * \mathrm{FREQ}_i/\mathrm{CHOICE} \tag{50}$$

$$\mathrm{UNIFORMITY}_i = \frac{\mathrm{VOLSEARCHED}_i * \mathrm{FREQ}_i}{\mathrm{CHOICE}}$$

This quantity (i.e. uniformity) is unity when only one size class is visible and tends towards zero with increasing numbers of size classes.

(d) Modelling hunger

Hunger seems best defined as a reverse sigmoid function of the gastric contents expressed as the weight of daily food intake (fig. 55). However there are no data from which the relationship could be established and the function used was chosen on the presumptions that stomach content volumes (fig. 45) represented 20-25% of daily food intake and trout whose stomachs contained 20-25cm^3 (nearly half distended) were about half satiated whilst those containing around 100cm^3 were fully satiated (daily food intake 400-500cm^3; hunger almost zero). Hunger was described as a function of the square root of stomach contents so that small but (computationally) non zero hunger values could be obtained for a substantial range of daily food intake values.

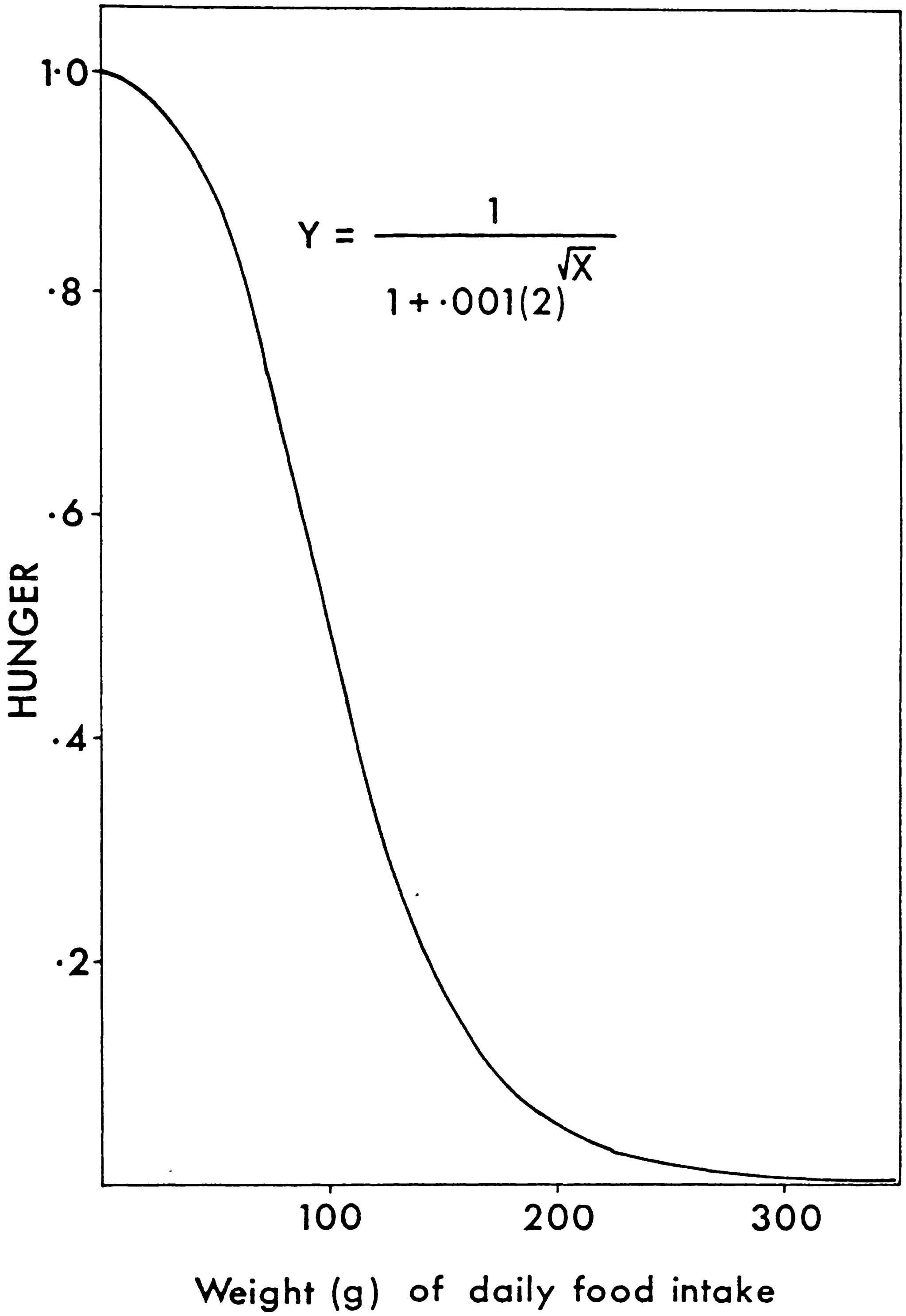


FIG. 55 The relationship between hunger and the quantity of food consumed daily by foraging trout.

(e) Smelt numbers attacked, escaping and eaten

The proportion of a given smelt size class likely to be attacked by foraging trout can now be defined by:

$$\text{ATTACKED}_i = \text{PROPSEEN}_i * \text{UNIFORMITY}_i * \text{HUNGER} * \text{TIMEINTERVAL} * \kappa \tag{51}$$

where κ is a scaling term defining the number of daily repetitions for this activity. ATTACKED_i can exceed unity but those eaten will always be a fraction of those attacked because some will escape. A smelt's ability to escape probably depends principally on burst swimming speed and this is largely a function of length. Thus the proportion of a given size class likely to evade capture might be described by:

$$\text{ESCAPE}_i = \frac{1}{1+ (1\text{E}6 * 0.78^{\text{LENGTH}_i})} \tag{52}$$

This describes low escapement by smelt smaller than 35mm but becoming significant for those larger than 45mm (cf. fig. 42; January 1982, March, April, October and December).

The proportion of smelt in a given size class which are eaten by trout can now be defined:

$$\text{EATEN}_i = \text{ATTACKED}_i - (\text{ATTACKED}_i * \text{ESCAPE}_i) \tag{53}$$

This quantity must be constrained between zero and unity because, although a smelt can be seen and attacked many times, it can be eaten only once.

The proportion surviving trout predation is:

$$\mathrm{NOTEATEN}_i = 1 - \mathrm{EATEN}_i \qquad (54)$$

and the total daily smelt intake (wet weight) by each foraging trout can be defined by:

$$\mathrm{TROUTFOOD} = \sum_{n}^{i=1} \mathrm{WEIGHT}_i * \mathrm{FREQ}_i * \mathrm{EATEN}_i / (\mathrm{TROUT} * \mathrm{TIMEINTERVAL}) \qquad (55)$$

where TROUT is the number of trout present in the habitat area under consideration as defined by algorithm 42.

In summary, size selectivity is based on smelt visibility, the quantity attacked is scaled according to the choice available and the trout's appetite whilst the proportion eaten is determined by the smelt's ability to escape.

6. Possibilities for further development

It would be interesting and informative to extend the model to include population processes of trout, bullies and koaro as all interact through predation and/or competition for food. In Lake Taupo predation by koaro and bullies is probably of little significance for smelt as adult bullies were strictly benthic (although smelt may be important food for bullies), adult koaro were rare in the lake and the number of smelt eggs eaten by bullies was very small in relation to the number present. Similarly, interspecific competition with smelt for food was probably minimal as bully and koaro densities were low compared with smelt and only their larval stages share the smelt's diet and pelagic habitat. Bullies and koaro comprised only a small proportion of the trout diet. However in other more productive lakes where bullies and occasionally koaro are relatively more abundant (Mylechreest unpubl. data) there may be significant interspecific competition for food amongst the larval fish and smelt may be less important in the trout diet. Thus bully and koaro interactions with smelt and trout might influence the growth and abundance of all species present.

Inclusion of trout population processes would be of particular value for development of fisheries management policies. However this would necessitate inclusion of models describing angling, trout reproduction, egg survival, juvenile growth, juvenile mortality, the size and abundance of food resources other than smelt as well as trout feeding selectivity in relation to body size. These aspects await investigation and consequently information on which suitable models might be based is not available. The model could be modified to predict population structure and abundance for several species in a multi-species competitive predator-prey system by definition of habitat zones, species movements and their population dynamics by interconnecting essentially similar models to those described above. However the modifications involved are extensive and beyond the scope of the present study.

CHAPTER 7 - THE BEHAVIOUR AND SENSITIVITY OF THE MODEL

In this chapter, the behaviour of the model is described, the logic controlling this behaviour examined and its sensitivity to parameter variation tested.

1. General Properties and Features of the Model

All simulations commenced with a smelt liberation equivalent to 3000 smelt per hectare which were evenly distributed over the size range 2-200mm and were equally divided between littoral and pelagic habitats. Dramatic year to year variation in simulated population characteristics always occurred for the first 3-5 years simulated but during the following five year period, seasonal patterns became more consistent, reaching maximum stability after about 15 years. Thus the final 1-3 years of a 20 year simulation were used for comparative purposes. Cyclic or steady state equilibria developed only under exceptional circumstances.

The model was first run with a standard set of parameter values (Table 8) and the resulting 'standard outputs' are shown in figs. 56 and 57. A series of simulation trials was then run, in each of which only one of the model parameters differed from the standard set so the output data were comparable. Where appropriate, one very high and one very low value for a given parameter was tested. The standard set of parameter values was chosen to describe features of a system similar to Lake Taupo so that simulated smelt population processes might be comparable with those occurring in Lake Taupo.

The effects of model components with built in seasonal variability (i.e. smelt maintenance requirements, their maturity rate and the rate of movement between habitat zones) were isolated from seasonal changes in model parameters (eg. food production, food particle size, trout abundance etc) by eliminating seasonal variation in all habitat features and examining seasonality in these separately. Thus, excepting trials where the effects of seasonality were under scrutiny, all habitat features remained constant throughout the year.

Table 8. Parameter values used to describe the standard system

Mean depth in littoral zone = 15m

Mean depth of pelagic zone = 110m

Ratio of littoral to pelagic habitat area = 0.05

Water clarity (Secchi depth) = 15m

Littoral food production = $1.0 g.m^{-2}.d^{-1}$

Modal size of littoral food = 4.0mm

Shape term for littoral prey size frequency distribution = 2.0

Pelagic food production = $1.0 g.m^{-2}.d^{-1}$

Modal size of pelagic food = 0.3mm

Shape term for pelagic prey size frequency distribution = 1.2

Minimum prey size = 0.001mm

Duration of spawning season = 365 days

Egg survival = 1.0

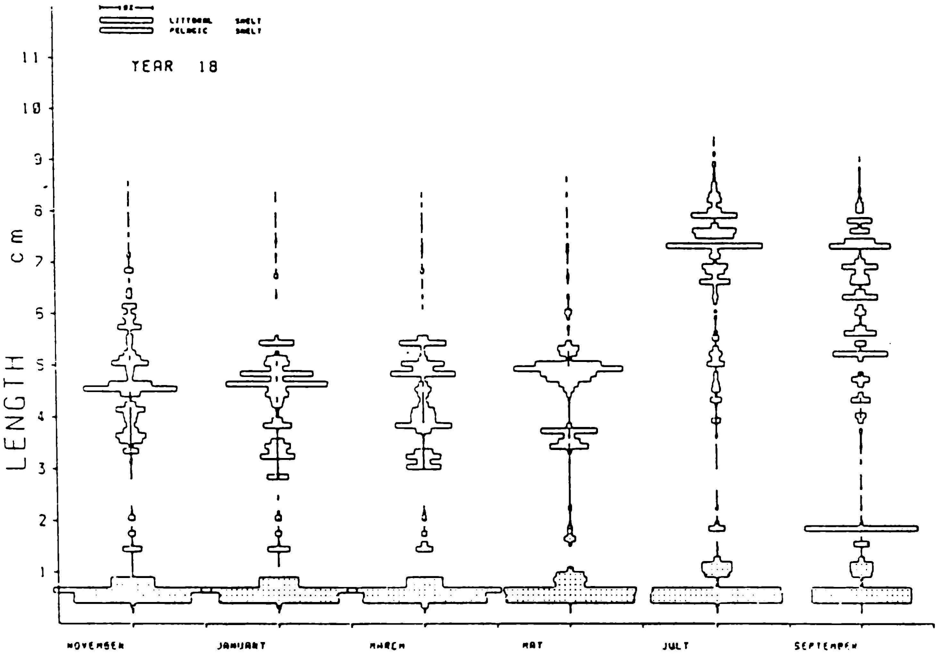
Trout stocking density = $2.0 Ha^{-1}$

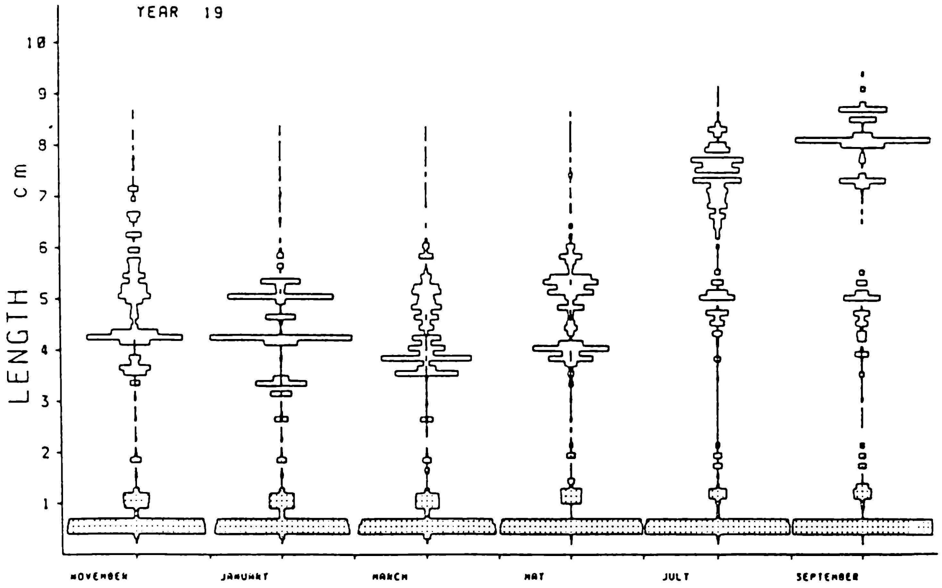
Bullies present? = No

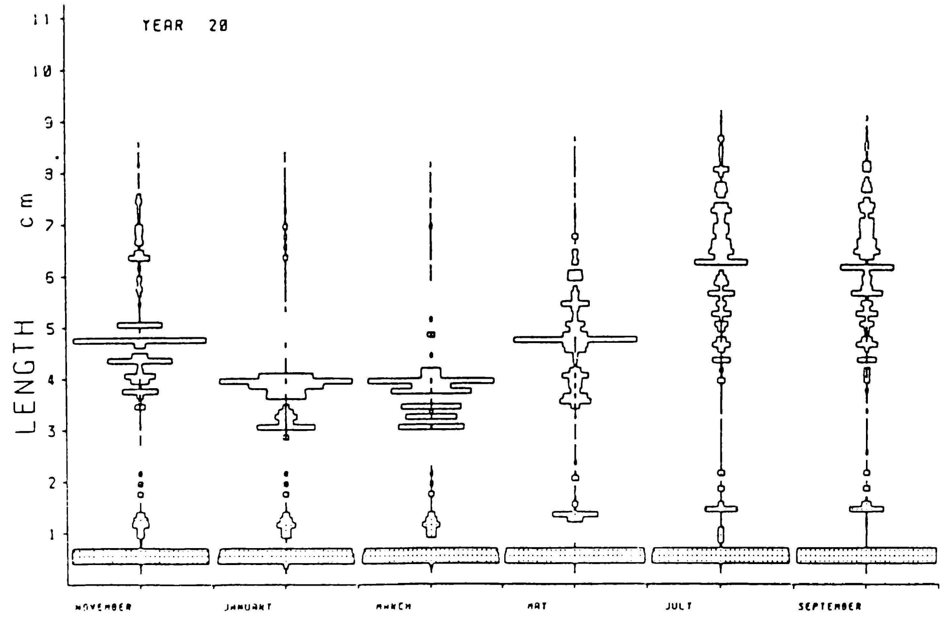
Output data consisted of bimonthly length frequency data and time series data for selected population parameters monitored at the end of each time interval simulated (i.e. 10 days). The parameters monitored were spawner densities, biomass, trout distribution and the weight of smelt eaten daily by trout. Length frequency data are presented only for the final year simulated, except in the standard run (fig. 56) where data for the final three years simulated are presented to illustrate annual variation. Time series data for selected population parameters describe changes occurring during the final three years simulated, except in the standard run (fig. 57) where parameters were monitored for six years. There was considerable variation in scale between data from different runs and so, to provide comparable data without excessive loss of detail, length frequency data are given as percent frequency distributions and population parameter data were scaled to occupy the available space on the paper. Consequently, ordinate scales for diagrams illustrating seasonal changes in selected population parameters are not consistent between runs.

FIG. 56

Simulated smelt length frequency distributions in the "standard" system. The habitat features which characterize this system are given in Table 8.


LITTORAL SMELT
PELAGIC SMELT
YEAR 18
LENGTH cm
1
2
3
4
5
6
7
8
9
10
11
NOVEMBER
JANUARY
MARCH
MAY
JULY
SEPTEMBER


YEAR 19
LENGTH cm
1
2
3
4
5
6
7
8
9
10
NOVEMBER
JANUARY
MARCH
MAY
JULY
SEPTEMBER


YEAR 20
LENGTH cm
1
2
3
4
5
6
7
8
9
10
11
NOVEMBER
JANUARY
MARCH
MAY
JULY
SEPTEMBER

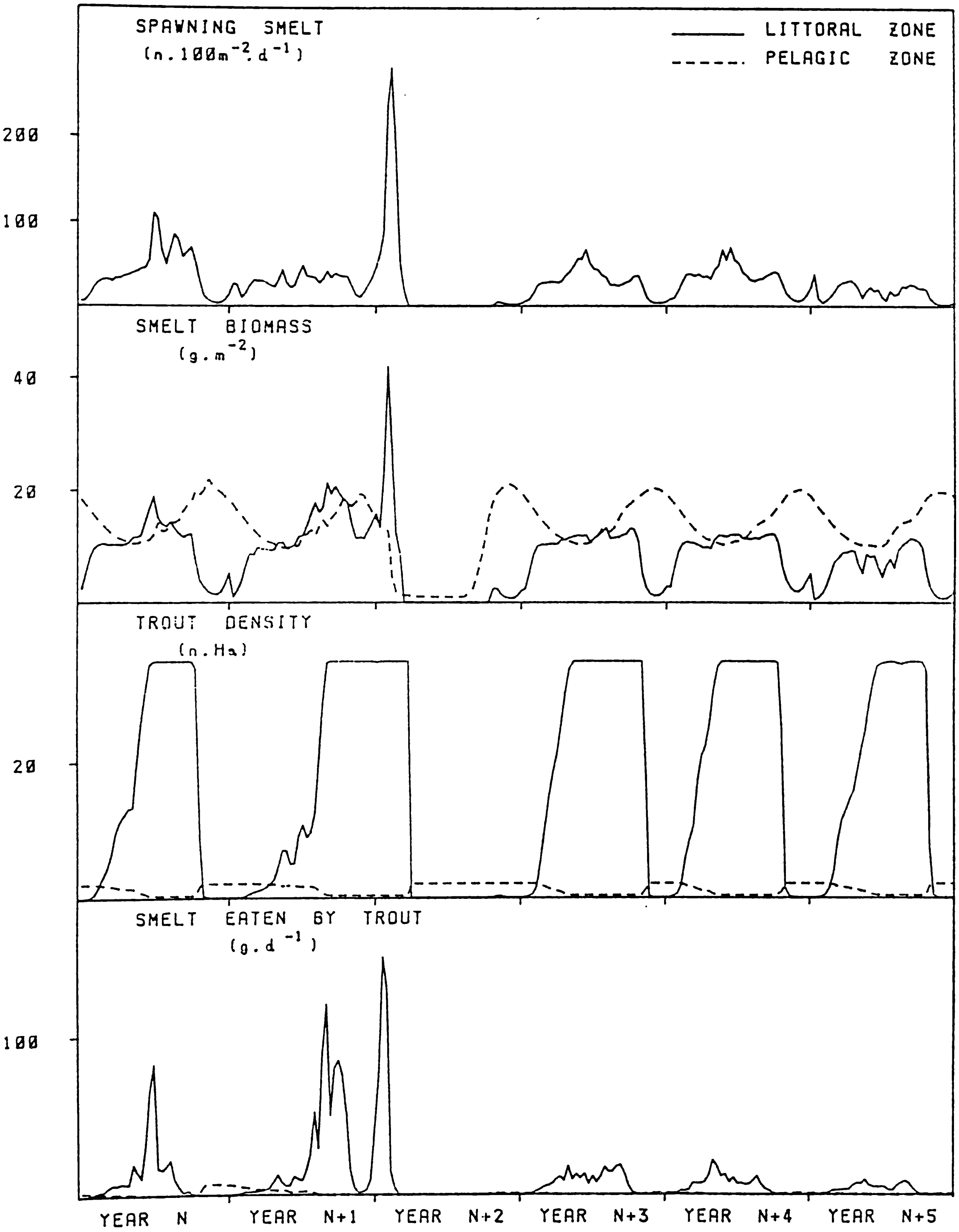


FIG. 57 Population parameters in the "standard" system during the final six years of a 20 year simulation. The habitat features characterizing this system are given in Table 8. N = 15

(a) Simulation Time and Length Intervals

All simulation outputs described were obtained using 1.0mm length intervals and a 10.0 day unit time interval. These units were chosen to ensure that program execution time was not excessive (i.e. < 2 hours for a 20 year period). However these large intervals caused the characteristically 'ragged' form of the length frequency distributions. When the unit length interval was reduced to 0.1mm and the unit time interval to 1 day, frequency distributions and the population parameters (spawner density, littoral biomass, quantities eaten by trout) were much more regular in appearance but execution time was unacceptable, being about 12 hours for a 4 year simulation. Modal lengths and length range were not affected, although the height of peaks in annual summary data were reduced slightly.

(b) Individual Variation in Feeding Vigour

Individual variation in growth was modelled through unequal allocation of food to the fish in each length interval. The number of smelt in each length interval was divided into three groups. The number in each group was determined by the ratio 0.3:0.4:0.3 and the food available to each length interval was allocated in the ratio 1.5:1:0.5. Thus 30% of the fish in each length interval were fast growing because they received three times as much food as the slow growers.

In the absence of growth variation the population processes ceased to operate when food intake and maintenance requirements were approximately equal and when the smelt were too small to be subject to predatory or spawning mortality. Under these circumstances, the smelt neither grew nor starved and the system became static. However this problem never arose when growth variation was incorporated into the model.

Two trials were used to examine the effect of different proportions of fast and slow growing smelt on simulated population length frequency structure. In one, length intervals were divided into fast, intermediate and slow growers according to the ratio 0.1:0.8:0.1 (low variation) and in the other, the ratio 0.4:0.2:0.4 was used. Increasing growth variation caused greater spread around the modal length of pelagic smelt but littoral length frequency distributions were not significantly affected (figs. 58 and 59). The 'ragged' shape of the distributions was also unaffected.

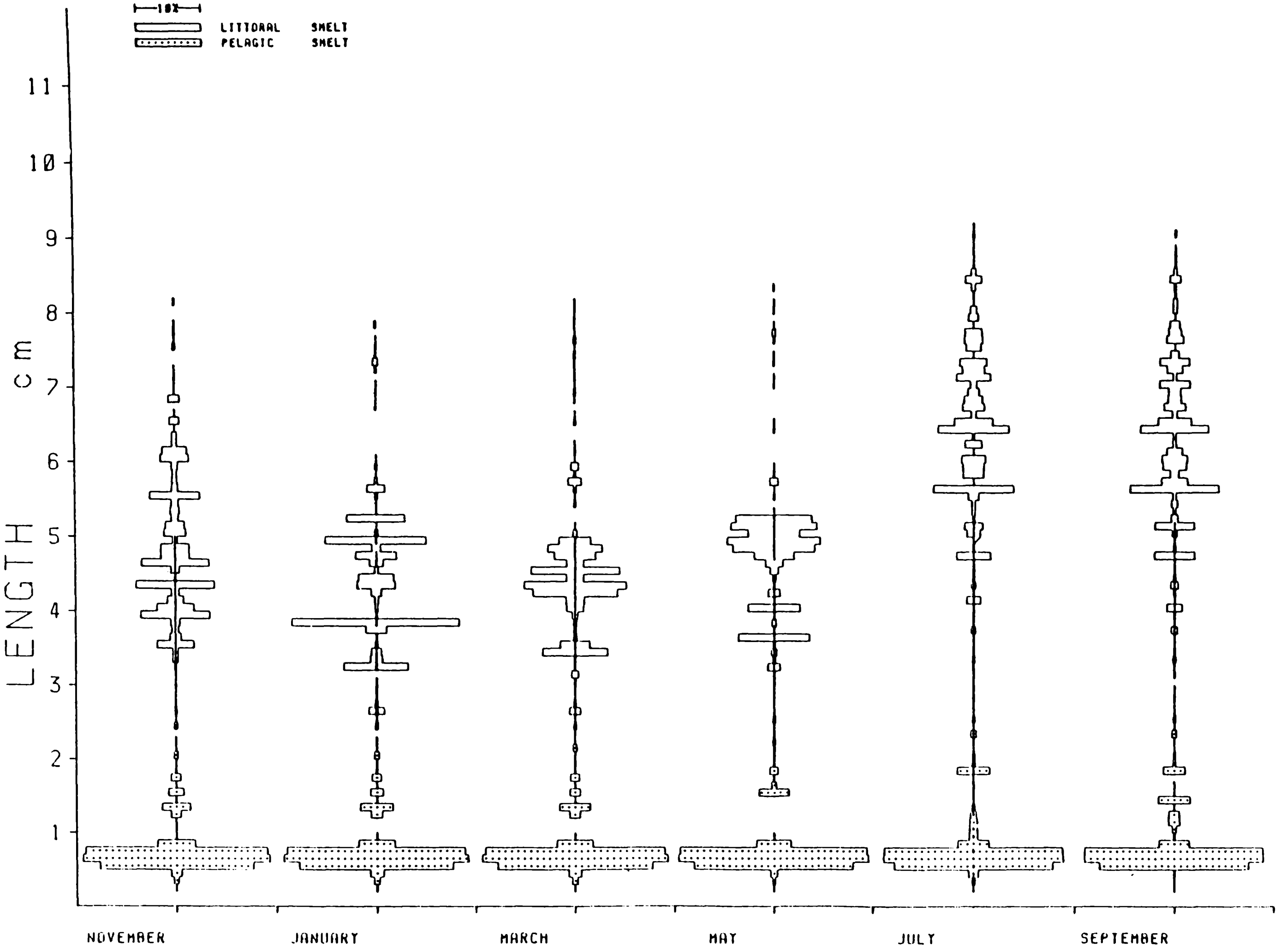


FIG. 58 Simulated smelt length frequency distributions after altering feeding vigour variability. Each length interval was divided into fast, intermediate and slow growing smelt according to the ratio 0.1:0.8:0.1.

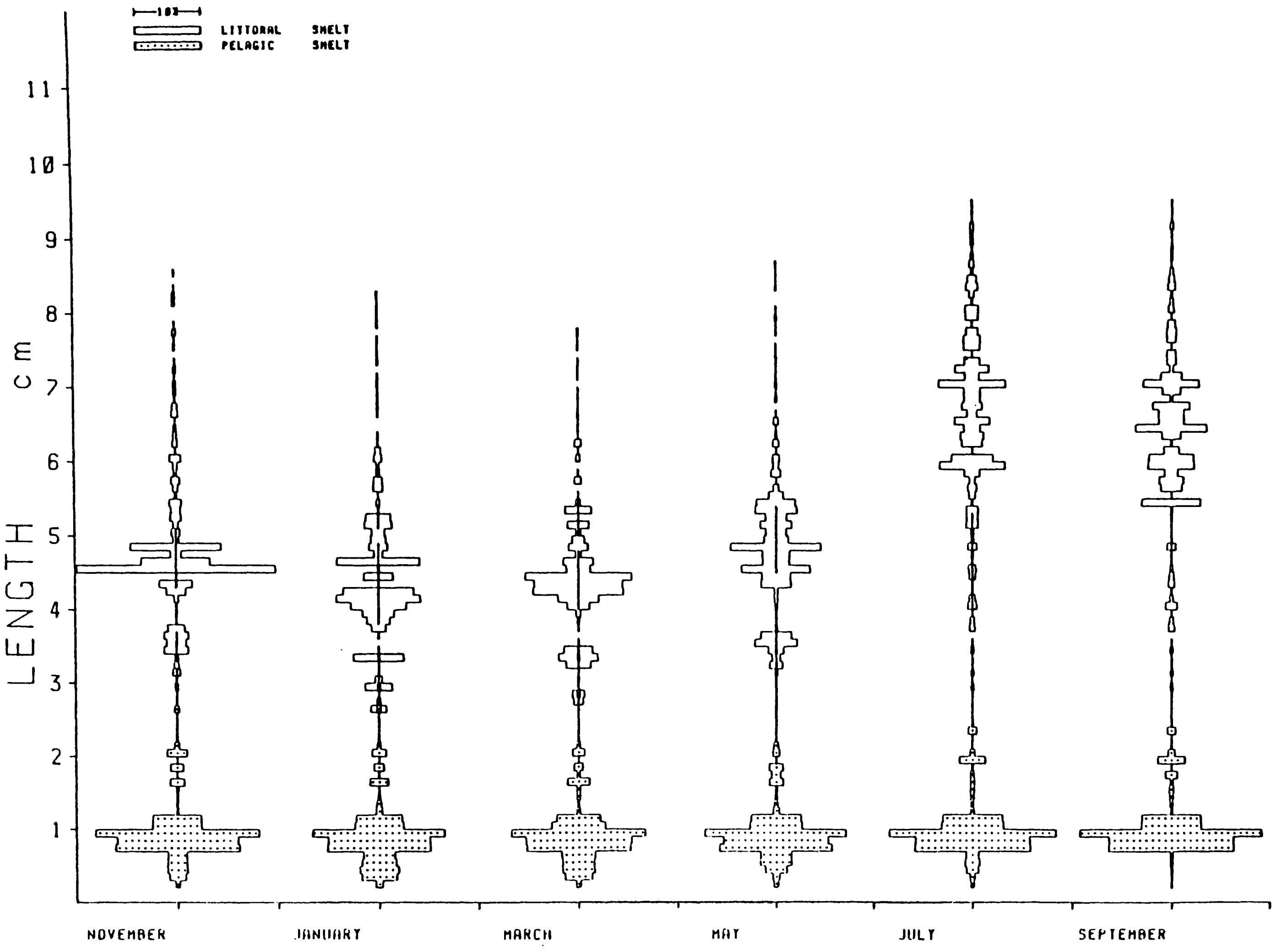


FIG. 59 Simulated smelt length frequency distributions after altering feeding vigour variability. Each length interval was divided into fast, intermediate and slow growing smelt according to the ratio 0.4:0.2:0.4.

(c) Diet Breadth and model behaviour

Diet breadth (fig. 52) was defined by the difference between upper and lower prey size limits which were described by increasing functions of length. For the standard run, diet breadth was defined by:

$$0.00724L^{1.69} - 0.001L^{1.6}$$

When the much narrower diet breadth (fig. 60),

$$0.007L - 0.003L$$

was used instead, the length frequency structure (fig. 61) remained essentially similar to the standard run but the largest smelt (> 70mm) were absent and spawner numbers, biomass and quantities eaten by trout (fig. 62) were reduced. This occurred because these limits encompassed a smaller proportion of the food size range and there was insufficient food available within the diet size limits of larger smelt to sustain growth. However when the slightly broader diet breadth,

$$0.002L^{1.6} - 0.001L^{1.6}$$

was tested, the system was not viable and the smelt became "extinct". This occurred because the diet breadth for smelt 2-6mm long was so restrictive (see figure inset in fig. 60) that they had insufficient diet breadth to obtain a large enough ration to grow. This diet breadth would have been viable if either the average size of pelagic food were smaller or if total food production had been substantially greater.

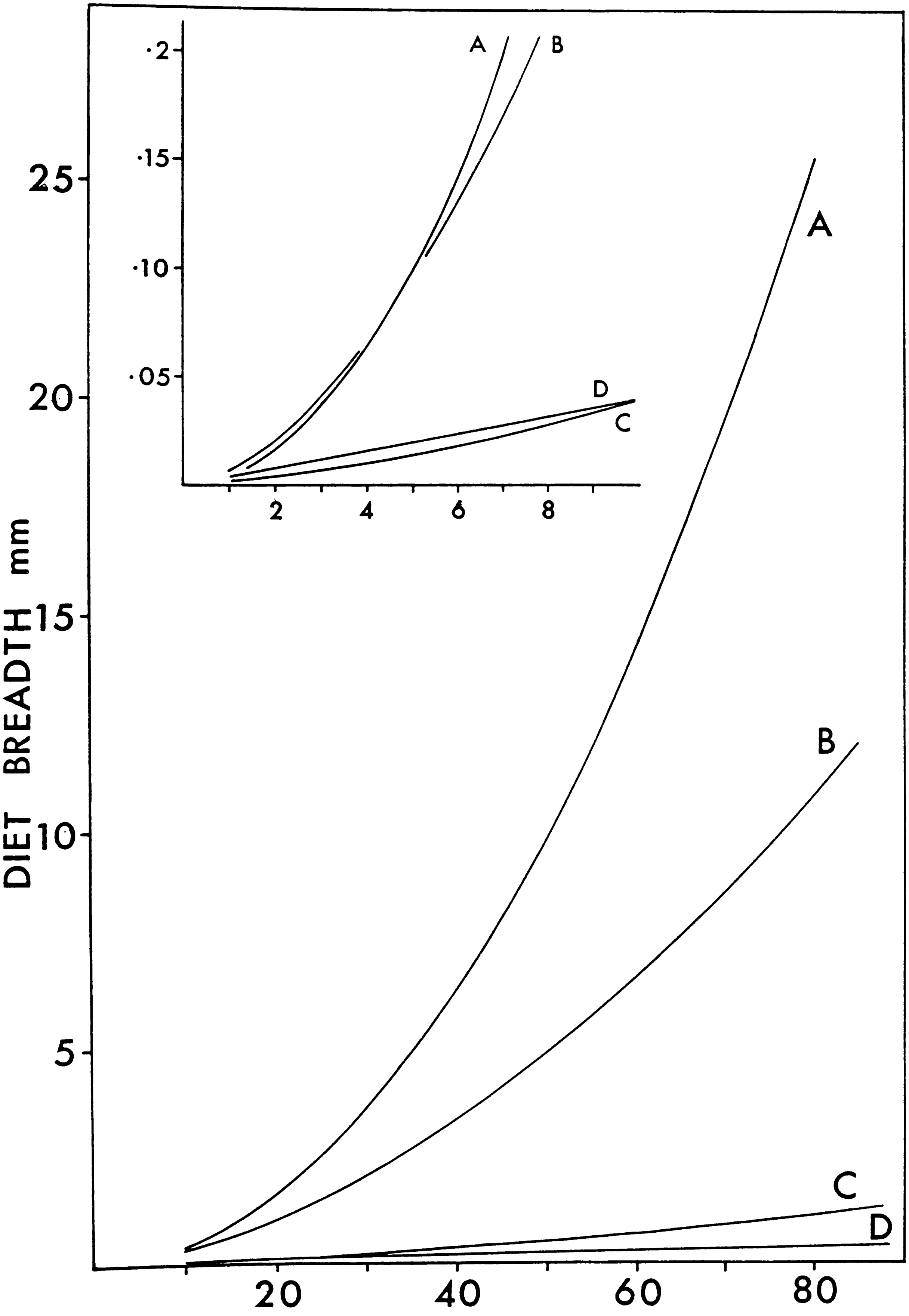
Fish with the diet breadth,

$$0.007L^2 - 0.003L^2$$

increased rapidly with length, had a high lower food particle size limit and, like fish with the diet breadth used in the standard run, had widely separated limits. The effects of these features were to cause a bimodal pelagic smelt length frequency distribution to develop (fig. 63) and depress smelt numbers in the littoral zone (fig. 64). Littoral smelt numbers were low because the high lower diet breadth limit prevented them feeding on small food items which comprised a major proportion of total food production. The modal length of pelagic smelt increased because the rate at which the quantity of food available for consumption increased with length was high. There were two factors which contributed to this. Firstly, because the diet breadth increased as a steep exponential function of length, substantially more of the food resource became available with only small increases in length. Secondly, because adult smelt numbers were low, their reproductive output was depressed and consequently competition for food amongst the larval smelt was not sufficient to limit growth until they reached 23-25mm. Thus modal lengths were determined by the rate at which the quantity of available food increased with fish length. The factors which determined this rate are diet breadth, the distribution of productivity over the prey size range and competition for the available resource.

FIG. 60

Relationships between diet breadth and length used in trials examining the effects of different diet breadths on smelt population parameters.


DIET BREADTH mm
25
20
15
10
5
20
40
60
80
LENGTH mm
A
B
C
D
·2
·15
·10
·05
2
4
6
8
A
B
D
C

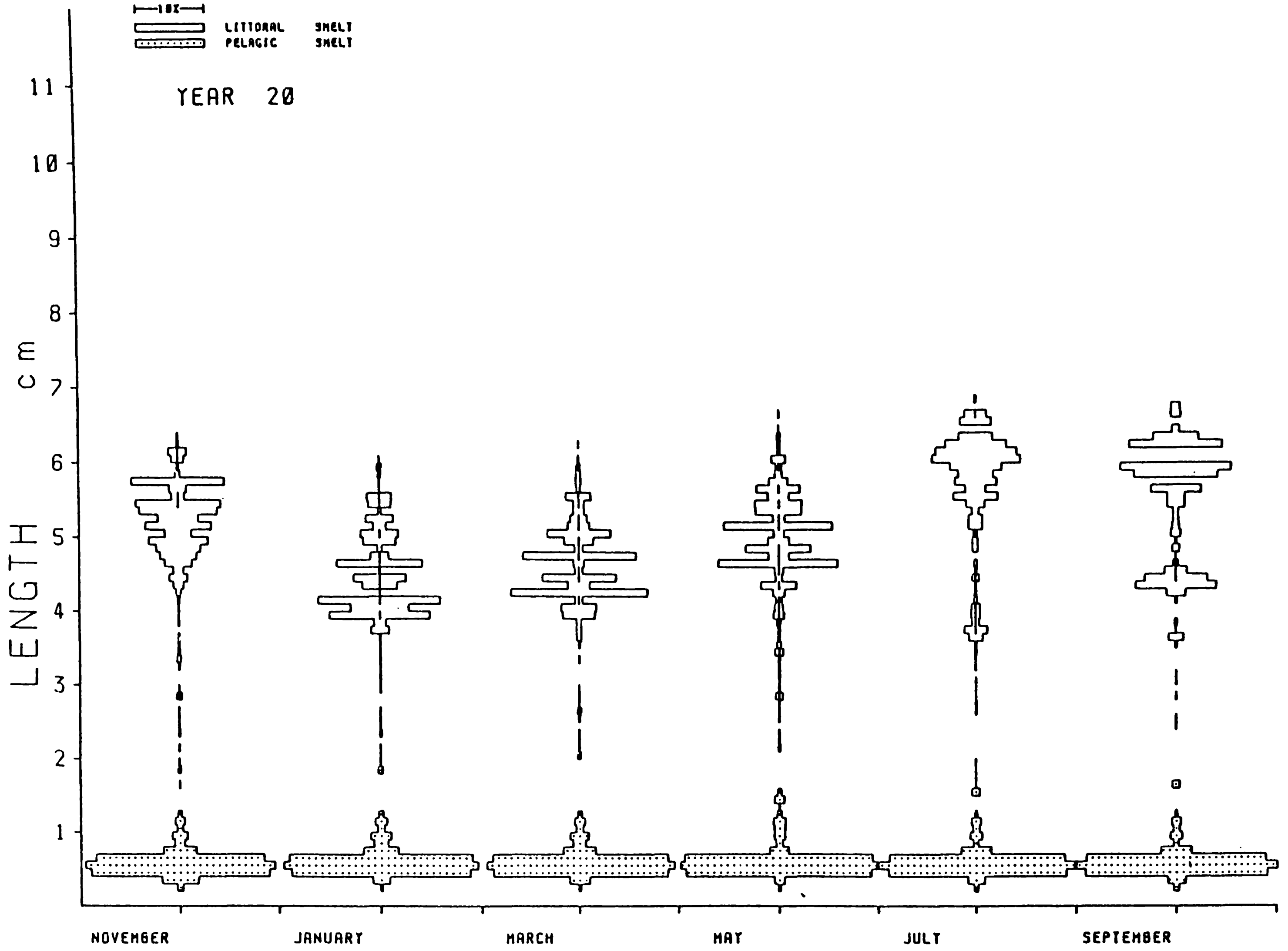


FIG. 61 Simulated length frequency distributions obtained when the diet breadth was described by 0.007L - 0.004L where L is length (mm).

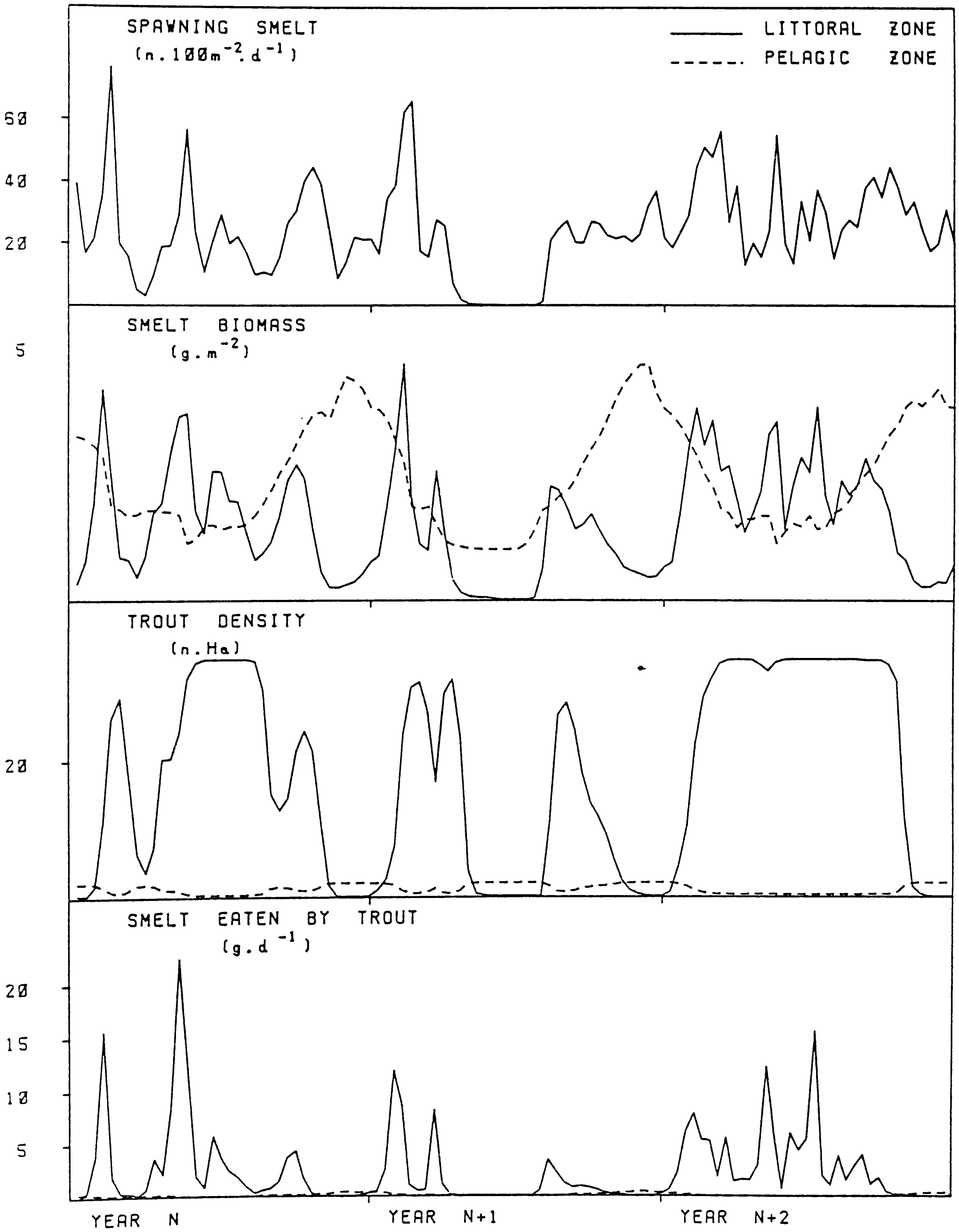


FIG. 62 Simulated population parameters obtained when the diet breadth was described by 0.007L - 0.004L where L is length (mm). N = 18

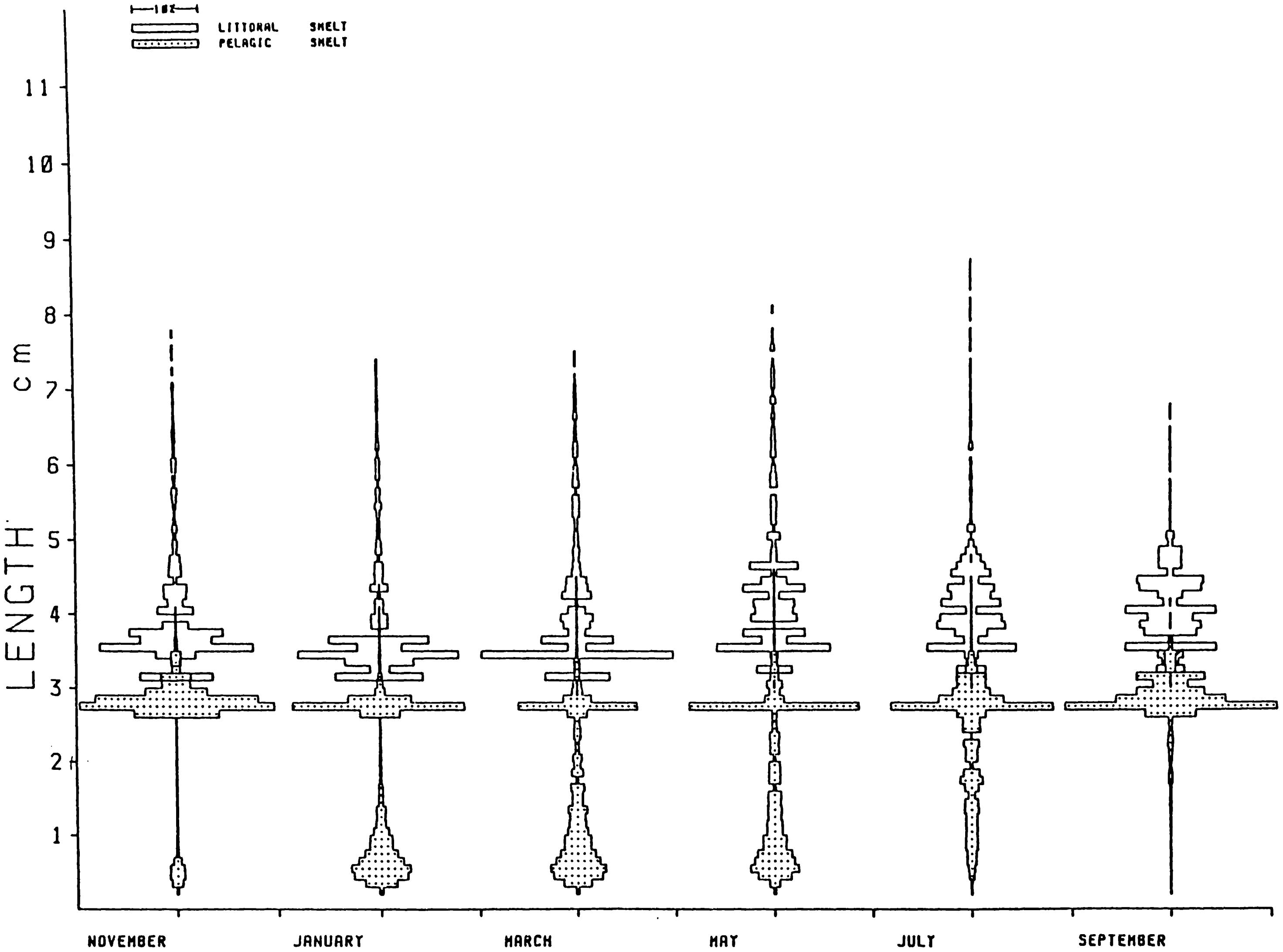


FIG. 63 Simulated smelt length frequency distributions obtained when the diet breadth was described by $0.007L^2 - 0.003L^2$ where L is length (mm).

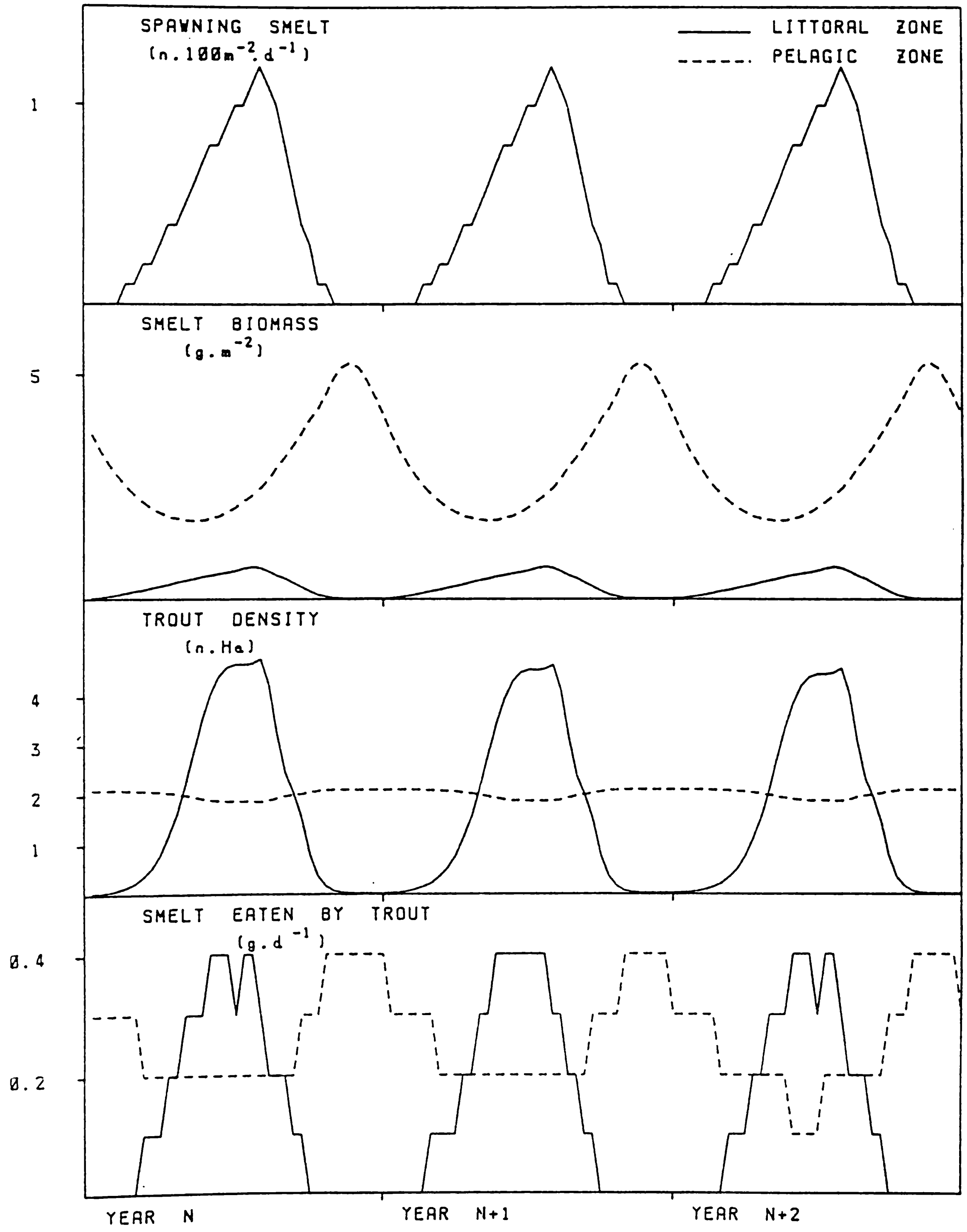


FIG. 64 Simulated population parameters obtained when the diet breadth was described by $0.007L^2 - 0.003L^2$ where L is length (mm). N = 18

(d) Morphological variation in diet breadth

The relationship between diet breadth size limits and fish length determines both the size range of potential competitors and, for a given prey size distribution, controls the proportion of the food resource which becomes available to a fish as it grows. This implies that population characteristics will be influenced not only by the relationship between diet breadth and fish length, but also by the relationship between diet breadth size limits and length. This is of particular interest as there is considerable morphological variation between lacustrine and migratory riverine smelt in their gill raker structure, number and head shape (McDowall 1979; Northcote and Ward 1984). It seems likely that these populations would therefore have different diet breadths and different food particle size limits, so that their abilities to utilize a given food resource would also differ. Thus two simulation trials were used to compare population parameters obtained for two similar and overlapping diet breadths with differing limits (fig. 65) to examine the performance of two forms of smelt.

The larger diet breadth limits resulted in a population with bigger juvenile smelt, fewer spawners, and reduced littoral biomass; pelagic biomass was unaffected (Table 9). These diet limits defined a diet breadth which embraced a smaller proportion of total food production and this limited the population's ability to utilize the food resource, despite having a broader total diet breadth. Increased access to larger prey, reduced competition and slightly broader diet breadth failed to compensate for inability to feed on the more abundant small food items. However the raised diet limits would have sustained greater littoral biomass and numbers of spawning smelt if larger prey were relatively more numerous. This behaviour of the feeding model suggests that for a given prey size distribution, there is an optimum diet breadth defined by limits which maximize food resource utilization and minimize the size range of potential competitors diminished with the rate at which diet breadth limits increased with length, the optimum represents a compromise between generalist and specialist feeding strategies.

The behaviour of the feeding model implied that a narrow diet breadth or specialist feeding strategy would be adaptive when the size structure of the food resource does not vary with time and when there is intense competition for it. Conversely, a broad diet breadth or generalist feeding strategy would be appropriate if the prey size distribution was variable or if there was little competition for available food. Thus intensity of competition may be the key factor which determines whether specialization or generalization will be the optimum feeding strategy for a given food resource.

Table 9. Population parameters obtained for the final six years of a twenty year simulation for two forms of smelt whose diet breadths were defined by different food particle size limits. One form (left) was characterized by larger and more widely separated food particle size limits (fig. 65). Data are daily means (± 95% confidence limits) calculated for the whole year.

	DIET BREADTH = $0.00724L^{1.69} - 0.002L^{1.6}$			DIET BREADTH = $0.007L^{1.6} - 0.001L^{1.6}$		
		BIOMASS			BIOMASS	
YEAR	SPAWNERS	LITTORAL	PELAGIC	SPAWNERS	LITTORAL	PELAGIC
15	25.2±5.3	8.0±1.3	14.3±1.1	61.1±13.3	10.3±1.6	14.1±1.2
16	26.6±5.7	8.6±1.5	13.7±1.1	59.3±11.0	10.4±1.3	14.1±1.3
17	29.2±7.0	9.0±1.4	12.2±0.9	59.9±10.4	9.9±1.4	14.2±1.3
18	28.6±21.0	6.7±3.1	7.5±2.2	45.7±7.4	9.6±1.2	14.1±1.3
19	24.9±4.8	8.0±1.2	15.0±1.1	57.8±11.4	9.7±1.9	13.9±1.1
20	31.3±6.0	8.3±1.4	14.9±1.3	48.4±14.1	9.1±1.7	14.1±1.3

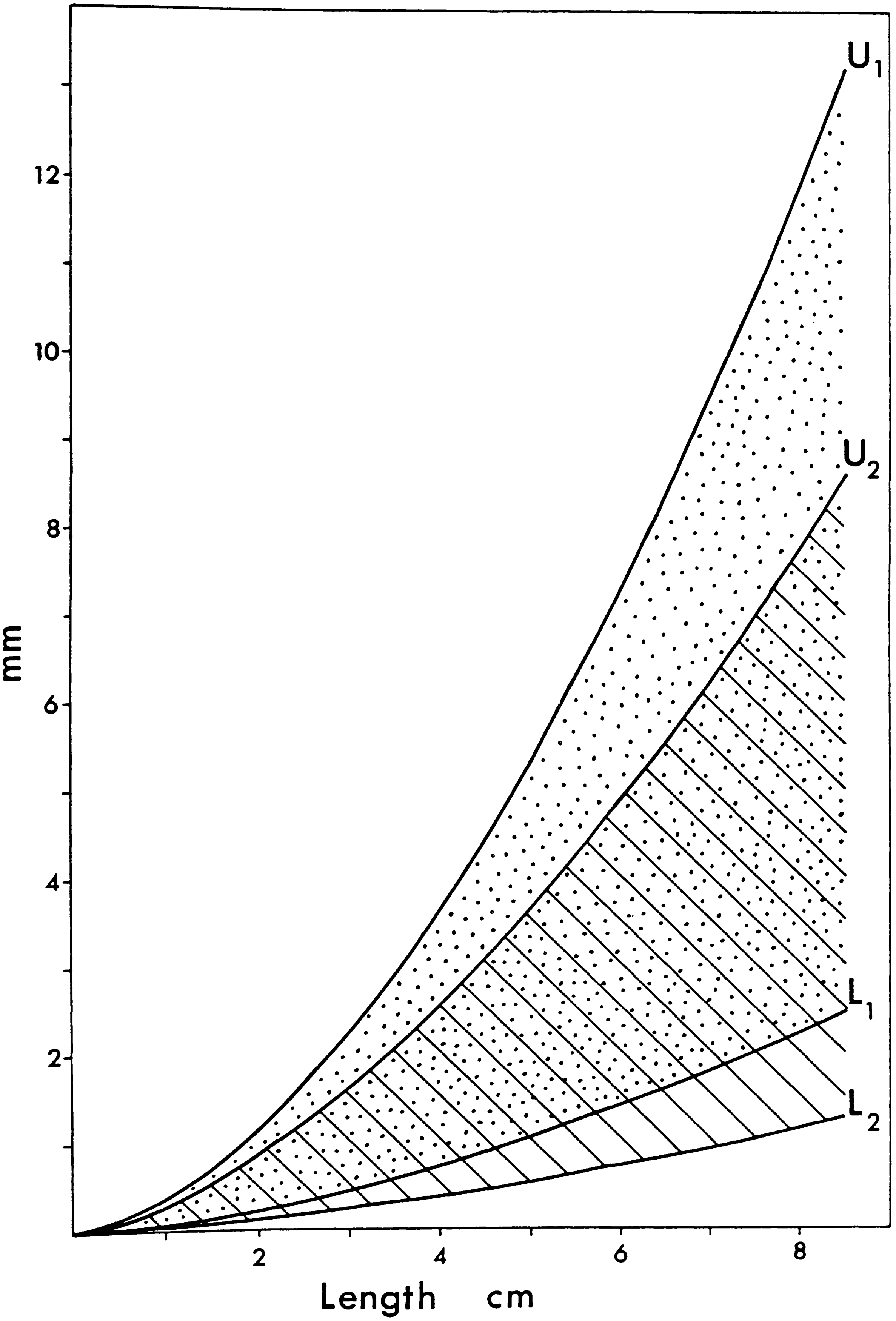
FIG. 65

Two similar diet breadths with different diet breadth limits. The stippled area represents a broader food particle size range which includes larger items and is defined by the limits U_1 and L_1 where,

$$U_1 = 0.00724L^{1.69} \quad \text{and} \quad L_1 = 0.002L^{1.6}$$

The shaded area repesents an overlapping, narrower food particle size range which includes smaller items and is defined by the limits U_2 and L_2 where,

$$U_2 = 0.007L^{1.6} \quad \text{and} \quad L_2 = 0.001L^{1.6}$$


U1
U2
L1
L2
mm
2
4
6
8
10
12
2
4
6
8
Length cm

The differences between the size distribution of prey species available at sea, in rivers and in lakes may account for certain differences between lake resident and anadromous smelt populations (McDowall 1970, 1972, 1979; Woods 1968). The lake limited smelt populations of the central North Island are derived from liberations of migratory Waikato River stock but major morphological and meristic differences now exist between these and the present Waikato River population (McDowall 1972, 1979). When compared with lacustrine smelt populations such as that which occurs in Lake Taupo, Waikato River smelt have fewer gill rakers, more vertebrae, larger but fewer eggs and a heavier body form (Northcote & Ward 1984). The major biological difference between Waikato River smelt and lacustrine populations is the more extreme migratory behaviour of the former, as their larvae develop in estuarine or coastal waters and return to the lower river system as immature adults where they feed, mature and spawn. This behaviour is analogous to pelagic larval development and the spring migration into littoral habitat; the difference being in the distances separating juvenile from adult habitats.

If spawning occurs some distance from coastal feeding areas then emergent larvae will require sufficient energy reserves to ensure survival whilst drifting downstream towards the feeding area. However in a lake, such reserves are unnecessary because of the proximity to larval feeding habitat and therefore the requirement for large eggs and larvae with high energy reserves may not be important in a lake system. The zooplankton of estuarine and coastal habitats is usually more diverse both in size and species composition than occurs in lake habitats. One would therefore expect an advantage from an opportunist feeding strategy which permits exploitation of whatever species are readily available.

Short, widely spaced gill rakers, an elongated body form and large larval size which characterize migratory Waikato River smelt may be adaptations for feeding on larger bodied evasive prey; longer closely spaced gill rakers may reduce the maximum suction velocity generated by the buccal-opercular pumping action and reduce efficiencies of feeding on evasive zooplankton (Wright et al. 1983). Presumably such feeding apparatus is well suited for opportunist feeding on insects and epibenthic fauna which abound in the lower Waikato River and tributary lakes. In contrast, zooplankton in lakes is less diverse and not infrequently dominated by small bodied cladocerans and rotifers. Simulations suggested that the greatest single source of mortality is juvenile starvation. Therefore one would expect strong selection for more specialized feeding apparatus which could improve feeding efficiency on the zooplankton size range available. This would necessitate inclusion of smaller species in the diet and greater numbers of longer and more closely spaced gill rakers, characteristics of Lake Taupo smelt, would achieve this, but at the expense of feeding efficiency for large evasive prey. Thus their effective upper prey size limit may be somewhat lower than for similar sized migratory smelt. Simulations indicated that raised diet breadth limits increased the growth of adult smelt if large prey were present, and this could account for the size difference between sympatric lake resident and migratory smelt in Lake Waahi (Northcote and Ward 1984). Similarly, the combined effects of reduced diet breadth limits and the generally smaller prey available in lakes would account for the dwarfism characterizing all central North Island smelt populations.

2. Model sensitivity to variations in habitat features

Model sensitivity to variation in the major influential features of the lake habitat is examined in this section. The effects of increases in each feature in relation to standard values (Table 8) are summarized in Table 10 and are each described in this section.

Table 10. The effects of increases in habitat variables on selected population parameters. Data represent increases (+), decreases (-) or no significant change (0) in population parameters following an increase (in relation to the values describing the standard system) in the habitat variables listed.

	PELAGIC ZONE			LITTORAL ZONE			
	Modal Length	Biomass	Wt eaten by trout	Modal Length	Spawner density	Biomass	Wt eaten by trout
Modal size of pelagic food	0	0	-	0	+	+	+
Modal size of littoral food	0	0	0	+	-	-	-
Minimum prey size	+	0	0	0	0	0	0
Pelagic shape term	+	0	+	-	-	-	-
Littoral shape term	0	0	0	0	+	+	+
Pelagic prey production	0	+	0	-	+	+	+
Littoral prey production	-	0	0	+	+	+	+
Restricted spawning season	+	0	+	0	+	0	0
Trout Nos	0	0	0	0	0	0	0
Littoral habitat	-	0	+	+	-	-	-
Pelagic depth	0	0	-	0	0	0	0
Littoral depth	0	0	0	0	0	0	-
Turbidity	0	0	-	0	0	0	-
Egg Mortality (0.8)	+	0	0	0	0	0	0
Larval mortality	+	-	+	0	0	0	0

(a) The smelt food resource

(i) The Distribution of Productivity over the Prey Size Range

In the model, diet breadth was a fixed morphological feature and therefore the principle variable which determined modal length was the distribution of productivity over the prey size range as described by a Weibull density function. The shape of the Weibull function was defined by three parameters: the minimum particle size, the modal size and the shape term which determined the distribution's kurtosis and skewness (fig. 66). The effects of variation in these parameters were examined separately for both the littoral and pelagic food resources.

(ii) Modal Food Particle Size

Sensitivity to a tenfold (0.1 to 1.0) increase in the modal size of pelagic food items was considerable. When the modal size of pelagic food items was 1.0mm, growth of the smallest smelt was slow and there was a persistent mode at 2-4mm in length (fig. 67). However, once through this "bottleneck" they grew rapidly and were soon recruited to the littoral population where numbers of spawners, smelt biomass and quantities eaten by trout were high (fig. 68). In contrast, when the modal prey size was only 0.1mm, smelt in the pelagic zone had a bimodal length frequency distribution, the primary mode varying seasonally between 25 and 33mm in length (fig. 69). Numbers of smelt recruited to the littoral population were reduced because the pelagic food resource could sustain only small numbers of smelt large enough to move into the littoral zone. Consequently spawner densities, biomass and quantities eaten by trout were low and the trout found more smelt to eat in the pelagic zone (fig. 70).

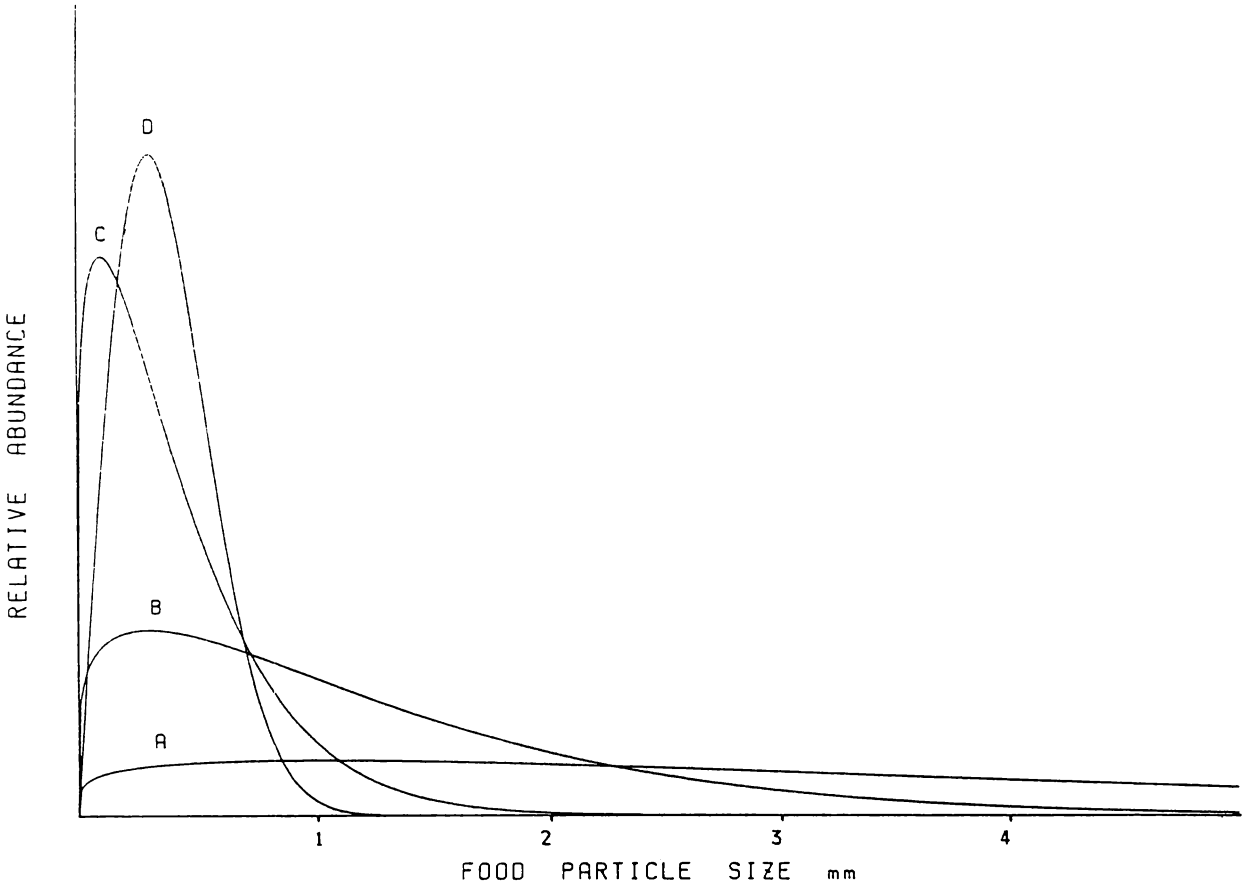
Both systems were characterized by erratic annual cycles and appeared unstable. When the pelagic prey size was large the system was unstable because the large reproductive population produced far more offspring than could be sustained by pelagic production of food items within the larval smelt's food particle size limits. This caused a bottleneck in larval development and periodically inhibited recruitment to the adult population thereby temporarily depressing breeding and reducing larval competition, allowing further larval development and, later, increased egg production. However, when pelagic prey were small, larval growth was rapid and the bottleneck occurred at 24-30mm. This restricted the number able to join the littoral population and breed. Consequently, when pelagic smelt densities were low following depressed spawning activity, those present grew larger and were able to join the littoral population and breed. This accelerated larval recruitment causing further competition which depressed growth in the pelagic zone sufficiently to curtail movement into the littoral zone and halt further reproduction. Hence the cyclic instability of this system.

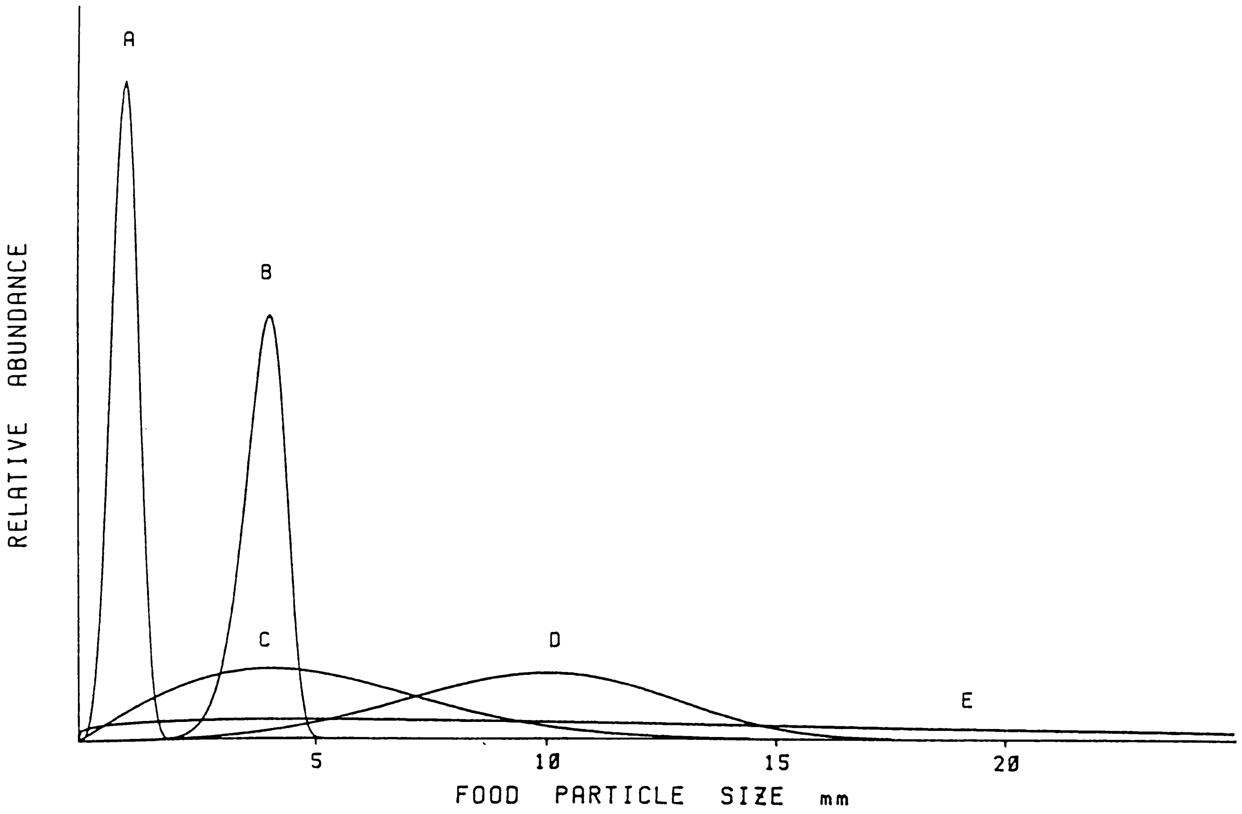
Variation in the modal size of littoral food was found to have little effect on population processes as a tenfold increase (1.0 to 10.0mm) caused only minor changes in population length frequency structure (fig. 71 cf. fig. 73). Modal lengths of littoral smelt increased by ca. 5mm when littoral prey were small (fig. 71) but when larger prey were available, big smelt (> 60mm) were always present (fig. 73). However spawner densities, littoral biomass and quantities eaten by trout were reduced (fig. 72 cf. fig. 74) because a significant proportion of the littoral food resource was larger than the upper food particle size limit for littoral smelt. In the standard run (figs. 56 and 57), the modal size was 4.0mm and littoral biomass was greater than was obtained when the modal prey size was either 1.0 or 10.0. This indicates that there was an optimum modal prey size which supported a maximum sustainable fish biomass at a given rate of food production for fishes with specific diet breadth characteristics.

FIG. 66

Some Weibull density functions describing the distribution of productivity over the prey size range in the pelagic zone (above) and in the littoral zone (below). The parameters which define each curve are given below.

Pelagic zone	Modal Size (mm)	Minimum Size (mm)	Shape term
A	1.0	0.001	1.2
B	0.3	0.001	1.2
C	0.1	0.001	1.2
D	0.3	0.001	2.0
Littoral zone			
A	1.0	0.001	4.0
B	4.0	0.001	10.0
C	4.0	0.001	2.0
D	10.0	0.001	4.0
E	4.0	0.001	1.2


D
C
B
A
RELATIVE ABUNDANCE
1
2
3
4
FOOD PARTICLE SIZE mm


A
B
C
D
E
RELATIVE ABUNDANCE
5
10
15
20
FOOD PARTICLE SIZE mm

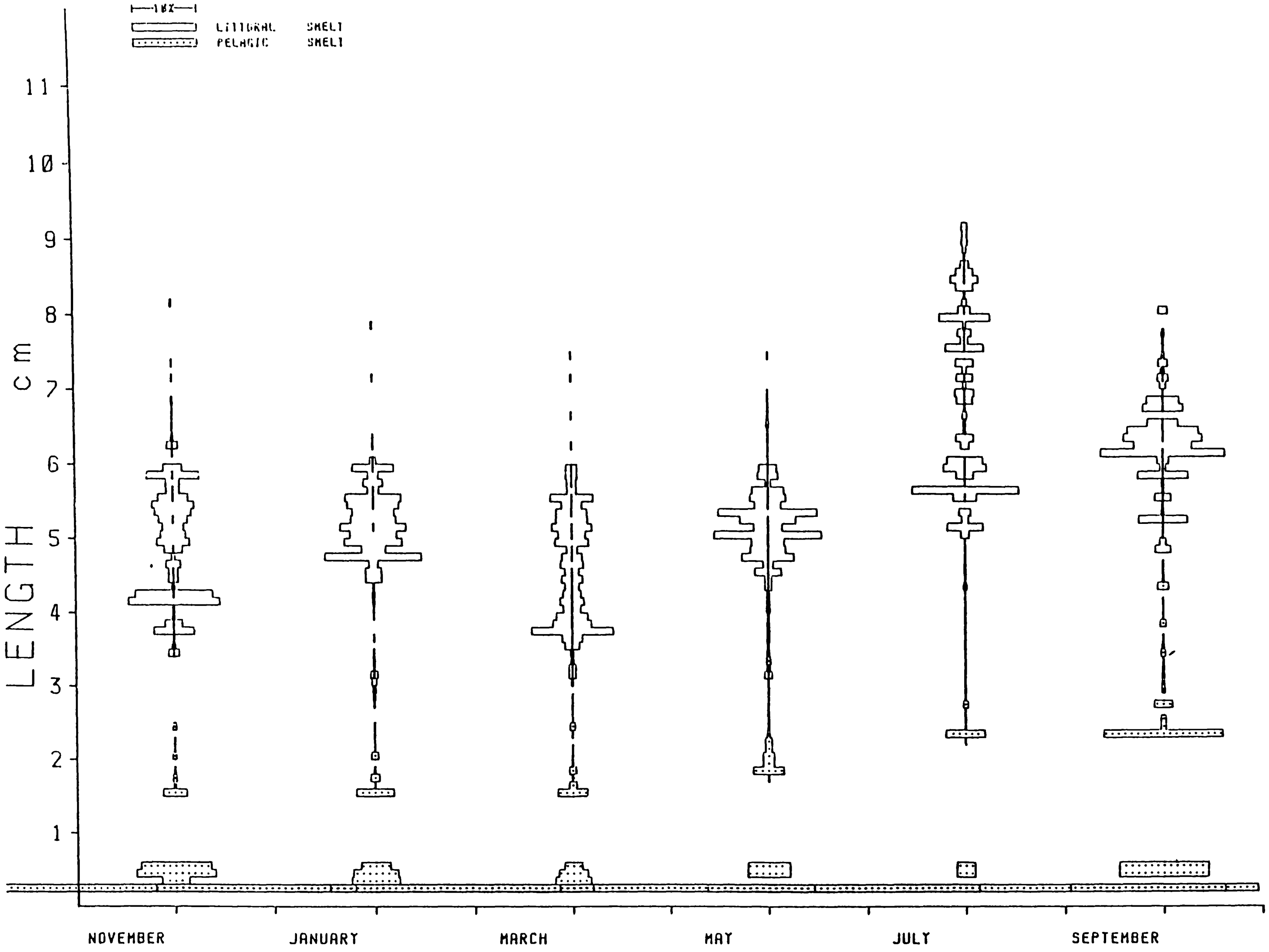


FIG. 67 Simulated smelt length frequency distributions when the modal size of pelagic prey was 1.0mm.

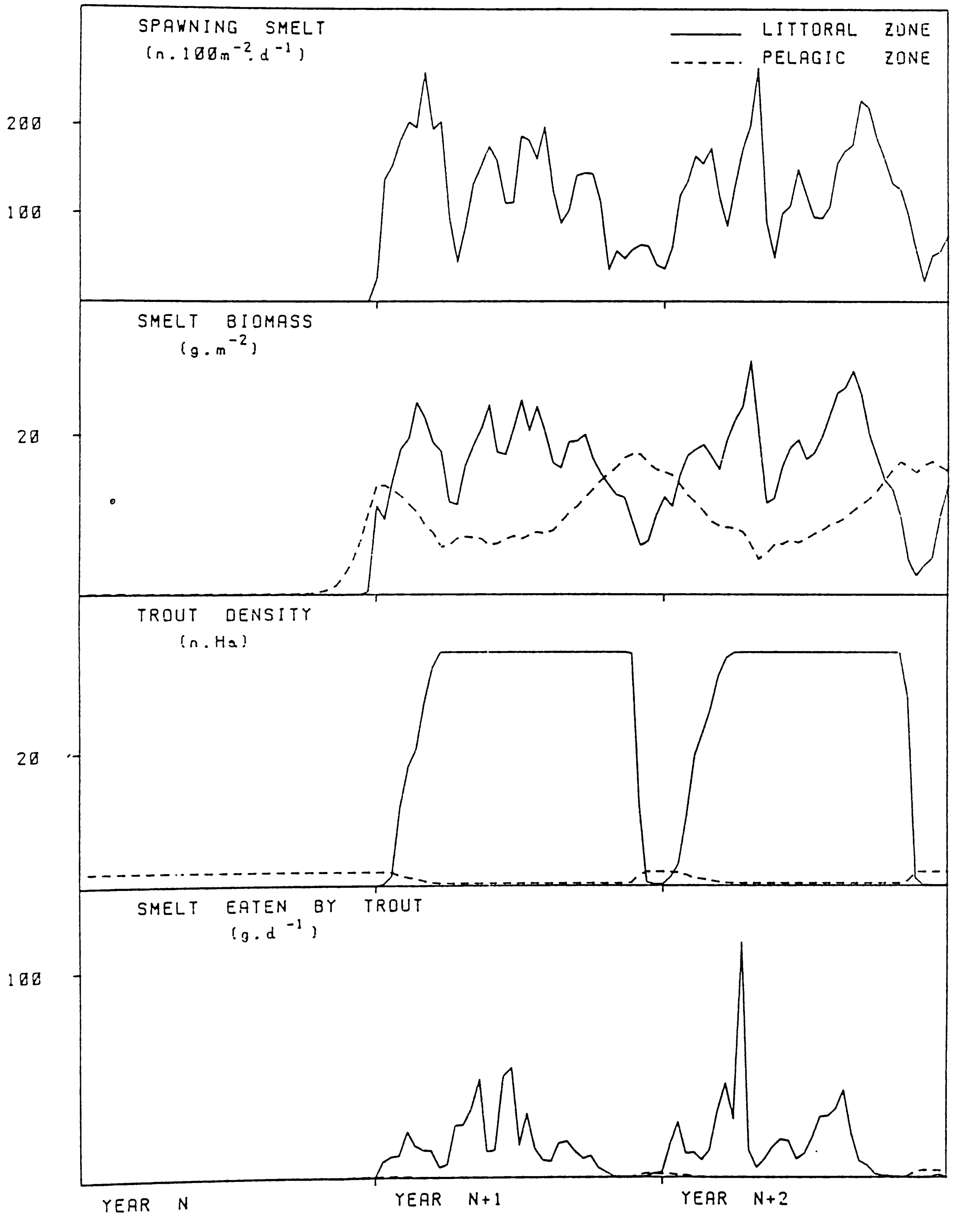


FIG. 68 Simulated population parameters when the modal size of pelagic prey was 1.0mm. N = 18

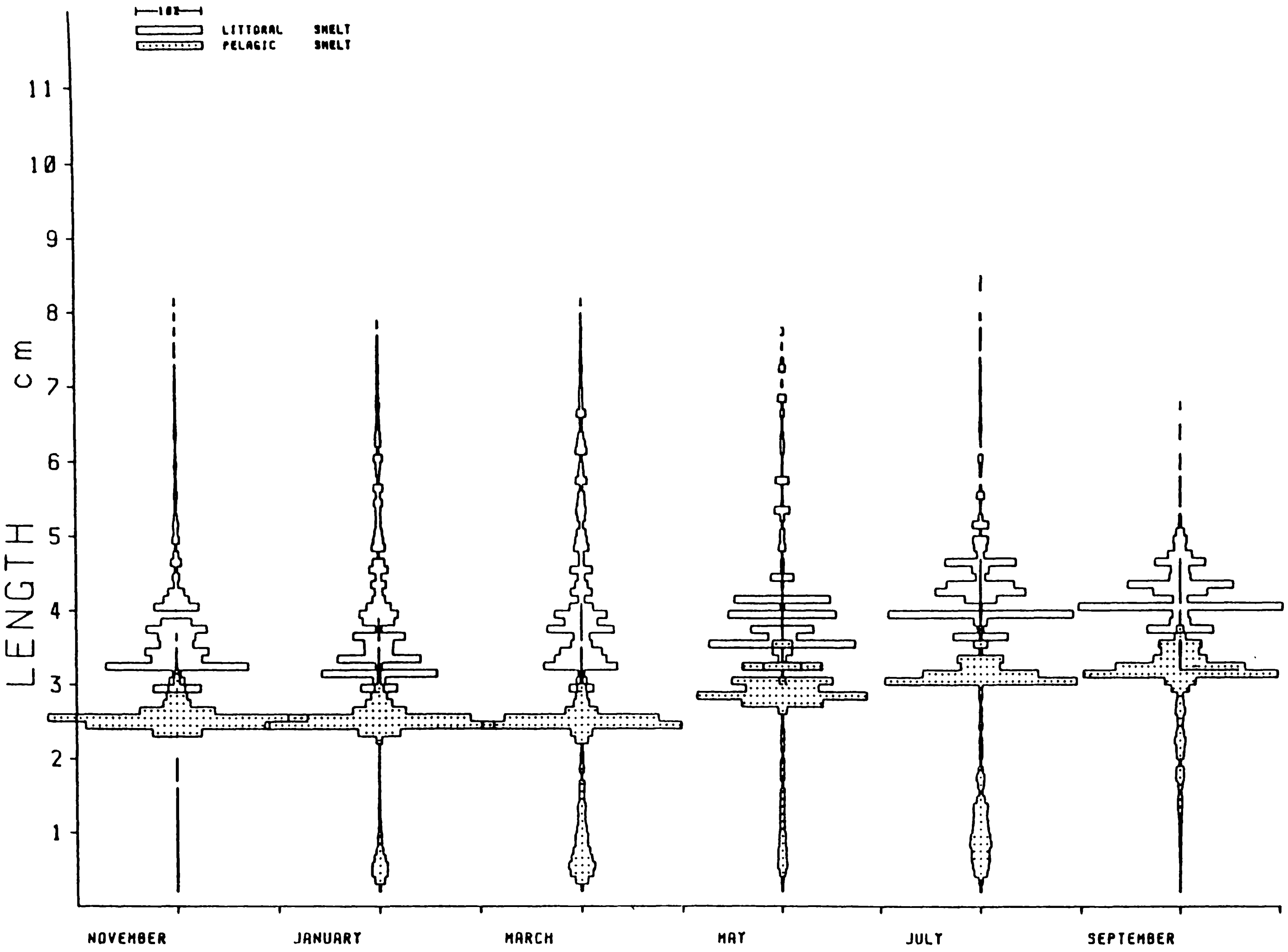


FIG. 69 Simulated smelt length frequency distributions when the modal size of pelagic prey was 0.1mm.

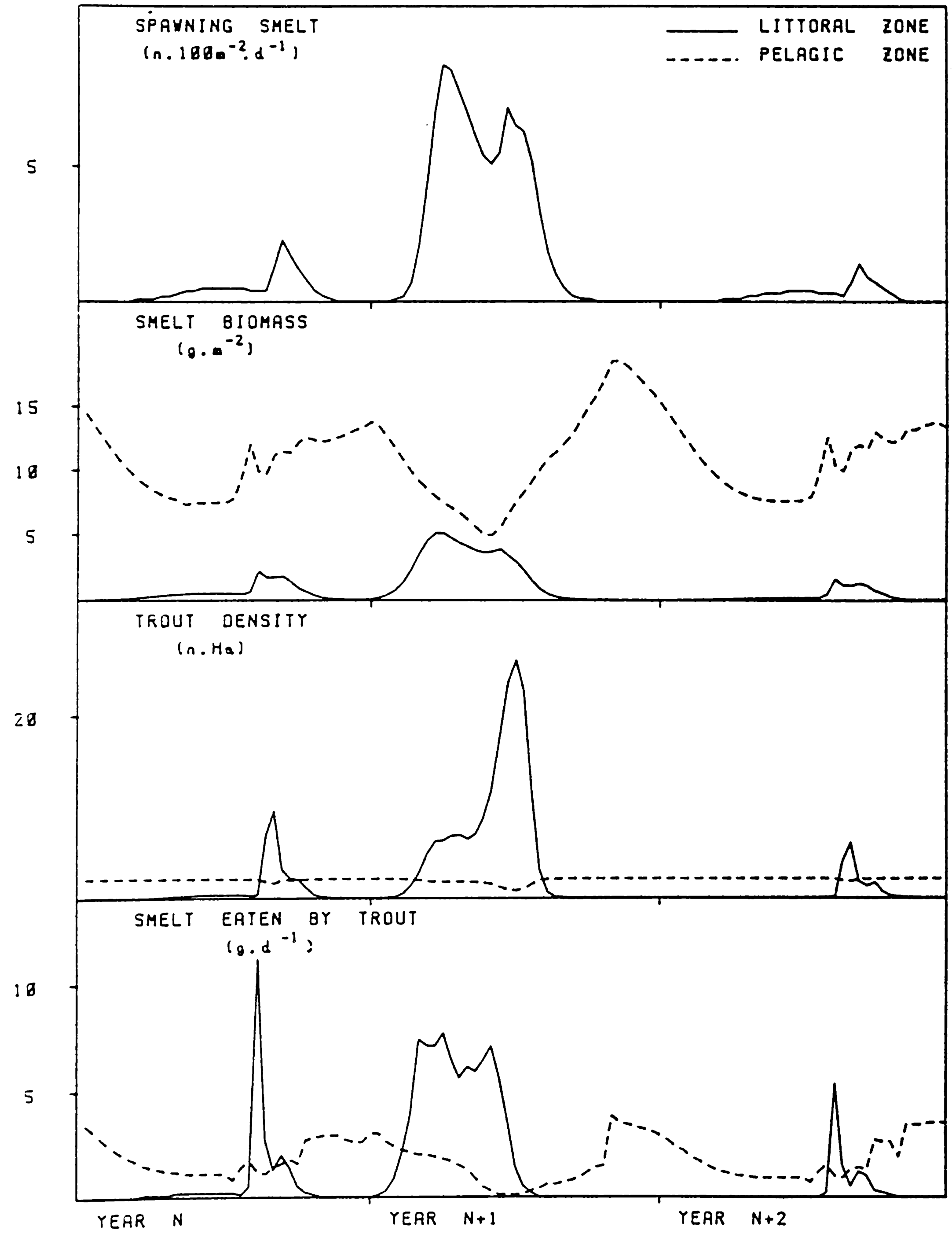


FIG. 70 Simulated population parameters when the modal size of pelagic prey was 0.1mm. N = 18

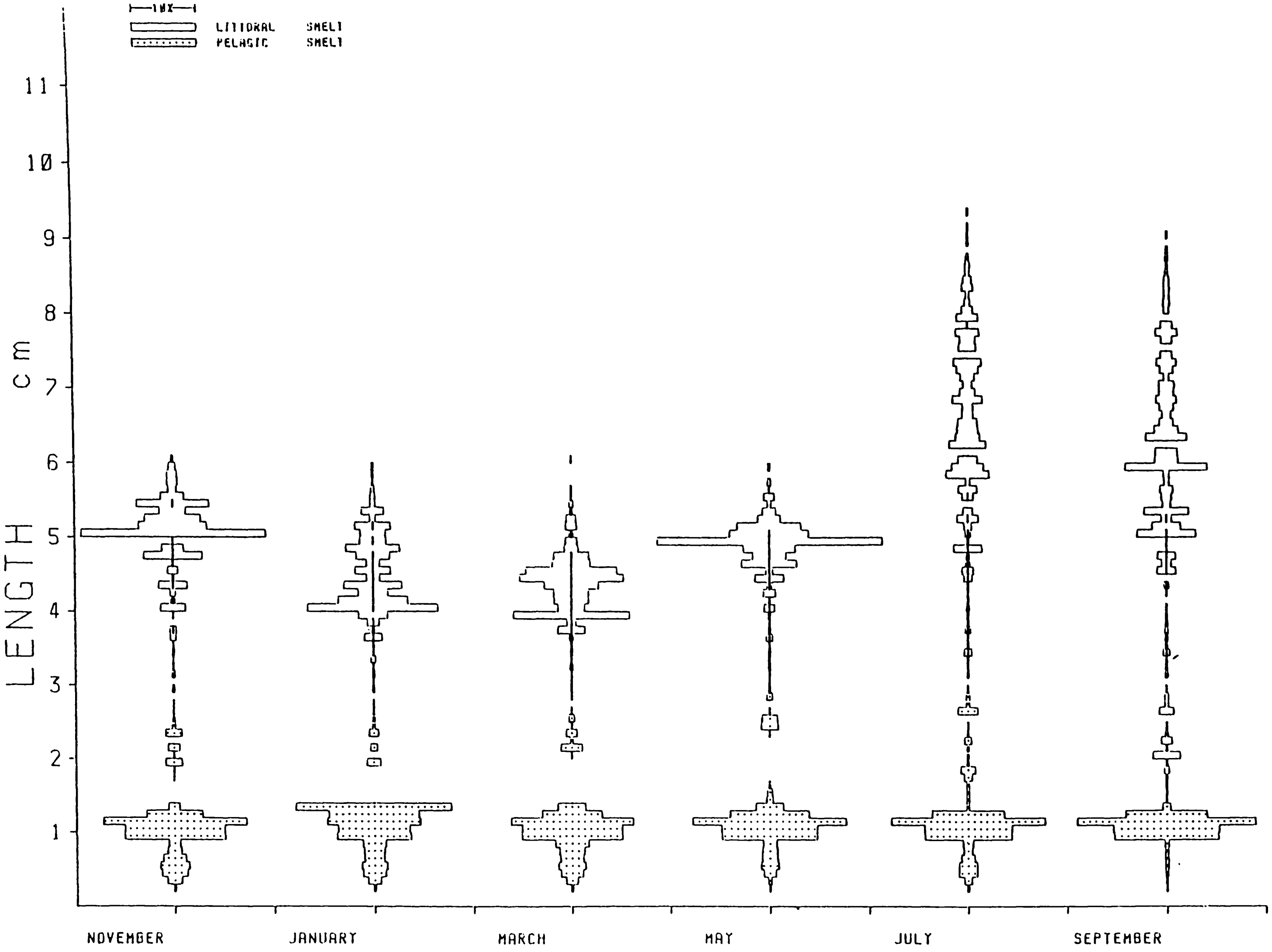


FIG. 71 Simulated smelt length frequency distribution when the modal size of littoral prey was 1.0mm.

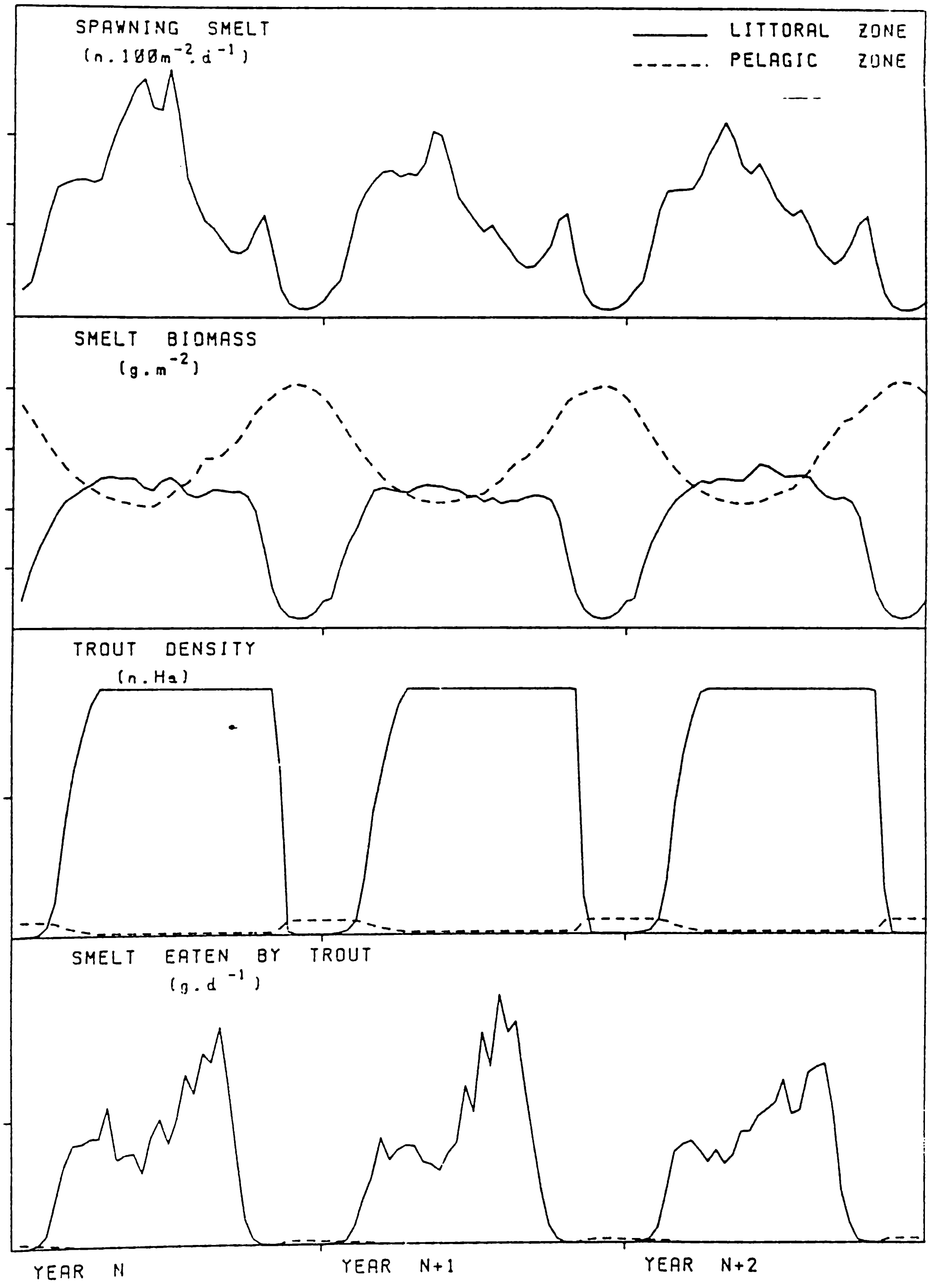


FIG. 72 Simulated population parameters when the modal size of littoral prey was 1.0mm. N = 18

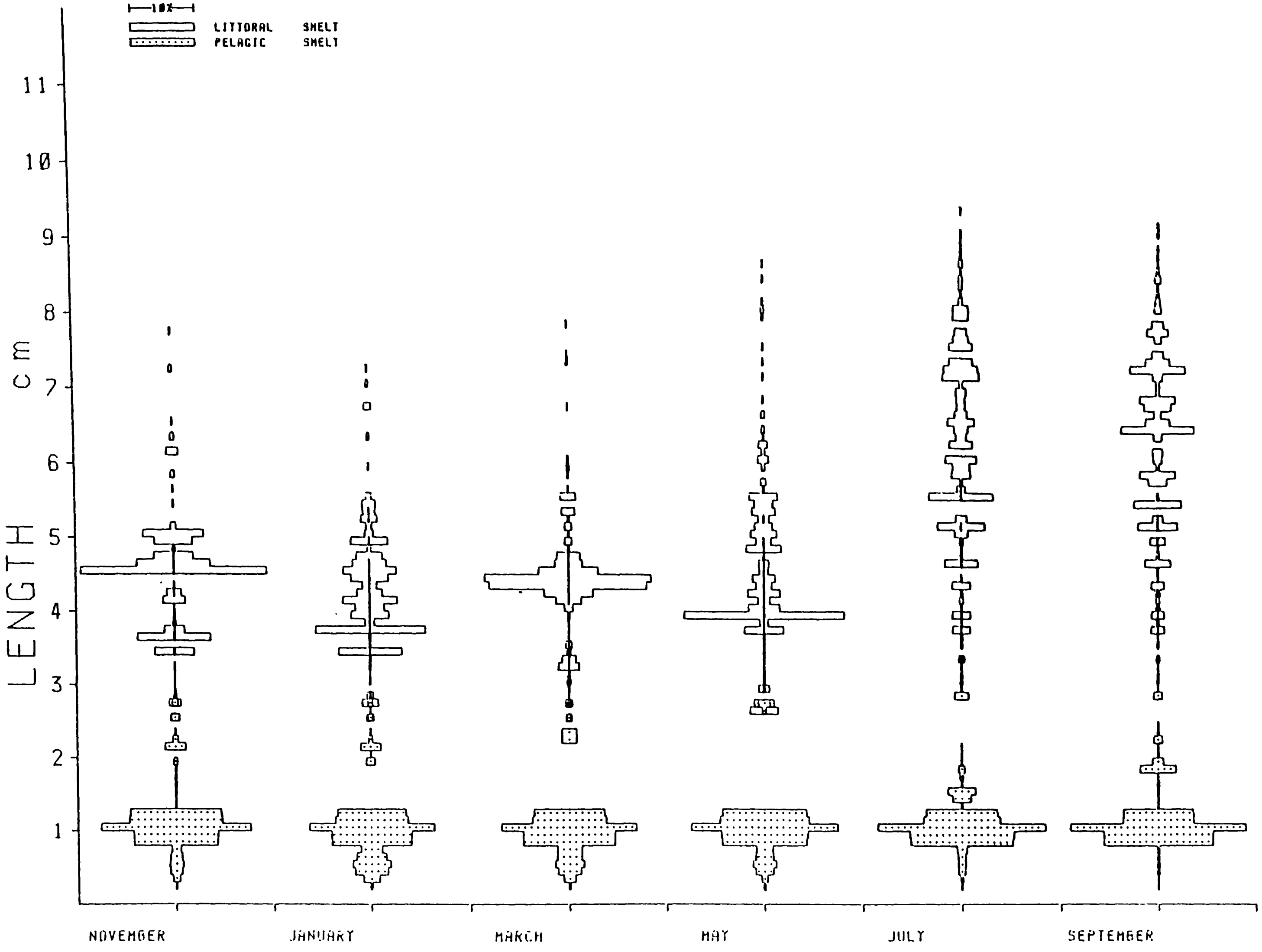


FIG. 73 Simulated smelt length frequency distributions when the modal size of littoral prey was 10.0mm.

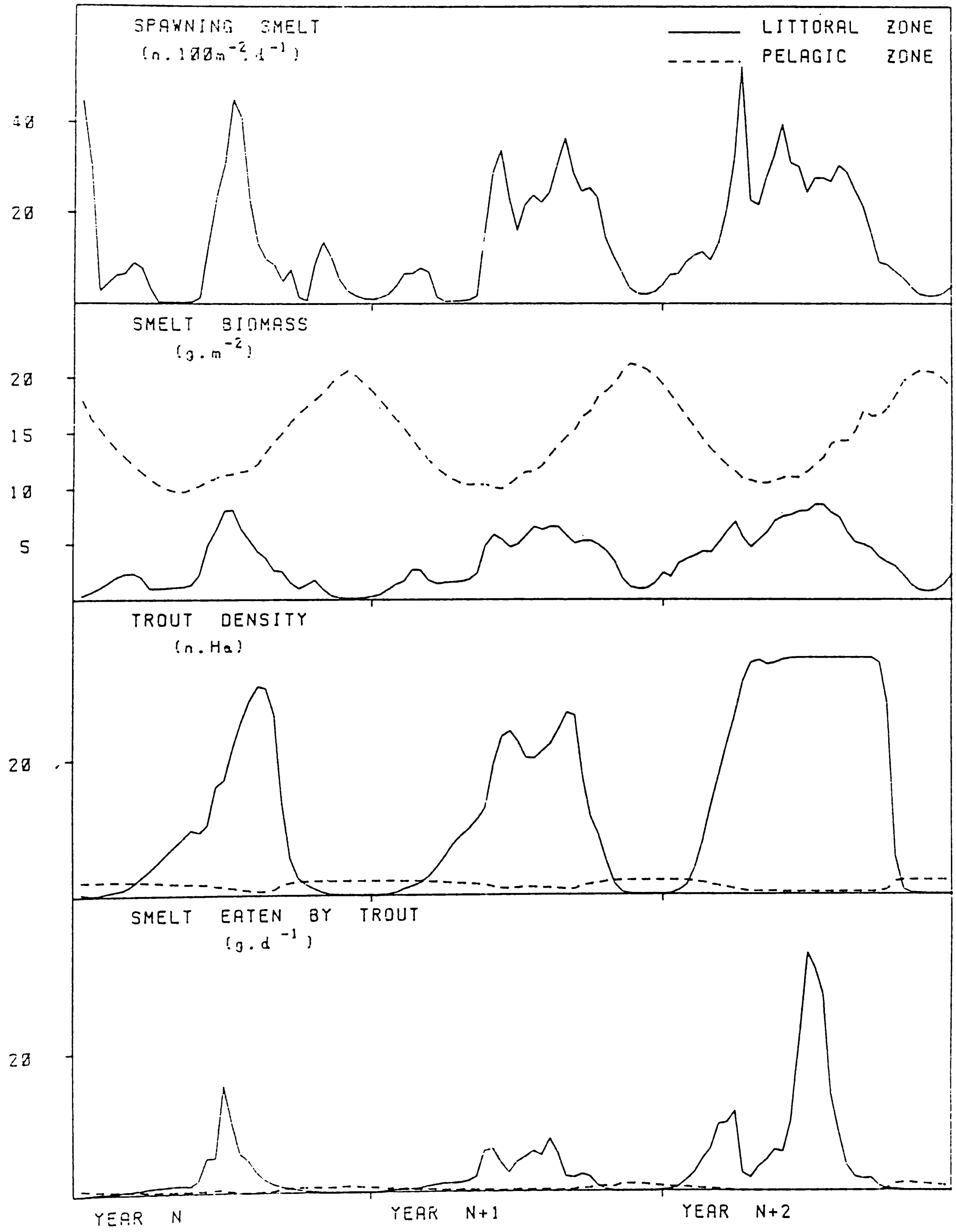


FIG. 74 Simulated population parameters when the modal size of littoral prey was 10.0mm. N = 18

(iii) Food Particle Size Range

The food particle size range was controlled by two parameters, the minimum prey size and the shape term (fig. 66). A small increase in the minimum prey size from 0.001m (the standard value) to 0.05mm, caused the modal length of pelagic smelt to increase from 3-6mm to 11-18mm (fig. 56 cf. fig. 75) but littoral length frequency structure, spawner densities, biomass and quantities eaten by trout were not significantly affected. The modal length of pelagic smelt grew in response to the larger minimum prey size because this accelerated the rate at which food availability increased with length for larval smelt less than 12mm long. Larger smelt were not affected because their lower diet limit was greater than the minimum prey size and consequently, length frequency structure and abundances in the littoral zone were little affected.

The shape term, which determined the distribution of production over the prey size range in the pelagic zone (fig. 66), was increased from 1.2 (the standard value) to 2.0. This raised the proportion of pelagic production available to larval smelt and reduced that available to larger ones. The result was a particularly stable system characterized by bimodal pelagic length frequency distributions (fig. 76 cf. fig. 56), low littoral smelt densities and a largely pelagic trout population which obtained much of its smelt forage from the pelagic zone (fig. 77 cf. fig. 57). Littoral smelt density and their reproductive output was low because pelagic growth conditions restricted the number reaching sufficient size to be recruited to the littoral population. This restraint on reproductive output and only minor competitive restriction of growth were the dominant factors promoting the stability of this system.

Two littoral prey size ranges having shape terms 10.0 and 1.2 were tested for comparison. The former distribution was skewed to the left and covered a limited size range (2-5mm) whilst the latter was skewed to the right ranging from 0.1 to 13mm (fig. 66). When the littoral prey size range was restricted, spawner densities, littoral biomass and quantities eaten by trout were slightly higher and smelt larger than 65mm were present only in winter. Apart from this, the population length frequency structure was not greatly affected by considerable changes in the prey size distribution because adult smelt diet breadths were so extensive that major changes in the distribution of productivity over the prey size range were required to significantly alter on the proportion of food production lying within their upper and lower prey size limits.

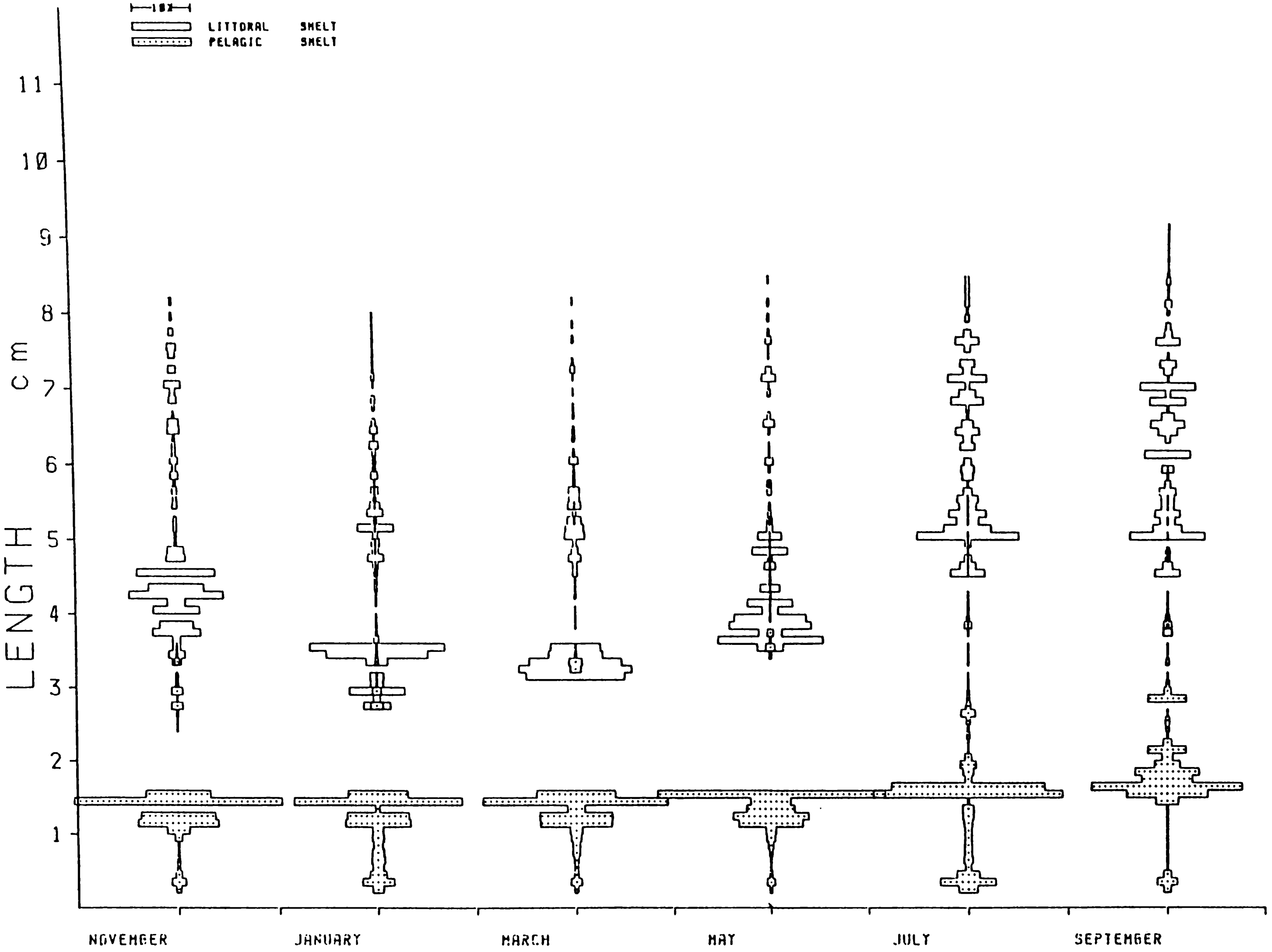


FIG. 75 Simulated smelt length frequency distributions when the minimum prey size in both littoral and pelagic habitats was 0.05mm.

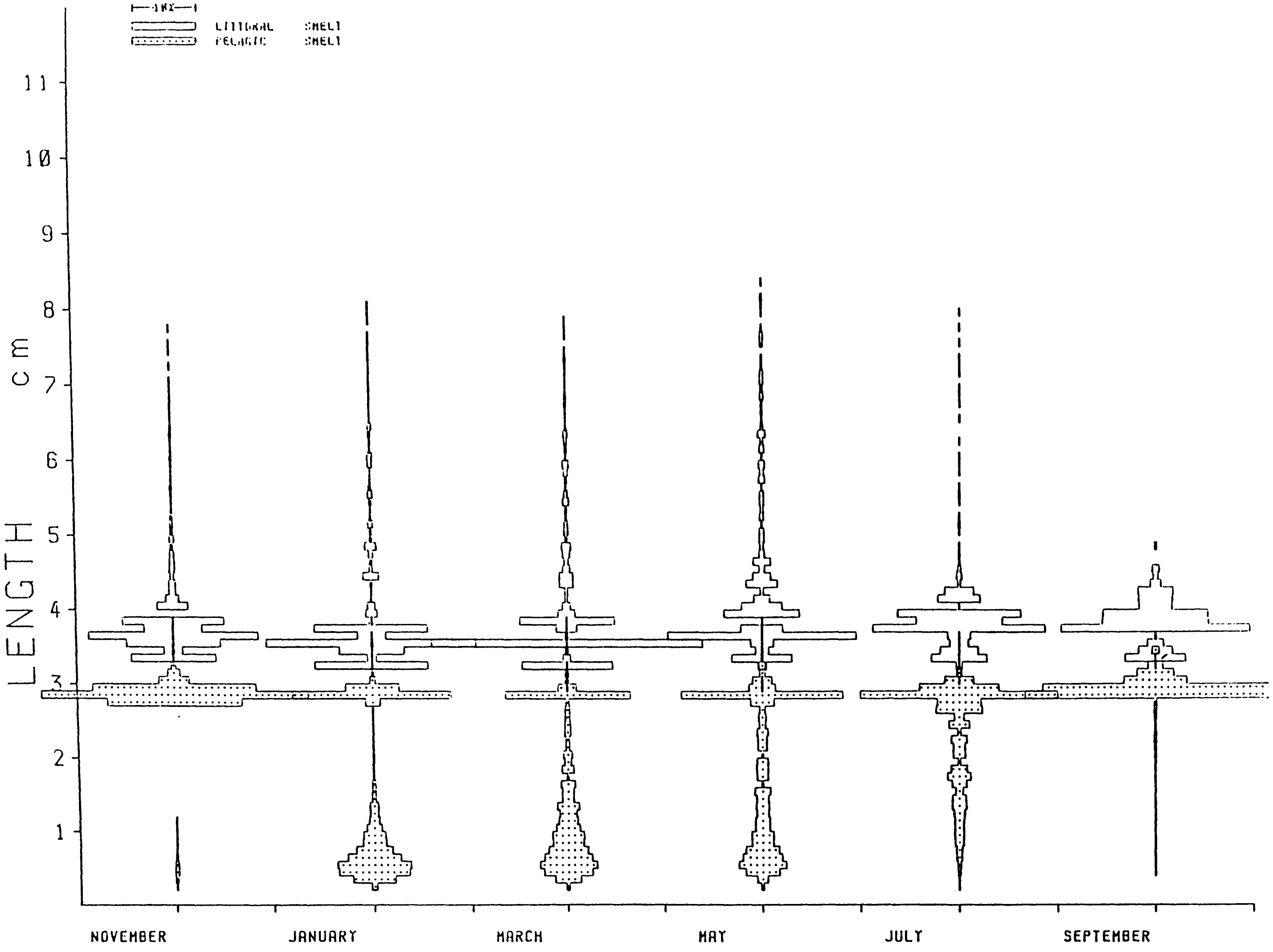


FIG. 76 Simulated smelt length frequency distributions when the pelagic shape term was 2.0.

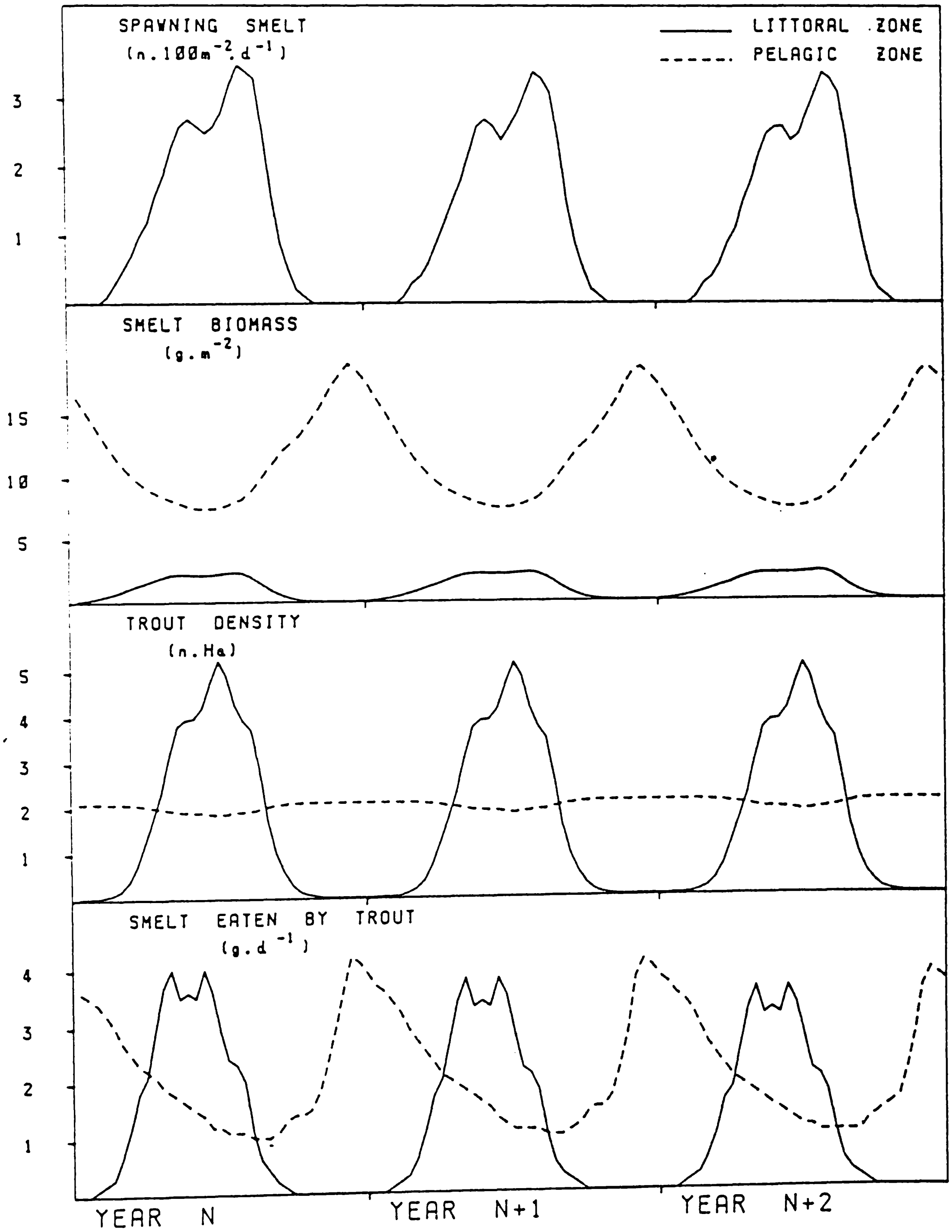


FIG. 77 Simulated population parameters when the pelagic shape term was 2.0. N = 18

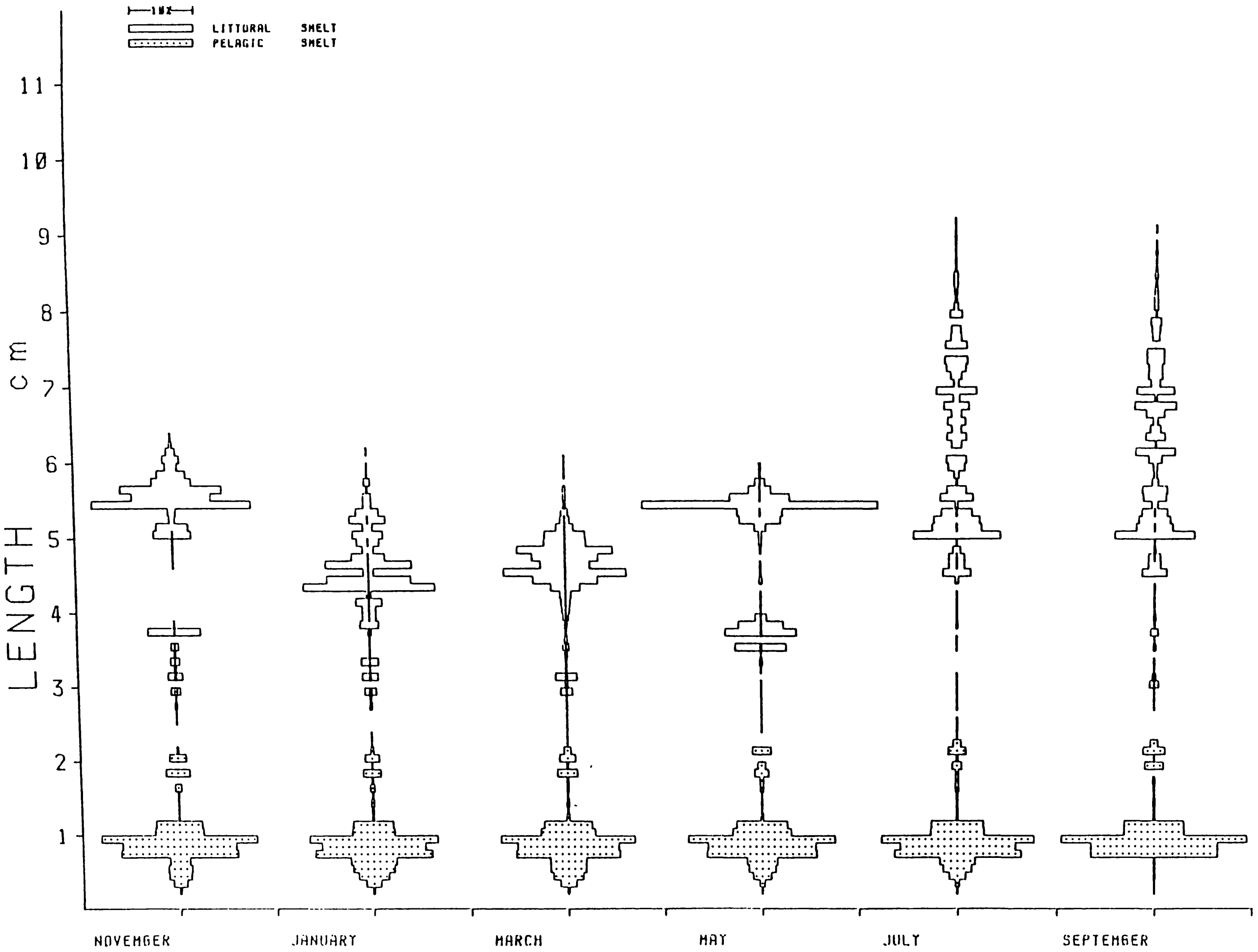


FIG. 78 Simulated smelt length frequency distributions when the littoral shape term was 10.0.

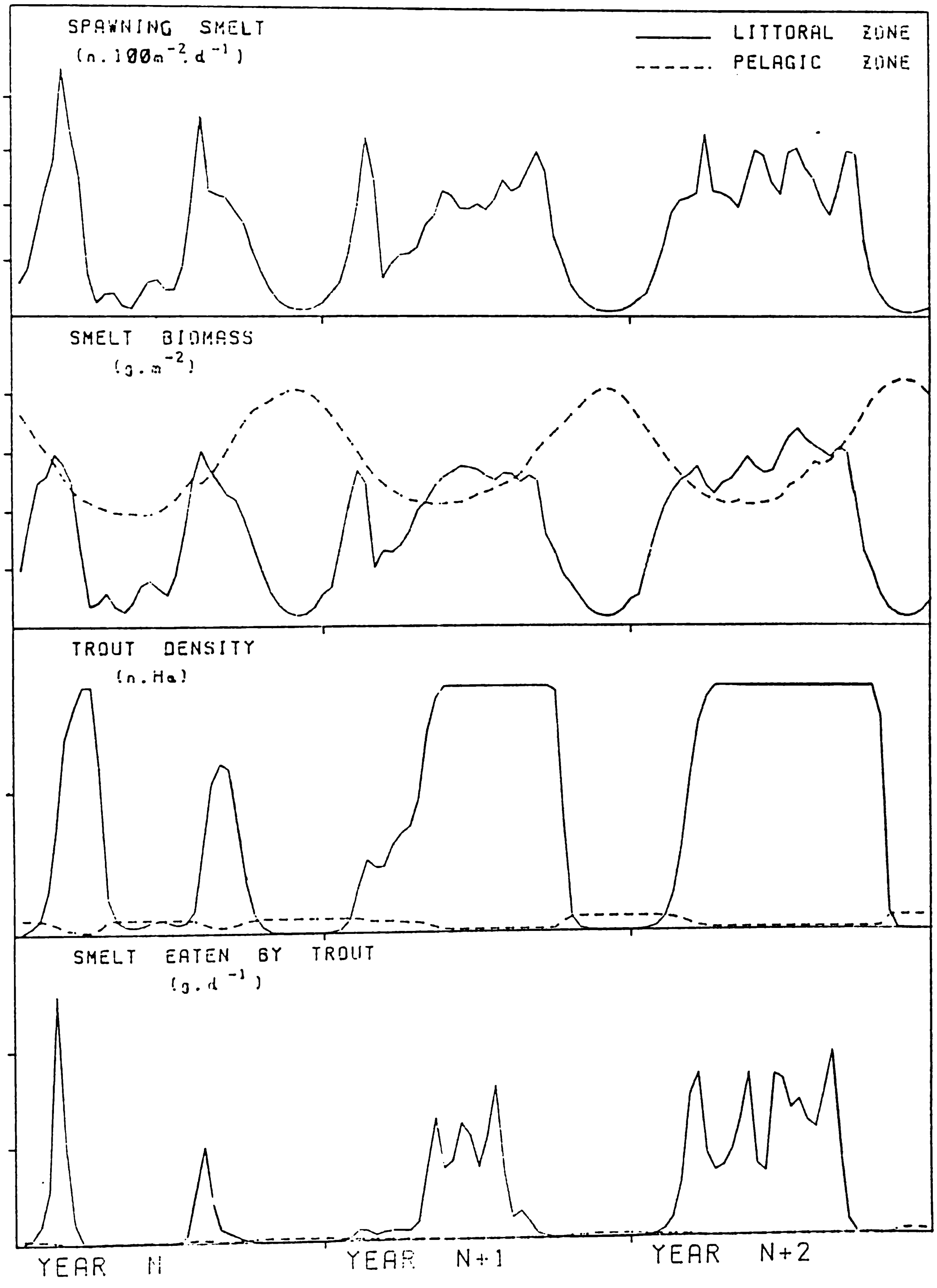


FIG. 79 Simulated population parameters when the littoral shape term was 10.0. N = 18

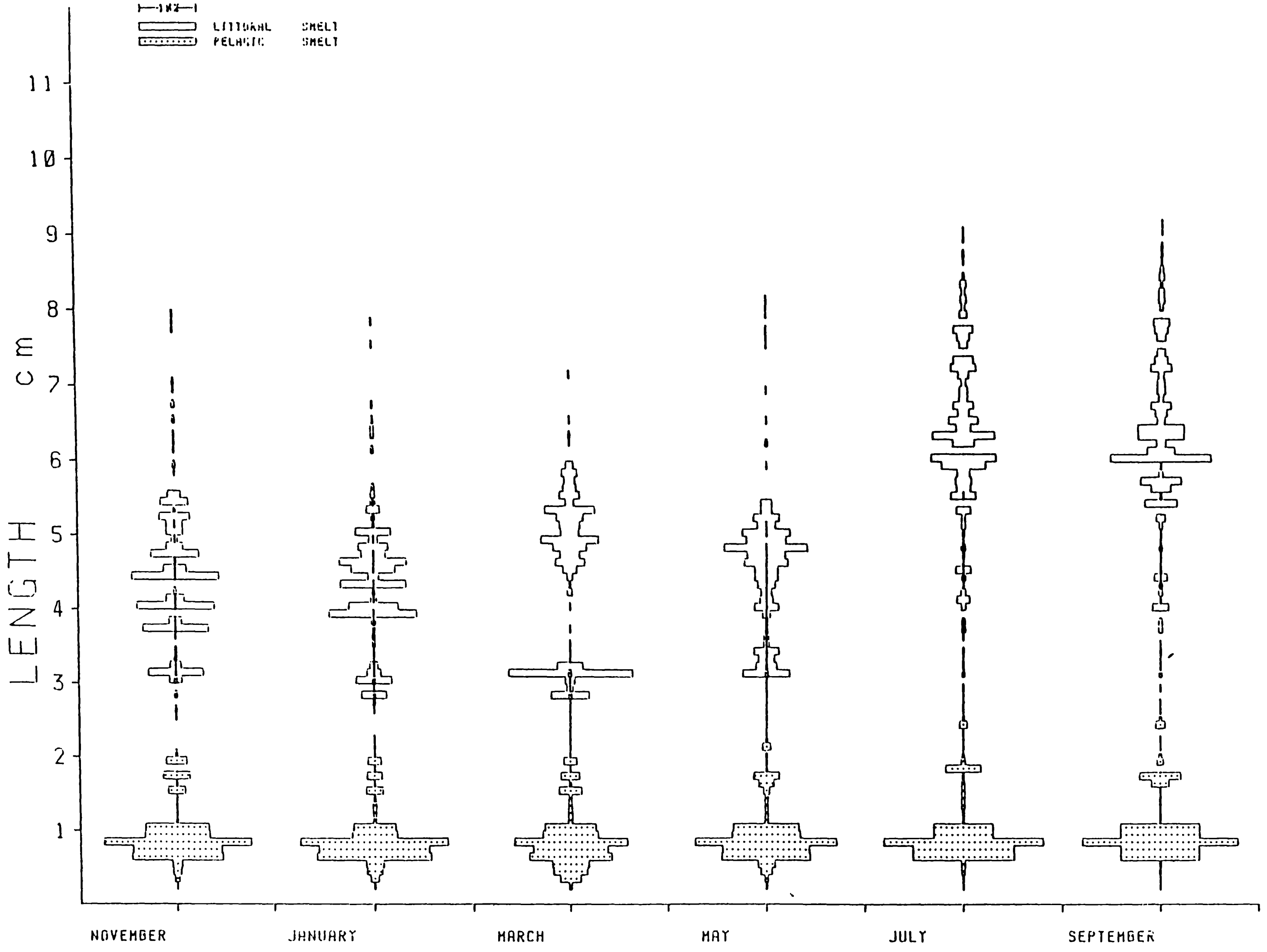


FIG. 80 Simulated smelt length frequency distributions when the littoral shape term was 1.2.

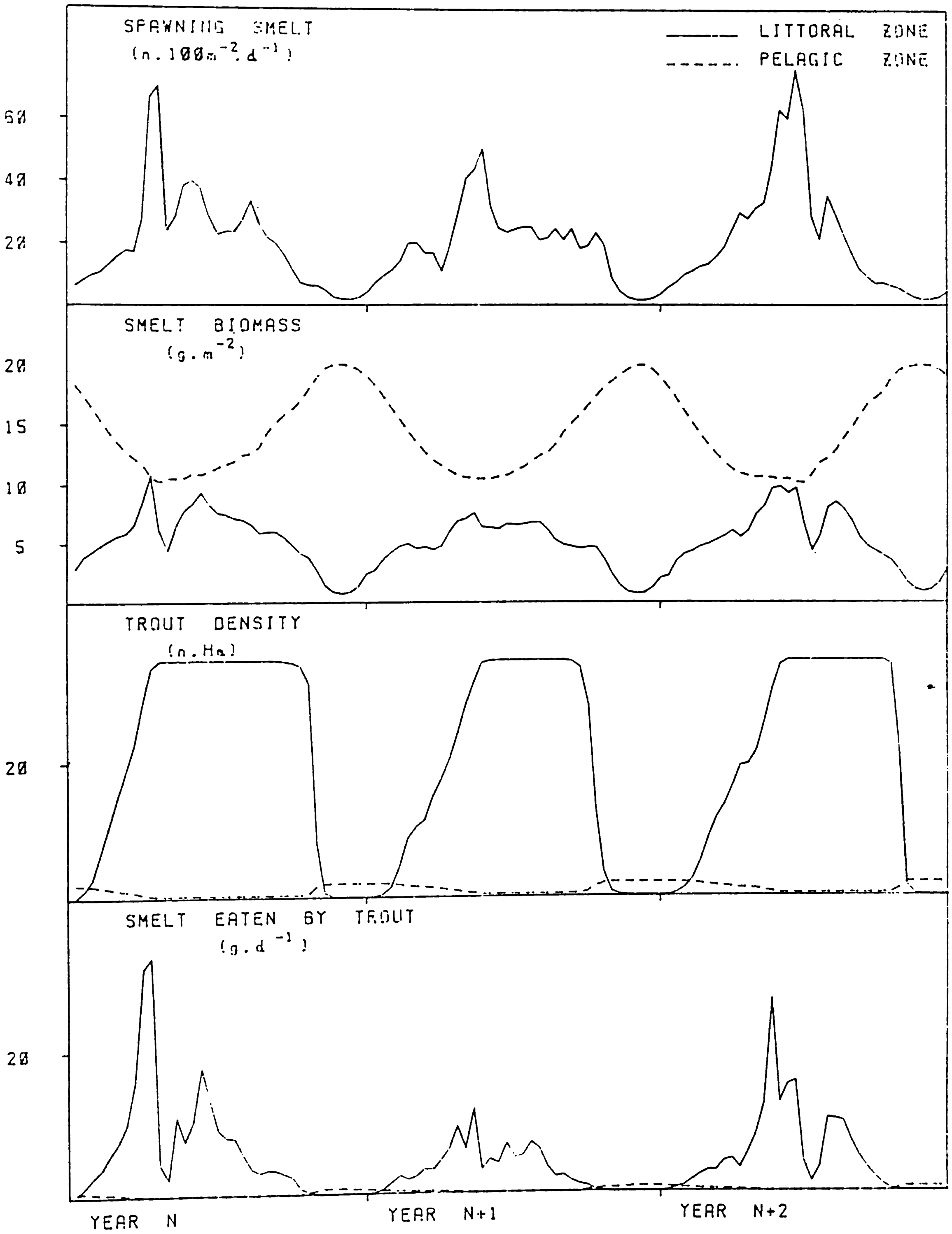


FIG. 81 Simulated population parameters when the littoral shape term was 1.2. N = 18

(iv) Food Production

Daily food production was examined separately for the pelagic and littoral habitat zones. For each zone, two trial runs using the values $0.1g.m.^{-2}.d^{-1}$ and $5.0g.m.^{-2}.d^{-1}$ to describe daily food production were compared to examine the influence of different levels of food productivity on smelt population processes.

The fifty fold increase in pelagic food production had little effect on pelagic smelt length frequency distributions but changes to other population parameters were dramatic. Modal lengths of littoral smelt decreased by up to 20mm (fig. 82 cf. fig. 84). Pelagic biomass increased ca. 40 fold and littoral biomass about five fold (fig. 83 cf. fig. 85). Quantities of smelt eaten by trout increased ten fold but their feeding remained confined almost exclusively to the littoral zone. It seems that enhanced pelagic production caused greater numbers of smelt to be recruited to the littoral population and so intensified competition for the littoral food resource, resulting in depressed growth by littoral smelt.

When littoral production was only $0.1g.m.^{-2}.d^{-1}$, spawner density, smelt biomass and littoral growth was reduced even further (figs. 86 and 87), to the extent that the population's reproductive capacity was impaired. This reduced the number of larval smelt entering the pelagic zone and consequently competition for food did not restrict their growth until they reached 9-12mm in length. Increasing littoral food production to $5.0g.m.^{-2}.d^{-1}$ resulted in a considerable increase in the size and reproductive output of littoral smelt (figs. 88 and 89); the latter intensified competition for food amongst the larval smelt and so depressed their growth, causing their short modal length. Littoral biomass increased about three fold whilst quantities eaten by trout only doubled in response to a fifty fold increase in littoral food production. Thus in a system where pelagic habitat is relatively extensive compared with littoral habitat, changes in pelagic food production influence smelt abundances more dramatically than similar changes in littoral food production and the difference between littoral and pelagic food production is an important factor controlling the growth of adult smelt.

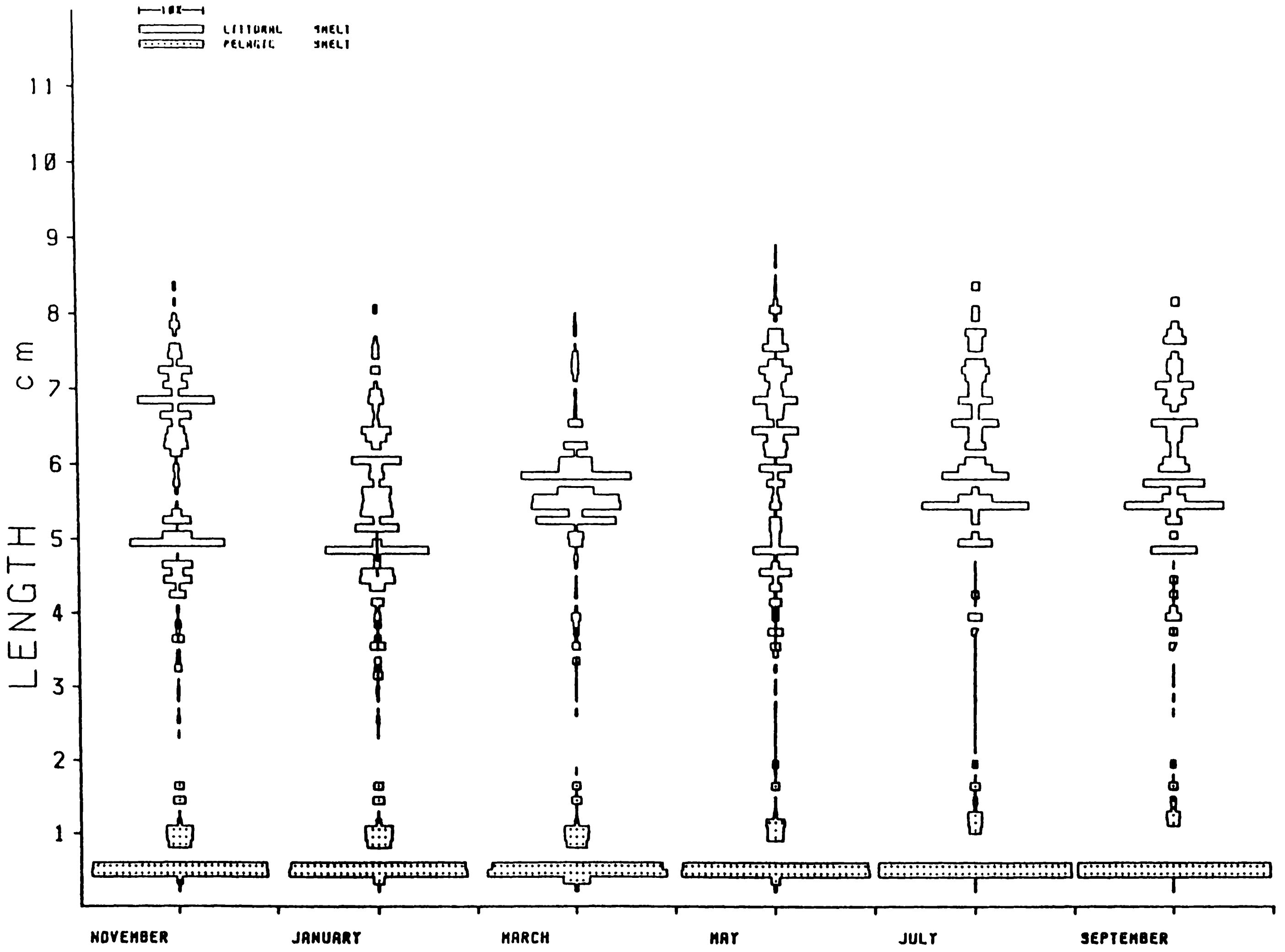


FIG. 82 Simulated smelt length frequency distributions when pelagic food production was 0.1g.m.$^{-2}$.d^{-1}.

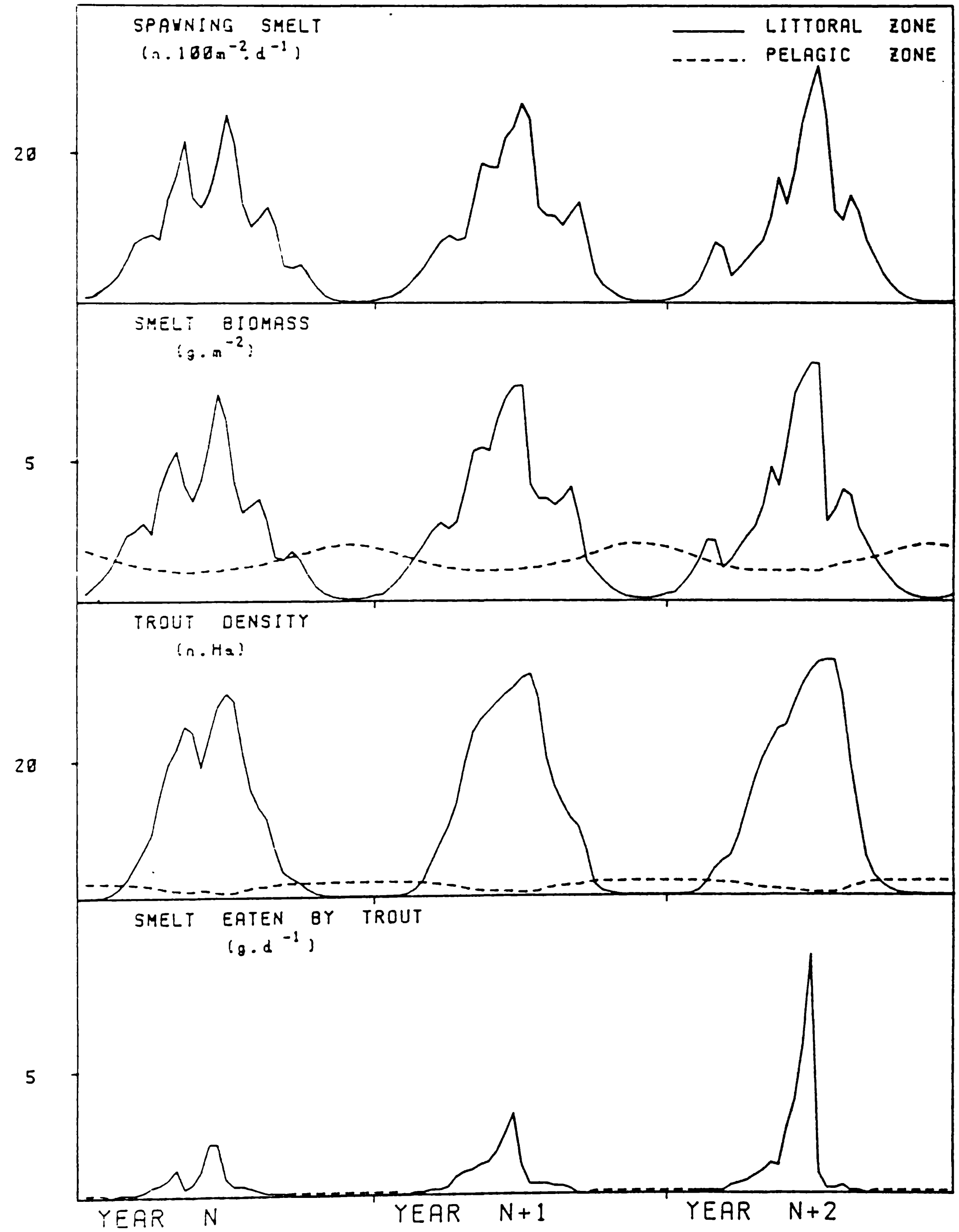


FIG. 83 Simulated population parameters when pelagic food production was 0.1g.m.$^{-2}$.d^{-1}. N = 18

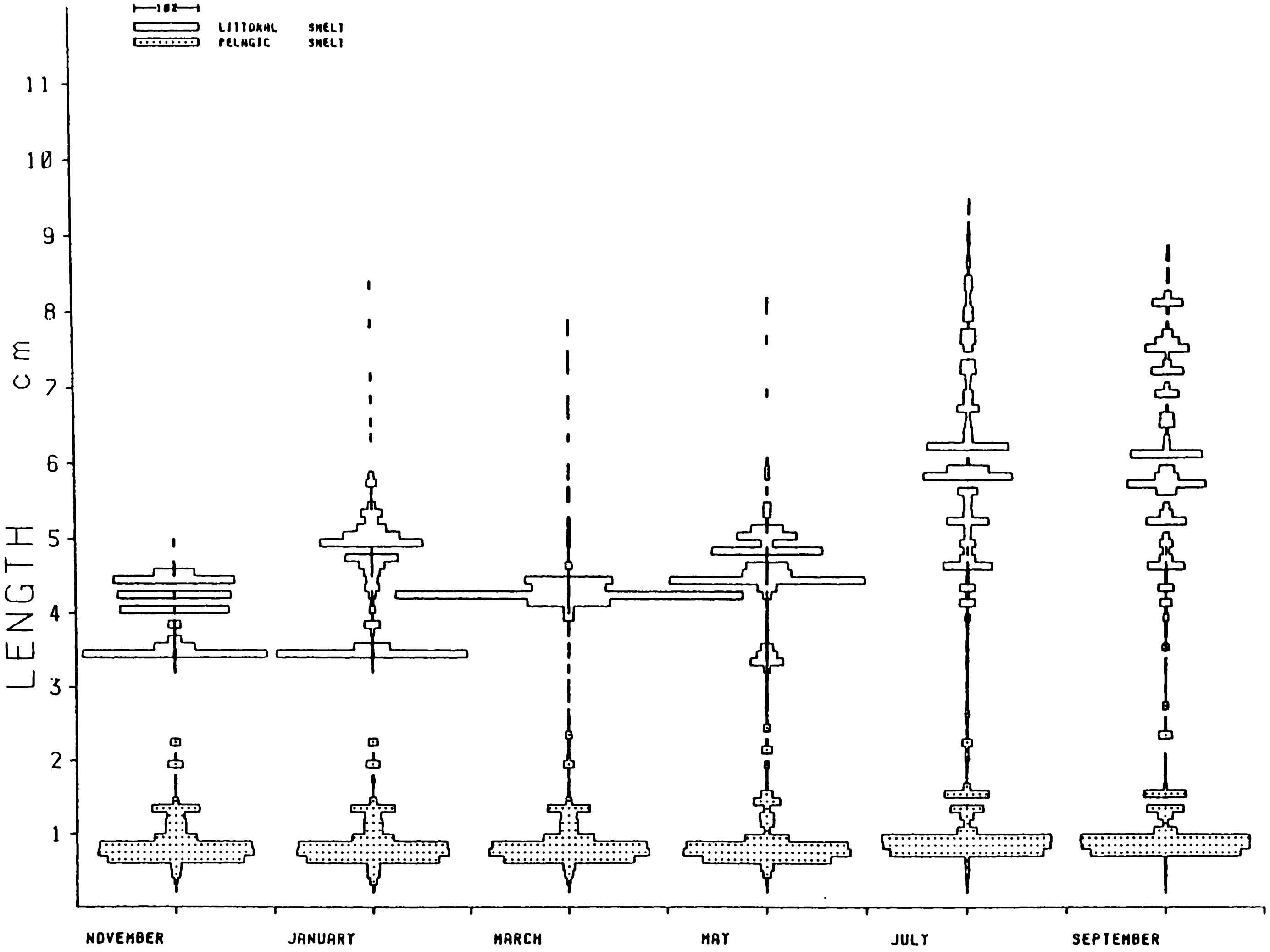


FIG. 84 Simulated smelt length frequency distributions when pelagic food production was $5.0 g.m.^{-2}.d^{-1}$.

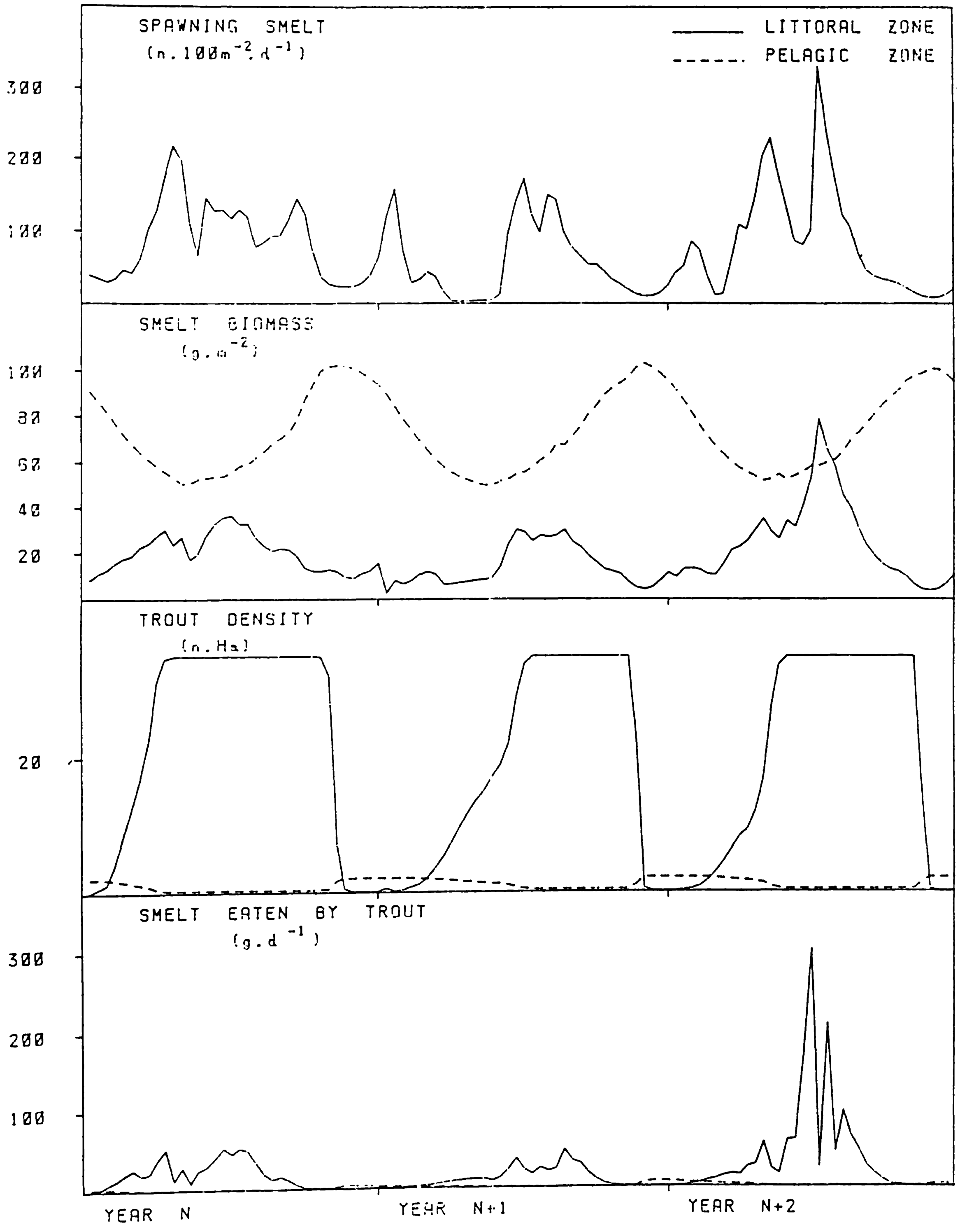


FIG. 85 Simulated population parameters when pelagic food production was $5.0g.m.^{-2}.d^{-1}$. N = 18

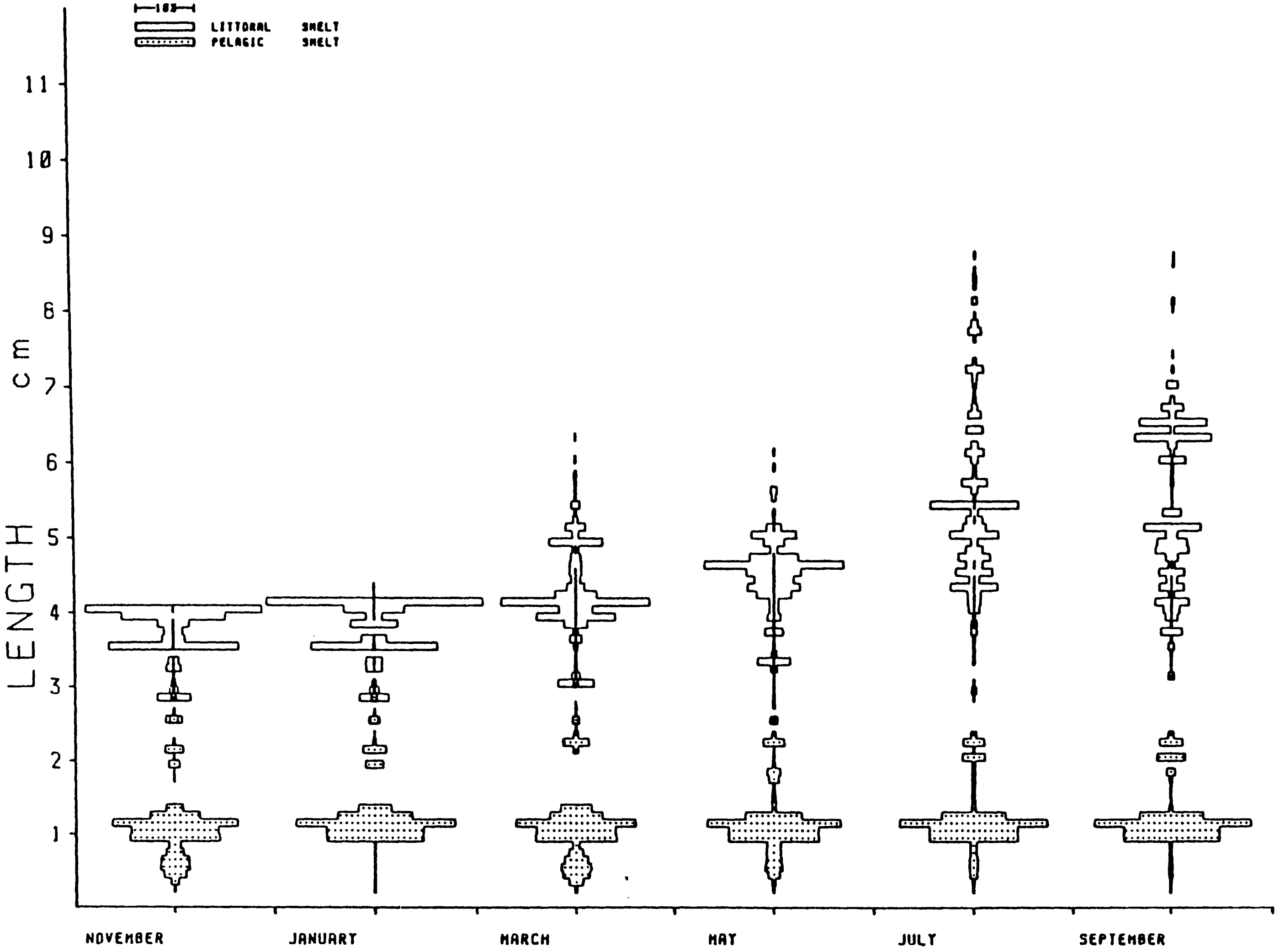


FIG. 86 Simulated smelt length frequency distributions when littoral food production was 0.1g.m.$^{-2}$.d^{-1}.

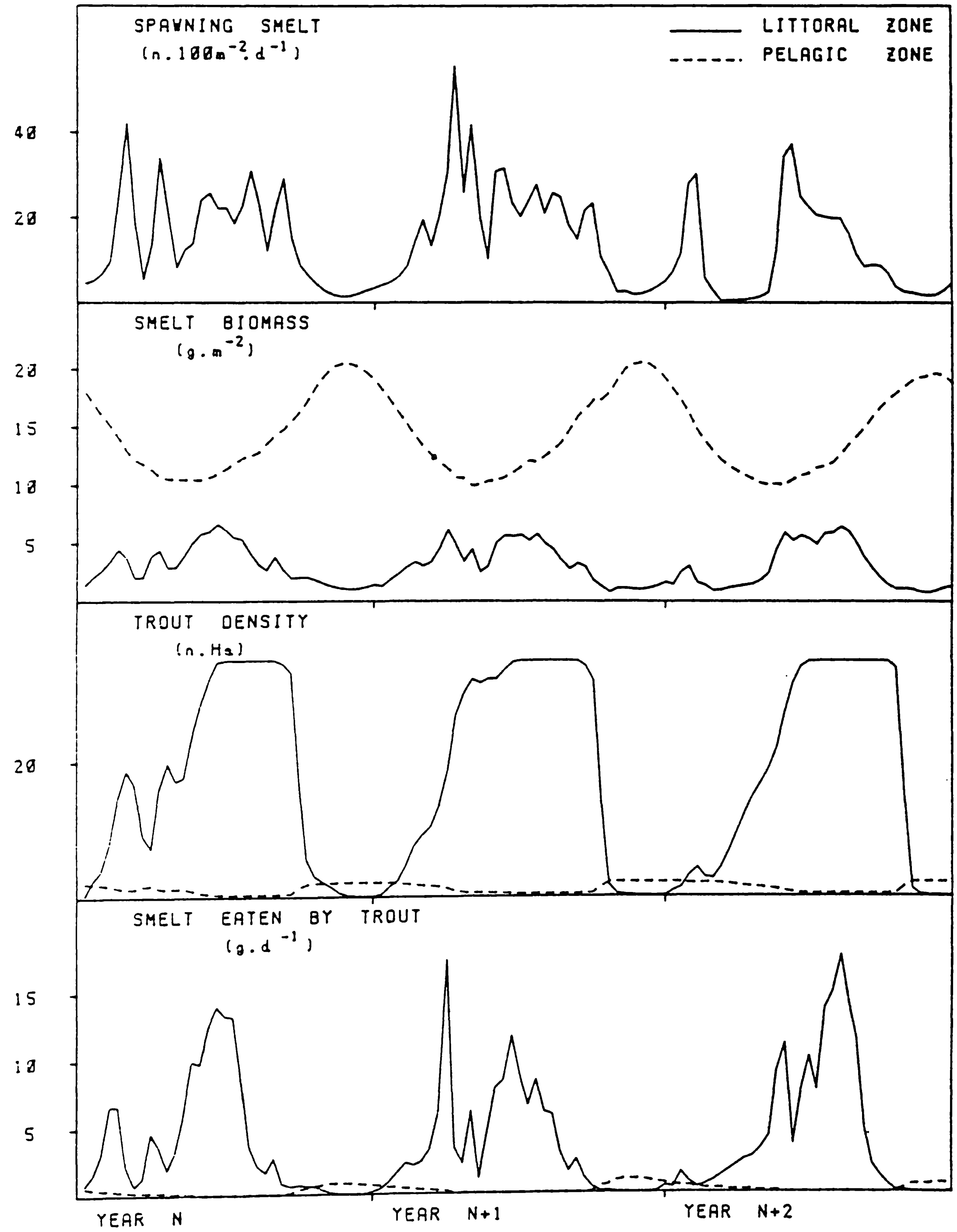


FIG. 87 Simulated population parameters when littoral food production was 0.1g.m.$^{-2}$.d^{-1}. N = 18

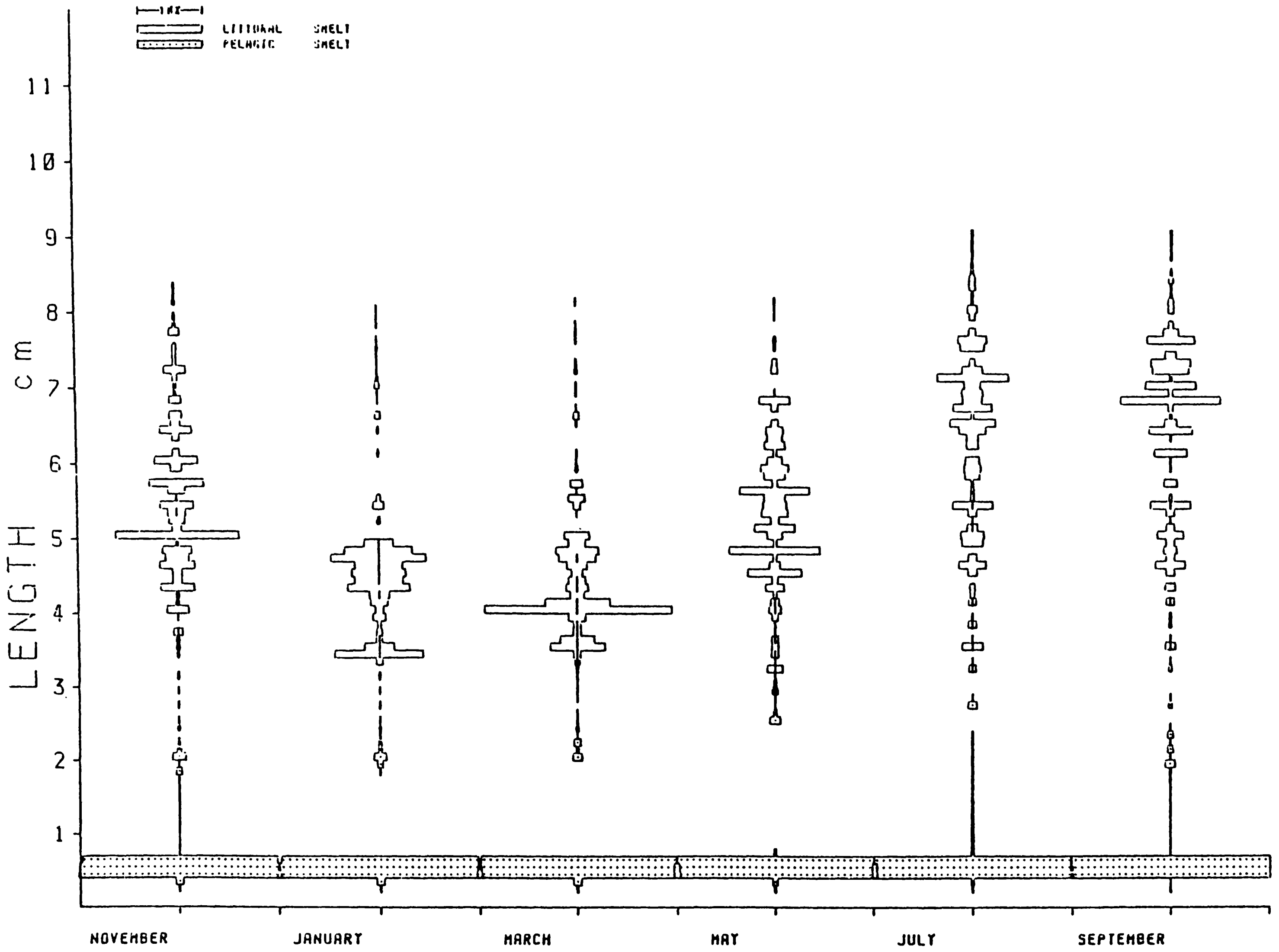


FIG. 88 Simulated smelt length frequency distributions when littoral food production was 5.0g.m.$^{-2}$.d^{-1}.

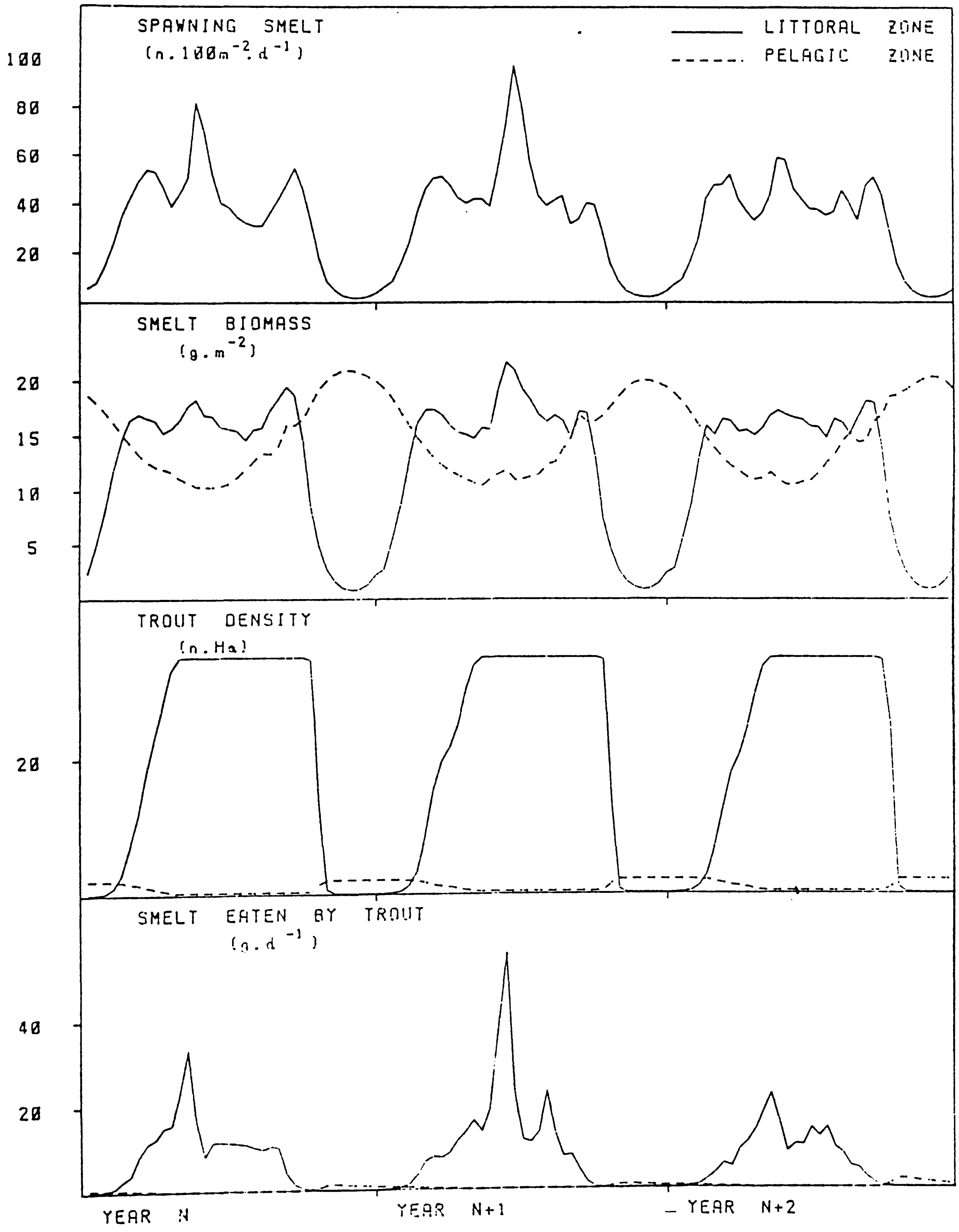


FIG. 89 Simulated population parameters when littoral food production was $5.0g.m.^{-2}.d^{-1}$. N = 18

(b) Seasonal Variation in the Size and Quantity of Food

Seasonal variations in the modal prey size, the shape term describing the distribution of productivity over the prey size range and total food production were described using a cosine wave function (Equ. 25). In each case, the seasonal cycle was normal in shape as the exponent determining the kurtosis of the cycle was unity. The effects of seasonality in each of these three parameters were examined separately for both habitat zones.

(i) Seasonality in the Modal Food Particle Size

Seasonality in the modal size of pelagic prey, ranging from 0.1mm on February 1st to 1.0mm on August 1st, caused a minor increase in the modal size of pelagic smelt, from 2-5mm in August to 6-9mm in January (fig. 90). It also raised the size of littoral smelt (cf. fig. 56), caused a winter peak in spawner densities and littoral smelt biomass and caused two annual peaks in littoral trout abundance and the weight of smelt eaten there (fig. 91). The winter peak in spawner densities and littoral biomass occurred because the large size of pelagic prey available at that time permitted maximum numbers of pelagic smelt to grow large enough to be recruited to the littoral population. Thus seasonality in the average size of pelagic prey was more influential in determining seasonal timing of spawning than seasonal components built in to models describing movement and maturation. The small food particle size during summer restricted growth by pelagic smelt larger than 20mm and this limited recruitment to the littoral population, which restricted spawner abundance and littoral biomass there. Thus, in the littoral zone there were fewer smelt sharing the available food resource and consequently they attained a larger size than occurred in the absence of seasonal variation in the modal prey size.

Seasonality in the modal size of littoral food items (1.0mm on February 1st to 10.0mm on August 1st) caused a minor (ca. 5mm) increase in the modal length of littoral smelt during winter (fig. 92). Of more significance however, peaks in spawning activity, littoral biomass and quantities eaten by trout (fig. 93) occurred during early and late summer when the maximum proportion of the available food resource was within the food particle size limits of littoral smelt. These quantities were greater than occurred when the modal prey size was constant at either 1.0mm (fig. 72) or at 10.0mm (fig. 74). Improved food availability resulted in raised smelt biomass rather than accelerated growth and so it seems that recruitment to the littoral population was sufficient to prevent more food becoming available to individual smelt. Thus smelt growth was little affected but sustainable biomass increased in response to improved food availability.

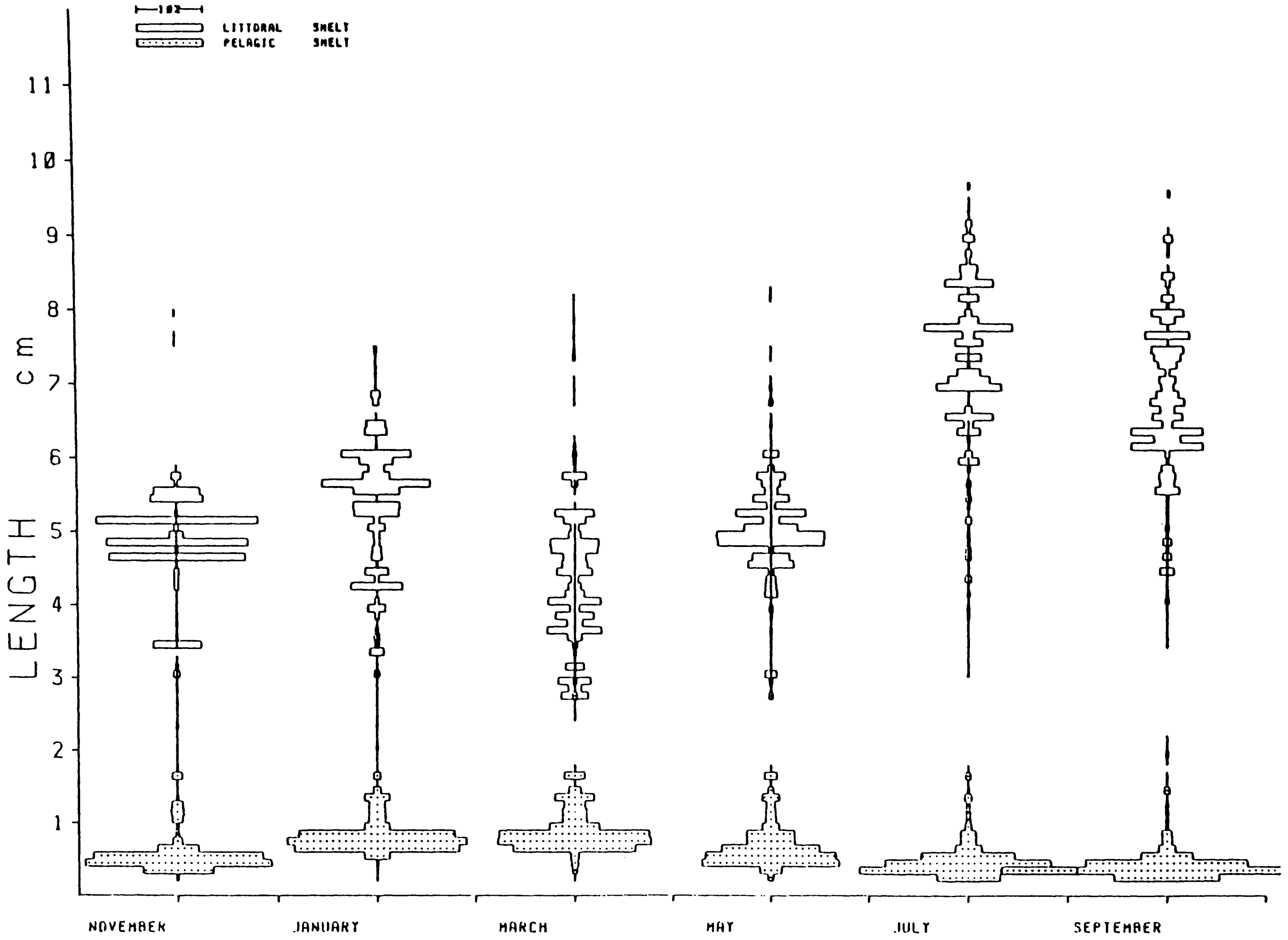


FIG. 90 Simulated smelt length frequency distributions when the modal size of pelagic prey varied seasonally, from 0.1mm on February 1st to 1.0mm on August 1st.

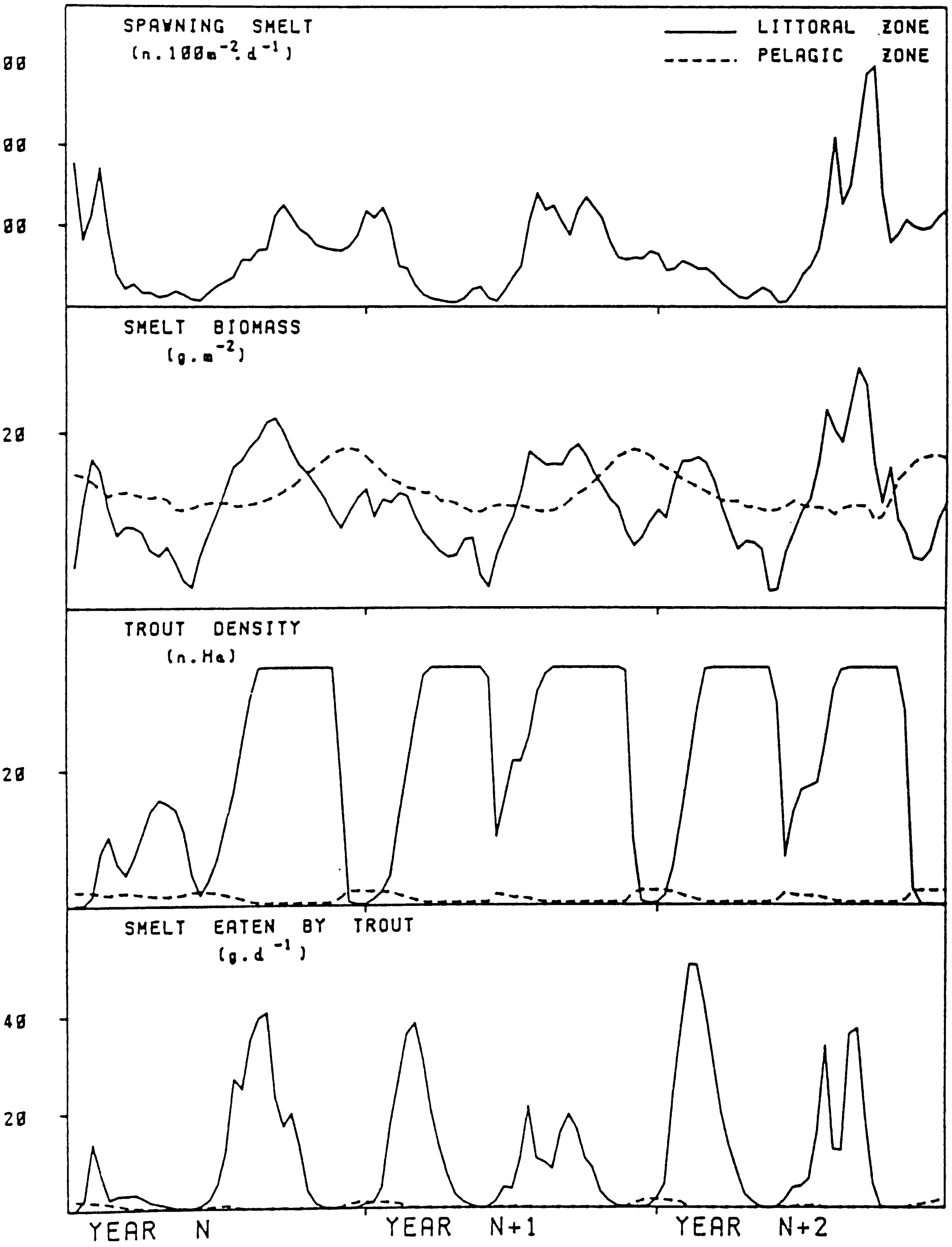


FIG. 91 Simulated population parameters when the modal size of pelagic prey varied seasonally, from 0.1mm on February 1st to 1.0mm on August 1st.

N = 18

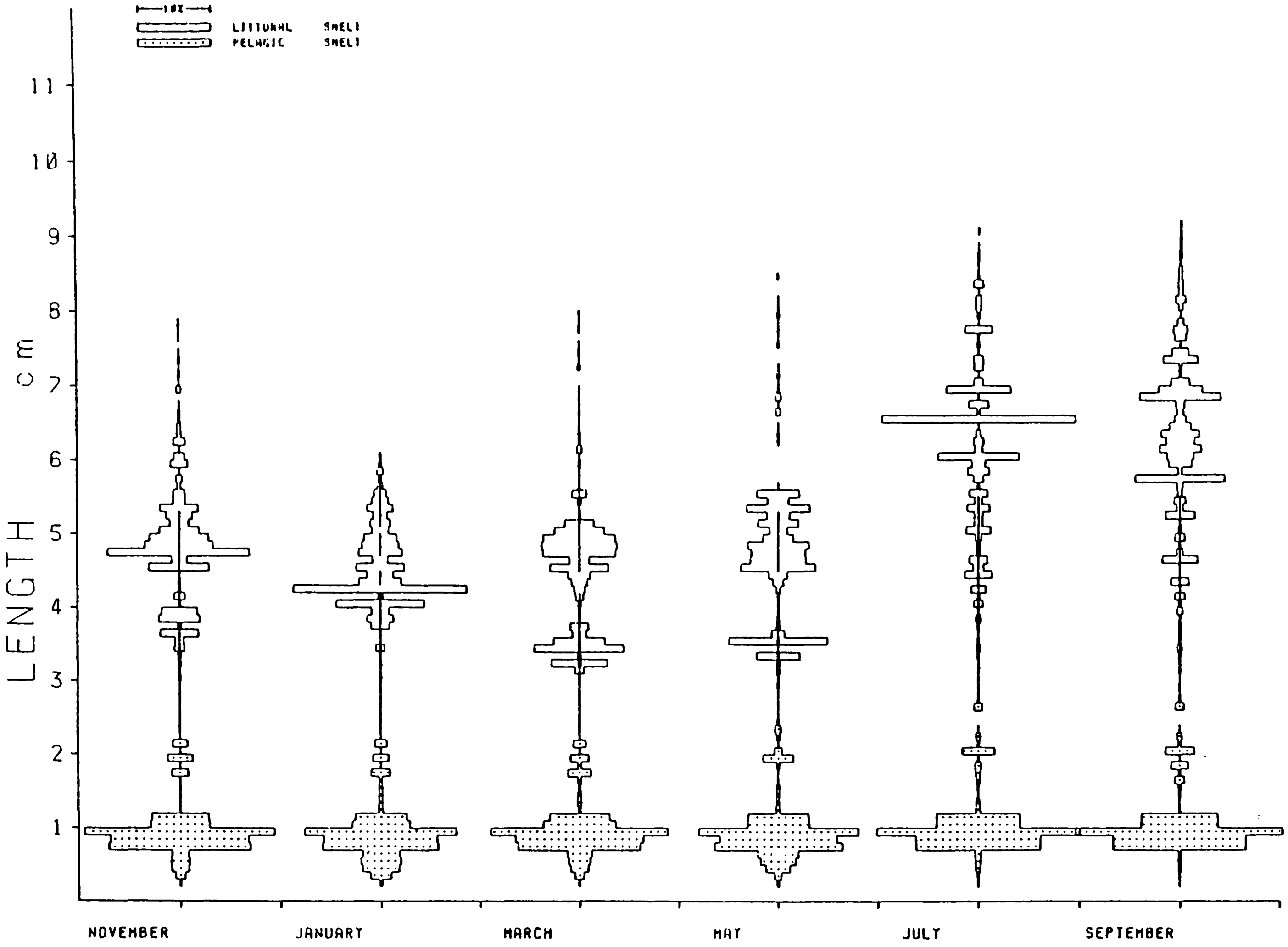


FIG. 92 Simulated smelt length frequency distributions when the modal size of littoral prey varied seasonally, from 1.0mm on February 1st to 10.0mm on August 1st.

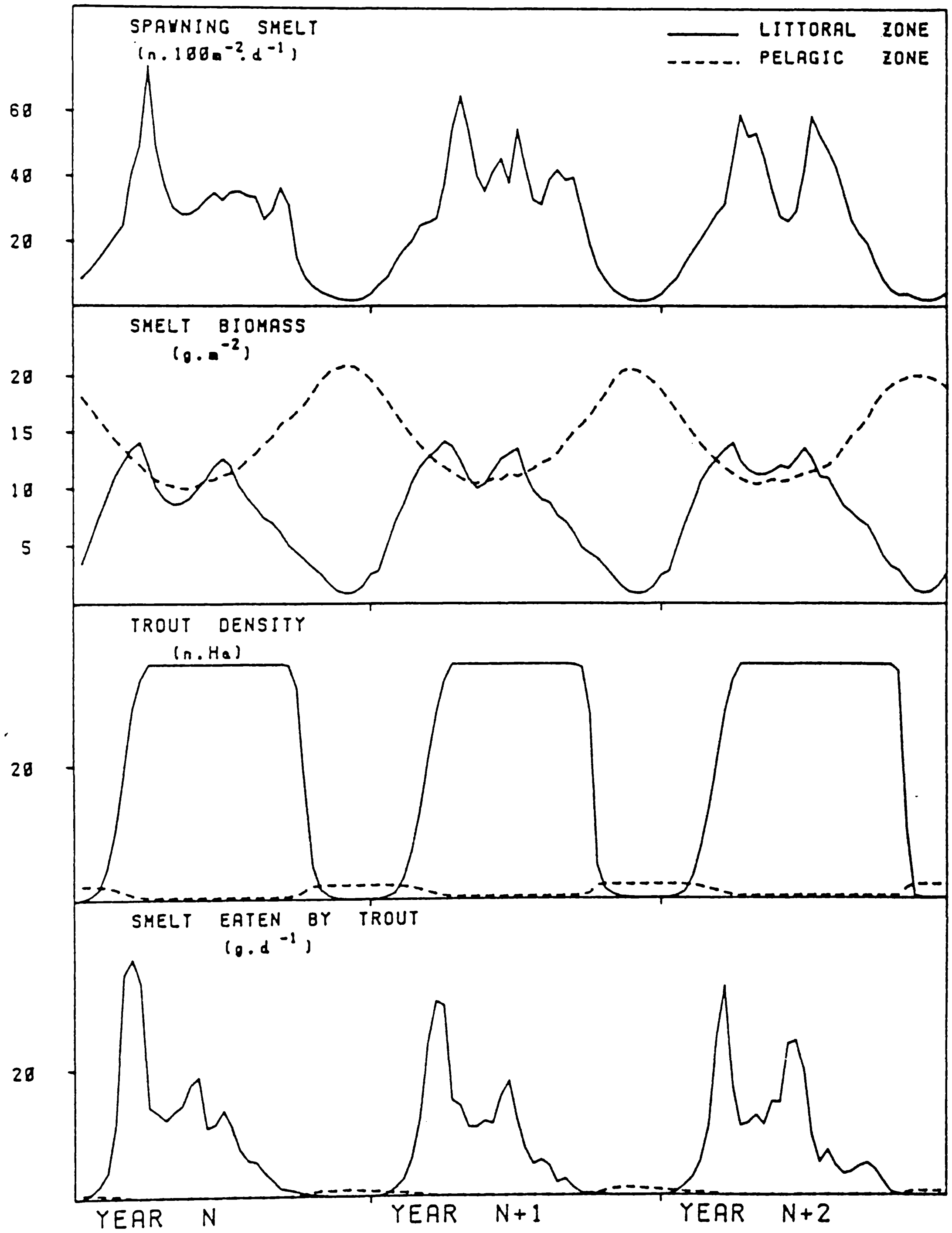


FIG. 93 Simulated population parameters when the modal size of littoral prey varied seasonally, from 1.0mm on February 1st to 10.0mm on August 1st.

N = 18

(ii) Seasonality in the Shape Term

The range of variation (1.2 on August 1st to 4.0 on February 1st) tested was the same for both the littoral and pelagic prey size distribution but, because the modal sizes were different, the ranges of prey size in the pelagic and littoral zones also differed. The variation used described a limited size range of mainly small items during summer (0.001 to 1.1mm in the pelagic zone and 2.0 to 5.0mm in the littoral zone) but included more large and some smaller items in winter (0.001 to 5.0mm in the pelagic zone and 0.001 to 13.0mm in the littoral zone).

Seasonal variation in the pelagic shape term caused the modal length of pelagic smelt to increase gradually after January as larger prey became more abundant (fig. 94). However the prey size range available was always restrictive, allowing few smelt to grow large enough to be recruited to the littoral population. Consequently littoral smelt densities were low (fig. 95), those present grew rapidly and large smelt (> 60mm) comprised a major proportion of the population.

Cyclic variation in the littoral shape term had comparatively little effect on either pelagic or littoral smelt length frequency structure (fig. 96) as the diet breadth size limits of adult smelt were sufficiently extensive to ensure that the proportion of food production available was little affected by these changes in the prey size range. Large smelt were relatively scarce during summer so that spawner densities, littoral biomass and quantities eaten by trout were also slightly depressed (fig. 97). This occurred because there was insufficient food available in late summer to sustain large smelt. Thus it seems that seasonal cycles in the distribution of productivity over the size range of pelagic prey can be a major factor controlling both population length frequency structure and abundances of adult smelt in the littoral zone. Variation in the littoral prey size distribution has comparatively little influence - affecting the abundances of only the largest smelt.

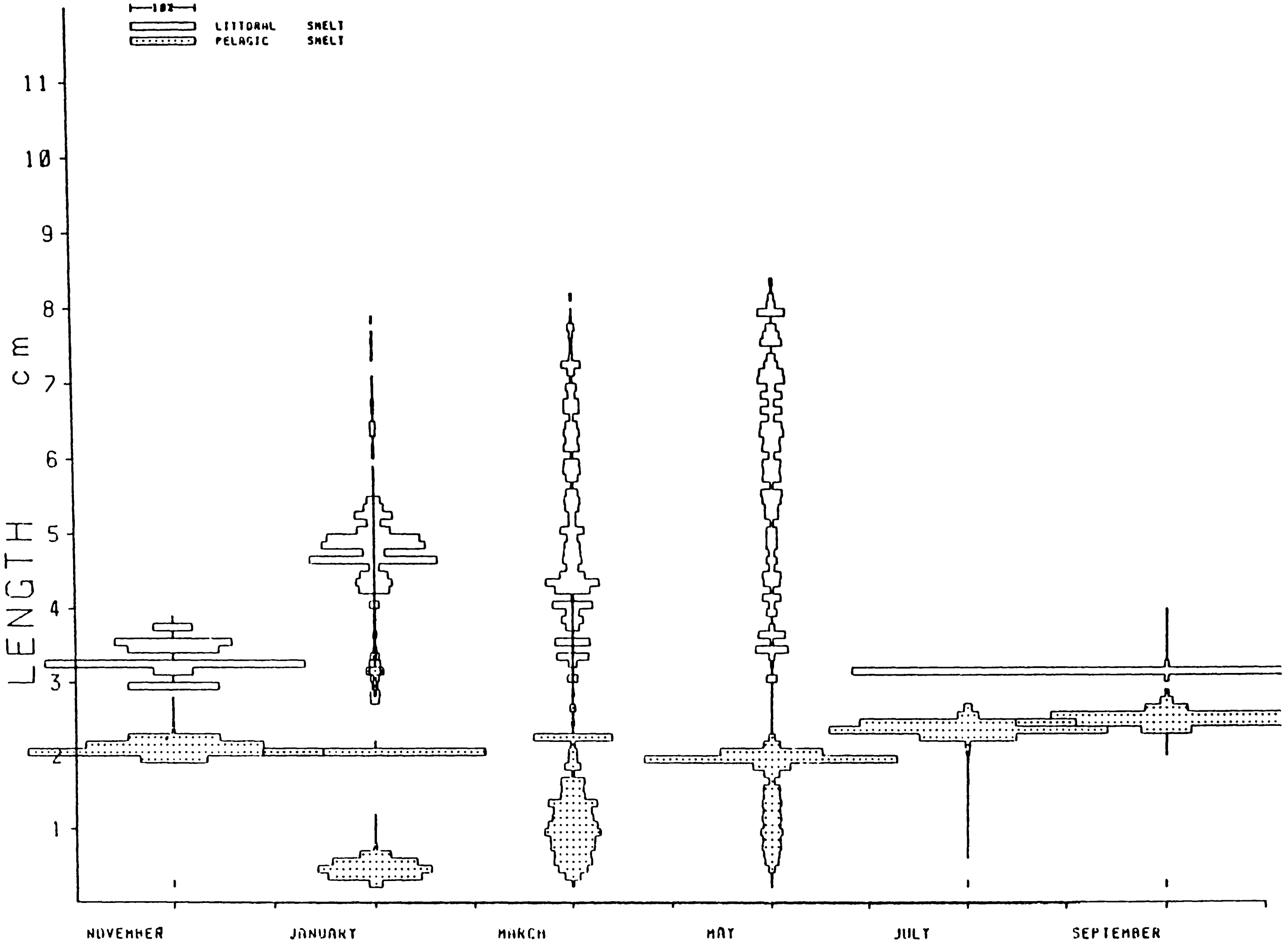


FIG. 94 Simulated smelt length frequency distributions when the shape term for the pelagic prey size distribution varied seasonally from 1.2 on August 1st to 4.0 on February 1st.

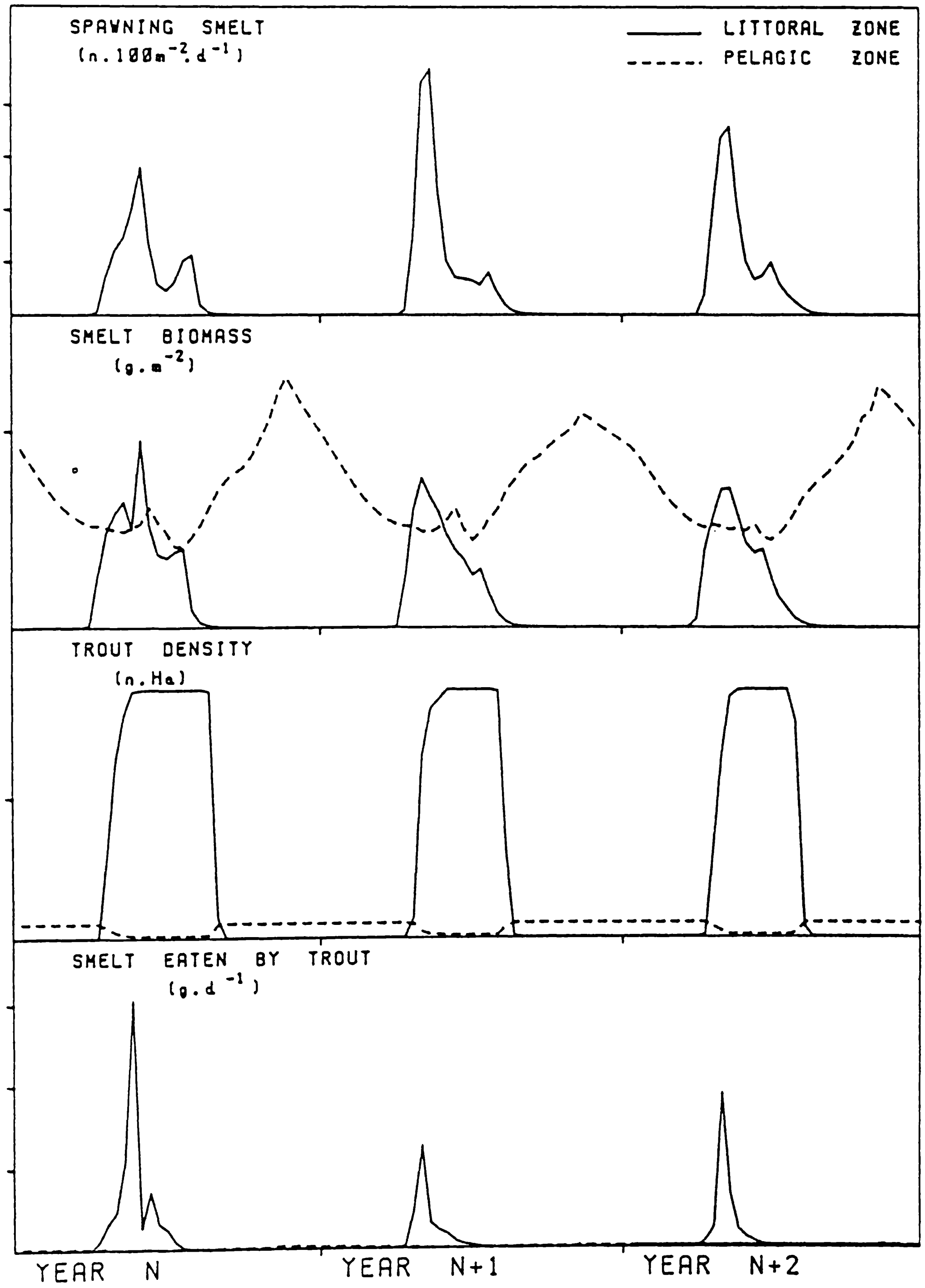


FIG. 95 Simulated population parameters when the shape term for the pelagic prey size distribution varied seasonally from 1.2 on August 1st to 4.0 on February 1st. N = 18

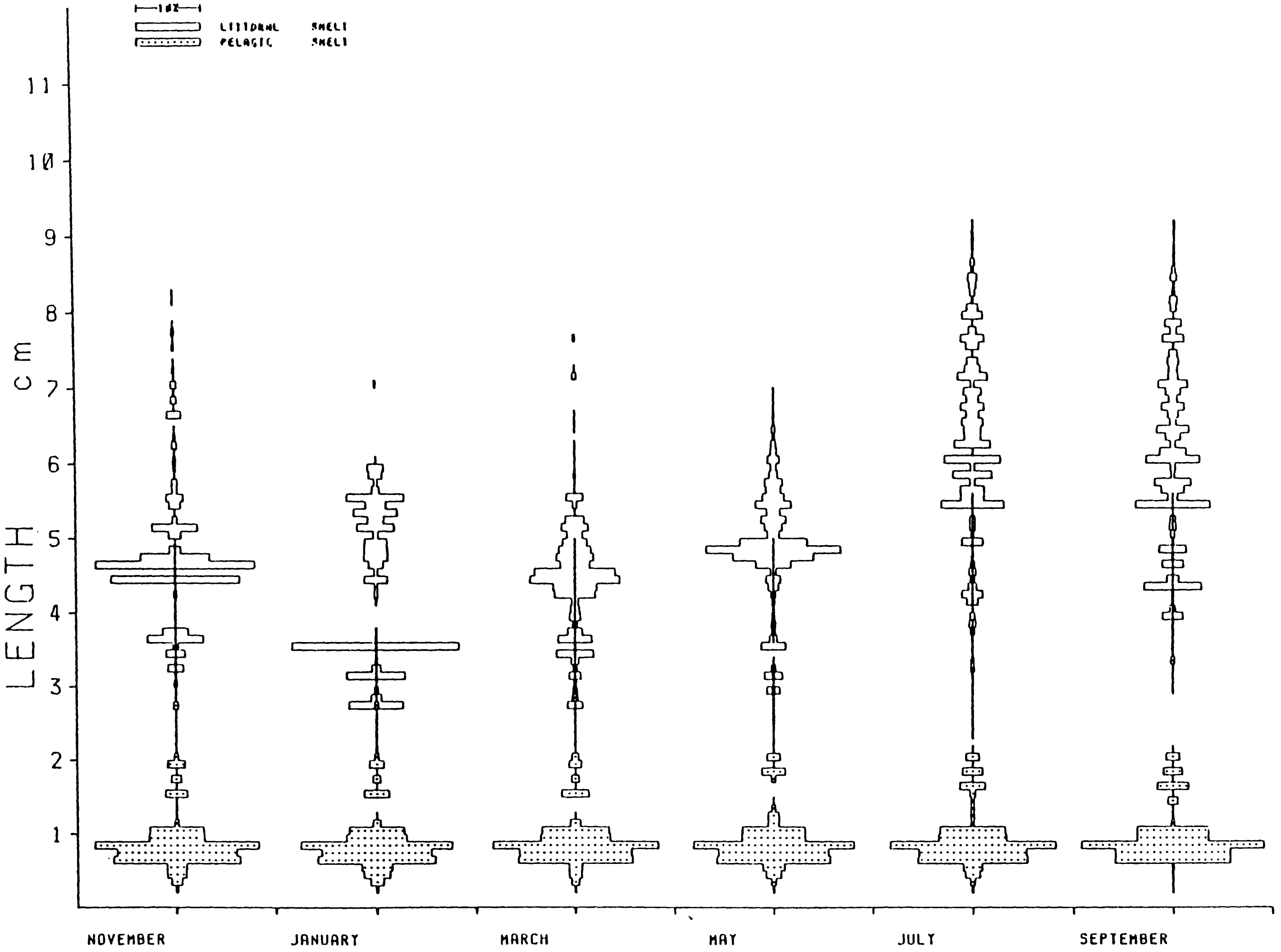


FIG. 96 Simulated smelt length frequency distributions when the shape term for the littoral prey size distribution varied seasonally, from 1.2 on August 1st to 4.0 on February 1st.

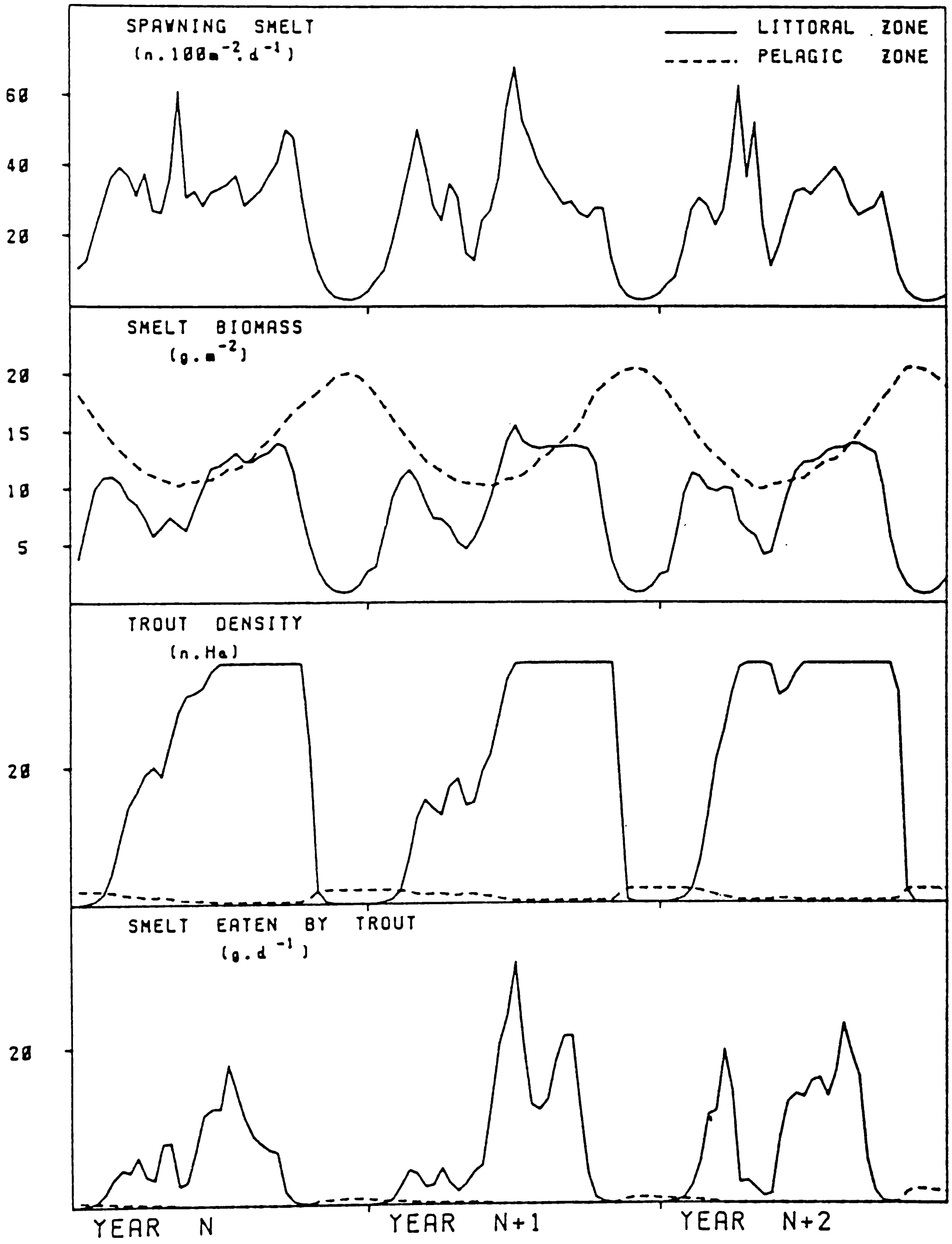


FIG. 97 Simulated pöpulation parameters when the shape term for the littoral prey size distribution varied seasonally, from 1.2 on August 1st to 4.0 on February 1st. N = 18

(iii) Seasonality in Food Production

Seasonal variation in pelagic food production, ranging from $0.1 g.m^{-2}.d^{-1}$ on February 1st to a maximum at $5.0 g.m^{-2}.d^{-1}$ on August 1st caused development of a bimodal length frequency distribution in pelagic smelt (fig. 98), but had little effect on length frequency structure of littoral smelt. The second mode in the pelagic smelt length frequency distribution developed as the food resource increased during autumn and decayed as the food resource diminished in spring. Growth in the pelagic zone, movement into the littoral, and spawning activity (fig. 99) were associated with the period of increasing food production and were not greatly influenced by inherent seasonality in models describing movement, maturation and maintenance requirements.

The seasonal cycle in pelagic food production caused development of a bimodal length frequency distribution because, from January to July, the balance between food production and the intensity of competition maintained by newly recruited larval smelt resulted in a net increase in the amount of food available to size classes longer than about 10mm. Starvation occurred when the balance reversed in August and the food resource diminished.

Seasonality in littoral food production ($0.1 g.m^{-2}.d^{-1}$ on August 1st to $5.0 g.m^{-2}.d^{-1}$ on February 1st) had little effect on population length frequency structure (fig. 100) because recruitment from the pelagic population always maintained sufficient feeding competition to prevent the increase in food production resulting in more food being available to individual smelt. Thus length frequency distributions were unaffected but littoral biomass (fig. 101) increased considerably.

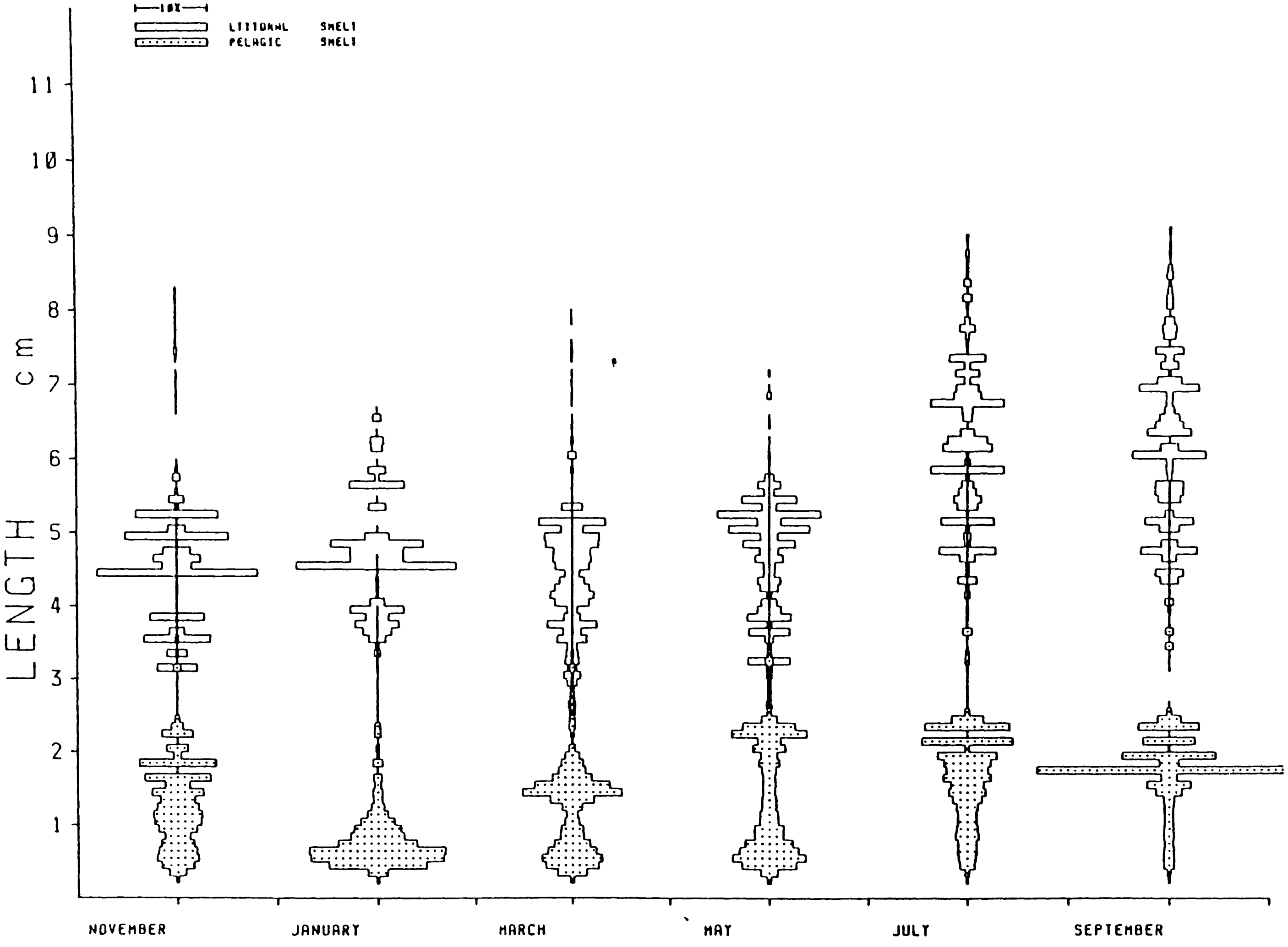


FIG. 98 Simulated smelt length frequency distributions when pelagic food production varied seasonally, from 1.0g.m.$^{-2}$.d^{-1} on February 1st to 5.0g.m.$^{-2}$.d^{-1} on August 1st.

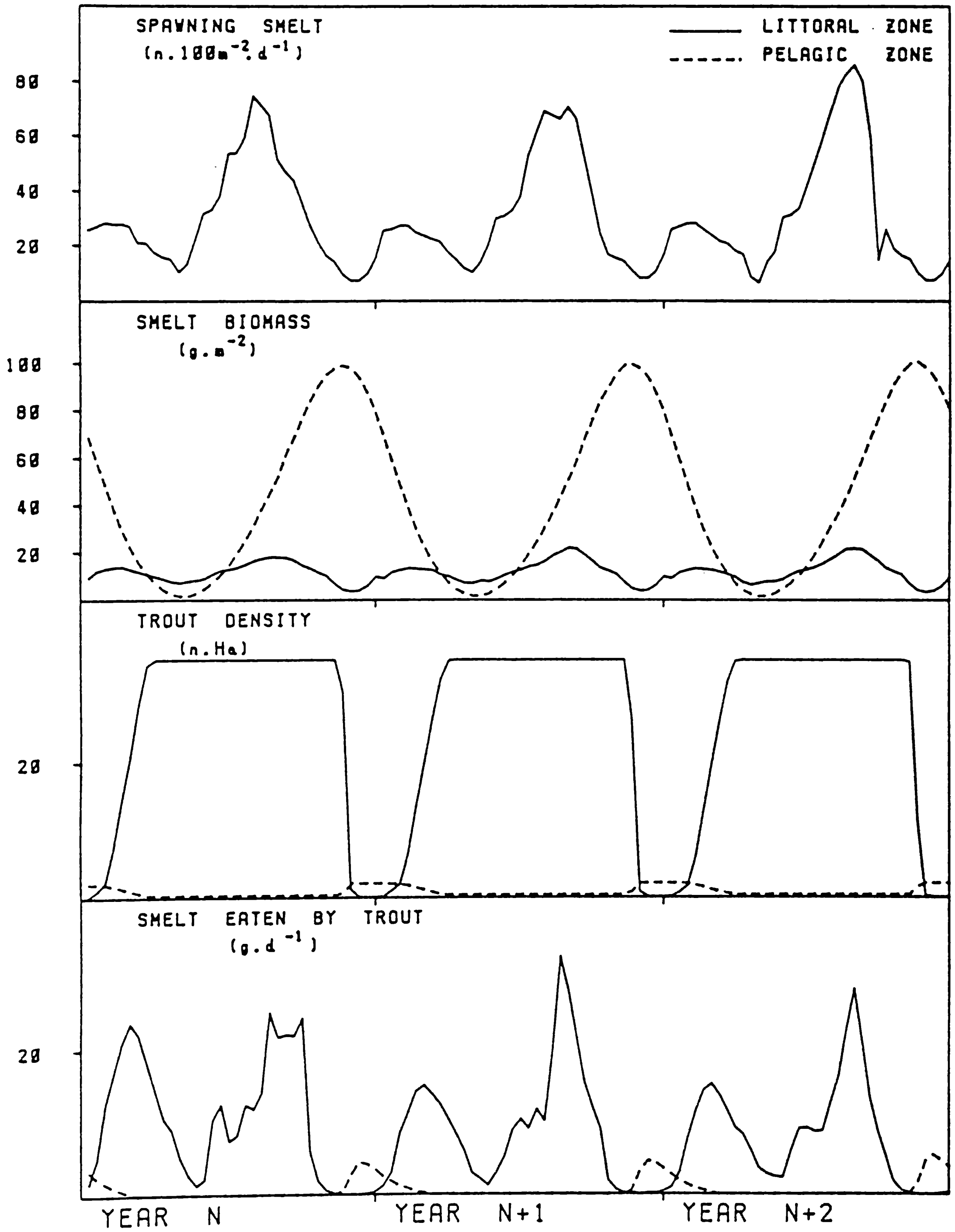


FIG. 99 Simulated population parameters when pelagic food production varied seasonally, from 1.0g.m.$^{-2}$.d^{-1} on February 1st to 5.0g.m.$^{-2}$.d^{-1} on August 1st. N = 18

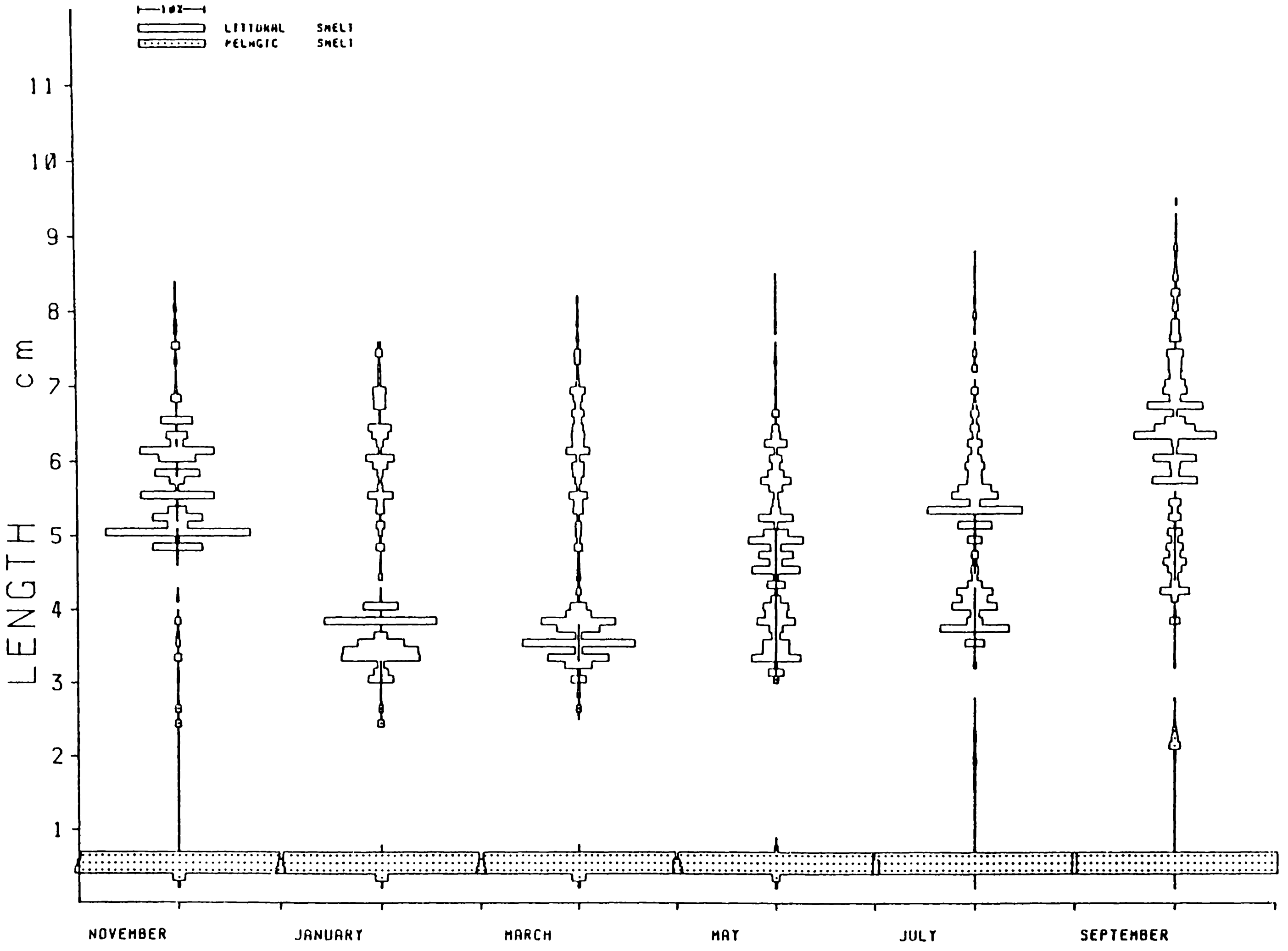


FIG. 100 Simulated smelt length frequency distributions when littoral food production varied seasonally, from 0.1g.m.$^{-2}$.d^{-1} on August 1st to 5.0g.m.$^{-2}$.d^{-1} on February 1st.

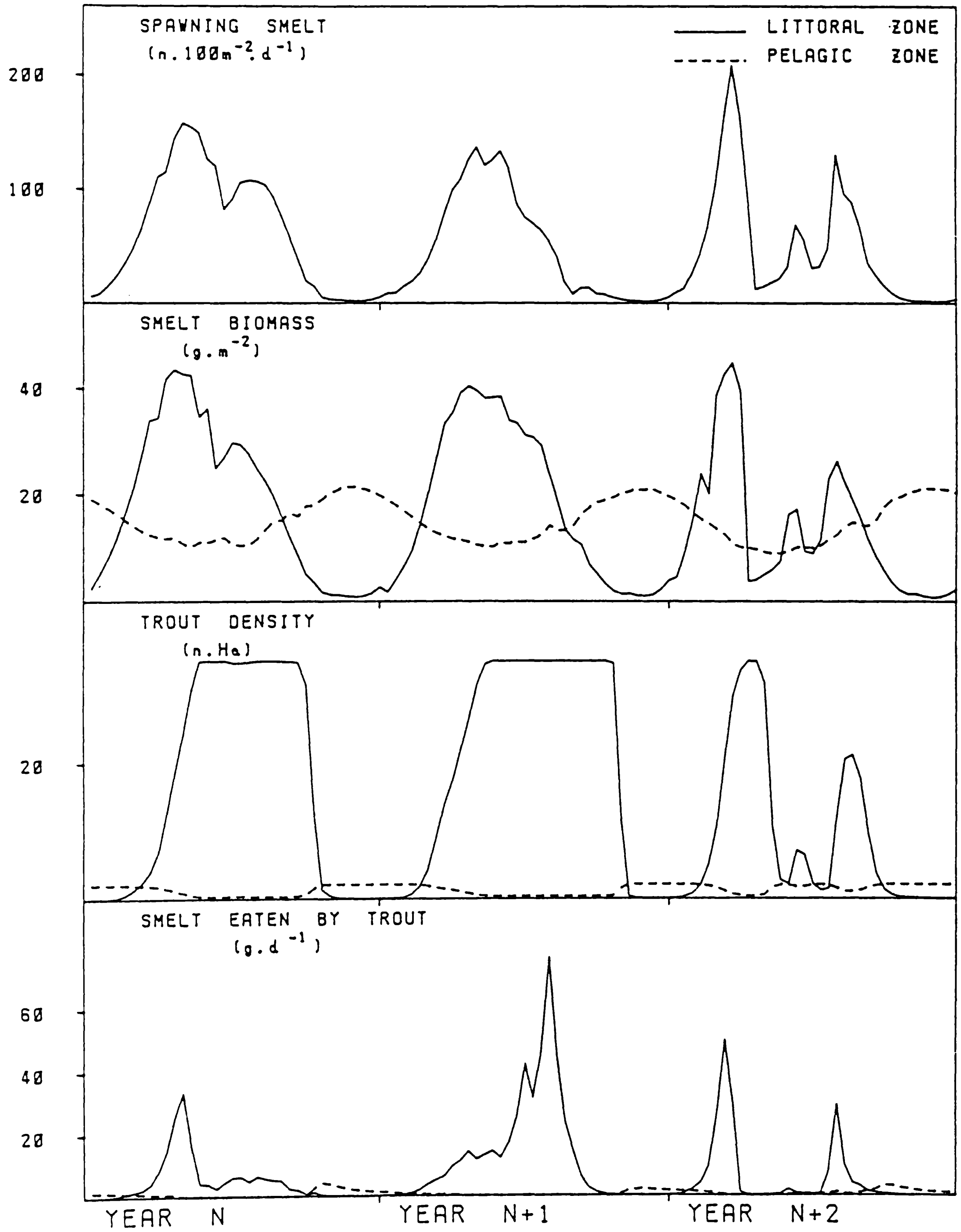


FIG. 101 Simulated population parameters when littoral food production varied seasonally, from 0.1g.m.$^{-2}$.d^{-1} on August 1st to 5.0g.m.$^{-2}$.d^{-1} on February 1st. N = 18

(c) Trout Predation

The trout predation model described selection for the larger more visible smelt, whose escape ability also increased with length. The intensity of selection increased with the abundance of large smelt and the quantity eaten was maximal when highly visible smelt, not quite large enough to evade capture, were particularly abundant (fig. 102). Thus both the intensity of selection and the quantity eaten were usually strongly correlated with smelt biomass per unit water volume. In previous simulations where the pelagic zone was very much deeper (110m) than the littoral zone (15m), the littoral smelt biomass per unit volume was relatively high and the smelt present were always larger and more visible. Consequently, trout predation occurred predominantly in the littoral zone. Predation in the pelagic zone increased when habitat conditions restricted the population's reproductive capacity so that large pelagic smelt became relatively more abundant.

The effects of trout predation on smelt population processes were examined by varying trout stocking density in the standard system. Length frequency distributions were not affected by the presence of trout (fig. 103 cf. figs. 56 and 104) and densities up to 100Ha^{-1} had little effect on population length frequency structure (fig. 104). Intense cropping at high trout densities did reduce littoral smelt biomass (fig. 105 cf. fig. 57) but numbers of spawning smelt and the weight of smelt eaten by trout were not affected although annual variation in these parameters was reduced. Thus it seems that trout predation has little influence on smelt population processes.

The relationship between the weight of smelt eaten daily by individual trout and their stocking density in the standard system (fig. 106) demonstrated that reduction in trout food intake caused by increased competition for the available smelt was small, even for a two order of magnitude increase in trout stocking density. However, annual variation was substantially greater at low stocking densities and therefore, assuming correlation between attainable trout size and the weight of smelt eaten daily, one would expect the biggest trout to occur when stocked at $2.0Ha^{-1}$, largely because of the annual variation which characterized the system at low trout stocking densities.

The ability of this system to support such high predation rates depended on adequate recruitment to the littoral population to compensate losses due to predation. Therefore, factors which influence recruitment might also be expected to influence the relationship between trout stocking density and trout growth.

The effects of a restricted spawning season at high stocking density were examined by increasing the trout stocking density in the standard system to $50Ha^{-1}$ and limiting the smelt spawning season to 30 days (i.e. October).. The quantity of littoral smelt eaten by trout was reduced only slightly but the weight of pelagic smelt eaten increased by ca.35% (Table 9). However the population length frequency structure (fig. 107) was almost identical to that obtained with a 30 day spawning season when the stocking density was only $2.0Ha^{-1}$ (fig. 112). Thus, for the standard system, the combined effects of high trout densities and a restricted smelt spawning season caused only minor reductions in the quantity of smelt eaten by trout and increased predation caused little change in smelt population processes. This result occurred because predatory mortality allowed smelt, which would have otherwise died of starvation, to develop and grow. Starvation mortality diminished as predatory mortality increased.

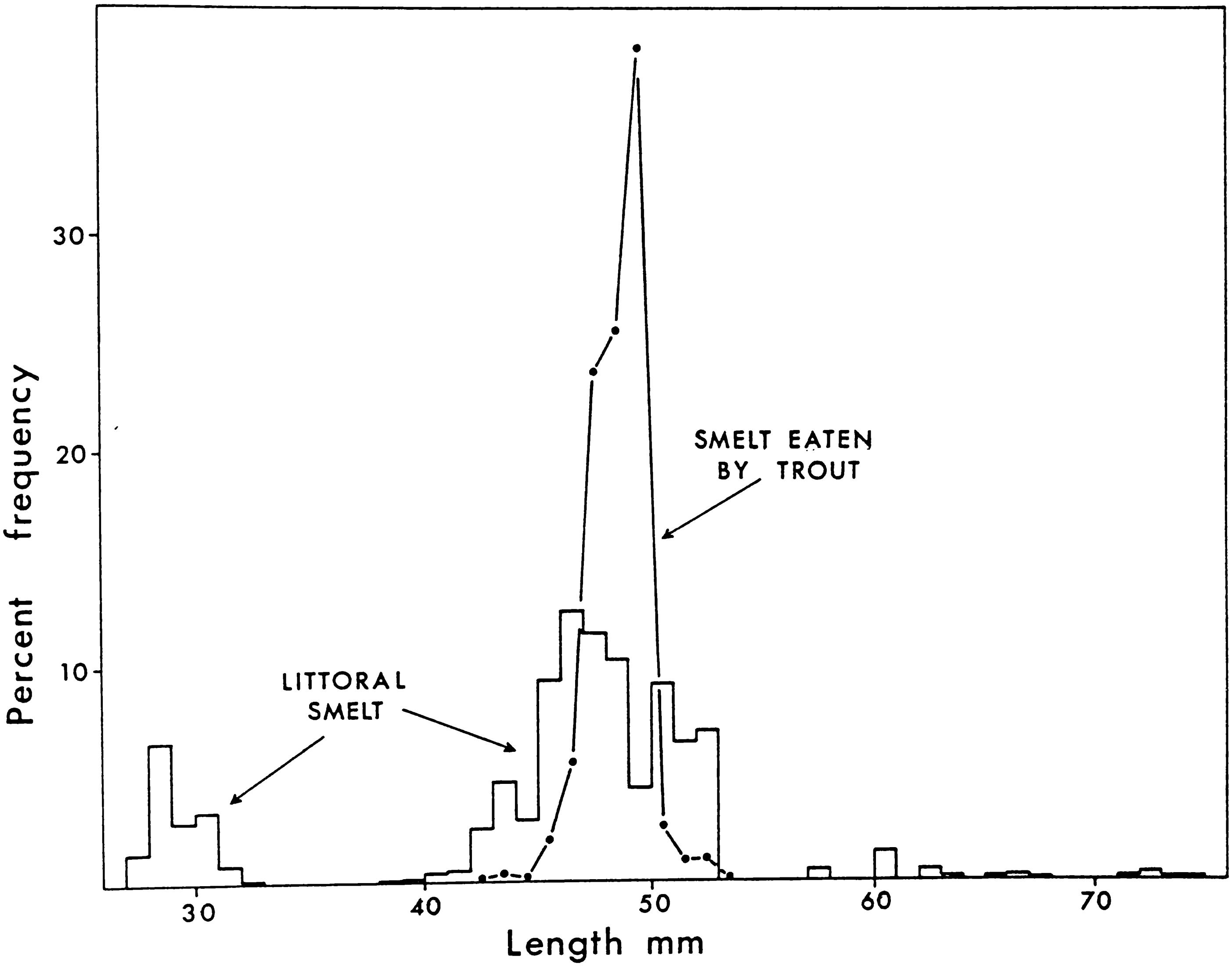


FIG. 102 Simulated length frequency distributions of smelt present in the littoral zone (histogram) and eaten by trout.

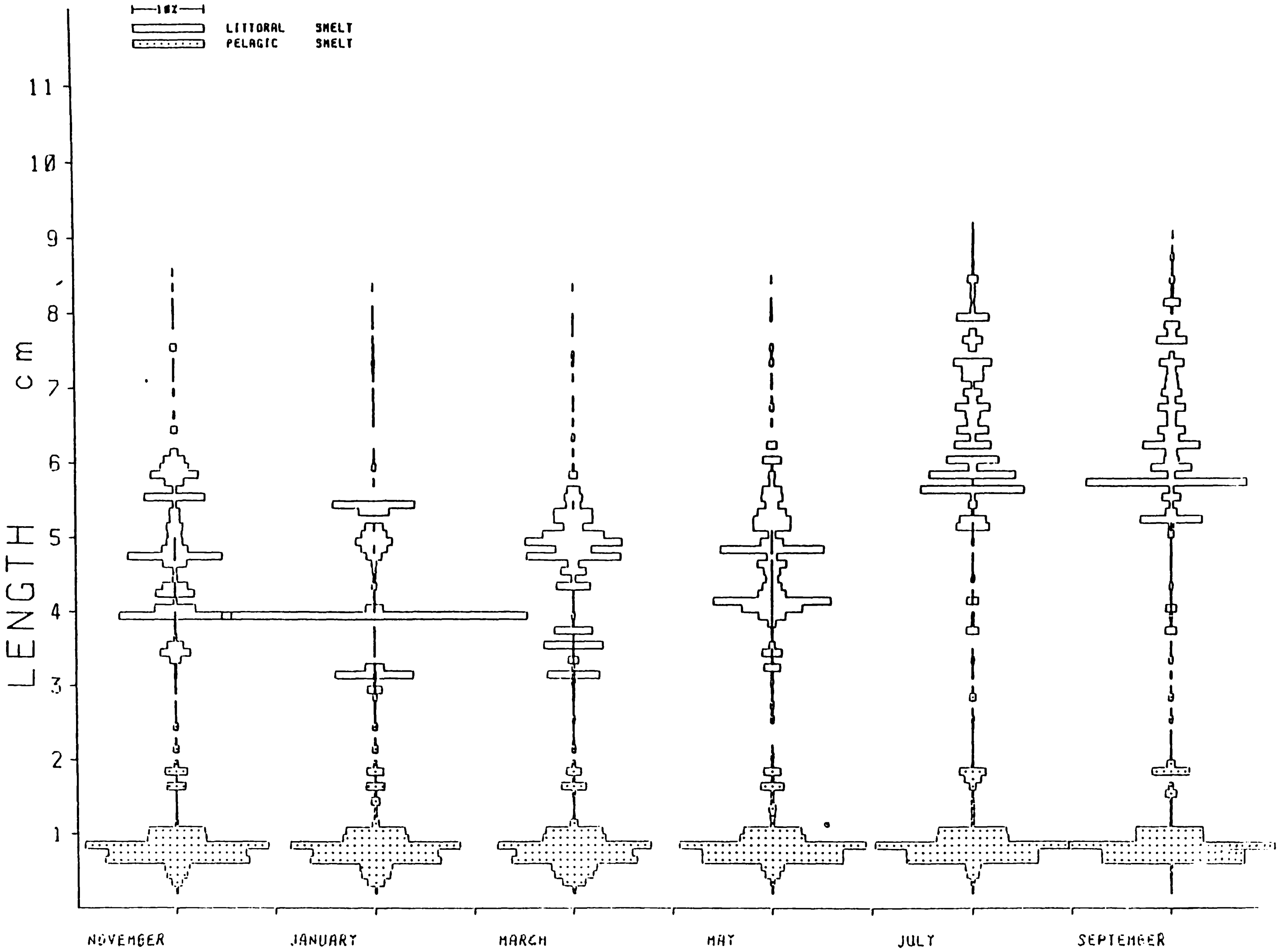


FIG. 103 Simulated smelt length frequency distributions when trout are absent from the system.

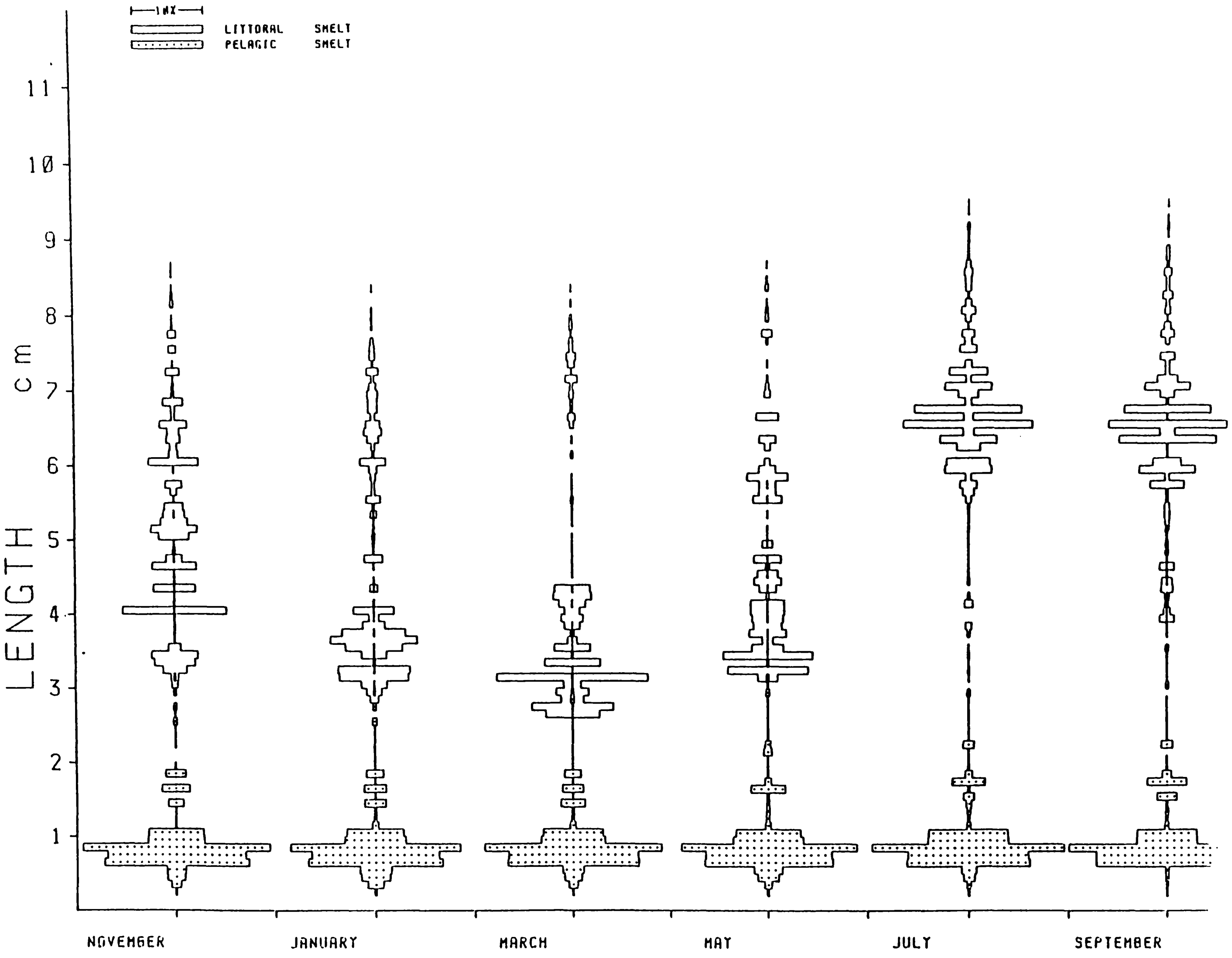


FIG. 104 Simulated smelt length frequency distributions when trout are stocked at $100 Ha^{-1}$.

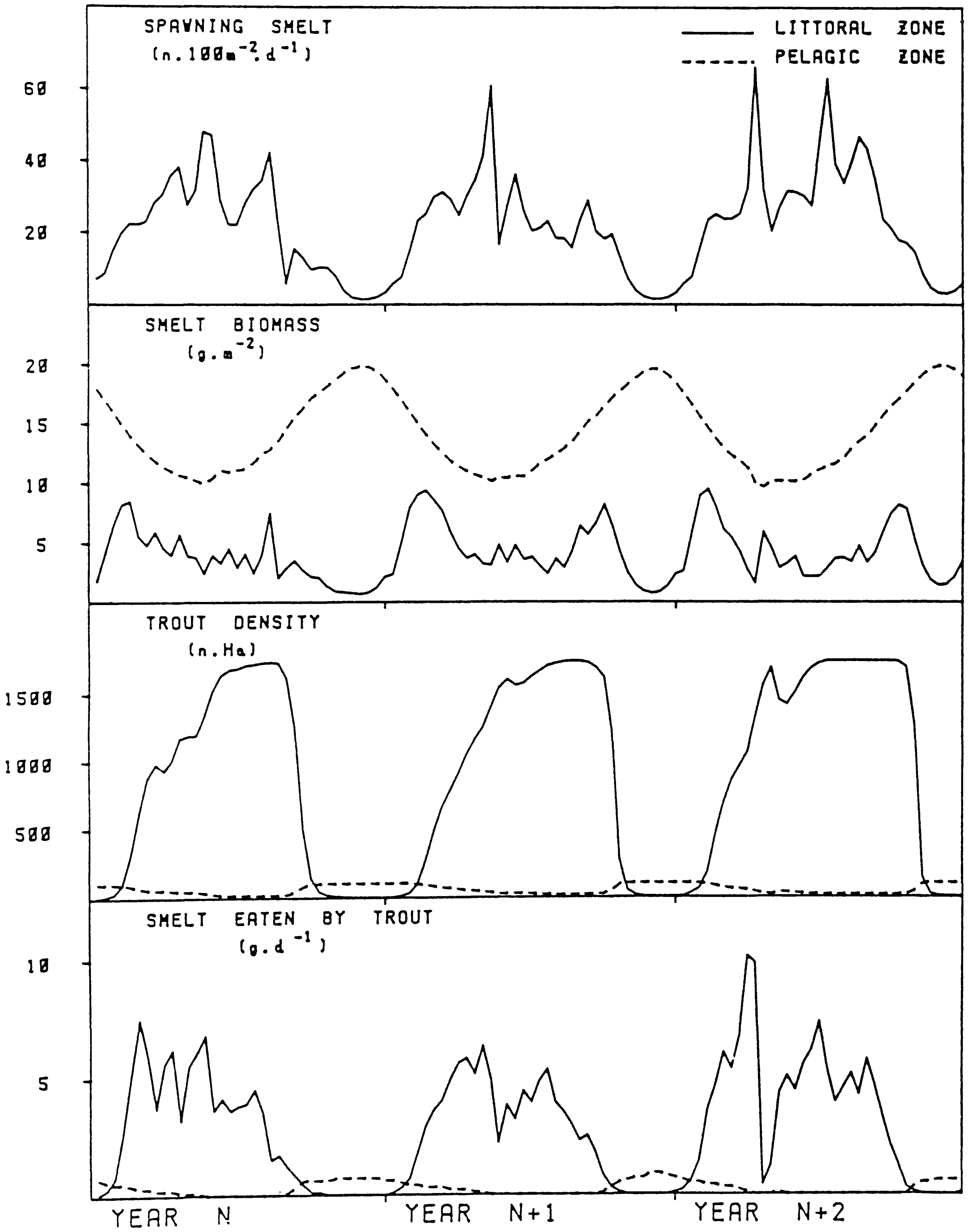


FIG. 105 Simulated population parameters when trout are stocked at $100Ha^{-1}$. N = 18

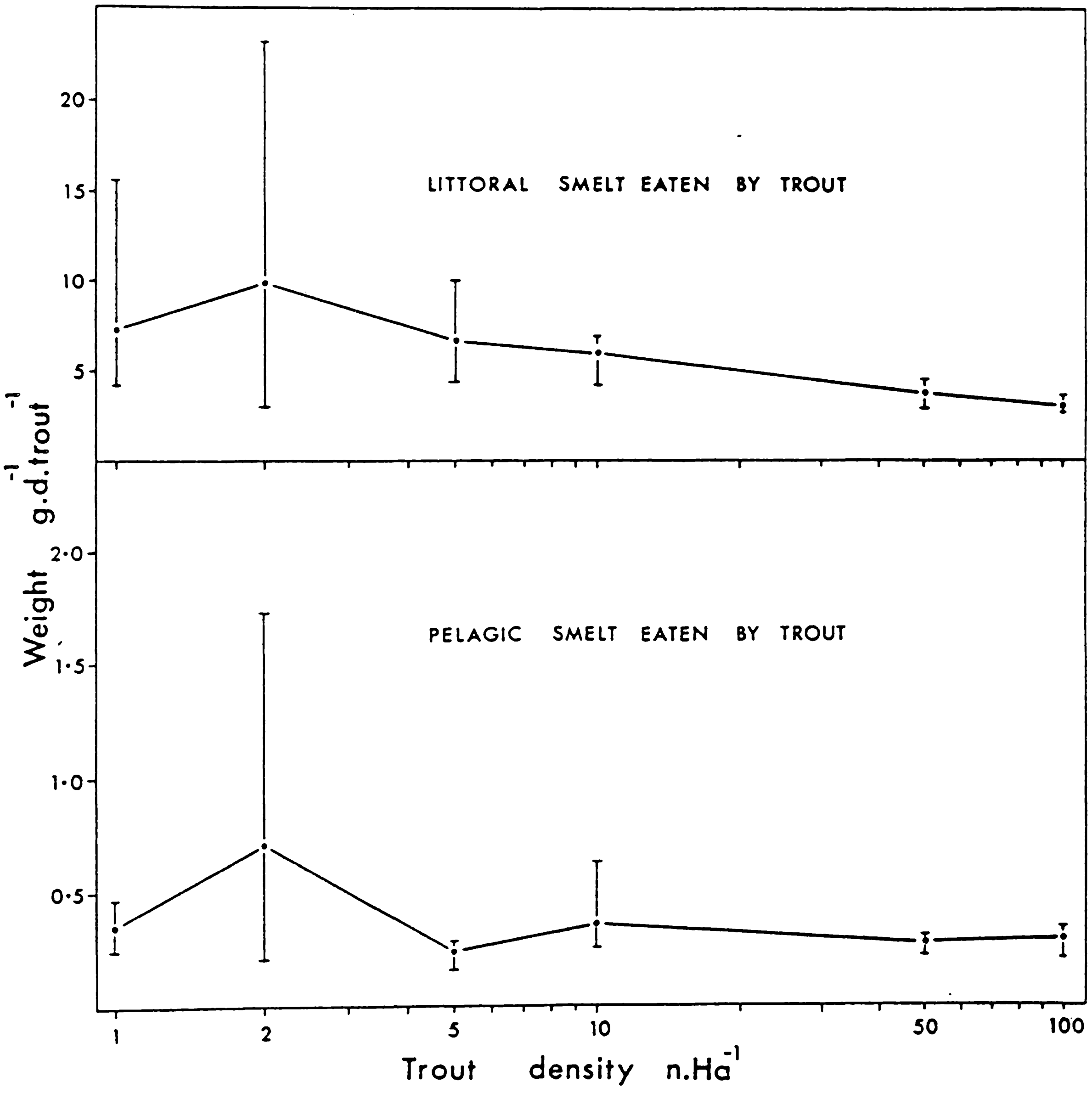


FIG. 106 The relationship between trout stocking density and weight of smelt eaten daily by individual trout. Data are mean weights (g) of smelt eaten daily. Vertical bars indicate the annual range of variation in the final six years of twenty simulated.

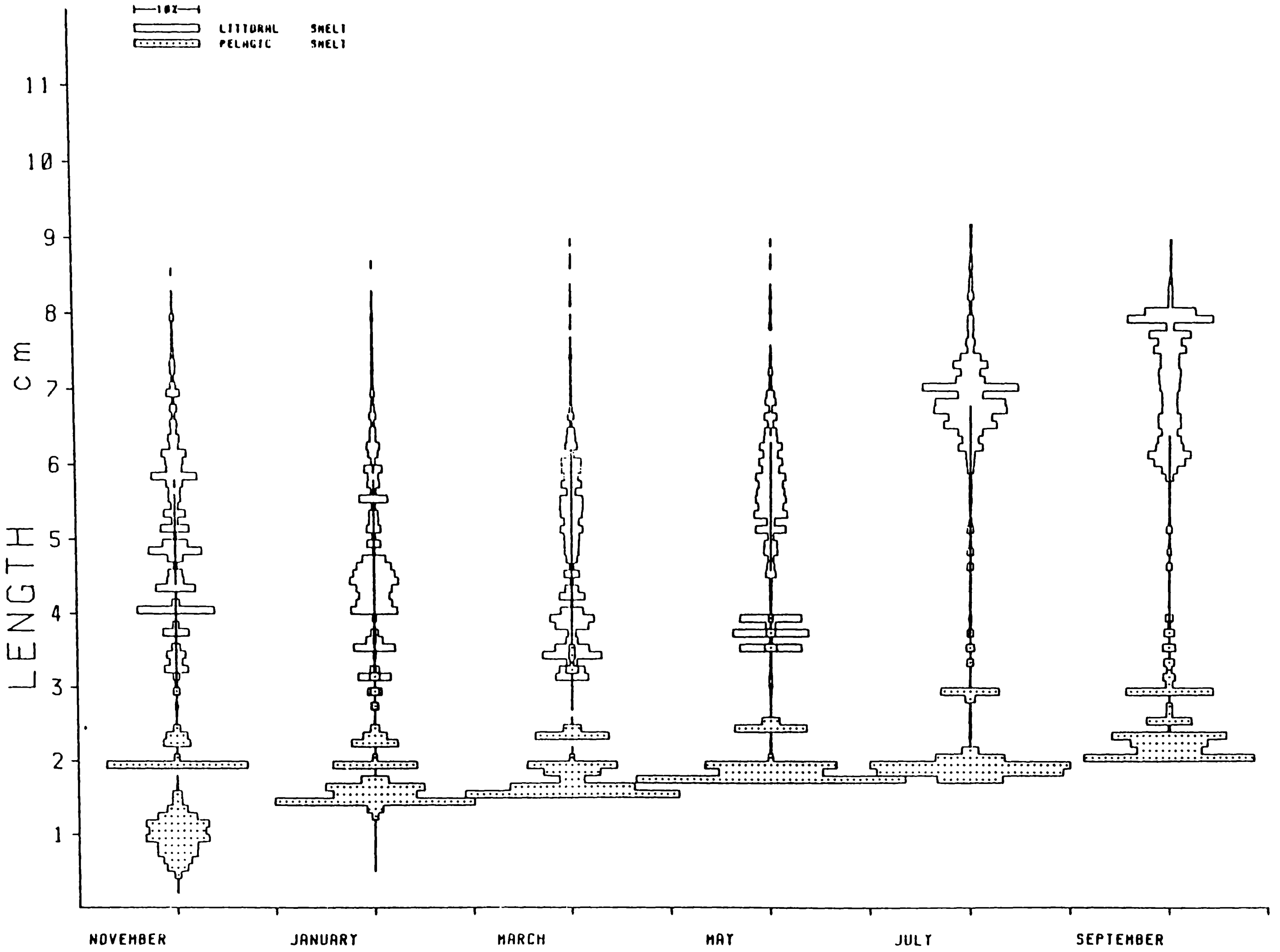


FIG. 107 Simulated smelt length frequency distributions when spawning was confined to the month of October and trout were stocked at $50Ha^{-1}$.

Table 11. The effects of trout stocking density and duration of the smelt spawning season on the weight of smelt eaten daily by individual trout. Data are mean weights (g) of smelt flesh eaten daily during each of six years simulated.

	Stocking density = 2.0Ha^{-1}				Stocking density = 50Ha^{-1}			
	360 Day Spawning		30 Day Spawning		360 Day Spawning		30 Day Spawning	
YEAR	Litt.	Pel.	Litt.	Pel.	Litt.	Pel.	Litt.	Pel.
15	10.1	1.72	3.4	.29	3.8	.30	3.5	.37
16	23.2	1.73	4.3	.24	4.3	.28	3.6	.46
17	10.3	.15	6.5	.26	4.5	.28	3.0	.35
18	7.0	.20	3.7	.32	3.6	.27	2.8	.33
19	5.3	.25	4.7	.29	2.9	.25	2.9	.40
20	3.0	.23	2.5	.45	3.3	.21	2.5	.30
$\bar{X}$	9.8	.71	4.2	.31	3.7	.27	3.1	.37

(d) The relative extents of littoral and pelagic habitat

In all previous simulations, the ratio of littoral to pelagic habitat area was 0.05, which approximates the ratio for Lake Taupo. The relatively limited extent and shallow depth of littoral habitat resulted in considerable concentrations of adult smelt when they moved into the shoreline areas to breed and feed on the larger food items available there. This increased the intensity of feeding competition in the littoral zone and provided a concentrated food resource for foraging trout. It therefore seems likely that variation in the relative extents and depths of littoral and pelagic habitat zones would influence smelt population processes and the trout-smelt predator-prey relationship.

Two trials were used to examine changes which occur when littoral habitat is more extensive. In each case, all habitat features other than the ratios of littoral to pelagic habitat (0.2 to 1.0) were the same as in the standard system. When the relative extent of littoral habitat was increased five fold (L:P = 0.2), littoral smelt were larger, particularly during summer (modal length 46-52mm cf. 30-40mm) and the secondary pelagic smelt modal length (11-16mm) decreased in relative size (fig. 108 cf. fig. 56). Spawner densities, littoral smelt biomass and the difference between littoral and pelagic trout densities all decreased (fig. 109). When littoral and pelagic habitat areas were equal in extent, these parameters decreased further, the trout population became largely pelagic, feeding predominantly on small pelagic smelt (fig. 110) and littoral smelt reached even greater size (fig. 111).

The relative decreases in pelagic habitat raised the density of larval smelt. This increased the intensity of feeding competition, slowed the growth of pelagic smelt and limited recruitment to the littoral population. Littoral feeding habitat was more extensive, which further reduced feeding competition and therefore supported rapid growth, resulting in the generally large size of littoral smelt. Because smelt were generally large, their maturity rate and associated spawning mortality rate was high and this prevented littoral biomass reaching the sustainable maximum (i.e. $10\text{-}20 g.m^{-2}$). The weight of smelt eaten by trout decreased when littoral habitat was more extensive because smelt within their preferred size range were scarce. There were high densities of larval smelt 2-6mm long in the pelagic zone and low densities of large smelt in the littoral and these were generally large enough to avoid capture. Neither population group provided adequate trout forage.

Slow growth in pelagic waters limited the number of smelt moving into the littoral zone and this restricted the abundance of medium sized smelt which trout eat. Larval growth would have improved given an increase in the relative abundance of large pelagic food items (i.e. greater modal size or smaller shape term), seasonal variation in pelagic food production or a brief spawning season. Any of these would have increased recruitment to the littoral population, depressed growth there, increased littoral biomass and enhanced the forage supply for trout feeding in the littoral zone.

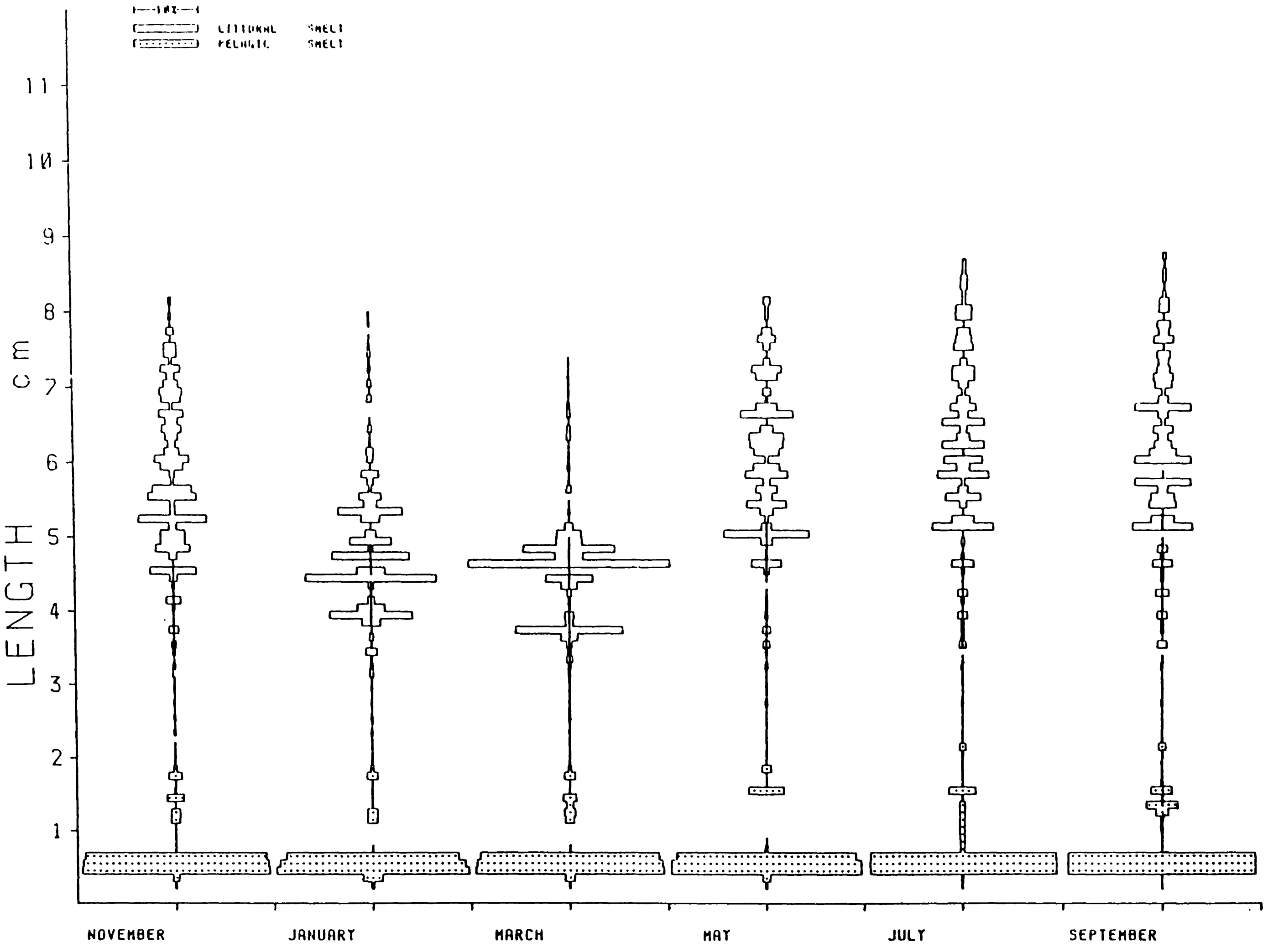


FIG. 108 Simulated smelt length frequency distributions when the ratio of littoral to pelagic habitat area was 0.2.

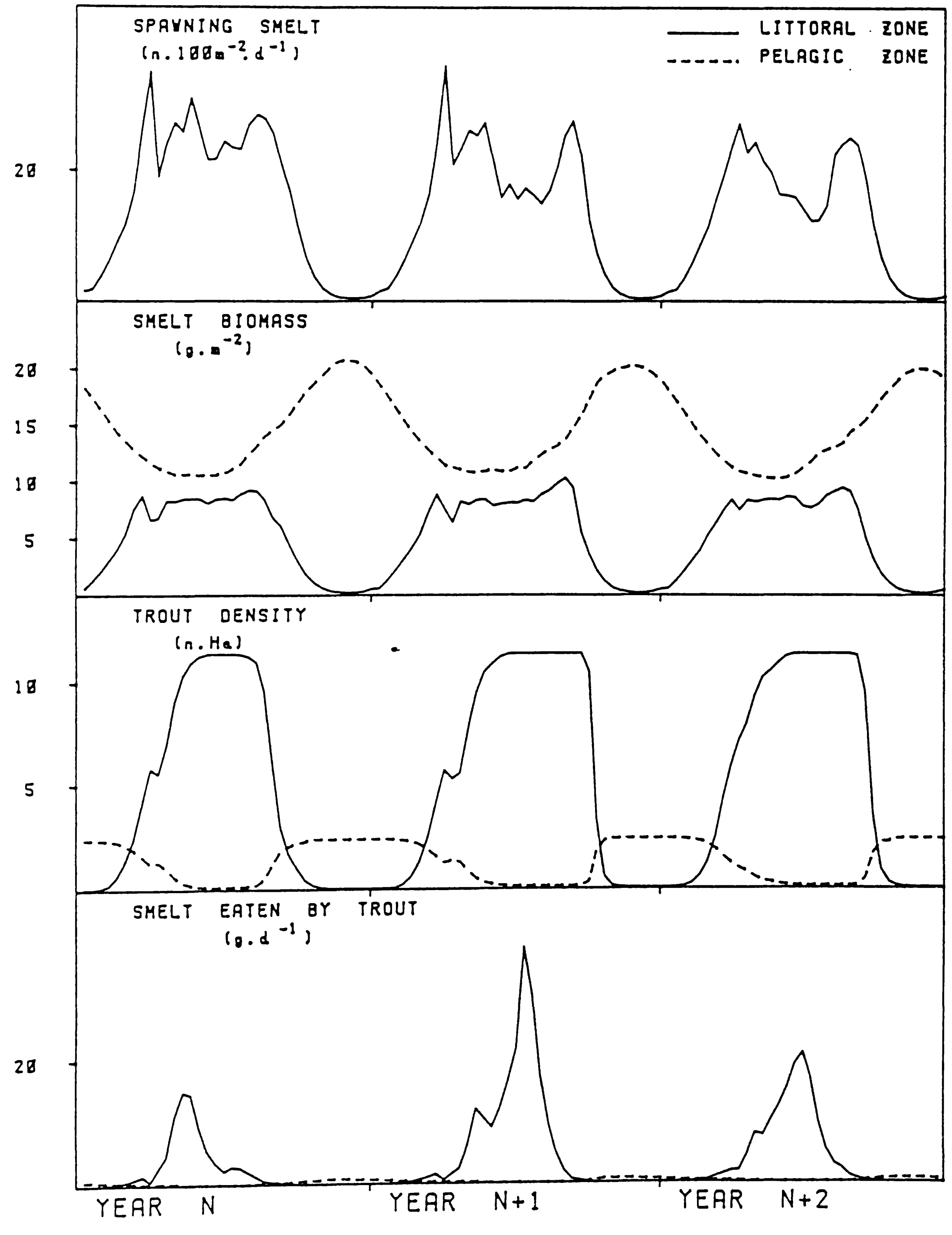


FIG. 109 Simulated population parameters when the ratio of littoral to pelagic habitat area was 0.2. N = 18

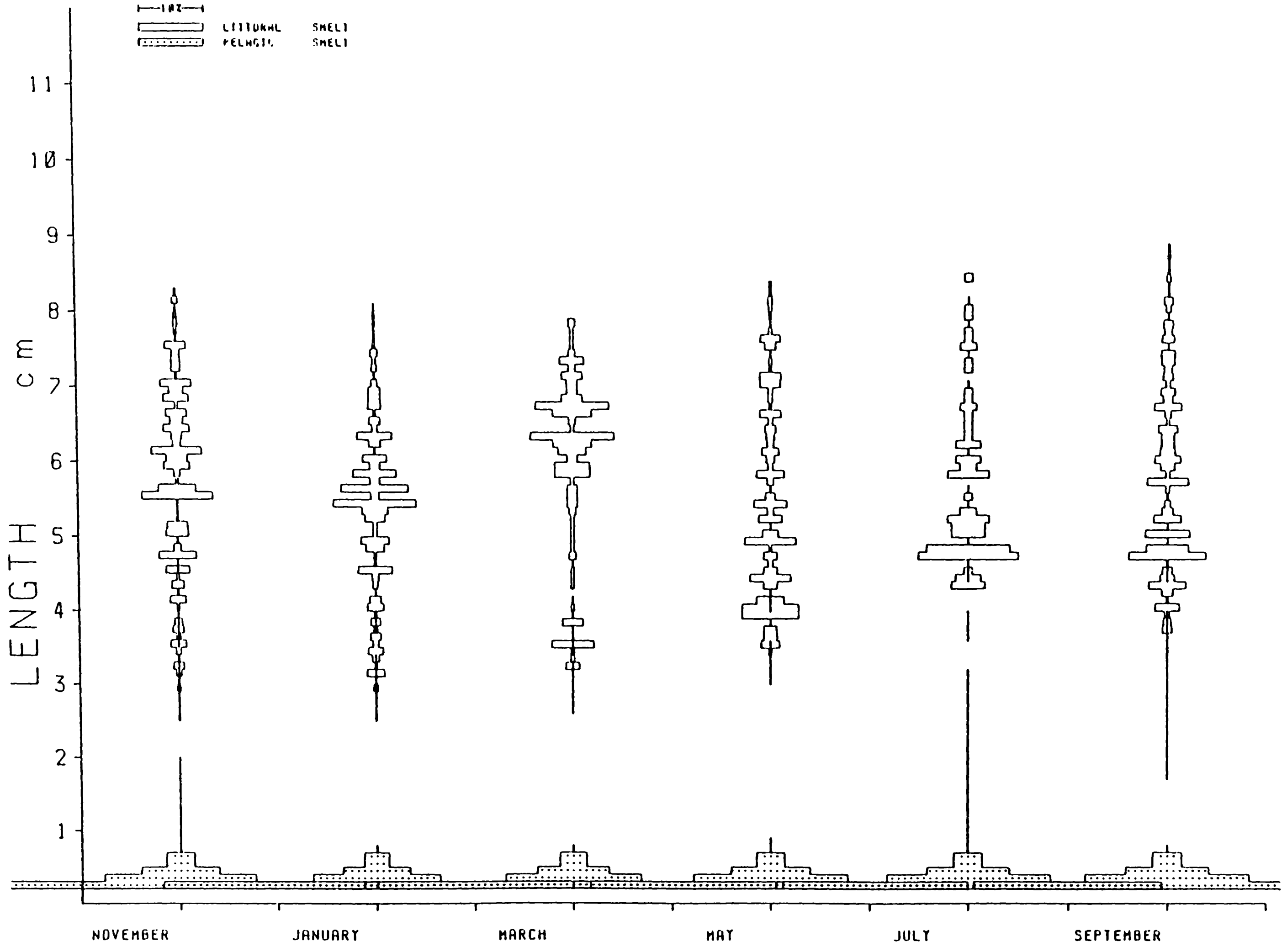


FIG. 110 Simulated smelt length frequency distributions when the ratio of littoral to pelagic habitat area was 1.0.

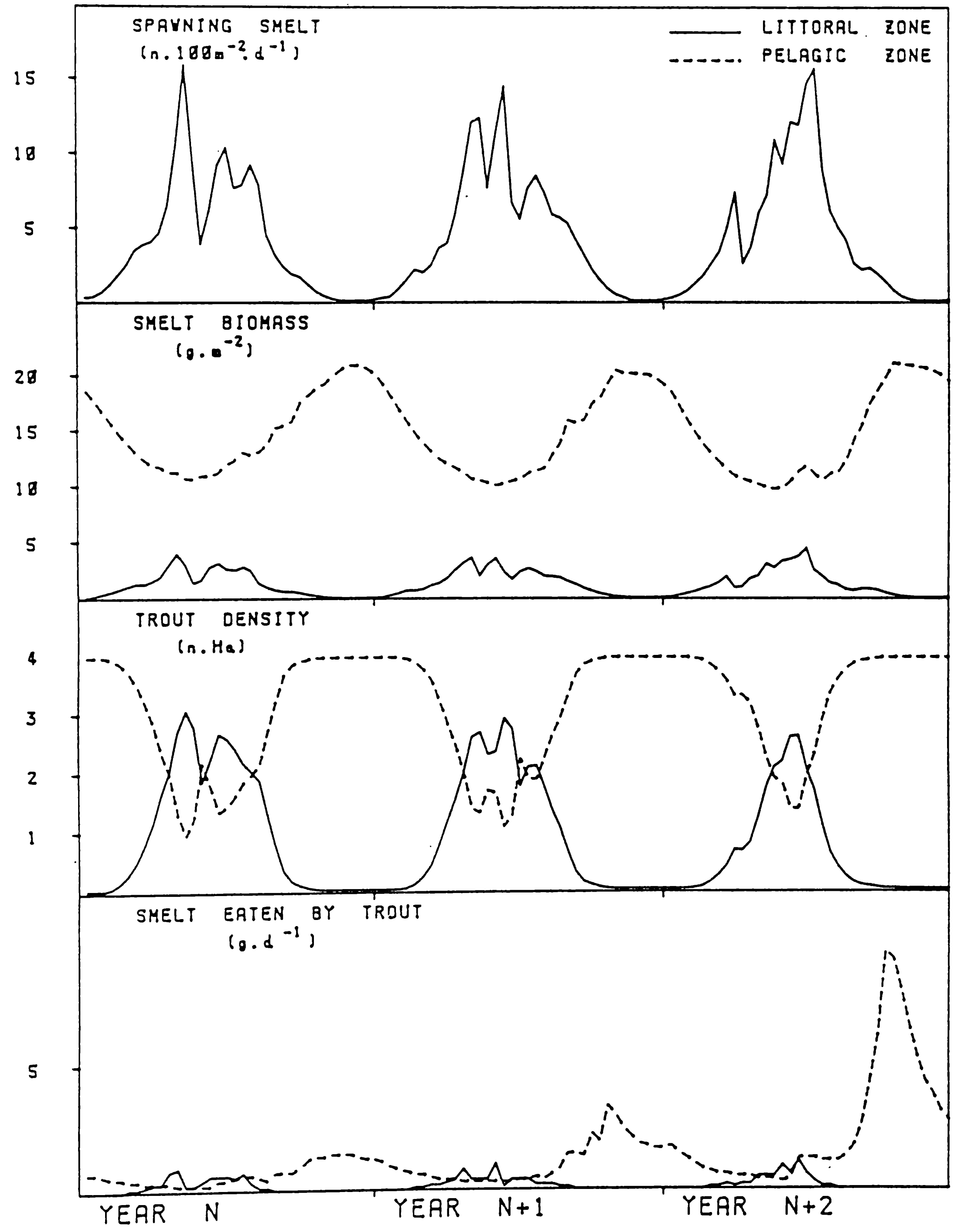


FIG. 111 Simulated population parameters when the ratio of littoral to pelagic habitat area was 1.0. N = 18

(e) Modal length groups and age structure

In each of the simulations described above, the spawning season was continuous, with maximum maturation in late summer. Consequently the formation and development of modal length groups was determined more by factors influencing growth than by cohort recruitment and development. Modal length groups formed when a growth bottleneck occurred and remained static until a change in the food resource, body maintenance requirements or the competitive environment caused an increase in the ration available for growth. However, recruitment was usually sufficient to prevent such changes raising an individual's food intake. Instead, the food resource was shared by more fish and consequently, enhanced food availability increased sustainable biomass but did not change modal lengths. Thus individual fish grew through modal length bottlenecks which were held static by recruitment; individual growth was independent of variation in modal lengths and the number of year classes present was not always related to the number of modal length groups. However, if recruitment were restricted, then the force maintaining the stability of modal length groups would also be limited and one would expect growth of modal lengths to approximate individual growth and the number of modes present to be indicative of the number of year classes present.

A trial in which the spawning season was restricted to only 30 days (i.e. October) was run to examine growth of modal length groups and from these, ascertain the age structure of the simulated population. Length frequency data demonstrated that the mode representing 0^+ larval smelt (fig. 112) grew slowly from ca. 10mm in November to 20mm in September. The 1^+ age group was represented in November by a secondary pelagic modal group at 19-24mm. This year class grew slowly during the summer but many were recruited to the littoral population where they formed a secondary modal length group during March and by the end of May became the dominant age class. Between May and July smelt densities diminished rapidly, partly due to emigration by smaller smelt and partly because of intense trout predation (fig. 113). The reduction in smelt density increased the amount of food available to remaining smelt, which grew rapidly, becoming large enough by late July to avoid feeding trout. Thus these smelt were two years old during October when most reproduced and died. A few survived, reaching ca. 90mm before spawning and death at 3 years of age. This mimics the population structure of Lake Taupo smelt (fig. 13). However, when an arbitrary source of length dependent larval survival (as in Equ. 37),

$$\text{DAILY SURVIVAL} \quad = \quad 1 - 0.3(0.9)^{L}$$

describing high mortality for small larvae but negligible mortality for those larger than 35mm, was included in the system, pelagic growth accelerated and most smelt matured at one year old. A few survived, reaching ca. 80mm before spawning and death at two years of age. This suggests that if only size, and not age, at sexual maturity is under genetic control, then the age structure of a fish population would be largely determined by the growth rate of juveniles. Sources of mortality which restrain competition for food will enhance juvenile growth and permit sexual maturity to occur at an earlier age. Thus trout predation, which does not affect juvenile smelt, is unlikely to influence the age structure of smelt populations (fig. 113 cf. fig. 107).

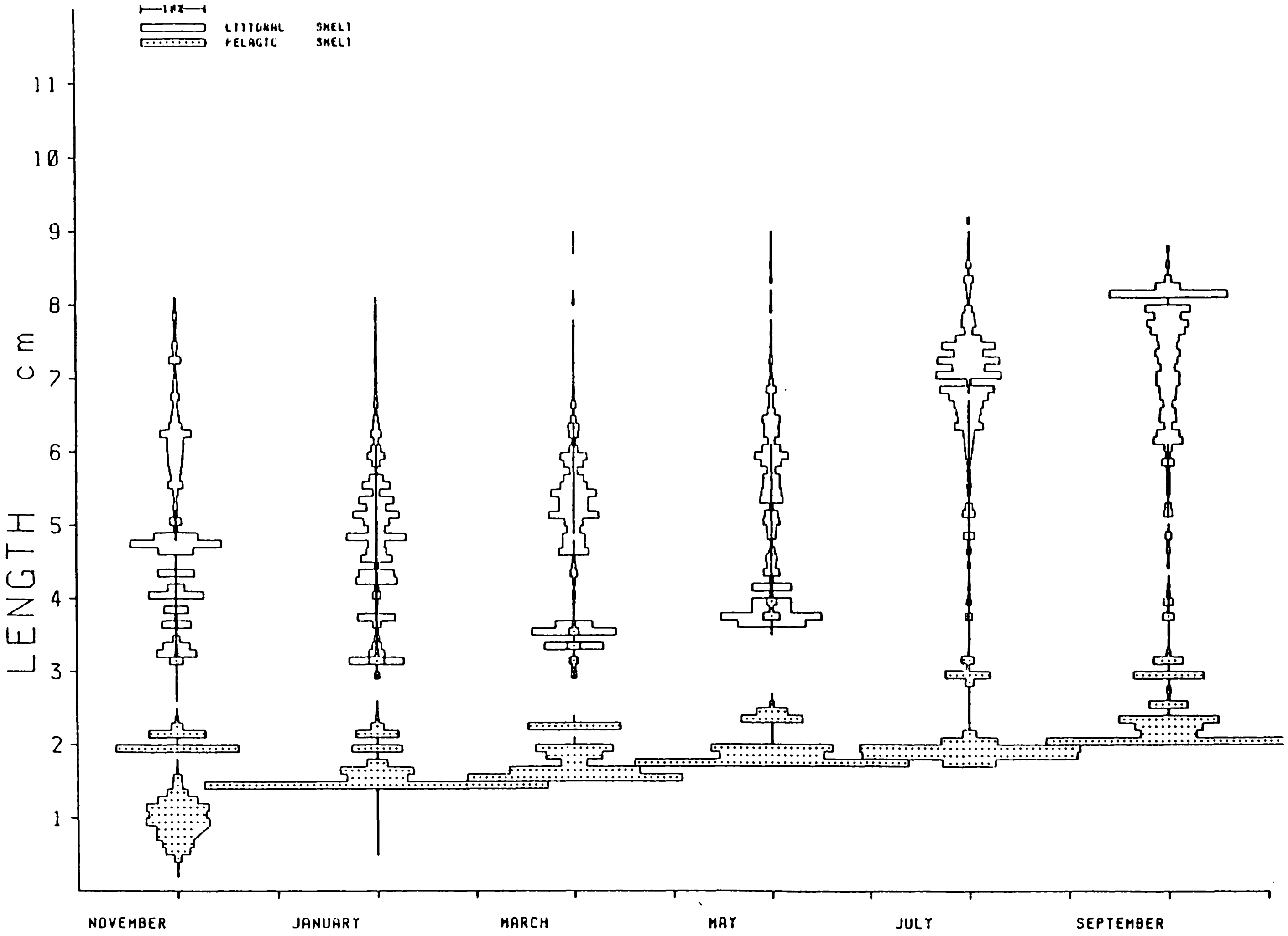


FIG. 112 Simulated smelt length frequency distributions when spawning was confined to the month of October.

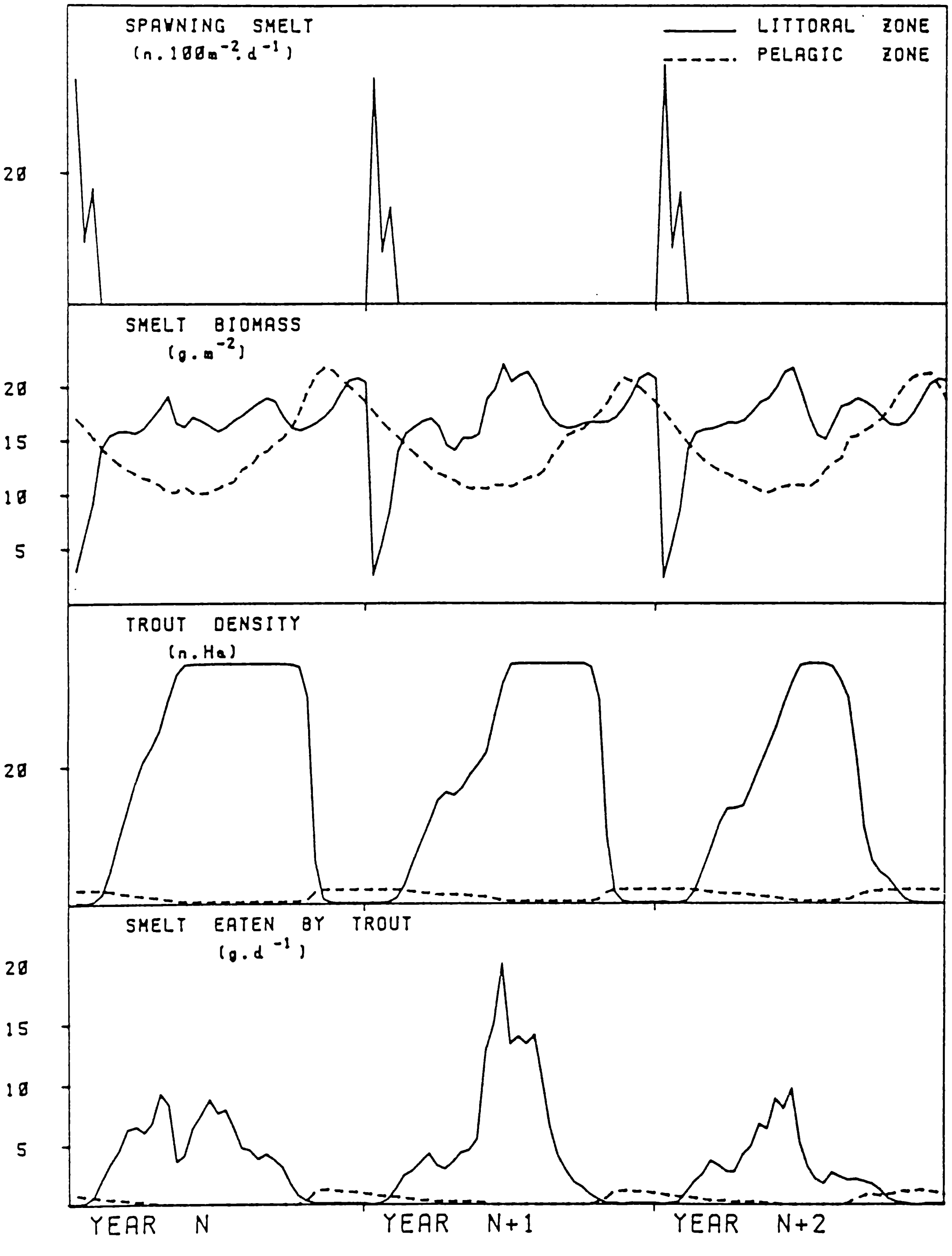


FIG. 113 Simulated population parameters when spawning was confined to the month of October. N = 18

CHAPTER 8 - GENERAL DISCUSSION

1. Smelt biology and interactions with trout

The Lake Taupo smelt population consisted of three year classes. The juvenile (0+) year class occupied only the pelagic zone and fed exclusively on plankton. The adult (1+) year class occupied both littoral and pelagic zones, feeding on a greater variety of invertebrates, including littoral insect larvae and terrestrial (winged) insects floating near the surface. The senior (2+) year class contained relatively few smelt which either failed to mature and spawn at two years of age or survived spawning. These were substantially larger fish and fed predominantly on larval bullies.

Recently hatched larval smelt belonging to the 1979 year class became abundant during summer (January 1980) and grew relatively fast throughout the autumn and winter, reaching nearly 30mm (fork) length by October 1980. Growth was slow throughout the summer and by March 1981 their mean length was only 34mm FL. Growth again accelerated during late autumn and they reached ca. 43mm FL by November 1981 when the majority commenced spawning. Eggs were scattered over sandy areas along beaches in water less than about 3.0m deep and in the lower 200-400m of tributary streams. The major Western Bay streams were used much more extensively than those on the southern and eastern shores of the lake where beach spawning habitat was very much more extensive. Female smelt spawned in pulses separated by a 6-8 week recovery period whereas males apparently maintained sexual activity for an extended period. Thus although peak spawner densities were observed in November, utterly spent and emaciated smelt were not found until January, when they quickly became abundant, particularly in streams where foraging trout were scarce.

The major sources of egg mortality were habitat perturbations caused by extreme weather conditions. Wave action scoured eggs from amongst the heavier sand grains while extended calm spells permitted growth of algal mats and accumulation of fine organic detritus which probably impeded oxygen supply to developing eggs. In streams, eggs were scoured by freshes and extensive algal mats developed during prolonged periods of drought. The proportion of dead eggs in samples was correlated with temperature but not with their density. Dead eggs were infected by a fungus but it remains unclear whether the fungal hyphae were the cause of death or were merely saprophytic.

It seemed that there was no significant predation on larval smelt and it is likely that starvation was the principal source of larval mortality. Trout stomachs contained few smelt less than 30mm FL and none less than 25mm FL although other small items such as larval bullies (12-20mm TL) and *Daphnia carinata* were occasionally eaten. Estimates of the abundances of different sized smelt in trout stomachs were probably biased towards larger, comparatively slowly digested smelt, but it seems unlikely that larval bullies or *Daphnia* could be recognised whilst smelt less than 25mm FL were not. Thus it was concluded that larval smelt were not important in the trout diet.

Trout preyed principally on the adult (1+) year class and for most of the year these usually comprised over 80% by volume of items eaten. Both maximum littoral trout abundances and maximum quantities of smelt found in their stomachs occurred when smelt were concentrated in the littoral zone for breeding. Trout selected the larger smelt available and the intensity of selection was correlated with measures of smelt abundance. Thus the trout predation rate was dependent on both smelt size and density and consequently trout obtained most food when smelt densities were high. Therefore, factors which cause persistently high densities of large smelt in places where they are accessible to feeding trout will increase their utilization as forage, promote good trout growth and raise predatory mortality amongst adult smelt.

Trout are effective surface and midwater feeders, responding primarily to visual cues (Ware 1972). Their vision is directed forward and upward during feeding (Ahlbert 1976) and this probably explains their preference for feeding on smelt both in Lake Taupo and in the other central North Island lakes (Smith 1959; Rowe 1984), despite the presence of abundant benthic bullies and freshwater crayfish (*Paranephrops planifrons*). Their feeding efficiency would be enhanced by factors which increase smelt densities and make them more visible. Thus smelt spawning habitat requirements, their prolonged breeding season, the relatively limited extent and shallow depth of littoral breeding habitat compared to pelagic growing habitat and the clear waters of Lake Taupo are important factors which enhance smelt availability to foraging trout. The shallow depth and limited extent of breeding habitat cause high concentrations of adult smelt to develop, whilst their prolonged reproductive habits and the duration of suitable breeding conditions ensure that these concentrations persist for many months. However, one would not expect either comparable littoral smelt densities or comparable utilization by foraging trout in lakes such as Lake Okataina or Lake Waikaremoana which are deep and similar to Lake Taupo in trophic status but have convoluted shorelines and relatively extensive littoral habitat (Jolly and Brown 1975). Smelt utilization would also diminish if water turbidity were sufficient to limit the trout's reactive distance. The benefits for trout feeding derived from spatially restricted reproductive habitat depend on the absence of territorial smelt breeding habits and of density dependent sources of egg mortality, so that the extent of reproductive habitat does not easily become a factor limiting smelt population size. Trout predation itself could be a sufficiently significant source of mortality to influence choice of spawning habitat. In places where persistently high densities of breeding smelt develop there would be some selective advantage to be gained from spawning in locations which are inaccessible to foraging trout. This could explain why Western Bay streams were intensively used by foraging trout whilst apparently suitable tributary streams elsewhere were not. The scarcity of suitable beach spawning habitat in the Western Bay area compared to that available along southern and eastern shores would have caused generally greater densities of spawning smelt to develop there and so would have increased the risk of trout predation near Western Bay beaches. Consequently there was probably more reproductive advantage in spawning in streams which provided a secure refuge from trout predation. If the only reason for stream spawning was predator avoidance then this would explain why smelt spawned in the lower 200-400m of tributary streams, despite the abundant spawning habitat available further upstream. Feeding trout were always numerous near stream mouths but few entered the streams to feed on smelt. Thus once smelt moved a few metres into streams, the risk of trout predation was greatly reduced and in the absence of density dependent sources of egg mortality, there was no advantage in using all available spawning habitat. If feeding was a significant factor influencing stream utilization then one would expect smelt to be more widely dispersed throughout accessible stream habitat in order to minimize feeding competition and maximize utilization of the resource, as seems to occur in anadromous smelt populations of the Waikato and Wanganui river systems where they penetrate considerable distances upstream (Northcote unpubl. data; Stickland pers. comm.).

Simulations indicated the importance of pelagic prey production and the prey size frequency distribution in controlling littoral smelt abundance. Food productivity and the prey size distribution controlled both levels of smelt abundance and size whilst seasonality in these determined seasonal patterns of smelt size, abundance and reproduction. If pelagic zooplankton were large or their productivity high then greater densities of large juveniles were sustainable allowing more to be recruited to the littoral zone. However, intense competition was associated with high littoral smelt densities and this depressed adult growth. Thus increases in either the size or production of food in the pelagic zone are likely to result in increased littoral smelt abundances but will depress the average size. Simulations indicated that such changes would enhance trout feeding. The benefits of increased littoral smelt density would outweigh disadvantages associated with smaller smelt size.

In the absence of genetic control, seasonality in zooplankton size and productivity would be the key factors controlling seasonal timing and persistence of littoral smelt concentrations; simulations indicated that seasonal timing of maximum littoral smelt biomass and spawner density would precede peak pelagic zooplankton size and productivity. In Lake Taupo, peak phytoplankton productivity occurs in winter (White et al. 1980), whilst maximum zooplankton size and abundance occurs in the spring (fig. 26 and also Forsyth and McCallum 1980) but adult smelt densities were maximal in late November - a little later than simulations would predict. However, this is not surprising when genetic control of reproductive strategy is considered. Egg production is maximal if reproduction precedes a period of increased mortality, such as would occur following a peak in food availability for adults. However larval survival requires an abundance of suitably small prey and in Lake Taupo, these are not available during winter when egg production could potentially be maximal. Therefore spawning at this time would be largely unsuccessful whereas delaying spawning until suitable food for freshly hatched larvae was available, would improve juvenile survival. Thus it seems that optimum seasonal timing of spawning must be a tradeoff between timing for maximum egg production, larval survival and acceptable risks of egg mortality during incubation. Clearly prolonged egg development could bridge the time gap between optimum periods for egg production and larval survival, but the likelihood of gales or floods causing serious mortalities probably restricts the viability of this option. It seems that the favoured strategy of Lake Taupo smelt was to delay spawning until availability of small zooplankton was imminent and littoral food started to become abundant, to retain some somatic reserves and to feed on the larger food items available there whilst a second batch of eggs matured to be spawned later in the season. Those smelt which spawned early in the season also laid the biggest eggs. Presumably, these hatched larger larvae and, being large, were better equipped to feed on the zooplankton size range available in spring, when small zooplankton were scarce. As summer progressed, the size of eggs laid diminished, presumably because minute prey are normally plentiful in autumn and no significant feeding advantage was conferred by hatching large larvae. The spawning season was also prolonged by individual variation in seasonal timing of spawning. Presumably some survival advantage is conferred by breeding outside the peak spawning period if competition for food is a significant source of larval mortality, or if seasonal timing of food availability is variable. Simulations suggested that feeding competition amongst larvae is likely to be an important influence under a variety of diverse conditions and therefore one would expect some spawning to occur whenever there was a reasonable likelihood of larval survival, and this probably included eight months of the year - as indicated by the presence of smelt eggs in spawning areas and larval smelt in nocturnal ringnet tow samples from October until May.

In summary, the key features of Lake Taupo and its smelt population which enable the system to sustain an exceptional rainbow trout fishery are the large ratio of feeding to reproductive habitat for smelt, the absence of density dependent sources of smelt egg mortality, the long duration of suitable conditions for spawning, larval development and significant post-spawning survival. These factors interact to promote a prolonged spawning season throughout which the larger members of the smelt population are concentrated in the littoral zone where they are accessible to trout and the trout are available to anglers.

2. Simulation model performance, limitations and deficiencies

The principal objective of the simulation study was to predict smelt population processes and smelt utilization by foraging trout in relation to influential habitat features. It was argued that each of the population processes (growth, reproduction, mortality and migration) were both size and density dependent and must therefore be treated as being interdependent and inseparable. Consequently the population length frequency structure is of major importance because it largely controls the rate of each population process and is itself modified by the operation of each process. The population length frequency structure was therefore used as the central unit of the simulation model. Thus the most rigorous test of the model's ability to predict smelt population processes must be through comparison of real smelt length frequency distributions and those predicted by the model for a particular lake. One would need to compare time series length frequencies of smelt in each habitat zone, of ripe smelt and of smelt eaten by trout. If real and simulated distributions were similar then predictions for less sensitive parameters such as areal biomass, spawner densities and quantities eaten by trout could also be expected to be accurate, although the converse would not necessarily be true.

Seasonal patterns in smelt abundance and length frequency structure for a series of diverse lakes await presentation (Mylechreest unpubl. data) and detailed information on seasonal patterns of invertebrate size, distribution and abundance has yet to be collected. It is therefore not yet possible to determine how closely habitat related variation in smelt population parameters corresponds to that which would be predicted by the simulation. Nevertheless some broad comparisons with the Lake Taupo system and with rainbow trout feeding patterns in other central North Island lakes

(Rowe 1984) corroborate the more general aspects of model predictions.

In Lake Taupo, three smelt year classes were generally present. One occupied only the pelagic zone; the others were found in the littoral zone (fig. 13) but probably occupied both habitats. Littoral smelt were largest in early spring at the start of the spawning season when phytoplankton productivity was maximal (White et al. 1980) and zooplankton were generally large. In late summer, towards the end of the spawning season, when pelagic phytoplankton productivity was minimal and zooplankton were generally small, littoral smelt were also mostly small. Littoral trout densities and quantities of smelt eaten by foraging trout were associated with high smelt densities in the littoral zone and in winter, when smelt were confined to pelagic waters, trout stomachs contained generally little food and few smelt. All these features of the Lake Taupo trout-smelt system were reproduced in simulation trials.

Rowe (1984) in his review of food and feeding patterns of lake-dwelling rainbow trout in the Rotorua lakes showed that the percentage occurrence of smelt in trout stomachs was higher in deep, clear, oligotrophic lakes than in smaller, shallow, turbid, eutrophic lakes except in Lake Rotorua. He attributed this trend largely to differences in water clarity which reduced predation efficiency but did not account for anomalous trout feeding in Lake Rotorua. Simulations indicated that trout predation on smelt would diminish with increasing depth, turbidity, and ratio of littoral to pelagic habitat area. Thus the trend described is as simulations would predict. Lake Rotorua, whilst shallow and eutrophic,is large and has an extensive pelagic zone. Simulations would predict greater utilization of smelt forage in this lake than in other similarly turbid eutrophic lakes with relatively more extensive littoral habitats because smelt would be more concentrated in the littoral zone of Lake Rotorua. Interestingly, smelt comprised a greater proportion of the Lake Taupo trout diet than was observed in any of the Rotorua lakes. This also is predictable because the ratio of littoral to pelagic habitat area is considerably smaller for Lake Taupo than for any of the Rotorua lakes. Thus whilst turbidity may be a significant factor influencing utilization of smelt by trout, factors which cause persistent concentrations of large smelt to develop are also important.

Although the model adequately described the major characteristics of the Lake Taupo smelt population, trout movements and feeding on smelt as well as reported variation in smelt utilization in different lakes, the detail of certain simulated parameters were less satisfactory. In most of the simulation trials, the modal length groups representing pelagic larval smelt were more persistent and generally covered a lesser range of lengths than was observed in the Lake Taupo population. This probably occurred in part due to a deficiency in the design of the model and in part because there may be a relationship between smelt size and their starvation mortality rate. Simulated frequencies were associated with integer length intervals whilst growth was added as weight. Smelt grew to join a new length interval only if the new weight was equivalent to that of the next length interval. Thus small smelt required a disproportionately large food intake to grow in comparison with that required by large smelt and consequently, for small smelt, the balance between food intake and maintenance requirements was often such that they neither grew nor starved. The consequences of this were exacerbated by the assumption that starvation mortality was independent of smelt size. Smelt dissections indicated that fat reserves were never present in larval smelt less than 25mm in length but were usually present in adult smelt. One would therefore expect greater mortality in response to starvation amongst larval smelt than amongst adult smelt. However, until experimental work is undertaken to determine the relationship between smelt size and the starvation mortality rate, appropriate size dependent starvation mortality cannot be incorporated into the model.

Modal lengths of adult smelt in the littoral zone were somewhat larger than were observed in the Lake Taupo population, even when the modal size of littoral food was set at 1.0mm. This may be because food items which are actually available to littoral smelt are only those present in midwater or on the surface. The abundant and generally larger bodied epibenthic invertebrates, on which the modal prey size (4.0mm) was based, may not be a part of the food resource generally available to littoral smelt. If this is the case then the modal prey size was unrealistically large and would account for the difference between simulated and actual modal lengths of littoral smelt. Clearly, a detailed comparison of the size range of species eaten by smelt and those species present is required to determine the nature of the food resource actually utilized by smelt.

The trout predation model treated smelt as being evenly distributed throughout the water column. This does not occur in reality, as echograms collected during October suggested (figs. 15 & 16). Consequently, a trout foraging in the pelagic zone is likely to encounter greater smelt densities and feed more effectively there than the model would predict. Thus the model underestimated both the quantity of smelt eaten and trout density in pelagic waters. However this deficiency is not easily remedied. Neither smelt nor trout distribution in the water column has been described and the operation of key factors which determine their depth distribution remain unknown. Thermal and chemical stratification as well as the vertical distribution of zooplankton are likely to be important control factors but prediction of these and resulting smelt and trout distribution is not yet possible. Perhaps the most feasible approach would be to use descriptive dat~~e~~ from echograms to define seasonal patterns in the distribution of smelt in the water column for the particular lake under consideration.

The basic smelt unit modelled was a size class interval, not an individual smelt. This was a convenient approach for considering the interaction of length and density dependent processes, but could not consider genetic changes in population characteristics, such as egg size, diet breadth and expected seasonal timing, size and age at maturity. These clearly differ both within and between populations (Woods 1967, McDowall 1979, Northcote and Ward 1984) and variation in habitat features presumably promotes these differences. However, to allow for genetic changes, the basic modelling unit would have to be an individual smelt as natural selection operates on the individual. Each fish would have associated dynamic features such as length, weight, age and other fixed genetic features which would be passed on with some variability, to the fishes' progeny. The magnitude of each inherited feature to be associated with each offspring could be drawn from a normal distribution of values with arbitrary variance but with the mean value corresponding to that of the parent. This approach would enable changes in population genetics to be accounted for and models describing life history patterns (e.g. movements and maturation) could be based on patterns which prove successful in the system under consideration, rather than being based on predetermined models fitted to observational data. Furthermore, if the basic unit of simulation were an individual fish, then feeding models based on the components of feeding mechanics and behaviour (search, choice, pursuit, attack and retention) could be used. Perhaps an choice, pursuit, attack and retention) could be used. Perhaps an adaptation of the tactical feeding model described by Wright and O'Brien (1984), could be incorporated to provide additional realism and generality. However their model would require considerable modification to accommodate competition amongst different sized fishes. Difficulties associated with this approach are not insurmountable, but the programme required to simulate a system based on individual characteristics is substantially more complex and would consume inordinate computer time.

3. Implications for management

The major objectives of fisheries management for Lake Taupo are to maintain trout size, abundance and availability to anglers. Both field work and theoretical simulations indicated the importance of smelt abundance, size and distribution in making them a useable forage resource and in determining the location of feeding trout. The value of smelt as a forage base depends on factors which promote high densities of adult smelt in places where trout can feed on them. In Lake Taupo, pelagic zooplankton production and the limited extent of smelt spawning habitat are the most important factors causing localized concentrations of smelt to develop. The trout gather to feed in such places (i.e. off beaches and near stream mouths) and anglers fishing the lake direct much of their effort to these localities. Wind induced currents can cause pelagic smelt concentrations to develop near reefs and promontories and during winter these places become the most productive areas for angling. Clearly these major morphometric features of Lake Taupo and the biological characteristics of smelt are not suitable for manipulation in pursuit of management objectives. However small scale maintenance of suitable spawning habitat conditions in specific localities is required to maintain productive angling in these places between November and April. Local environmental changes which will cause deposition of silt and organic detritus or will increase current velocities sufficiently to scour smelt eggs or will promote growth of algal mats can be expected to diminish the value of the locality for smelt spawning, trout feeding and angling.

There appears to be only one locality where enhancement of smelt spawning habitat could easily be undertaken and would be likely to improve angling there. The Waitahanui river, a stable spring-fed stream on the north-eastern shore, has a stone embankment at the mouth which was installed to stabilize the position of the river mouth and to reduce erosion of the surrounding lakeshore reserve. This substantially shortened the channel length between the main road bridge and the lake, increased the river's gradient there and resulted in water velocities which are excessive for smelt egg deposition. Smelt have been abundant here in the past as Jolly (1967) obtained large samples during 1958 and Burstall (pers. comm) observed abundant smelt at Waitahanui early in the 1950's. However at present they are absent from the lower river. Removal of the stone embankment, allowing the river to extend its channel by several hundred metres, thereby reducing flow velocity in the lower reaches, would enhance this area for smelt spawning, trout feeding and angling. However intense utilization by spawning smelt, comparable to that which occurs in Western Bay streams, is unlikely to develop as beach spawning habitat is extensive in the vicinity of Waitahanui.

Concern has been expressed that lake level fluctuations, associated with use of Lake Taupo as a reservoir for hydro-electric power generation, could be a detrimental influence on smelt spawning habitat and egg survival. The association between lake levels and smelt breeding conditions has been reinforced because anglers associate years in which lake levels are high in spring with exceptional smelt densities and good fishing. However, the lake level rarely changes by more than 10cm in a week and, although there is no statutory restriction on the extent of the drawdown zone, annual lake level variation is generally less than 1.5m. Sampling indicated that few eggs were present in water less than 50cm deep and Jolly (1967) demonstrated that egg development time is brief, being about ten days. There is therefore no possibility that significant numbers of smelt eggs could be stranded by present lake level management practice. The association between high densities and a raised lake level is probably one of common causation. High lake levels occur following a period of high rainfall and if runoff is a major source of the lake's nutrients, one would expect periods of raised limnetic productivity to be associated with periods of high runoff. Simulations indicated that small changes in pelagic food production would result in considerable differences in littoral smelt densities and it seems likely that this is the cause of annual variations in smelt abundances in Lake Taupo. Thus periods of high rainfall raise the lake level and would cause high littoral smelt densities; high lake levels as such do not indicate exceptional breeding conditions for smelt.

Lake Taupo is expected to experience a slight increase in productivity following forestry and agricultural developments in the catchment (White et al. 1983), and this will cause changes in certain smelt population parameters. Simulations indicated that considerable changes in littoral food production had little influence on smelt population processes, but small changes in pelagic food production were influential. Therefore the nature of changes in smelt population processes are likely to depend on how the zooplankton respond to raised primary production. If larger zooplankton become more abundant in summer, more 1+ smelt will be sustainable and this will lead to increased densities of adult smelt when they move into shoreline areas during the following spring. Their average size may decrease if peak zooplankton abundance in winter is unaffected, but if this also increases, the smelt size and growth rates will not change, although sustainable biomass will increase. Trout feeding will benefit and their growth will improve.

If summer zooplankton are unaffected, or if only small zooplankters such as rotifers become more abundant whilst the abundance of larger-bodied winter zooplankton increases, then the summer "bottleneck" will remain, causing more starvation mortality amongst 1+ smelt. However after this period, winter growth will be more rapid and adult smelt will reach a greater size. Adult densities in the littoral may be reduced but their biomass will increase and trout feeding will benefit, unless the smelt are able to grow large enough to consistently avoid capture by foraging trout. A "slight" increase in productivity is most unlikely to have such dramatic consequences.

The size of the Lake Taupo rainbow trout population would probably not respond to increases in smelt abundance because availability of juvenile rearing habitat is finite and such habitat may be fully utilized. Whilst there is no published evidence to support (or oppose) this view, the size of adult trout runs returning to tributary streams to spawn suggest that many more return and spawn than are required to saturate rearing habitat. Every winter, 1000-2000 adult trout pass upstream through the fish trap located on the Waihukahuka stream (a tributary of the Tongariro; discharge ca. $0.1m^3.s^{-1}$) above which there is about 400m of stream available for spawning and juvenile rearing. The winter run through the trap on the Tokaanu stream (discharge ca. $1.9m^3.s^{-1}$), which flows directly into Lake Taupo, is 2000-3000 trout and there is only about 600m of stream channel available for spawning and rearing above the trap (Dept. Internal Affairs, unpubl. data). The extent of redd superimposition in these and other streams, the year round presence of breeding trout, and the number of fry produced, suggest maximum utilization of breeding habitat. Fingerlings are abundant in streams for most of the year (Dept. Internal Affairs, unpubl. data) but trout less than 30cm long are rarely caught by anglers fishing in the lake and fingerlings were never taken in beach seine hauls at Waihaha. Thus it seems likely that juvenile trout remain in streams until they are large enough to feed on smelt in the lake. Presumably they grow rapidly once in the lake and consequently trout less than 30cm are rare in the anglers' catch.

Thus circumstantial evidence suggests that the size of the Lake Taupo rainbow trout population is probably limited by the extent of juvenile rearing habitat. Extensive stream protection measures are in force and at present there seems to be only limited opportunities for enhancement of rearing habitat in the lake tributaries. Thus there is probably little potential for significant increases in the trout population. However, deterioration of stream habitat quality or intense angling pressure could reduce the population size. The widely held belief that reductions in trout population size will cause changes in trout growth rates (Burstall 1983) was not supported by simulation studies which indicated that the quantity of smelt eaten by trout was almost independent of trout stocking density. The weight of smelt eaten by trout was most sensitive to factors controlling the density of smelt 30-55mm long, and extreme trout stocking rates had little impact on this, even when the spawning season was restricted to only 30 days. This occurred because predatory mortality allowed smelt, which would have otherwise died of starvation, to develop and grow. Thus variation in trout growth rates will be associated with changes in smelt density but not with changes in trout density. Therefore, in Lake Taupo, environmental management should continue to be directed at maintenance and enhancement of stream habitat suitable for use by juvenile trout. An increase in the size of the trout population can be expected to raise anglers' catch per unit effort but will not depress the size of their fish.

The suggestion that trout growth is almost independent of their population density has profound implications for stocking practices in other central North Island lakes. These lakes are stocked with hatchery reared yearlings obtained from annual strippings of Lake Taupo trout running into the Tokaanu stream. The lakes (except Lake Taupo) are stocked annually with varying numbers of juveniles: the numbers depending on lake area and growth performance of trout in each. Hatchery reared trout typically comprise 30-90% of the anglers catch and stocking rates range from 1-4 trout per hectare in the large lakes and up to 20 trout per hectare in small lakes (Dept. Internal Affairs, unpubl. data). Simulations indicated that increases in stocking density of 1-2 orders of magnitude will have little effect on either smelt population processes or on trout growth. Year to year variation in the growth of trout stocked at 1.0 per hectare will be greater than variation associated with an increase of up to 100 trout per hectare, even if the smelt spawning season is brief. If this prediction is correct then substantially increased stocking rates could be used to improve angling success in many of these lakes without any significant reduction in trout growth. Thus management for high catch rates and management for trophy fish are not mutually exclusive objectives. However, where smelt is the principal forage species, then both management objectives are achievable only in lakes whose morphometry and/or productivity consistently support high smelt densities.

Comparison with stocking densities applied to rainbow trout fisheries in Western Alberta lakes (Donald and Anderson 1982) indicates that trout stocked at 100-500 fish per hectare can grow to a comparable size to that attained by trout in central North Island lakes. The comparison must be treated with caution because there are major differences both between the forage species present in these and central North Island lakes and between the climates of the two regions. Nevertheless the comparison clearly demonstrates that stocking densities of up to two orders of magnitude greater than are used in the larger lakes of the Rotorua district can sustain trout of a size which would be acceptable to anglers fishing these lakes. Thus, if optimisation of trout stocking rates for size and catch rate in these lakes is to become a management objective then two areas for further investigation are to be recommended. Firstly the relationship between trout stocking rates and trout growth in lakes whose trout populations largely consist of hatchery reared trout should be determined and secondly, consideration should be given to testing and further development of the simulation described above. Such tools can significantly enhance predictive assessment of fisheries management options for different lakes.

APPENDIX 1

ESTIMATION OF AVOIDANCE BY SMALL PELAGIC FISHES FROM A QUANTITATIVE SAMPLING DEVICE

(a) Introduction

Small fishes are amongst the most difficult members of the pelagic community to sample quantitatively because their wariness, flight speed and size range may readily enable them to avoid capture in many sampling nets. The larger fish present may evade the sampler and the smallest may be lost through the mesh. Consequently catch data will underestimate fish densities and give biased estimates of population size frequency structure. In the absence of totally efficient sampling devices, it is therefore desirable to estimate escapement for all sizes of each species caught so that appropriate corrections may be made to catch data.

Fleminger and Clutter (1965) calculated the "apparent minimal peripheral escape zone" for six copepod species using the ratio of numbers caught in two different sized nets. They assumed that the effective sampling area of the smaller net was proportional to the ratio of catches taken in two nets:

$$\pi r_e^2 = \pi r_1^2 \frac{C_s}{C_1} \qquad (1)$$

where r is the effective radius, C_s and C_1 are numbers caught in smaller and larger nets respectively and r_1 is the radius of the larger net. The width of the apparent minimal peripheral escape zone was defined by:

$$r_s - r_e$$

where r_s is the radius of the smaller net. The peripheral escape zone was estimated from the relation :

$$r_s - r_1 (C_s/C_1)^{0.5} \qquad (3)$$

Unfortunately, this method requires the untenable assumption that the larger net fished with complete efficiency. Similarly, a method involving comparison of night and day larval anchovy catches to estimate probability of capture (Zweifel and Smith, reported by Webb and Corolla 1981) assumed complete catchability at night and no diurnal variation in abundance.

Gilfillan (reported by Clutter and Anraku, 1968) considered the peripheral escape zone to be a linear function of towing speed:

$$E = k/S; \quad k = x_o u_e \qquad (4)$$

where S is the net's speed, x_o is the organism's mean reaction distance, and u_e is the organism's mean escape speed. Both x_o and u_e were assumed to be independent of net size and speed so that k could be considered constant and the ratio of numbers of animals caught by each net would be proportional to their catching efficiencies.

That is,

$$\frac{C_1}{C_2} = \left[\frac{r - k/S_1}{r - k/S_2} \right]^2 \qquad (5)$$

or alternatively,

$$\frac{C_1}{C_2} = \left[\frac{r_1 - k/S}{r_2 - k/S} \right]^2 \qquad (6)$$

where C_1 and C_2 are numbers of animals caught at speeds S_1 and S_2 or in nets of radii r_1 and r_2. The value of k can be found by rearrangement of (5) or (6) thus:

$$k = \frac{r \left[\sqrt{\frac{C_1}{C_2}} - 1 \right]}{\frac{1}{S_2} \sqrt{\frac{C_1}{C_2}} - \frac{1}{S_1}} \qquad (7)$$

or

$$k = \frac{S \left[r_1 \sqrt{C_2} - r_2 \sqrt{C_1} \right]}{C_2 - C_1} \qquad (8)$$

This approach assumes that the filtration efficiencies of both nets are complete; that k is independent of both net speed and net size; that there is no deviation from the shortest effective escape direction; that towing lines or bridles do not influence avoidance behaviour of target species.

Tranter (1967) estimated the filtration efficiencies (f) of a variety of net designs and found that f for nets lacking conical mouth openings was between 0.8 and 0.9. However it can be shown (i.e. by substitution in equations 7 and 8) that estimates of k are not particularly sensitive to reductions in filtration efficiency to ca. 0.8.

Gilfillan's field trials indicated that k was nearly constant regardless of towing speed or net size. Barkley (1972) however argued that factors such as noise levels, mesh losses, hydrodynamic behaviour etc would depend on net size and towing speed and so could be expected to influence an animal's response to an approaching net and therefore influence k. It has generally been assumed that organisms choose the optimum escape direction so that the peripheral escape zone (E) can be defined by k/S (Barkley 1964, 1972). However the effects of deviation between chosen and optimum escape routes on estimates of the peripheral escape zone (E) await examination.

Fleminger, Clutter and Smith (reported by Clutter and Anraku 1968) presented evidence for avoidance caused by the towing line in front of the net, suggesting that the effective fishing area for nets with towing lines or bridles in front of the net mouth might be a band lying between the peripheral escape zone and a void around the centre of the net. Clearly then, estimates of a net's catching efficiency based on estimates of E or k can apply only to nets lacking net mouth obstructions.

Clutter and Anraku (1968) point out that frequency of response, direction and rate of movement have probability distributions rather than fixed values so that some variance about E must be expected. Since k is dependent on reaction distance and flight speed, which are characteristics likely to differ between species and between different sized individuals of the same species, k must be estimated for each component of the catch (Barkley 1972). However as some catch components are represented by only a few individuals, the difficulties caused by the generally patchy distribution of pelagic animals will be exacerbated. Thus the difference between C_1 and C_2 which is used to estimate k will in part be caused by the patchy distribution of the animals rather than by differences in their ability to avoid the net. If the vagaries of patchiness exaggerate the catch of animals in the larger or faster net then k will be overestimated. However if the catch in the smaller or slower net is such that more are caught than would be expected from differences in net size or towing speed, the solution for k becomes imaginary (i.e. the square root of a negative number). If different sized nets are used, this occurs when

$$C_s > C_l r_s / r_l$$

and for different net speeds when

$$C_s > C_f$$

C_s and C_f being catch components taken in slower and faster nets respectively. These problems are more likely to arise when differences in net size or speed are small but as these differences increase, the tenuous assumption that k is not influenced by net size or speed becomes more important.

This dilemma can be circumvented and possible dependance of E on net size examined by fitting a model describing catch ratios in terms of net radius, filtration efficiency (f) and the peripheral escape zone:

$$\frac{C_{in}}{C_{im}} = \left[\frac{\sqrt{f}r_n - E_{in}}{\sqrt{f}r_m - E_{im}}\right]^2 \qquad (9)$$

where C_{in} and C_{im} are numbers of catch component i taken in nets of radius r_n and r_m. E_{in} and E_{im} are apparent peripheral escape zone widths of catch component i for nets n and m respectively. It seems reasonable to think of E as a multiplicative function of flight speed, reaction distance and net velocity as indicated by Equation 4, but, since flight speed and reaction distance are generally dependent on the animal's size, it follows that the interaction could equally well be described by a function of the animal's length. Reaction distance may also be influenced by net design features such as its size, colour, speed etc and by environmental conditions such as water clarity and light intensity which affect the fishes' ability to see the approaching net. Reaction distance may also be influenced by the behaviour of other organisms in the vicinity. It therefore seems that a model describing E for a particular species caught in a specific net design should be a function of the animal's size, and of net radius, speed and perhaps certain environmental parameters. E should be a multiplicative function of these variables, tending towards zero if net speed were infinite or the animal's size (escape ability) were minute.

Thus the width of the peripheral escape zone (E) for a particular net design and under constant environmental conditions might be described by:

$$E_{in} = aL_i^b r_n^c S_n^d \qquad (10)$$

where L_i is a measure of size defining catch component i and a, b, c, and d are fitted coefficients. Once E_{in} is known then the catching efficiency of net n for catch component i can be determined and estimates of the population length frequency distribution, density and biomass corrected for net avoidance.

This study tests the utility of this model, explores possible mechanisms of avoidance and examines the effects of deviation between chosen and optimum escape routes on estimates of the peripheral escape zone.

(b) Methods

Three dropnets of 40cm, 58cm and 78cm mouth diameter were constructed (fig. 1) so that their proportions were identical. They were designed to fish from the surface to any depth required, closing and containing the catch when the attached line was held fast. Each dropnet was made with 1.2mm Monyl nylon mesh. This mesh retains Lake Taupo (New Zealand) smelt (*Retropinna retropinna*) larger than about 15mm in length. Lead weights were attached to the outside of the steel ring to give average speeds of 0.91 $m.s.^{-1}$ (range ± 0.02 $m.s.^{-1}$). The nets were fished in rotation from a drifting boat between the surface and 100m depth (bottom ca. 105m) and retrieved by winch until sixteen replicate samples for each net were collected. All samples were taken from the vicinity of the Karangahape cliffs, Lake Taupo on 11 October 1982. Each catch was washed from the net and stored separately in 1% formaldehyde solution. In addition, a 1.2 x 8m beach seine net of 2.0mm mesh size was used to collect a littoral smelt sample. Total body length (TL) and length to the caudal fork (FL) were subsequently measured under a dissection microscope and data were grouped into 1.0mm length intervals for further analysis.

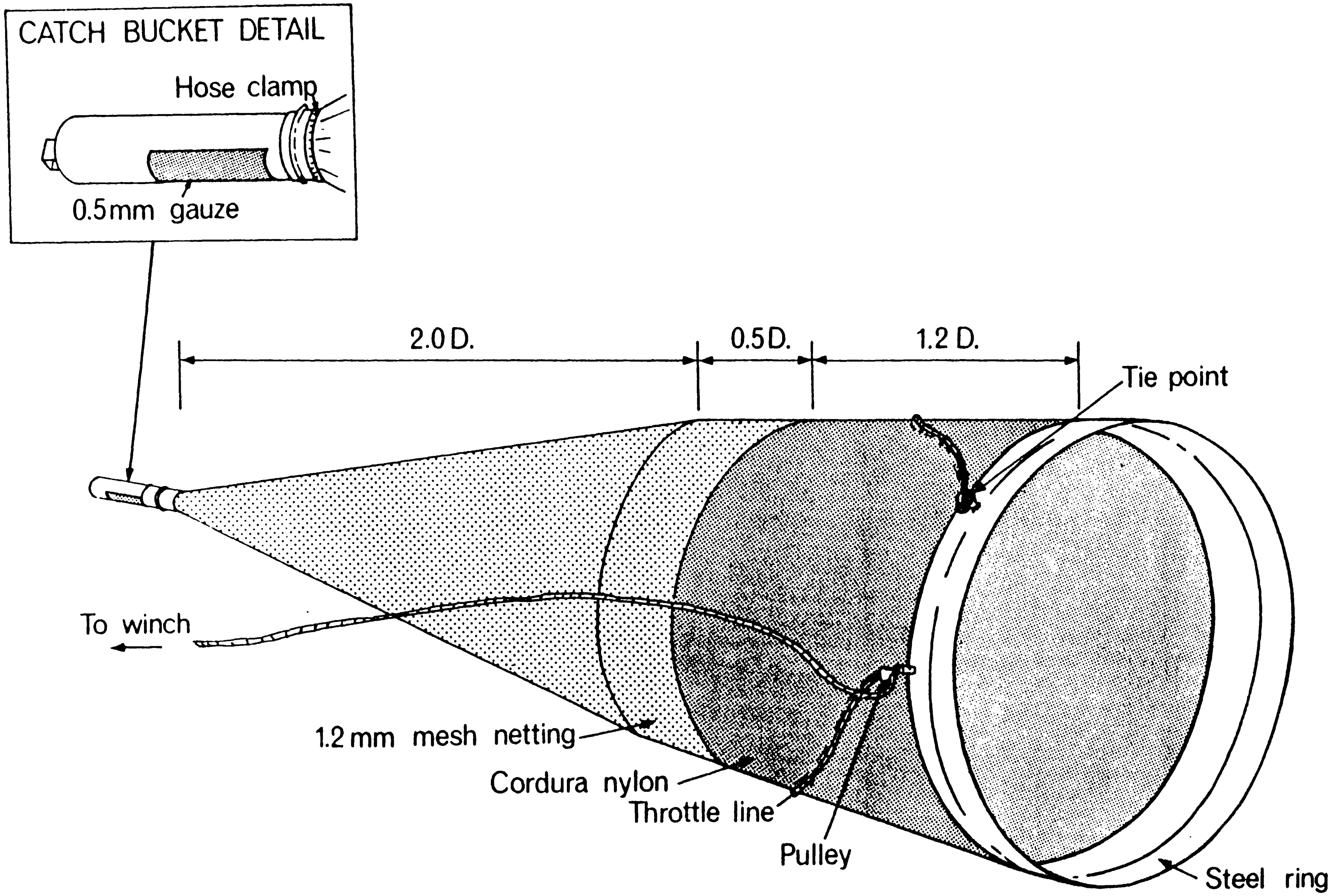
(c) Results

Smelt densities, as estimated from each replicate sample were 30 - $60m^{-2}$ except when shoals were encountered, when densities were as great as $250m^{-2}$ (fig. 2). Modal density estimates and the mean and maximum size caught, increased with the size of the dropnet used (fig. 3) suggesting that sampling efficiency improved with net size.

FIG. 1

Dropnet design.

Each net consisted of a truncated cone and cylinder of Monyl nylon gauze attached to a cylinder of Cordura nylon and the dimensions of each component were proportional to the diameter (D) of the mouth of each net. The throttle line was fastened to the steel ring, then threaded around the nylon cylinder in an elliptical fashion through 'D' ringlets spaced at 10cm intervals before passing through a swivel pulley mounted on the steel ring.


CATCH BUCKET DETAIL
Hose clamp
0.5mm gauze
2.0 D.
0.5 D.
1.2 D.
Tie point
To winch
1.2 mm mesh netting
Cordura nylon
Throttle line
Pulley
Steel ring

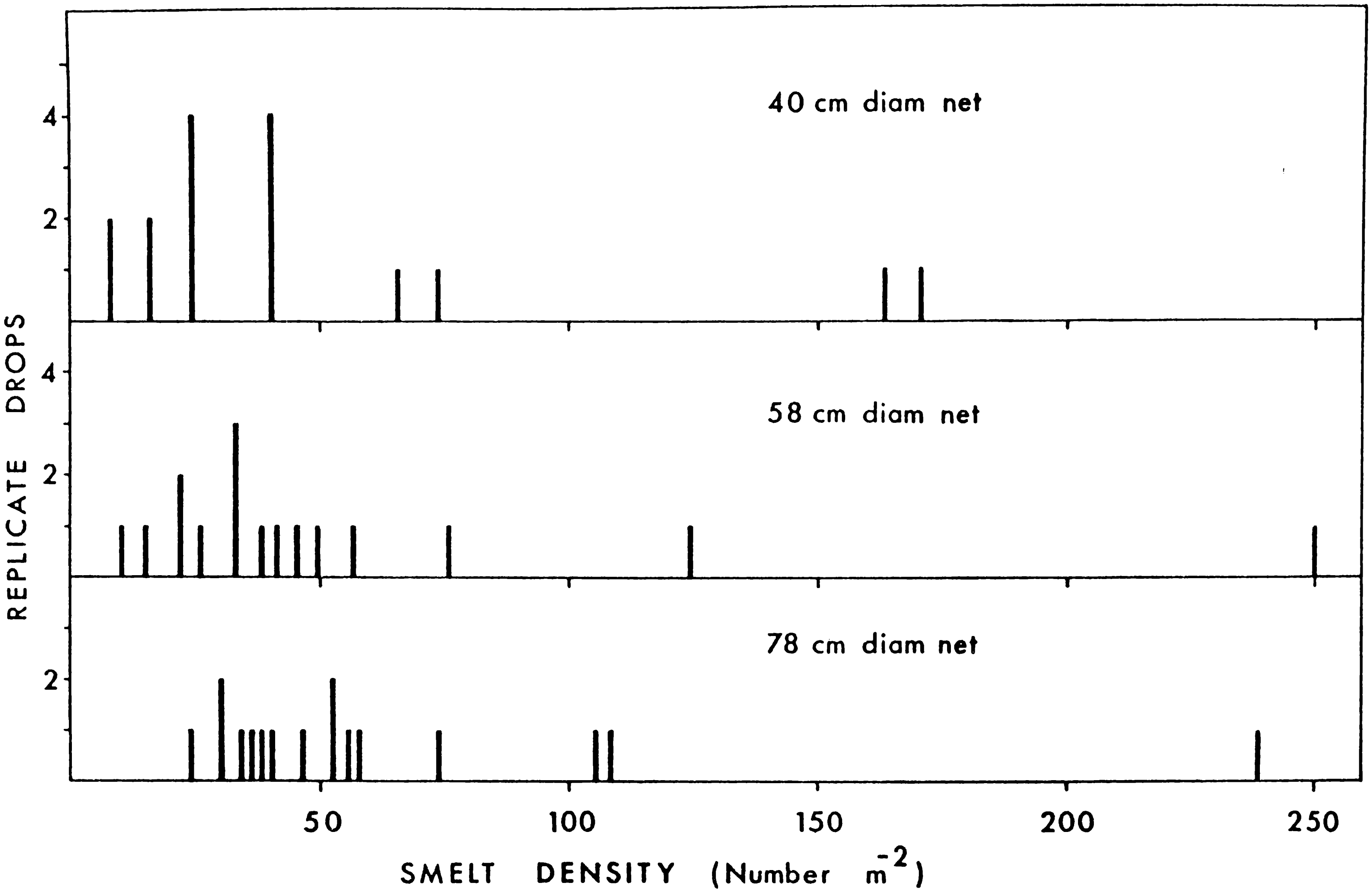


FIG. 2 Smelt density estimates based on replicate catches in three dropnets, each descending at 0.91m.s^{-1}. The bars indicate the number of replicate drops for which the same density estimate was obtained.

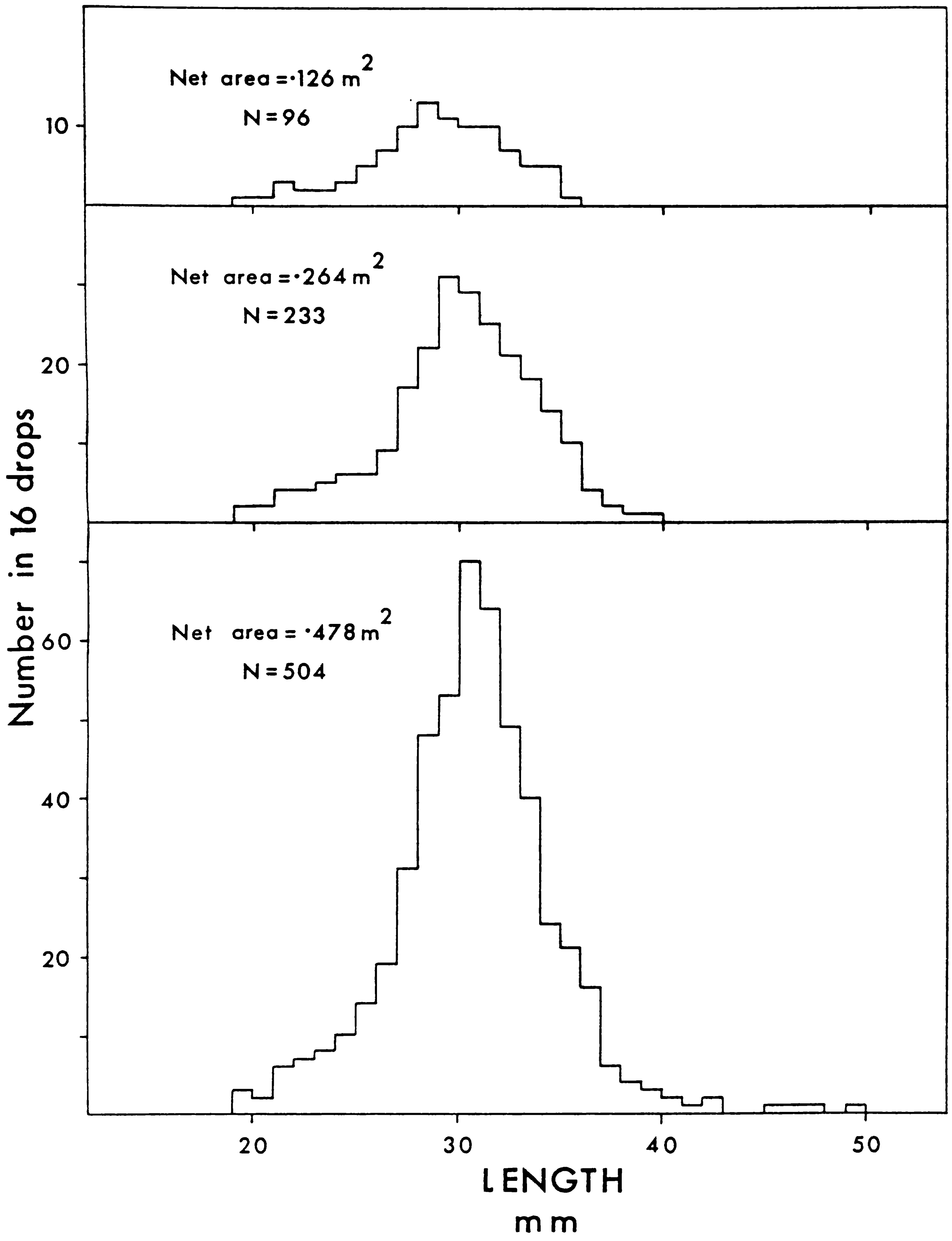


FIG. 3 Length frequency distribution of smelt caught in dropnets of three different mouth sizes.

Length frequency data from combined replicate samples were used to calculate catch ratios for each net-fish size combination and an iterative procedure was used to fit each of a series of models (Table 1) to these data. The fitting procedure was constrained so that zero catches could not be predicted for any length or net combination for which smelt were actually caught. Only 15.3% of total catch ratio variation was attributable to differences in net size (i.e. E = 0 and f = 1) but 51.5% was accounted for when E was proportional to length and this increased to 76.5% when E was described by an exponential function of length. The fit improved to account for 80.6% of total variation when net size was included in the model, but was not sensitive to variations in net filtration efficiency (f). Consequently fit improved little when the best fitting combination of exponents and filtration efficiency were found. Nevertheless, the value obtained for f is within the range of those given by Tranter (1967) for nets of similar construction.

TABLE 1. Best fitting coefficients obtained for models describing the width of the peripheral escape zone (E). Values held constant are indicated by *. The r^2 value is the percentage of total catch ratio variation accounted for by each model.

MODEL	a	b	c	f	r^2
(i) $E = 0$				*1	15.28
(ii) $E = aL^bS^{-1}$	.5808	*1		*1	51.13
(iii) $E = aL^bS^{-1}$	7.167E-4	2.826		*1	76.513
(iv) $E = aL^br^cS^{-1}$	1.427E-8	7.963	-2.502	*1	80.623
(v) $E = aL^br^cS^{-1}$	1.219E-8	7.996	-2.517	0.845	80.624

Thus the best description of the relation between smelt length and net size was a curve whose slope increased rapidly with smelt length and moved to the right with increasing net radius (fig. 4).

The effective fishing area (FA) of each dropnet,

$$\pi\left(fr_n - E_{in}\right)^2 \qquad (11)$$

was estimated for each length interval and corresponding catch frequencies were corrected for avoidance and the net's filtration efficiency. The corrected density for each length interval i sampled using net n was defined by:

$$C_{in}/FA_{in} \qquad (12)$$

and corrected estimates of areal smelt density (fig. 5) were obtained by summation of corrected densities for each length interval taken in replicate samples.

The length - weight relationship, fitted by least squares regression was described by:

$$W = 1.316E\text{-}7L^{4.053} \qquad R^2 = 0.97 \qquad (13)$$

where FL is fork length expressed in millimetres and W is weight in grams. Mean areal biomass estimates were obtained from the summation

$$\sum C_{in}W_i/FA_{in} \qquad (14)$$

Correction for net avoidance raised estimates of all population parameters (Table 2). Estimates of smelt density were particularly sensitive to correction for avoidance (fig. 5 cf. fig. 2) and corrections for the largest 2 - 3 smelt length classes taken in each net accounted for much of the difference between corrected and uncorrected estimates of smelt density and areal biomass. Eliminating data from these length intervals for calculation of parameters considerably improved agreement between estimates obtained using different dropnets.

Correction of smelt length frequency distributions (fig. 6) raised smelt frequency estimates, particularly for the larger smelt. This resulted in a significant increase in the mean length estimated from catches taken in the smallest dropnet ($p<.001$) but only minor increases in mean length for samples collected in the two larger dropnets ($p>.05$). Comparison of length frequency distributions suggest that corrected frequencies for smelt larger than 31mm caught in the smallest net and perhaps those larger than 44mm taken in the largest net overestimate true abundances. The size frequency distribution of smelt collected in a beach seine haul (fig. 7) demonstrated the existence of a modal size group 40 - 50mm long and their presence in samples caught in the largest net indicated that these adult smelt were also present in pelagic waters. However even the largest dropnet failed to reveal their abundance.

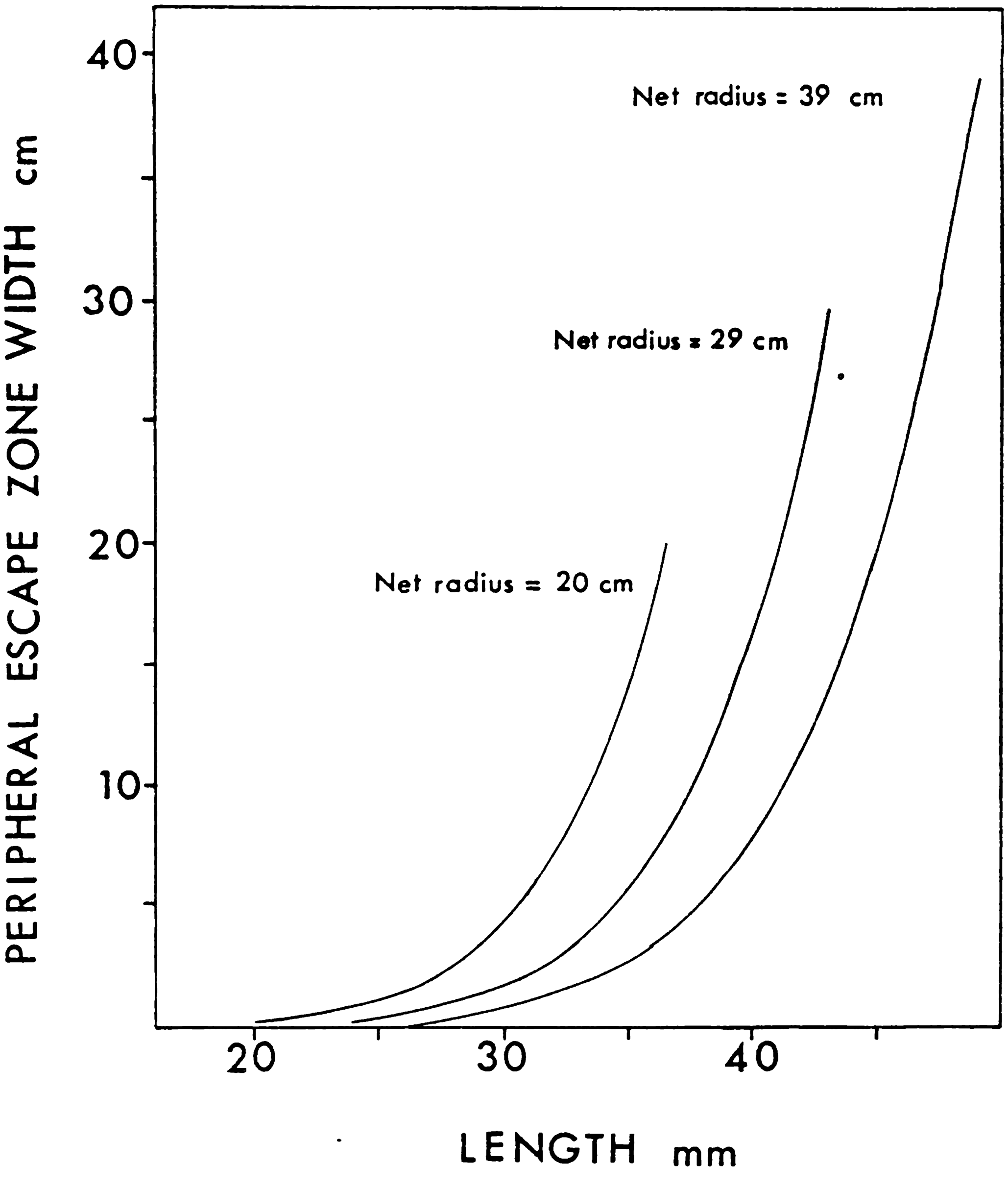


FIG. 4 The relationship between the width of the peripheral escape zone (E), smelt length and net size determined from the ratio of catches taken in different sized nets.

TABLE 2. Smelt population parameters based on raw catch data uncorrected for net avoidance (A), data corrected for avoidance (B), and corrected data for all but the largest smelt taken in each net (C).

	A			B			C		
NET RADIUS (cm)	20	29	39	20	29	39	20	29	39
LENGTH RANGE (mm)	19 - 35	19 - 39	19 - 49	19 - 35	19 - 39	19 - 49	19 - 33	19 - 37	19 - 42
MEAN LENGTH (mm)	28.4	29.6	30.3	30.6	30.2	34.0	29.1	30.0	30.4
MEDIAN DENISTY (n.m.$^{-2}$)	32	34	44	53	47	62	53	47	62
DENSITY RANGE (n.m.$^{-2}$)	8 - 171	11 - 250	24 - 235	10 - 764	16 - 422	30 - 308	10 - 395	16 - 392	30 - 308
MEAN BIOMASS (g.m.$^{-2}$)	5.32	7.29	9.72	11.65	11.41	29.71	10.36	10.73	12.4

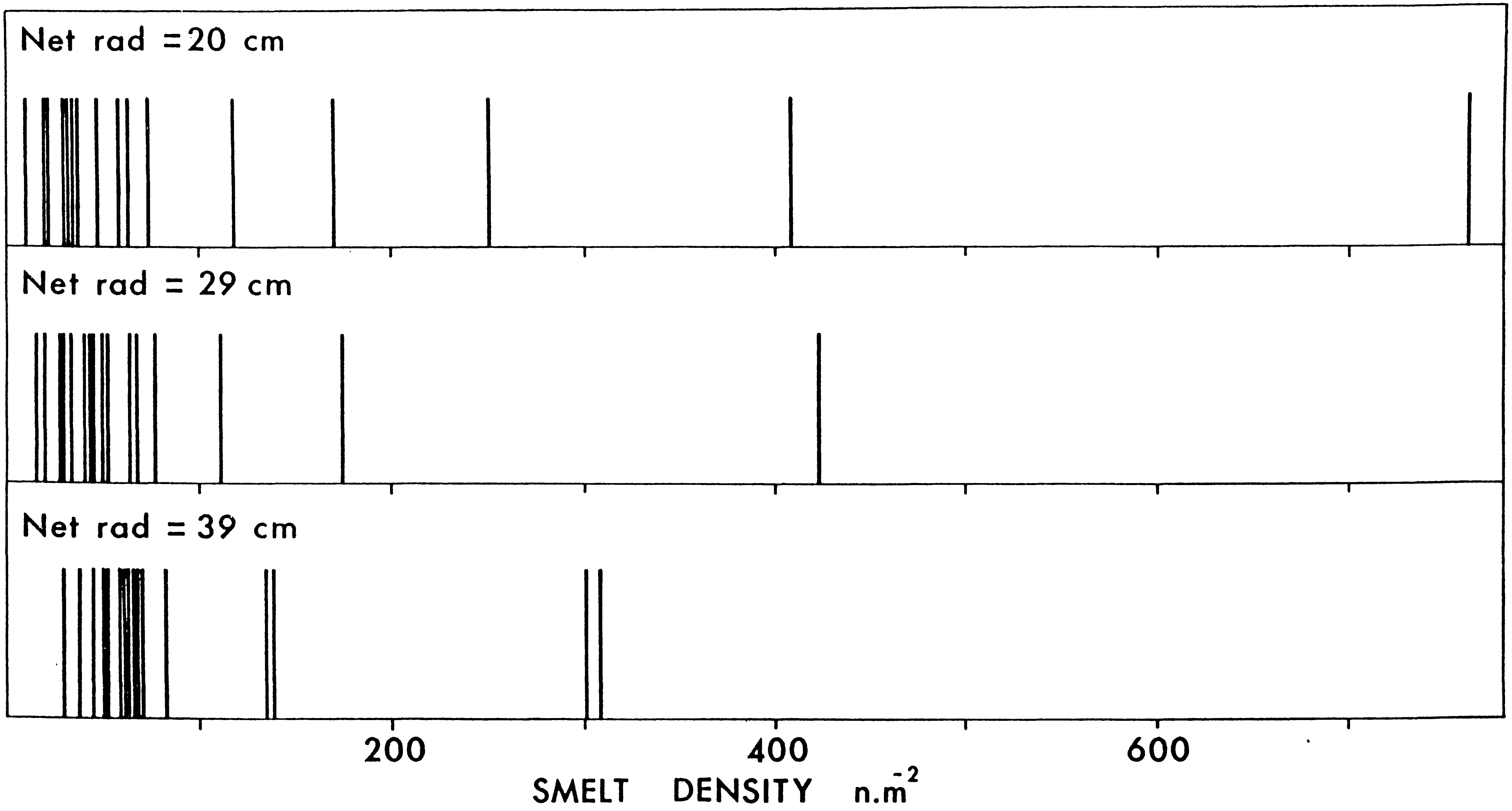


FIG. 5 Smelt density estimates corrected for avoidance. Data are 16 replicate drops for three dropnets each descending at $0.91 m.s^{-1}$.

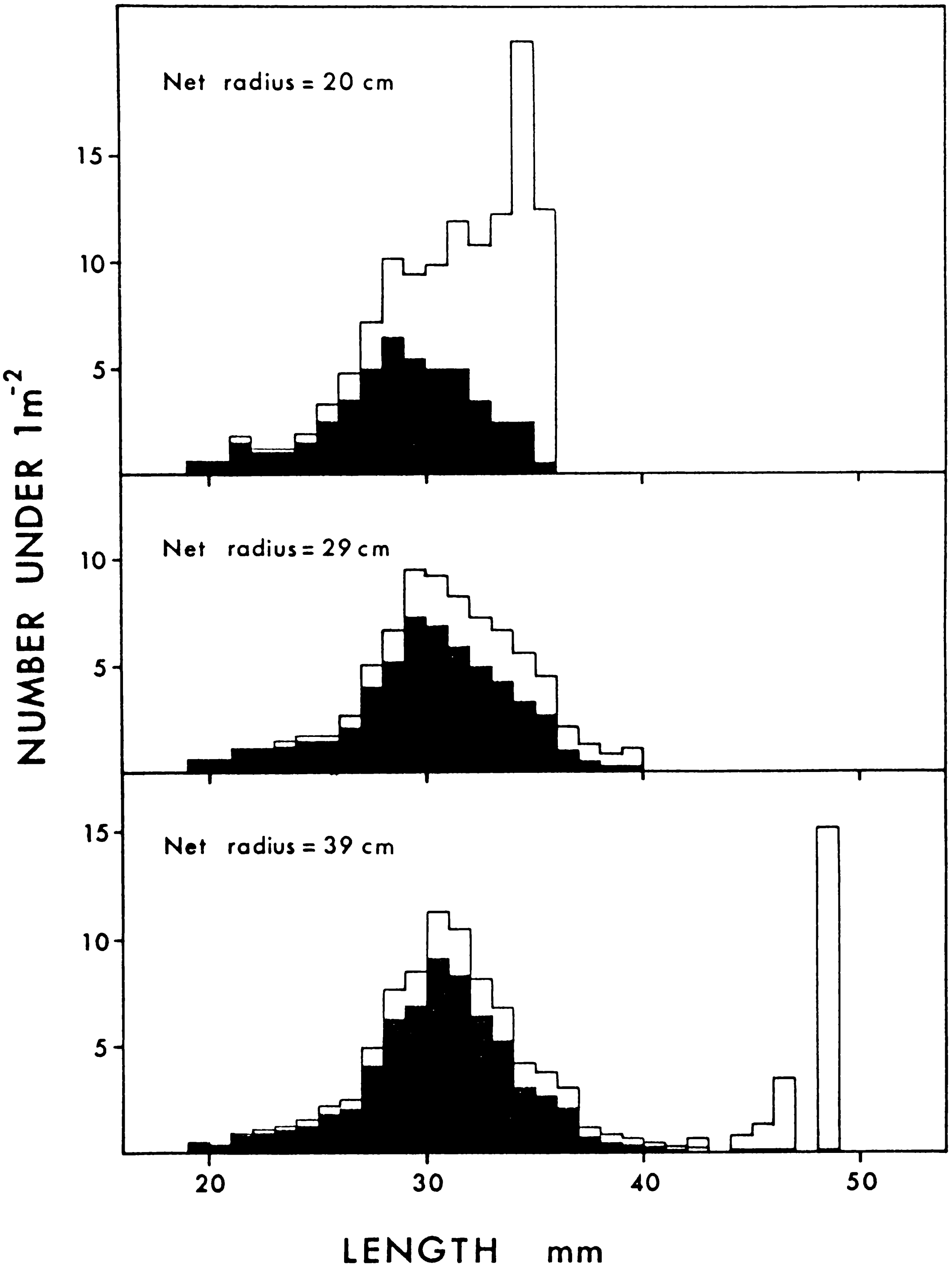


FIG. 6 Length (TL) frequency distributions of smelt caught in three dropnets before (black) and after correction for net avoidance.

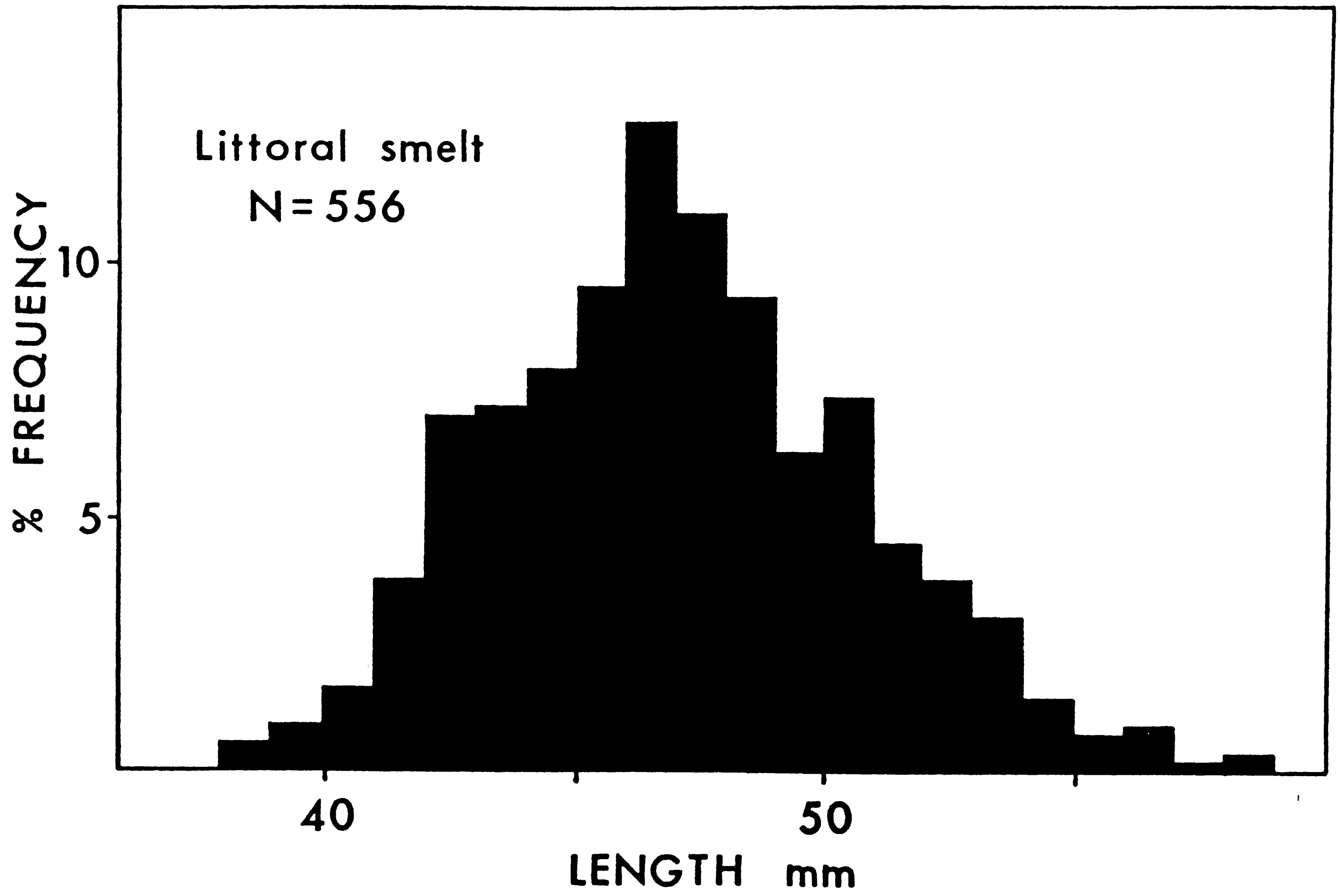


FIG. 7 The length (TL) frequency distribution of smelt collected in a beach seine net.

(d) Avoidance in practice and in theory

The curves for E derived from the catch data indicated that the width of the peripheral escape zone increased with smelt length but decreased with net size (fig. 4). Reaction distance and escape ability would be expected to increase with fish size (Dill 1974; Webb and Corolla 1981) and if these were approximately proportional to length then E would increase exponentially with length. Thus the observed relationship between E and smelt length was consistent with theory. Descriptive modelling of catch ratio data indicated that E was inversely related to net radius and therefore not proportional to k. The inverse relationship betwen E and net size indicates that E is not proportional to k, although Anraku and Clutter (1968) and Barkley (1972) assumed that it was and treated E as independent of net size.

(e) Random escape routes

Net size related variation in E can result from differences in net perimeter curvature if the target species often choose a suboptimal escape route (fig. 8). A fish located X cm inside the net's path capable of travelling J cm between commencing evasion and the net's arrival where:

$$J = k/S \qquad \text{(cf. Equ. 4)} \qquad (15)$$

will avoid capture if $J>X$ and if it chooses the optimum escape route. If the chosen route is suboptimal then the probability of capture (PC_{XJ}) will depend on the difference between J and X and on the angular deviation between optimum and chosen escape routes (fig. 9).

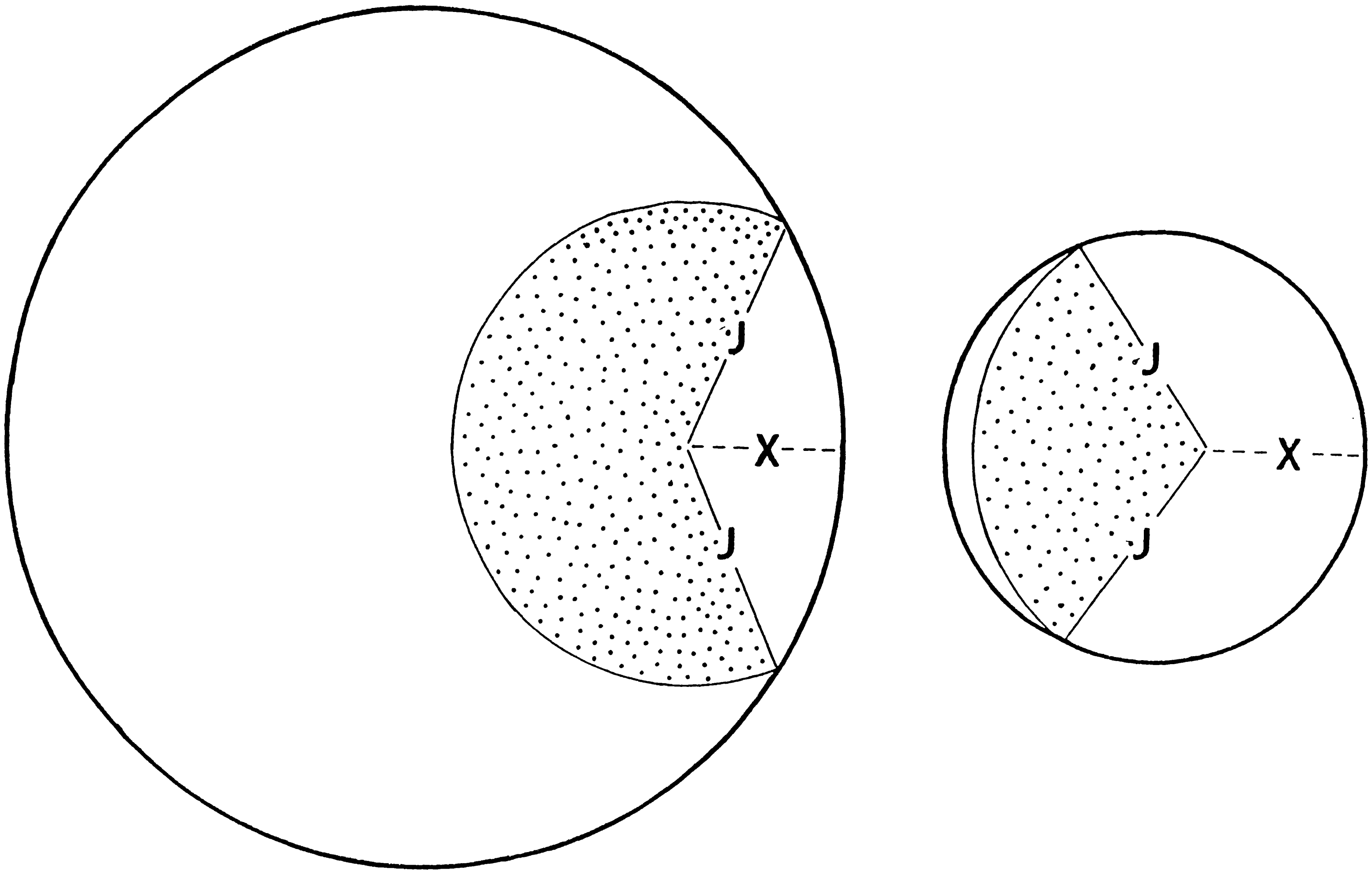


FIG. 8 Escape directions which will result in capture (shaded) of an organism located Xcm from the net's periphery and capable of swimming Jcm between commencing evasion and the arrival of different sized nets.

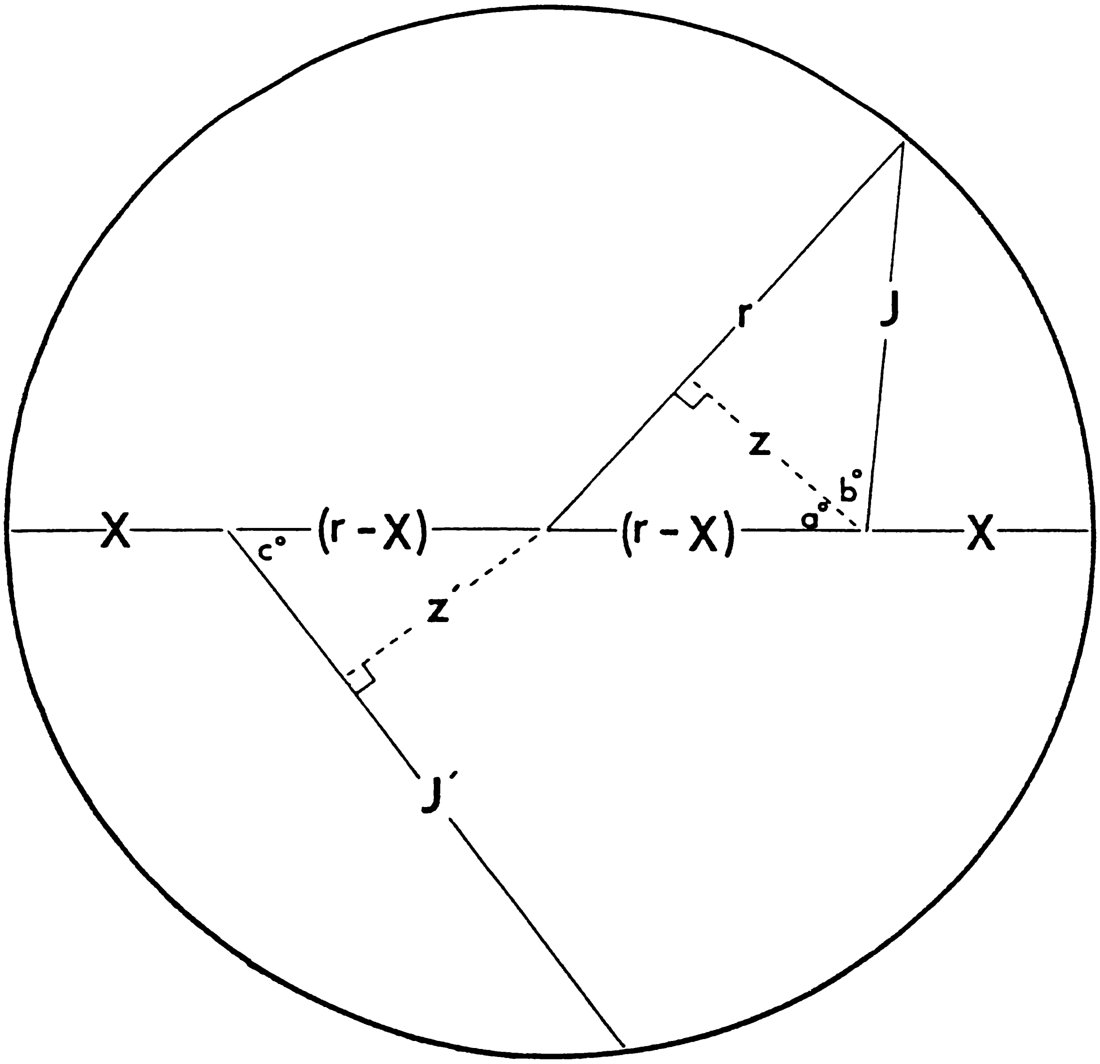


FIG. 9 Calculation of probability of capture (PC_{XJ}) when escape directions are chosen at random.

when $J \leqslant (r^2 + (r + X)^2)^{0.5}$

$PC_{XJ} = 2(a^0 + b^0)/360$

else $PC_{XJ} = 2c^0 /360$

The angular range of ineffective escape directions (C^0) which will result in capture, can be defined

when $J \leqslant \left(r^2 + (r + X)^2\right)^{0.5}$

by $C^0 = 2(a^0 + b^0)$ (see fig. 6) (16)

where $a^0 = \mathrm{Cos}^{-1}(z/r-X)$ and $b^0 = \mathrm{Cos}^{-1}(z/J)$

$$z = \left[J^2 - \left[\frac{(r-X)^2 - r - J^2}{2r} \right]^2 \right]^{0.5}$$

and when $J > \left(r^2 + (r + X)^2\right)^{0.5}$

C^0 is defined by $2c^0$ (17)

where $c^0 = 2\mathrm{Sin}^{-1}(z/r - X)$

$$z = \left[r^2 - \left[\frac{(r-X)^2 - r - J^2}{2r} \right]^2 \right]^{0.5}$$

If the direction of escape is chosen at random then the probability of capture for a fish belonging to catch component J and located X cm inside the net's patch (PC_{XJ}) is defined by:

$$PC_{XJ} = C^0/360 \qquad (18)$$

The mean probability of capture (PC_J) for fish evenly distributed in front of the net can be approximated by the summation:

$$\sum_{r - 0.5I}^{X = 0.5I} PC_{XJ} \left[\frac{\pi (r - X + 0.5I)^2 - \pi (r - X - 0.5I)^2}{\pi^{2}} \right]$$

which reduces to :

$$\sum_{r - 0.5I}^{X = 0.5I} \frac{PC_{XJ} 2I(r-X)}{r^2} \qquad (19)$$

where I is the increment between successive X values. E was estimated from the difference between actual and effective net radii:

$$E_{rJ} = r - (PC_J r^2)^{0.5} \qquad (20)$$

The relationship between escape ability (J) and E was found to be described by a concave curve which moves to the right with increasing net size (fig. 10). Thus when the escape route direction is chosen at random, the width of the peripheral escape zone is not proportional to escape ability. However net size related differences in E obtained from catch data (fig. 4) are substantially greater than those which can arise from differences in peripheral curvature if escape routes are chosen at random. Thus choice of suboptimal escape routes can, at best, explain only part of the observed variations in E.

(f) Escape route selection based on net perception

Intuitively, both random and optimal selection of escape routes seem unlikely because an animal's ability to choose a successful escape route probably depends on its location (X) inside the path of the net, on the extent of its sensory field (s_0) and on the size of the net. If the animal is able to perceive the whole net mouth (i.e. $s_0 \geqslant 2r-X$) then sufficient directional cues should be available to permit choice of an appropriate, perhaps optimal route out of the net's path, leading to successful net avoidance if $J>X$. However, if the animal can perceive only the closest part of the net perimeter, then it can respond only to this, probably by moving further into the path of the net, avoiding capture only if $J > 2r-X$.

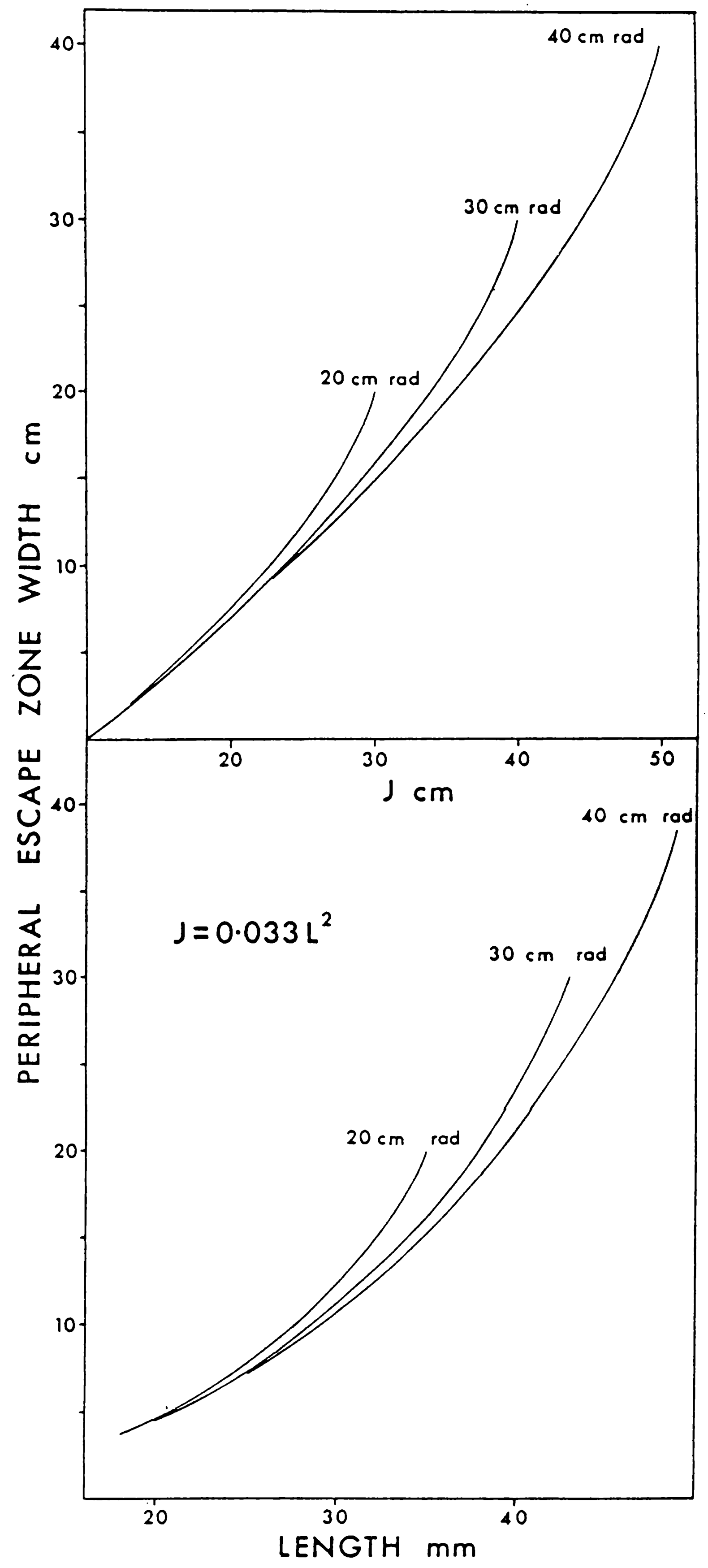


FIG. 10 The relationship between the width of the peripheral escape zone (E), escape ability (J), smelt length and net size obtained by simulation when the escape direction is chosen at random.

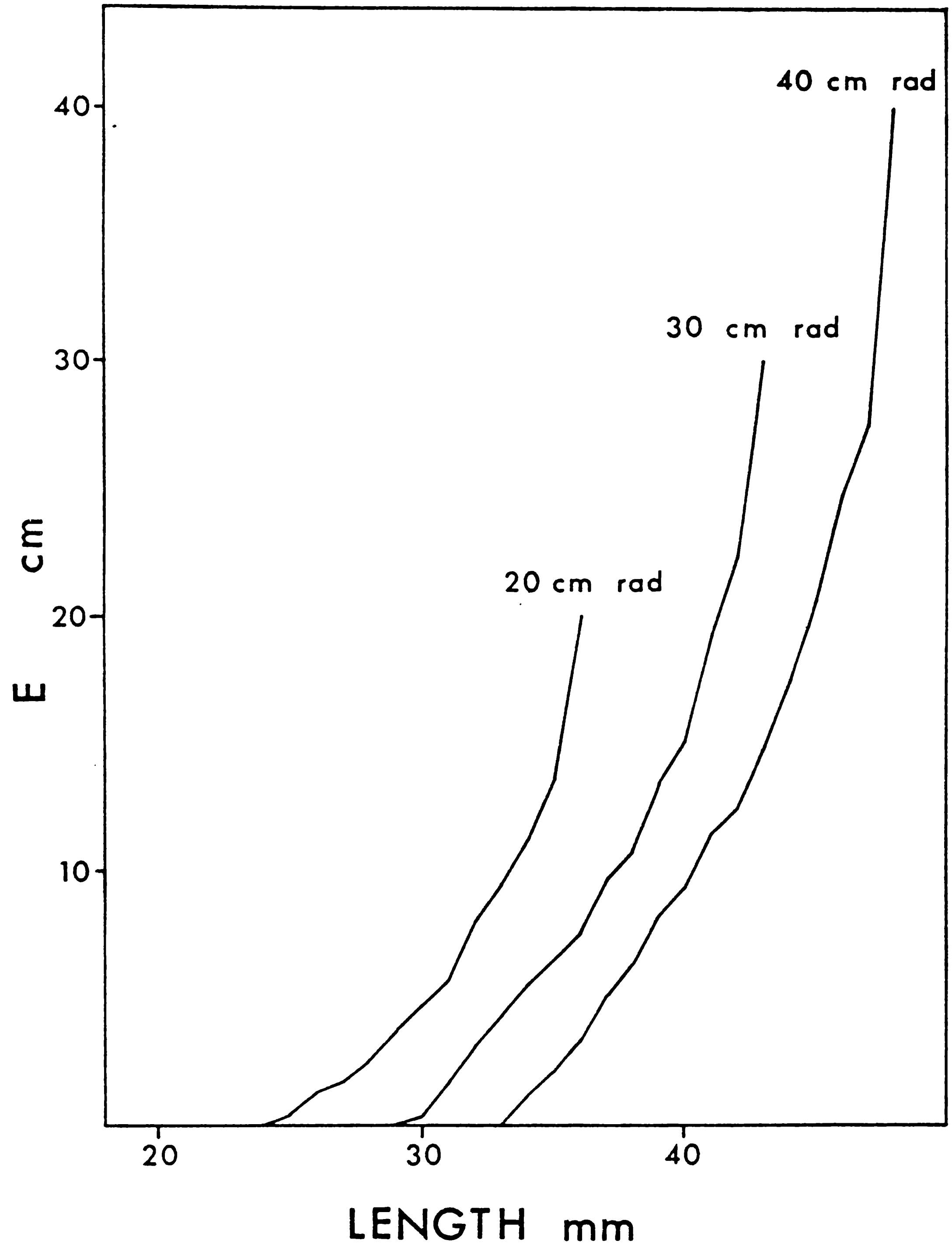


FIG. 11 The relationship between the width of the peripheral escape zone (E), smelt length and net size obtained by simulation when the chosen escape direction depends on whether the smelt can perceive all or only part of the net.

This concept of net avoidance, controlled by directional cues, is easily simulated given the simplifying assumptions that the chosen escape route is always perpendicular to the net's periphery, the fish are evenly distributed in front of the net's mouth and they do not respond to the behaviour of others present.

Mean probability of capture for animals distributed evenly across the net's path was estimated using equation 17 and the width of the peripheral escape zone E estimated from equation 18. Appropriate coefficients for exponential functions of length describing s_0 and k in terms of smelt length were found using an iterative procedure which fitted simulated E values to those predicted by equation(iv) given in Table 1. The best fitting exponential functions (fig. 11) were:

$$s_0 = 8.82E\text{-}3L^{2.36} \qquad \text{and} \qquad k = 0.414L^{2.44}$$

where L was expressed in millimetres, s_0 in centimetres and the units of k were $cm^2.s.^{-1}$. When the sampler is a dropnet, s_0 is the radius of the sensory field overhead and this may not be equivalent to the forward or lateral sensory fields which would be appropriate parameters for use with samplers which fish horizontally rather than vertically.

The simulated relationship between E, smelt length and net size exhibited essentially the same features as the relation determined from catch ratio data (fig. 11, cf. fig. 4).

(g) Discussion

Observed consequences of avoidance can be accounted for if smelt choose the shortest route away from the net's path when they perceive the whole net but choose an escape direction normal to the nearest point on the net periphery when only part of the net is perceived. This behaviour generates a peripheral escape zone which increases in width with fish size (i.e. escape ability) but decreases in width for larger nets. The radius of the sensory field above the smelt and their escape ability were both described by exponential functions of their length.

The sensory field would be expected to increase exponentially with smelt length due to incomplete sensory organ development in smaller smelt. Escape ability could increase exponentially for two reasons. Firstly, as smelt become more corpulent and muscular with increased length (Equ. 13), their swimming ability probably increases correspondingly. Secondly, reactive distance may increase disproportionally with length because larger and older smelt may be more experienced in avoiding large approaching objects. Dill (1974) found that reactive distance in rainbow trout (*Salmo gairdneri*) increased exponentially with length and increased further with experience.

Random choice of escape routes generated a relation between E, smelt length and net size which was similar to that which the directional cue model indicated. However, neither the steepness of the curves describing the relation between E and escape ability nor their displacement to the right with increasing net size were consistent with the form of the relationship indicated by catch ratio data. Thus the hypothesis that smelt react to the approach of a net by flight in randomly chosen directions is rejected.

The directional cue model predicts that E is not proportional to net size and only proportional to net speed when the sensory field is greater than the net diameter. Catch ratio data indicated that the relation between E and net size was consistent with this predication but, in the absence of catch data for the same net fished at different speeds, the actual relation between E and net speed remains unknown. However, for models fitted to catch ratio data, E was considered proportional to net velocity. Thus if the mechanistic directional cue model incorporates the essential components of net avoidance, then estimation of net velocity required to achieve a given fishing efficiency should be based on this rather than on the descriptive models fitted to catch data.

Net descent speed required to catch smelt of a given size at a specified efficiency level can be estimated using s_0, k and E. Given that a minimum acceptable fishing efficiency (F) is decided upon then the maximum width of the peripheral escape zone is defined:

$$E_{max} = r - (r - Fr^2)^{0 \cdot 5} \qquad (21)$$

If the sensory field is greater than the net diameter then, according to the model, all fish will choose the optimum escape route.
F is achieved when

$$S = k/E \qquad (22)$$

When the sensory field is less than the net's diameter but greater than its radius (i.e. $2r>s_0>r$), only those smelt lying within s_0 - r cm of the net's centre are expected to choose the shortest escape route.

The proportion expected to choose this is :

$$\left[\frac{s_0 - r}{2}\right]^2 \qquad (23)$$

According to the model, fish outside this area can perceive only part of the net perimeter and are expected to avoid this by swimming across the net's path. Consequently a slower net velocity will achieve the desired fishing efficiency for fish near the net's periphery. Thus F is achieved when net descent velocity is:

$$S = \left[\frac{k}{E}\left(\frac{s_0-r}{r}\right)^2\right] + \left[\frac{k}{2r-E}\left[1-\left(\frac{s_0-r}{r}\right)^2\right]\right]$$

If the sensory field is less than the net radius then only those fish lying between the net periphery and $r - s_0$ cm from the centre are expected to respond to the net by moving away from the periphery further into the net's path and for these, F is achieved by a particularly slow net speed:

$$S = \frac{k}{2r-E}\left[1-\left(\frac{s_0-r}{r}\right)^2\right]$$

Net avoidance caused only slight reduction in mean smelt length estimates but bias in density and biomass estimates was more significant. The nets were least effective at sampling large smelt and correction for the ability of these fish to avoid the net accounted for much of the difference between raw and corrected sample estimates. Perhaps the most important smelt population feature indicated by the correction for avoidance was the likely presence of a second modal group of ca. 45mm TL, which was confirmed by beach seine catch data. Nevertheless, detection of these fish required use of a sufficiently big and fast net to catch at least a few of them and there was no indication that these smelt might be members of a second modal size class. Similarly, correction for avoidance was a prerequisite for determining whether smelt larger than 35mm TL were scarce or merely avoiding capture. Clearly then, catch data must be corrected for avoidance before sample length frequency structure can be interpreted with confidence. This correction is essential when examining time series length frequency data as otherwise the effects of mortality or emigration, which depress absolute abundance, cannot be separated from growth which reduces catchability.

The width of the peripheral escape zone was found to be a rapidly increasing concave function of length, indicating that for the larger smelt present a small change in length substantially reduced their catchability. When this was low, the correction factor was large and consequently, population parameter estimates were particularly sensitive to small differences in the number of the largest fish caught. The vagaries of patchiness or anomalous avoidance behaviour become major sources of variation when catching efficiency is low and if these sources of variation in population parameter estimates are to be minimized then estimates should be based on catch data for a specified size range which the sampler catches at or above a known minimum level of efficiency. The upper size limit would be defined by an arbitrary minimum for the net's fishing efficiency and the lower size limit fixed by the minimum size retained by the mesh used. Thus population parameter estimates would apply only to animals within the size range specified.

The foregoing analysis of net avoidance does not allow for differences in avoidance behaviour between shoaling fishes and those swimming singly. It seems likely that a shoal of fish in the net's path will move as a group choosing approximately the same direction away from the net (Anraku and Clutter 1968) and that the movement of some individuals will be elicited by the behaviour of others rather than perception of the approaching net. Thus for a given catch component, both k and the chosen escape direction may vary depending on whether the animals were swimming singly or shoaling. This could account for some of the residual variation in the model fitted to catch ratios after variation associated with smelt length and net size was accounted for. The mechanistic directional cue model would be quite inappropriate for describing avoidance by shoaling fish. Ideally, two models for avoidance are required: one being applicable when animals respond individually and the other if they swim as a group. The principal difficulty with this lies in determining the fish density at which the latter model would be more appropriate.

The concept of the peripheral escape zone is probably only appropriate for sampling devices lacking net mouth obstructions as a towing line or bridle in front of the net mouth must be expected to elicit avoidance behaviour and for these nets, the peripheral escape zone is unlikely to account for all escapement observed. As Fleminger and Clutter suggested, (reported by Anraku and Clutter 1968) the net's effective fishing area may lie between a central void and the peripheral escape zone. Models for avoidance based on reaction to the towing line, bridle and net perimeter await development.

Previous methods used to estimate net avoidance have depended on the assumption that all animals in the path of the net respond to its approach by moving in the direction most likely to result in successful net evasion. The assumption was necessary because analytical estimation of E was dependent on the algebraic convenience conferred when E is proportional to k. However neither descriptive modelling based on catch ratio data nor mechanistic modelling using theoretical components of avoidance support the assumption. It therefore seems that iterative numerical fitting procedures which consume large amounts of computer time are required to obtain the best estimates of net avoidance.

APPENDIX 2

Smelt length frequency data.

The following tables give the number of ripe male, female and non-reproductive (i.e. juvenile, immature and spent) smelt caught in beach and stream seine hauls.

1. Waihaha Beach
2. Whanganui stream
3. Waihaha river
4. Waihora stream
5. Five Mile Bay
6. Waitahanui river
7. Lake Rotongaio outlet
8. Hatepe river
9. Tauranga - Taupo river
10. Waimarino stream
11. Waiotaka stream
12. Tongariro river at Blind Mouth
13. Kuratau river
14. Whareroa stream

TABLE 1   Length frequency data for smelt collected in seine hauls at Waihaha Beach

LENGTH	24.8.79 2010 hrs; 2			19.9.79 1200; 1			19.9.79 1600; 4			19.9.79 2000; 3			20.9.79 2400; 2			20.9.79 0400; 2			20.9.79 0800; 3			20.9.79 1000; 3			20.9.79 1500; 2			4.10.79 1130; 4			4.10.79 2230; 1			16.10.79 1130; 1			16.10.79 0930; ½		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
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37																					2									2									9
38			1																		2									1						1			24
39	1		1			1															1			2			1			1						1			33
40	1		2	1		5						1									2		1	7							1					1	1		63
41	3		1	3		4						1							1		6			5						1			1						99
42	3	2	5	5		11			1			1									11	1	2	3		1			1	1	2		1			1	4	4	125
43	7	6	9	3	3	15				1		4							1	1	10	2	1	3					1	1	7	4	4				8	5	105
44	4	4	10	5	10	11						1			1				2	5	6	2	1	3				1			6	4	7				10	7	93
45	6	4	11	2	6	6				2	1	4							1	7	7		3	4			1	1			2	7	5				7	14	87
46	6	5	24	2	5	7				2	1	6								8	4	1	1	4						2	4	7	2				6	22	58
47	6	7	23		5	2				1	2	4		1						3	3	1	6	3							2	6	2		1		1	12	48
48	6	9	20		2	1				3		2							1	5	2		4	1							1	18	4				1	9	27
49	1	10	11								2	5									1	1	6	1								8	4					6	14
50	1	6	9							1	3										1		1									7	2					5	4
51		3	6		1					1	3									2			1			1						5	1					3	1
52		2	1					1			4				1																	4							
53			1								3	1																				2					1	1	
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56											82/1																					1						1	
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																																1							

TABLE 1 Cont'd

	26.10.79			28.10.79			13.11.79			27.11.79			27.11.79			27.11.79			27.11.79			28.11.79			29.11.79			29.11.79			28.11.79			10.12.79			11.12.79		
	2200; 2			1530; ½			0830; ½			1000; 1			1400; 1			1800; 1			2200; 1			0200; 1			0630; 1			10-00; 1			14-00; 1			2300; 1			1700; 1		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
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31																																							
32																																							
33																																							2
34															1																								2
35									5			1			1																		1						3
36						1			12			4			1			1									1			1			5						8
37						6	1		30			13			3			4									1			2			4			1			23
38						12	2	1	93			10	2	1	19			11									2			3			8				4		59
39			1	2		27	3	1	113			19	1	1	31	2		10									3			10			29			4	8	1	90
40	1			2		81	5		176			13	4		32	1		13				1					1		1	2	2		25	1	2	3	8		131
41			2	10	6	101	8	1	179	1	1	22	3	2	38	1		12	1		1	4	1				3		1	2	3		44	1	1	9	15	3	127
42	1			20	8	165	12	1	137	3	3	18	4	5	29	4	2	8		2	1		3				1		2	6	9	3	44	3	7	8	17	8	120
43	1			21	28	194	7	9	67	3	3	17	2	7	17	2	1	8	1		3	1	7	1				1		2	12	4	57	3	6	6	9	8	91
44		3		20	50	144	1	6	33	2	5	7	2	7	5	0		3.		2			7							3	6	10	27	4	5	4	10	8	42
45	1	4		16	60	99	1	4	4	1	1	7	1	2	9	2	1	2		4	1		11								2	13	27	2	8	6	2	8	25
46		1		13	61	73	1	3	3		3	1	1	1	2		1	1	1	4			11								1	17	8	1	8	3		4	10
47		4		8	61	44		3				2	1		1					9	4		10								1	12	5	1	9	2	1	2	4
48		1		8	59	11					1				1					8			12									11	5		4			2	2
49				4	40	10														2			11									2			2	2			1
50		3		1	36	4																	5									1	1			1		1	
51		1		1	24	2														3	1		4									1			1				
52		1			8															2			2																
53					7															1			2																
54		1			4															1			1																
55					2															1			1																
56																																							
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58																																							
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TABLE 1 Cont'd

LENGTH	13.12.79			29.12.79			29.12.79			10.1.80			11.1.80			23.1.80			23.1.80			23.1.80			23.1.80			24.1.80			24.1.80			24.1.80			8.2.80		
	0900; 1			1015; 1			2315;1			1530; 1			0100; 1			0900; 1			1300; 1			1700; 1			2100; 1			0100; 1			0500; 1			0930; 1			1100; 1		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																					2			1			1												
27																					3			2			1												
28																					8			2			3												
29																					23			9			4												
30												1						13			48			27			4												1
31												2						41			63			66			4									4			5
32						1						3						100			95			145			6						1			16			13
33			2									10						173			98			248			3									29			17
34			9			2						17						162			105			246			1									23			17
35			20			4						25						136			73			205										N	N	24			17
36			28			2						25						90			54			160										O	O	12			18
37			48			1			1			23			1			60			29			118			1							N	N	8			11
38	1		77			8						21						36			22	1		129			2							E	E	1	1		10
39	1		69	1		5	1					40				2		46			15	2		109			1						1			2	1		9
40	3		49	1		11	3			2		42				3		28			13	7		35	1								1	P	P	2	3		1
41	3	2	38			22	5		6	7		42				4	1	25	1		9	8		38	1		3							R	R		3	1	1
42	3	2	19	4	3	17	5	7	6	7	4	34				8	2	26	1	1	12	6		24	2		2			1	1		1	E	E		3		1
43	3	2	9	3	3	19	6	15	7	3	4	25	1			7	3	16		2	10	2		17	2		2	1	1	1		1		S	S		3	2	2
44	3	1	5	4	3	3	3	12	3	2	2	21				4	5	4	1	1	1	2	3	10	1	1	2		1			1		E	E		4	1	3
45	2	3	6	2	4	6	2	25	2	2	2	9				3	3	1		1	3		1	5	1	1							1	N	N		1	1	4
46		1	2	2	8	7		35	1	2	2	8					1	4	1			1	1	3			1							T	T			1	
47				1	3	4		33		1	2	5					3	2			2		3	2	1		1		2			2							
48				1	4	1	2	41			2	4						1					1						1		1	1							
49					5	2		21	1			1		1				1			1	1				1													
50					1		1	10						1			1	1						2															
51					1						1												1															1	
52																	1	1																					
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TABLE 1 Cont'd

	9.2.80			21.2.80			21.2.80			5.3.80			20.3.80			20.3.80			20.3.80			20.3.80			20.3.80			21.3.80			21.3.80			21.3.80			5.4.80		
	2300; 1			1615; 1			2200; 1			1015; 1			0900; 1			1300; 1			1300; 1			1700; 1			2100; 1			0100; 1			0530; 1			0900; 1			1200; 1		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																							
27												2			1																					1			
28						1						4			9			6			6			3			1									5			2
29						4						12			31			27			27			2												22			7
30						11						36			96			72			72			22												39			62
31			1			28			1			88			254			187			187	N		70							N	N				74			149
32						65			2			118			297			244			244	O		116							O	O	1			77			309
33						72			3			127			318			282			282	N		155			2		N	1	N	N	1			81			451
34						74			6			119			323			264			264	E		115					O		E	E	3			54	1		506
35						71			10			109			296			192			192			69	N	N	1		N				2			49	2		474
36				1		57			7	1		88	1		275			111			111	P		53	O	O	1		E		P	P	2			48	5	1	409
37				1		47	1		4	2		55	1	1	221	1		104	1		104	R		47	N	N	1				R	R				68	6	1	399
38				1		41	2		11			54	3	2	167			63			63	E		25	E	E	2		P		E	E				66	17	9	236
39			1	5		33	2		10	3	1	44		2	131		1	35		1	35	S		14			3		R	2	S	S	1			36	22	17	181
40				8	1	21	1		16	2	3	43	2	1	84	1	1	24	1	1	24	E		8	P	P		1	E		E	E				26	34	37	165
41	2	1	2	3	3	18	3	1	13	3	3	33	2	5	48		4	16		4	16	N	1	8	R	R	1		S		N	N				24	26	51	120
42		2	2	4	4	17	3	6	12	5	3	31		14	27		3	7		3	7	T	2	4	E	E	1	1	E		T	T				27	21	72	99
43	3	2	1	4	7	18	1	4	9		5	16		11	26		4	4		4	4		2	2	S	S			N	1						15	14	90	50
44		5	1	3	12	12	1	2	3		7	6		9	8		5			5			1	1	E	E			T							10	4	51	22
45		6	1	4	9	6		3	6	1	5	13		6	5		5			5			2	1	N	N	1									4	1	45	20
46		6		1	13	5		1	4		2	10		1											T	T										2		23	11
47	1	8		1	6	1		1	3		1	2			1								1													4		11	8
48		6	1		6	2		1	3			3		2	1		1			1				1														6	1
49		2			2			2	1		2	1																										2	
50					3			1	1		1																										1	1	
51						1																																	
52																																							
53				1																																			
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55																																				1			
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TABLE 1 Cont'd

LENGTH	18.4.80			19.4.80			29.4.80			30.4.80			16.5.80			17.5.80			30.5.80			30.5.80			30.5.80			30.5.80			31.5.80			31.5.80			31.5.80		
	1230; 1			2300; 1			2200; 2			1530; 2			1515; 1			2130; 1			1200; 2			1600; 2			2000; 2			2400; 2			0400; 2			0800; 2			1200; 2		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																				1			
27																																							
28												1																											
29			1									9			2																								1
30			4									46			7						1			6															
31			13			4						145			17						2			10															9
32			33			15			1			250	N		27						8			39															27
33			58			12	N					305	O		59	N	N	1			25	N	N	94	N	N		N	N		N	N		N	N		N	N	53
34			63			10	O					298	N		60	O	O	1			42	O	O	108	O	O		O	O		O	O		O	O	1	O	O	75
35			60			13	N		1		1	252	E		46	N	N	1			40	N	N	98	N	N		N	N		N	N	1	N	N		N	N	98
36			61			13	E					171			33	E	E				41	E	E	79	E	E	1	E	E		E	E		E	E	1	E	E	76
37	1		48			10			2			157	P		20						28			43			1												58
38	2		50	1		10	P		1		5	133	R		22	P	P	2			8	P	P	24	P	P	1	P	P		P	P		P	P		P	P	13
39		1	36			2	R		1		4	91	E		14	R	R				7	R	R	1	R	R		R	R		R	R		R	R		R	R	8
40		4	29			4	E			1	11	78	S		13	E	E				3	E	E		E	E		E	E		E	E		E	E		E	E	4
41	1	4	19	1	1		S		1		13	54	E		12	S	S	1			2	S	S	1	S	S		S	S		S	S		S	S		S	S	1
42	1	10	9		1	4	E				12	40	E		9	E	E					E	E		E	E	2	E	E		E	E	1	E	E		E	E	
43		8	4				N			2	12	30	N		2	N	N					N	N		N	N		N	N		N	N		N	N		N	N	
44		3	1			1	T				8	16	T		2	T	T					T	T		T	T		T	T		T	T		T	T		T	T	
45			6					1			6	7		1																									
46			2					1			4	4																											
47		1									1	1																											
48		1									3				1																								
49						1					1																												
50																																							
51								1																															
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58																																							
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TABLE 1 Cont'd

	13.6.80			13.6.80			25.6.80			25.6.80			26.6.80			26.6.80			10.7.80			11.7.80			13.7.80			25.7.80			25.7.80			26.7.80			26.7.80		
	1530; 2			2300; 2			2115; 2			2115; *			1300; 2			1330; *			2045; 2			1315; 2			1130; *			1000; 2			1400; 2			1000; 2			1400; 2		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																							
27																																							
28												1																											
29																																							
30												1																					1						
31			2																								2						5						2
32			32						2				N	N	1	N		2	N			N	N				5						6						7
33		N	91	N			N					2	O	O		O		6	O			O	O		N	N	21	N	N		N		17	N			N		15
34		O	173	O			O					3	N	N		N		1	N			N	N		O	O	33	O	O		O		16	O		4	O		13
35		N	267	N			N		4			7	E	E		E		2	E			E	E	2	N	N	47	N	N	1	N		22	N		3	N		21
36		E	319	E			E		4			8			1			6							E	E	42	E	E	1	E		24	E		4	E		32
37			294						7			6	P	P		P		11	P			P	P				27						23			7			21
38		P	163	P			P		4		1	7	R	R	2	R		7	R			R	R		P	P	9	P	P		P		12	P		10	P		16
39		R	71	R			R		6	1		12	E	E	1	E		7	E			E	E		R	R	4	R	R		R	1	18	R		6	R		7
40		E	42	E			E		6			7	S	S		S		6	S			S	S	1	E	E	1	E	E		E		5	E		4	E		9
41		S	17	S			S		3		2	4	E	E		E		2	E			E	E		S	S		S	S		S		3	S		3	S	2	11
42		E	7	E			E		3		3	3	N	N		N		2	N		1	N	N	2	E	E		E	E		E			E		3	E	1	6
43	1	N	2	N			N	1	7		4	13	T	T		T	1		T			T	T	1	N	N		N	N		N			N	2		N		4
44		T	1	T	1		T	1	4		3	5													T	T		T	T		T			T	1		T		1
45								1				2						1															1		1			1	
46	1										5																												
47											1																												
48								1	1		2	1																											
49	1																			1																			
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TABLE 1 Cont'd

	26.7.80			26.7.80			27.7.80			27.7.80			27.7.80			10.8.80			10.8.80			10.8,80			21.8.80			21.8.80			22.8.80			22.8.80			4.9.80		
	1300; 2			2200; 2			0200; 2			0600; 2			1000; 2			1400; 2			1930; 2			2200; *			2230; 2			2300; *			0930; *			1115; 2			2200; 2		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																							
27																																							
28																																	1						
29															1																		1						
30															1															1			1						
31															4																		1						
32															7									1						1			4			2			
33	N		1	N	N		N	N	N	N	N		N		53	N			N	N				1	N	N		N		1			27	N	N	1			
34	O		1	O	O		O	O	O	O	O		O		98	O		1	O	O				6	O	O		O		5			67	O	O	1			
35	N		1	N	N	1	N	N	N	N	N		N		163	N			N	N				7	N	N	1	N		10			124	N	N	3			
36	E		3	E	E		E	E	E	E	E		E		201	E			E	E				12	E	E		E		14			152	E	E	2			1
37			2									2			209						1			17			1			30			153			3			
38	P		1	P	P		P	P	P	P	P		P		142	P		1	P	P				28	P	P	1	P		27			118	P	P				
39	R		2	R	R		R	R	R	R	R		R	1	86	R			R	R			1	22	R	R		R		19			45	R	R	6	1		
40	E		1	E	E		E	E	E	E	E		E	1	62	E			E	E	1			19	E	E		E		21		1	30	E	E	2			1
41	S		1	S	S		S	S	S	S	S		S	2	41	S			S	S	1			11	S	S		S		22			19	S	S	1			1
42	E		1	E	E		E	E	E	E	E		E	3	33	E	1	1	E	E	1		3	7	E	E	2	E	1	21			10	E	E				
43	N		1	N	N		N	N	N	N	N		N	5	11	N			N	N	2		3	5	N	N	1	N		14		1	7	N	N				
44	T	1	1	T	T		T	T	T	T	T		T	12	8	T			T	T			1	5	T	T		T	1	3			3	T	T				
45														5	3								1	3					3	5		1	3						1
46														2										2					1	1			2						
47														2	1								6	2					3	1			1						
48														1							1		6	1					3	1		1	1					3	
49																							1						1	2			1					2	
50																														2								2	
51														1										1														1	
52																							1						1										
53																													1										
54		1																											1										
55																							1	1					67;1										
56																													70;1										
57																													71;2										
58																													82;1										
59																													88;1										
																													89;1										

TABLE 1 Cont'd

LENGTH	4.9.80			5.9.80			17.9.80			17.9.80			17.9.80		
	2200; •			1100; •			0900; 2			1300; 2			1700; 2		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25															
26															
27															
28															
29															
30															
31															
32	N	N		N	N	2	N	N							1
33	O	O		O	O	0	O	O				3			2
34	N	N		N	N	1	N	N				7			2
35	E	E		E	E	3	E	E				17			4
36						4						21			4
37	P	P	1	P	P	2	P	P	2			35			9
38	R	R	4	R	R	2	R	R	2			30			6
39	E	E	3	E	E	2	E	E	0			24			16
40	S	S	2	S	S	2	S	S	1			19	1		33
41	E	E	5	E	E		E	E	1			17	0		45
42	N	N	4	N	N		N	N	1	1		15	2	1	48
43	T	T	6	T	T		T	T	1	1	3	15	0	0	34
44			4						0	0	1	10	1	2	19
45			0						1	0	1	10	2	2	12
46			1						1	1		2	1	4	9
47			1							1	1	0	0	3	1
48			1								2	1	2	2	1
49											1			1	
50														1	
51														1	
52															
53															
54															
55															
56															
57															
58															
59															

LENGTH	17.9.80			18.9.80			18.9.80			18.9.80		
	2100; 2			0100; 2			0500; 2			0900; 2		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												
31												
32	N	N	N	N	N	N	N	N		N	N	
33	O	O	O	O	O	O	O	O		O	O	
34	N	N	N	N	N	N	N	N		N	N	2
35	E	E	E	E	E	E	E	E		E	E	5
36												9
37	P	P	P	P	P	P	P	P		P	P	13
38	R	R	R	R	R	R	R	R		R	R	15
39	E	E	E	E	E	E	E	E	1	E	E	5
40	S	S	S	S	S	S	S	S	3	S	S	9
41	E	E	E	E	E	E	E	E	2	E	E	11
42	N	N	N	N	N	N	N	N	4	N	N	10
43	T	T	T	T	T	T	T	T	0	T	T	4
44									1			2
45												1
46												
47												
48												
49												
50												
51												
52												
53												
54												
55												
56												
57												
58												
59												

LENGTH	18.9.80			2.10.80			2.10.80			15.10.80		
	2200; •			1300; 2			2200; 2			1000; 1		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												
31												
32	N											
33	O											
34	N											2
35	E											3
36						1						4
37	P		1			1						18
38	R		1			4						23
39	E		3			6						26
40	S		3			12			1			29
41	E		4			15	1		0	5		56
42	N		5	5	1	17			0	7	4	49
43	T		2	2		30			1	8	8	48
44			1	0		22			1	9	6	20
45		2	2	1		11			0	3	5	21
46			1	1	1	7			0	4	11	16
47			0		2	1			0	2	18	11
48			2			2			1	1	13	3
49						0		1			4	1
50						0					8	
51						1						
52												
53												
54					1							
55												
56												
57		68;1										
58												
59												

TABLE 1 Cont'd

	15.10.80			30.10.80			30.10.80			30.10.80			12.11.80			12.11.80			12.11.80			24.11.80			24.11.80			24.11.80			24.11.80			24.11.80			25.11.80		
	2100; 2			1500; 1			2200; 1			2300; *			0930; 2			1530; 1			2230; 1			0800; 1/5			1200; 1/5			1600; 1/5			2000; 1			2400; 1			0400; 1		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																							
27																																							
28																																							
29																																							
30						1																																	
31						1																																	
32						4																					1												
33						6																					1						2						
34						15						1						3									1			2			2						
35						34			2			1		N	2			3						1			6			4			4						
36			2			61						7		O	1			8			1			1			22			11			16			1			
37			0			85				1		12		N	1			12			2			3			35			32			33			6		N	
38			3	1		102				2		15		E	2			22			1	2		13	3		75			55	1		79			16		O	
39			3	3		77			2	4	1	10	4			4	1	27			0	3		20	10		83	3		62	4		80	3		15		N	
40			5	3		79			0	5	1	14	3	P		3	0	31			0	11		34	14	1	100	10		98	8		90	3		24		E	1
41			2	9		69			0	9	6	7	7	R		7	0	25			4	18	5	48	24	2	98	16		108	10		86	4		36	1		
42		1	3	24	2	68			1	9	21	19	6	E		6	1	40	3		0	17	8	56	32	5	89	32	2	85	7	2	64	9		31		P	
43	1	0	2	28	6	86			2	15	31	14	7	S		7	1	34	3		0	22	8	49	31	6	55	24	6	62	6	1	39	11	2	27		R	
44		0		33	11	72	1		1	17	42	9	10	E		10	0	11	0		0	14	9	31	20	10	43	12	8	42	4	0	20	9	0	8		E	
45		2		20	21	70	1	1	1	8	60	19	11	N		11	1	6	1	1	2	8	13	19	10	13	29	9	9	28	3	1	12	6	0	8	1	S	
46	3	2		13	24	58		0	0	7	95	14	2	T		2	2	6	1		1	3	14	16	5	17	10	3	12	18		2	2	4	1	6		E	
47		3		4	34	35		0	1	5	99	10	2			2	3	5			2	4	21	10	4	17	10	2	10	14		1	1	2	0	3		N	
48	1	2		3	34	12		1	1	3	81	7	2			2	1			1	0	4	16	5	4	12	5	2	7	4		0	1	1	1	2		T	
49		0		2	19	4				2	57	3							1		1		14	1	2	8	2	1	11	3		1	1	2	1	1			
50	1	1			12	4				1	35	1											11	1	2	10	2		6	1					1	1			
51					3	1					17	1											6	1		3	1		4	1					1	1			
52					5	1					11												4	0		1			0						1	1			
53						0					1													1		2			2										
54						2					1															1													
55																																							
56																																							
57																																							
58																																							
59																																							

TABLE 1 Cont'd

	25.11.80			10.12.80			11.12.80			22.12.80			23.12.80			7.1.81			21.1.81			1.2.81			1.2.81			16.2.81			16.2.81			17.2.81			3.3.81		
	0800; 1			2200; 1			0830; 1			1130; 1			2145; 1			1215; 1			0900; 1			1330; 2			2300; 1			1715; 1			2215; 1			1200; 1			1430; ½		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																							
26																																				1			
27																																				3			6
28																																				3			17
29																														4						8			70
30												1			1			2						1						5						22			160
31									1			2			6			9						1			1			7						22			298
32									6			1			5			33			1			3						14	N					34			325
33									8			6			3			77			2			3						16	O					24			274
34						1			14			7			1			100			5			9						18	N		1			19			152
35									10			6			2			115			13			12						18	E					12			81
36									12			5			2			125			14			8						15						7			40
37									12			11			7	2		141			17			10			1			13	P					8			12
38									18	1		11			5	2		131	1		11			12						9	R			1		5			9
39	1					2	2		17	0		3			9	3		117	0		5			8					1	10	E		1	1		5			7
40	13			1		1	1		19	4		13	1		13	8		107	3		4	1		4			1	2	1	12	S		0	2		5			5
41	16			0		2	4	2	20	7		16	5		23	16	1	99	4	1	7	1		13			1	1	2	13	E		1	3	1	6			5
42	20	3		2		5	5	2	18	16	1	26	5		19	29	7	90	2	1	9	2		12				2	1	11	N		2	4	2	10	1	1	3
43	13	4		4	2	6	5	2	15	19	1	28	5		18	19	11	95	7	1	3	2		5				3	6	8	T		1	2	5	8	1	0	3
44	10	8		5	0	7	3	3	19	9	5	26	4		13	18	14	38	4	4	4	4		9				3	2	8			0	1	5	4		1	4
45	6	12		4	2	7	5	4	16	9	9	22	4		9	13	16	22	4	3	3	4		11	1	1	1	1	3	7			1	1	4	4		2	1
46	6	3		2	0	4	0	3	6	2	12	15	0	1	8	7	27	11	2	4	3	4	3	6			0		0	5		1	0	2	4	2		0	2
47	2	3		0	2	1	1	5	3	2	21	9	2	0	4	4	27	9	1	4	1	2	3	4			1		2	4		0	0	1	2	2	1	3	2
48		4		1	2	0		4	3	3	8	3	0	1	1	2	20	6	1	5			1	4					2	2		1	1	1	1	0			1
49		2		0	2	2		1	0	0	7	3	1	1	1	1	11	2		0			0	2						1				1	1	0			1
50		3		0	0	2		3	1	1	5	1	0	1	2	2	5	1		1			1	0				1		2					2	1			
51		1		1	1	1					2	1	0			1	2				1			2		1				1					2		2		
52		0									1		1				2							1						0									
53		1															1							1						1									
54																	0																						
55															1		1																						
56																																							
57																																							
58																																							
59																																							

TABLE 1 Cont'd

	7.3.81			17.3.81			17.3.81			30.3.81		
	2130; 1			0930; 1			1800; 1			1700; 1		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29									2			1
30									5			12
31						4			11			27
32			1			6			26			47
33			1			9			49			45
34			0			5			51			38
35			2			2			51			36
36	1		2			6			43			39
37	0		1			6	3		37	1		27
38	3		4			2	3	1	18	1		23
39	6		1	1		0	2	0	10	1		8
40	6	3	3	0		2	3	0	9	0		7
41	9	7	1	1		4	5	1	7	1	3	4
42	5	13	0	2	1	4	4	1	7	0	2	3
43	5	33	1	2	2	3	1	2	3	2	0	2
44	4	44		1	0	2	0	1	4	1	1	3
45	0	51		0	0		1	0	3		2	2
46	0	42		1	1		1	1	2			
47	0	22		1			1	0	2			
48	1	11		0			1	0	2			
49		7		1			0	1	1			
50		2					2		0			
51									1			
52												
53												
54												
55												
56												
57												
58												
59												

	15.4.81			15.4.81			27.4.81			27.4.81		
	1645; 1			2200; 1			1715; 1			2130; 1		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27			5									
28			9									
29			24									
30			67						4			
31			101			3	NONE PRESENT		10	NONE PRESENT	NONE PRESENT	
32	NONE PRESENT		150			2			25			1
33			129			3			35			2
34			92			8			38			1
35			54			5			45			1
36			42			5			40			1
37			24			5			41			1
38			15			4			28			1
39			12			1			16			0
40			6			1			7			0
41			3		1	1			4			1
42			5		1	1		1	3			
43			3					1	3			
44		1	1					0	2			
45		0	2					1	0			
46		0	1					2	1			
47		0						0				
48		1		1				1				
49								1				
50												
51												
52												
53												
54												
55												
56												
57												
58												
59												

	13.5.81			21.6.81			28.6.81			16.7.81			17.7.81		
	2000; •			1115; 1			2030; •			1600; 2			2245; •		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25															
26															
27						3									
28						9									
29			1			18						1			
30			3			39						0			
31	NONE PRESENT		8	NONE PRESENT	NONE PRESENT	86			1	NONE PRESEN	NONE PRESEN	2			1
32			6			105			6			1			9
33			11			120			9			1			18
34			8			78			12			1			17
35			9			42			10						32
36			3			22			18						43
37			5			10			26				1		55
38			2			1	1		28						49
39			3						21						29
40			3						14						24
41			3					2	12					1	18
42		1	2					4	14					2	24
43		0	1					6	9				1	1	20
44		1	1					6	4					2	16
45		1	1					6	4					3	10
46		0	1					3	2					3	8
47		1	0					4	1					4	4
48		1	0					1						3	0
49		1	1					0						2	1
50								1						1	
51								2						2	
52								1	1					2	
53								0						4	
54		2						2						1	1
55			1					1							
56								64;1						63;1	
57		1						66;1						66;1	
58								77;1						84;1	
59		1						94;1						86;1	
		98!1													

TABLE 1 Cont'd

	14.8.81			25.9.81			13.10.81			18.11.81			16.12.81			18.1.82			23.1.82		
	2300; *			2100; *			0930; 1			0915; 1			1700; 1			1200; 1			1800; }		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																					
26																					
27																					
28																					
29																					
30																					12
31	N																				26
32	O																	1			65
33	N											1			1			2			79
34	E		1						1			2			1			1			91
35			8						3			7			4			6			82
36	P		6						8			33			24			7			48
37	R		16						19			64			40			10			36
38	E		20	1					24			80	1		58	4		11	2		14
39	S		19	0		1			36	2		85	2		62	3		13	1		15
40	E	1	18	2		1			40	4		114	2		61	4		20	2		16
41	N	1	10	1		2			39	6		111	3	1	51	5		16	2	2	15
42	T	3	3	1		5	3	1	33	8		86	4	0	28	3	2	10	1	0	12
43		3	4	3	2	10	5	5	19	5	2	50	4	3	20	3	0	9	0	0	7
44		5	0	6	4	16	4	5	4	4	5	26	3	2	15	2	1	3	2	1	5
45		4	1	7	11	20	1	4	3	3	6	13	4	2	7	4	0	2	0	1	2
46		2		8	16	26	0	3	3	2	3	11		2	4	1	1	3	2	0	1
47		3		4	37	28	0	3	0	1	1	2		4	1	0	2	0	0	1	3
48		0		3	37	20	1	1	1	0	2	1		1	0	0	1	1	1		1
49		1		3	43	16		0	1	1	1			0	1	1		0			0
50				3	36	8		0			0			1				1			1
51		62;1		0	27	6		0			1			0				0			0
52		68;1		1	18	4		1			1			0				0			0
53		70;1			10	1		1						1				1			1
54		71;1			6	1															
55		72;1			2																
56		92;1			2																

TABLE 2   Length Frequency data for smelt collected in seine hauls in the Whanganui stream

	11.10.80			16.11.80			10.12.80			7.1.81			1.2.81			3.3.81			31.3.81			21.10.81			17.12.81			21.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																	
26																																	
27																																	
28																																	
29																																	
30																																	
31																		7			3												1
32																		12			5									1			8
33																		22			9												14
34												1						27			11									1			24
35						1												31			18			1						2			33
36						1			1			3				1		20			16			1			1			4	1		31
37						6			1	1		8			1	1		18		1	16			14			6			7	2		45
38			2			18			4	5		17			1	5		11		2	10			27	1		7	3	1	27	3	5	46
39			3	1		20			14	5		25			3	6		3	1	2	3			30	1	1	10	4		30	1	8	39
40	1		6	3		32	1		24	11		34	2	1	7	7	4	13		7	6	1		34	1	1	15	6	4	52	3	16	43
41	4	1	7	7	2	53	2		14	11	3	41	3	3	11	8	19	8	1	14	3	1	1	34	4	4	9	7	12	56	1	18	33
42	8	2	19	9		46	5	3	19	14	9	36	6	9	12	9	26	7		35	4	3	1	29	2	17	11	7	22	54		14	19
43	10	2	28	8	6	42		3	24	14	23	25	5	21	12	8	53	6	1	44	4	2	4	24	3	43	8	7	26	48		17	8
44	5	5	28	11		29	7	5	15	9	28	15	2	26	7	4	71	6		39	2	2	3	15	2	41	8	6	25	32		12	10
45	4	15	15	15	6	13	8	7	10	6	43	17	3	37	6		71	2		34		2	8	3	2	53	5	2	27	14	2	4	
46	4	15	16	10	9	16	6	13	9	5	56	6	1	30	4		48	2		30		1	6	2		52	3	1	16	12	1	2	
47	7	25	10	10	8	11	5	11	4	1	52	6		22	2		30		1	22		2	8	1		54		1	13	5		2	2
48	1	35	16	8	9	6	4	11	4	1	40	3		15	1		22			8		1	2			52	1		3	2	1		2
49	1	13	2	2	5	3		10	2		27	2		7	2		8			6			3			30			3				1
50		11	1	1	6	3		6			20			4	3		4			2	1	1				10				1			
51		8			4	3		3		1	13			4	1		2									5		1					
52		1			1			3			8				1											5			2				
53		2						2			6		1	1	1											2							
54							1				1												1			1			1				
55														1												1							

TABLE 3 Length frequency data for smelt collected in seine hauls in the Waihaha river.

	15.12.80			1.2.81			23.10.81			17.12.81			21.1.82			TIEKE FALLS 21.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																					
26																					
27																					
28																					
29																					
30																					
31																					1
32																					7
33																					5
34																					12
35															8						7
36			1												17						14
37			1						6			7			22			1			19
38			1			4			8	2		13			30			2	2		10
39	1		3	1		2			9	1		15	3		25			4	2	2	13
40	1		8	2		3			21	4		27	5	1	29			15		3	8
41	2		14	1		5			22	7	1	40	5	3	23		1	17		6	6
42	6		12	2		7	2	1	19	14	7	35	5	4	19		2	30		4	1
43	2		14		1	6		4	13	15	7	37	5	5	11		8	38	1	1	3
44	5	2	5	1	2	4		2	6	17	17	20		5	8		7	34		1	
45	1	2	7	2	3	3		2	3	5	22	23		3	5	1	17	20		1	1
46	2	2	2	3	3	4		3	2	4	18	16		3	4		19	12			
47	3	5	1	2	4	1				4	17	9		2	1		19	11		1	1
48	3	2	1	1				2		1	14	3					20	7			
49	1	1									9	1			1	1	16	5			
50	1	1			2					1	7					1	14	2			
51	1	1		1		1		1			1	1					10	1			
52											1						6	1			
53				1													3	1			
54											1						2	1			
55																	3				
56																	2				
57																	1	1			
																	1	1			
																		2			

TABLE 4. Length frequency data for smelt collected in seine hauls in the Waihora stream.

LENGTH	12.10.80			18.11.80			12.12.80			7.1.81			1.2.81			3.3.81			31.3.81			20.10.81			17.12.81			21.1.82			13.3.82		
	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																																	
26																																	
27																																	
28																																	
29																																	
30																																	
31																					3												
32																		2			5												2
33																		1			9									1			2
34																					11									1			2
35	N		1									2				1		3			18	N		3						2			7
36	O								4			5						5			16	O		6						1			2
37	N		3			1			7			4			1	2		2			16	N		15			2			4			2
38	E					2			7			6	2		1	3		7		1	10	E		15			1			12		2	4
39			3			4	2		10			18	1		3	5	1	8			3			16	1		3	1		17	1		1
40	P		1			3	1		18			24	3		5	9	3	5		1	6	P		18	1	1	5	3	1	21	2	2	
41	R		1	1		4	2		25	7	1	38	5	3	8	11	13	8			3	R		13	3	2	5	1	9	40		5	
42	E			4	1	4	2	1	17	8	4	43	11	10	13	7	27	12	1	4	4	E		10	2	6	6	3	24	38		3	
43	S		3	3	5	4	4	2	10	13	6	44	11	24	14	7	37	9	1	6	4	S	1	6	4	7	8	2	39	32	1	4	1
44	E			4	8	12	3	3	12	8	16	39	7	41	12	4	43	7		6	2	E	1	2	3	17	5	1	43	15		1	1
45	N	1	2	4	9	2	2	8	5	9	24	33	3	81	2	1	32	2		8		N	1	1	3	27	4	3	34	8		1	
46	T	1			19	4		8		4	26	13	2	90	1	1	25	4		8		T	1		1	36	1		33	2		1	1
47				1	24	3		7	2	1	24	7	2	57	1	1	17			6			2			33		1	25				
48				1	21	2		11		1	26	3	1	43	2		9	1		4						21	1		12	1		1	
49				1	12			6		2	22			26			4			2						8			3				
50		1			9			4			11	1		19			1			1	1					8			2				
51		1			4			1			9	1		8	1		1			1						4			1				
52					5			2		1	1			3																			
53					2						1			1																			
54					1			1			1			1																			
55																										1			1				
56																																	
57		1																															
58																																	

TABLE 5 Length frequency data for smelt collected in seine hauls at Five Mile Bay

	30.1.82			30.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25						
26						
27						
28						
29						
30						
31			1			
32			1			
33			5		N	
34			5		O	
35			1		N	
36			4		E	
37			2		P	
38	1		6		R	
39			8		E	
40	1		3		S	
41	1		6		E	
42	1		5		N	
43		1	6		T	
44		2	3			
45	1		4			
46	1	2				
47		4				
48		2				
49		2				
50		1				

TABLE 6 Length frequency data for smelt collected in seine hauls in the Waitahanui river.

	2.10.81			17.12.81			30.1.82			21.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29							NONE PRESENT					
30												
31												
32												
33												
34												
35												
36												
37												
38												
39												
40												
41												
42												
43												
44												
45												
46												
47												
48												
49												
50												

TABLE 7 Length frequency data for smelt collected in seine hauls in the outlet to Lake Rotongaio

	17.12.81			30.1.82			21.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25									
26									
27									
28									
29									
30									2
31						2			5
32						2			10
33						4			16
34			3			13			18
35						35			19
36			1			55			21
37			9			85			26
38			14			79	1		21
39			13	1		62	2	1	21
40			14	1		53	2	2	9
41			19		1	33	2	2	12
42	1		22	1	3	25	1	2	13
43		1	15	2		18	2	5	14
44		1	7		3	12		4	5
45	1		4		2	8	2	2	7
46		3	3		3	6	3	1	3
47	1	1	1	1	2	4		3	2
48		2		1	3	3		2	2
49		1			2	2	2	4	
50					2	1	2	3	2
51		1			1	1	1	3	
52					1			1	1
53								1	
54		1			1				
55								1	
56									
57								1	

TABLE 8 Length frequency data for smelt collected in seine hauls in the Hatepe river.

	2.10.81			17.12.81			30.1.82			21.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												
31									3			2
32						1			6			7
33			1			1			16			15
34			4			5			28			19
35			10			8			43			21
36			10			10			65		1	26
37			20	1		24	3		100	1		24
38			29			27	2		102	1	1	32
39	1		33			21	3		68	3	3	24
40			39			24	1	1	59	1	6	21
41			39	1		23	1	2	42		5	14
42		1	29	1	1	17	2	1	31	1	6	8
43		2	19	2		13	2	4	28	2	7	6
44		2	8	1		6	1		6	2		5
45			2	1	2	4	1	4	4	1	3	2
46		2	1	2	2	1	2	2	1	1	5	2
47		1	1		1	1			2			
48		3	1		1	2	1	1	1			1
49		1									1	
50		1							1		1	
51												
52							1		1			
53											1	1
54		1										
55												
56												
57									1			

TABLE 9 Length frequency data for smelt collected in seine hauls in the Tauranga-Taupo river.

	20.10.81			17.12.81			30.1.81			30.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25															
26															
27															
28															
29															
30												1			
31												3			2
32													N		1
33													O		
34		N						N					N		
35		O	1					O					E		
36		N						N							
37		E	1					E					P		
38													R		
39		P						P				1	E		
40		R				1		R					S		
41		E						E					E		
42		S						S					N		
43		E	1					E					T		
44		N						N							
45		T						T							
46															
47															
48															
49															
50															

TABLE 10 Length frequency data for smelt collected in seine hauls in the Waimarino stream

	20.10.81			17.12.81			30.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												
31												
32									1			3
33									1			11
34									5			17
35			3			1			9			21
36			4			4			16			14
37			6			7			23			16
38			17	1		12	1		32			16
39			28	5		21	1		34			16
40			33	6	3	25	1	1	39		3	19
41		2	30	7	4	29	1	8	39	1	4	16
42	1	5	33	7	7	22	3	9	33		5	9
43	1	9	42	10	21	21	2	9	22	1	3	8
44	3	7	34	6	23	13	1	12	14		1	4
45	1	15	20	6	18	9	1	8	8		4	2
46	1	14	16	2	18	8		6	7		2	1
47	2	16	14	2	12			4	1		2	
48	1	10	6	1	9	2	1	3	1	1	1	1
49	2	11	4		3			1				2
50	1	11	3		3			1				
51	1	5	1		1			1				1
52	1	3			1							
53	1	3										
54		1										
55		1			1							
56												
57												
58	1											
59		1										

TABLE 11 Length frequency data for smelt collected in seine hauls in the Waiotaka stream

	20.10.81			17.12.81			30.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												
31												1
32						1						3
33						1			1			1
34						5			1			3
35						8			1	N	N	
36			1			10			1	O	O	3
37			3	1		24			3	N	N	2
38			4			27			5	E	E	1
39			9			21			14			
40		1	12			24	1	1	15	P	P	
41	1	1	10	1		23	1	4	19	R	R	1
42	1		13	1	1	17	3	7	16	E	E	
43	1	5	14	2		13	2	10	14	S	S	
44		5	12	1		6	1	6	6	E	E	
45		5	11	1	2	3	3	6	2	N	N	
46		5	4	2	2	1	3	5	1	T	T	
47		6	3		1	1	3	7	3			
48	2	6			1	2		2	4			
49		2	2					1	1			
50		2						1	2			
51	1							1	1			
52								1				
53			1									
54												
55			1									

TABLE 12 Length frequency data for smelt collected in seine hauls in the Tongariro river at the Blind Mouth

	20.10.81			17.12.81			30.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25												
26												
27												
28												
29												
30												1
31									2			3
32						1			7			7
33	N								15			21
34	O								27			32
35	N		5			3			52			33
36	E		10			9			66			31
37			23			16			79	1		37
38	P		45	1		25	2		70			29
39	R		41	1		37	2		64		1	16
40	E		37	6	1	41	2	2	57	1	1	18
41	S		20	7	2	40	7	3	39			15
42	E	1	12	5	8	38	7	6	31		3	10
43	N		4	6	16	27	4	6	22	1	1	7
44	T			6	15	12	2	4	6		1	5
45		1		5	22	12	3	5	4		3	3
46				1	16	11		3	5	2	2	1
47		1	1		9	3	1	4	3		1	
48					7						2	
49					4	1					1	
50					3							
51					1			1		1		
52					1							

TABLE 13 Length frequency data for smelt collected in seine hauls in the Kuratau river

	15.12.80			31.1.81			21.10.81			17.12.81			21.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																		
26																		
27																		
28																		
29																		
30																		
31															1			1
32															2			6
33									1						2			7
34						1			1			6			2			21
35						2			7			6			15			29
36						7			16			16			27	1		35
37			2			7	N		33			43	1		54			59
38			3	2		10	O		49	3		59			58	5	6	71
39			10	1		15	N		39	5		62	1		57		8	50
40	2		13	2		18	E		29	10	1	62	1	2	52	1	11	35
41		1	20	5		31			19	10	3	53	4	2	38		13	25
42	8	3	12	4	3	33	P	1	17	18	11	34	3	4	32		11	14
43	5	6	16	3	8	44	R	1	12	17	16	28	3	6	27	1	7	12
44	4	6	18	2	10	20	E	2	1	10	13	11	2	9	12	1	7	5
45	2	15	12	1	9	9	S	5	4	7	18	7	2	4	7		5	1
46		12	2		9	4	E	3	2	2	18	6	2	3	2		1	
47	2	13	1	1	5	5	N	1		3	16	2		1			1	1
48		14	3		2	3	T			1	10						1	2
49		5			1					1	3	1		2			1	
50		2			1	1					1		1	1				
51		2			1						2						1	
52														1				
53		1																

TABLE 14 Length frequency data for smelt collected in seine hauls in the Whareroa stream

	15.12.80			31.1.81			21.10.81			17.12.81			21.1.82			13.3.82		
LENGTH	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R	♀♀	♂♂	N/R
25																		
26																		
27																		
28																		
29																		
30																		
31						2												
32						2												2
33						1												4
34						1												3
35			6			3	N	N	1						3			9
36			12	1		10	O	O	2						4			18
37			29			6	N	N	4			3			3			11
38			40	1		15	E	E	8			4			13		2	11
39			71	3		22			7			4			15	1		14
40	2	1	78	5		28	P	P	7	1		5	1		15			12
41	3		76	6	2	38	R	R	9	1		4	2	2	23		1	7
42	9	2	60	2	6	40	E	E	3	3		9	2	3	22			5
43	12	2	58	4	11	30	S	S	1	4	5	8	2	8	21		3	6
44	6	4	36	3	13	24	E	E		3	12	4		5	9	1	2	3
45	4	5	27	1	17	14	N	N		2	19	6		3	4		1	1
46	2	9	18		14	8	T	T		1	32	4			3		1	
47	3	6	5		11	4					37	3			1		1	1
48		9	7		11	3					45	2		2			1	
49		4	1		6	2				2	46				1			
50		3			3						35	1				1		1
51		1			1						23							
52		1	1								14							
53											7							1
54											4							
55																		
56																		
57											1							

APPENDIX 3

Length frequency data for smelt caught in dropnet samples and nocturnal ringnet tow samples. Fast tows (> $2m.s^{-1}$) are indicated by F and slow deep tows by S.

APPENDIX 3 - Pelagic smelt samples

SMELT LENGTH	20-9-79 Dropnet	4-10-79 Dropnet	11-11-79 Dropnet	28-11-79 Dropnet	13-12-79 Dropnet	5-1-80 15 min tow by day	7-1-80 15 min tow by night	25-1-80 20min tow by night	7-2-80 2300 hrs 15min tow	23-2-80 2400 hrs 15min tow	20-3-80 2200 hrs 15min S tow	20-3-80 2230 hrs 15min F tow	4-4-80 2115 hrs 15min ¼ moon	7-4-80 2045 hrs 15min no moon	19-4-80 No moon 15min tow
3								1				1			
4								3				4			
5							1	7				4			
6				1		2		19		4	3	3	1		
7				1	1	3	1	27	1	7	1	9	0		
8				1	3	3	3	34	3	5	0	12	3	1	1
9			1		1	8	2	39	2	6	2	10	0	4	1
10		1	1			3	2	36	4	2	1	15	2	3	2
11		1	1				2	35	6	3	2	18	0	7	2
12			1	2			1	30	5	0	3	13	3	9	4
13	1			3	1	2		29	4	3	3	10	4	11	9
14	1			3	1			27	5	4	0	12	3	10	7
15			1	6				24	2	4	3	14	2	11	7
16				2				17	4	6	2	10	1	9	5
17		1		1	1		1	12	2	2	2	7		11	5
18	3	5		2			1	8	3	5	1	3	1	15	1
19	1	1		2				2	4	2	2	8		12	3
20							1	3	3	4	1	5		11	4
21	3	1					1	2	5	1	3	4		9	4
22	1							2	6	4	1	3	1	3	2
23	2								3	2	0	3	1	4	2
24	2	1					1		5	0	1	1	1	7	3
25	7		1				1		8	1	1	3		11	0
26	3						1		2			2		10	3
27	7	2	1				2	1	3	2	1	1		6	1
28	12	5		1				1	2	2	2	1		4	1
29	9	5	1						3		2	2		5	2
30	13	1							2		2	1		4	2
31	13	2		1			2				1	0		3	1
32	2	3					1		3		3	1		1	1
33	4	2					2		7			0		3	2
34	2						1		6			1		2	1
35	1						3		5			1		1	2
36									2					1	0
37									2					1	1
38							1		3						0
39					1				1	1			1		1
40							1		3				1		1
41									5				1		
42							1		3						
43									1						
44															
45									1						
46															
47															
48							1								

Pelagic smelt samples cont'd

25-4-80 2145 hrs 15min tow ¾ Moon	13-5-80 2130 hrs 15min No Moon	13-5-80 30min I.K. Tow	14-5-80 1400 hrs 10 drops 40m	14-5-80 Noon 10 drops 60m	14-5-80 1300 hrs 10 drops 100m	30-5-80 2230 hrs 20min tow Full Moon	13-6-80 2015 hrs 20min Tow	25-6-80 2330 hrs 20min tow ½ Moon	27-6-80 1500 hrs 8 drops 40m	27-6-80 1600 hrs 50 drops 90m	27-6-80 1700 hrs 2 drops 105m	10-7-80 220 hrs 20 min tow No Moon	27-7-80 2115 hrs 20 min tow Full Moon	10-8-80 2100 hrs 20min tow No Moon
1														
2	1	1		1		2		2	1					
3	1	2	1			1		0						
1		1			1	3		1		1				1
2					2	2	1	0	1	1			1	1
1	2			3	2	0	2	1	0			1		
3	2			2	4	1	2	1	1		1	1		
0	1	1	1	2	5	1	0	1	3	1				1
3	3		3	2	3		0	0	1	0		1		1
1	1		1	4	5		1		1	2	1			0
1	4		2	5	4		0		0	1				1
1	5		4	4	4		1		0					0
	5		5	7	7		2		1		1	2		1
	3		6	5	3		2		1					1
	4		6	8	5		0		1	2				1
1	5		6	10	4		0		1	0		2		1
	3		2	10	2		0		1	2		0		0
	7		3	9	2		0		1	0		2		4
	4		3	6	0		1			1		4		3
	3		1	8	3		2			1		2		0
	0			7	1		4			0		2		6
	1			4	1		1		1	2		3		8
	1			2	2		1					6		10
	3			0			1					8		14
	2			1			0					8		13
	0			1			2	1	1			9		20
	0				1		5					7		15
	1				1	1	5					6		10
	2					1	5	1		1	1	9	1	12
2	2					0	3	1	1	2		3	1	7
1	1					1	1	1				4		5
1	1					1						3		2
1	0					0								1
	1					0							1	1
	1					1								0
						0								0
						1								1

Pelagic smelt samples cont'd

20-8-80 2100 hrs 20min Tow ½ Moon	6-9-80 1500 hrs 3 drops 60m	6-9-80 1600 hrs 1 drop 100m	6-9-80 2100 hrs 20min Tow No Moon	18-9-80 2100 hrs 20min Tow	4-10-80 1900 hrs 20min Tow No Moon	15-10-80 1915 hrs 20min Tow	31-10-80 2400 hrs 20min Tow No Moon	12-11-80 2100 hrs 20min Tow	24-11-80 2100 hrs 20min Tow	12-12-80 2045 hrs Surface trawl	15-12-80 2230 hrs 20min drop-net tow	16-12-80 2100 hrs 20min surface tow	16-12-80 2100 hrs 20min dropnet tow AFAP	7-1-81 2245 hrs 20min Dropnet tow	30-1-81 2330 hrs 20min Tow
											1				
								1	1					3	
								1	1					4	3
					1			2	1		1			6	7
						1		3	2		1			8	10
								4	4		2		2	10	9
					1			3	4		2		7	9	8
								0	10		4		7	7	6
			1					2	5		2		10	5	2
			1			1		1	5		1		6	3	2
		1	0		1			1	5		2		2	1	2
			1					2	0		1		3		4
			1			2		1	0		1		4		3
	1		0			0	1	0	1				4		2
	0		0			2	0	1	1				3	1	4
	1		1			1	1				2		1	1	2
	1					1							3	1	1
													0		2
							2						1		2
							1	1					1		4
							4	2							
						2	1	0							1
							0	3							2
			1				1	0							0
			2		1		2	2							3
			2		1		0	4						1	0
			3		0		2	1						1	2
			4		2		0	1						1	2
			5		1		2	2			1			2	1
			1		1		6	1			1			3	1
			4		2		4	1		1	1				1
1			3		4		0	1		3				2	2
			1	2	3		3			4			1	4	3
1			2		0		5		1	5		1		1	3
			0		4		1	1		5	1	1		1	2
			1		4		1			3			1	3	0
					1		1			1				2	0
					0	1	3		1	1				1	1
					1									2	0
										1					1
															0
															1
										1					

Pelagic smelt samples cont'd

31-1-81 20min Tow	16-2-81 2130 hrs	7-3-81 2000 hrs 20min Tow No Moon	17-3-81 2300 hrs 20min Tow ½ Moon	1-4-81 2330 hrs 20min Tow	15-4-81 2000 hrs 20min Tow AFAP	15-4-81 2030 hrs 20min Tow Slow & Deep	15-4-81 2100 hrs Alt. Slow & Fast Tow	27-4-81 2030 hrs Alt. Slow & Fast Tow	11-5-81 1800 hrs 30min Tow
1	2		2						
1	8	5	5	3	2		2	1	1
	18	8	14	5	0	2	1	3	
	36	11	13	5	1	1	2	6	
	48	15	11	4	2	1	5	8	2
	45	16	17	9	4	0	6	8	1
	48	12	19	12	2	3	5	9	1
	48	8	16	14	4	2	4	7	1
	39	5	21	16	4	4	6	5	1
	36	5	20	14	4	5	8	7	3
	28	4	16	13	2	4	6	12	1
	21	5	12	12		4	11	8	2
	14	7	10	8		3	10	11	5
	12	9	6	5		4	4	17	4
	9	11	4	6		1	2	11	3
	7	12	3	7		0	4	7	1
	5	10	5	2		1	3	5	
	3	9	2	2		1	1	1	
	1	9	3	4		1	2	1	
		8	3	4			2	8	1
		7	1	2			1	6	1
		6	0	4				5	
	2	6	1	4		1		5	
		6		1				5	1
		4		3			1	3	2
		3		2			1	4	1
		2		3		1	1	6	
		1	1	3				2	
				3				3	1
				1	1			1	
					1				
								1	
								1	
							1	1	
				1					
				1					

APPENDIX 4

A listing of the BASIC programme used to simulate smelt population dynamics and a brief description are given. The simulation structure is illustrated in fig. 49.

Lines	
100 - 480	Define standard parameter values.
110	Determines whether or not standard parameter values will be used.
480 - 850	Provide for input of different parameter values.
850 - 940	Define memory variable requirements.
940 - 960	Provide options for which data is required for output.
960 - 970	Print the parameter values used.
970 - 980	Describe the initial smelt liberation.
1040 - 1270	Move parameter values associated with each habitat zone into "working" variables.
1270 - 1490	Describe movement between littoral and pelagic habitat zones.
1600 - 2000	Simulate maturation, spawning and post-spawning survival.
2000 - 2010	Define the quantity and size distribution of the food resource.
2010 - 2030	Initializes variables used later.
2030 - 2500	Calculate food allocation to each length interval.
2500 - 2870	Define the extent of growth or starvation.
2880 - 3040	Simulate trout movements between the littoral and pelagic zones.
3040 - 3100	Define the number of smelt in each length interval eaten by trout.
3100 - 3400	Simulate egg hatching.
3400 - 4100	Print selected smelt length frequency data and data for certain population parameters.
19000 - END	Trap errors.

```
00100   ONERROR GOTO 19000
        LINPUT "Output to terminal or filename: <TT:> ";f$
        f$ = "TT" if f$ = " "
        open f$ for output as file 1%
        DATAFLAG$="N"
        declare double sslowa,ssuppa,foodintake
        declare double competitors,STARVSURV,area,HUNGER
        declare double R05,R07,ripe,MET,LITT,PEL
00110   INPUT  "DO YOU WISH TO ENTER DATA Y/N<No> ";DATAFLAG$
        dataflag$ = left(edit$(dataflag$,-1%),1%)

        PRINT #1,"This version is the standard run "
        PRINT #1,""
        PRINT #1,""
        PRINT #1,""

        MAX%                   = 200%
        TIMEINTERVAL%          = 10
        STOPDATE               = 7200
        STARTSUMMARYDATA       = 15
        DAYNOW%                = 0

        LITPELRATIO            = 0.05
        SECCHIDEPTH            = 15
        LITTDEPTH              = 15
        PELDEPTH               = 110
        MAXLITTEMP             = 15
        MAXPELTEMP             = 15
        MAXTEMPTIME            = 120
        MINTEMP                = 15

        EGGSURV                = 1
        SPAWNSEASON%           = 360

        MAXTROUTNOS            = 2
        MAXTROUTNOSTIME        = 120
```

```
MINTROUTNOS         = 2
TROUTNOSPEAKWIDTHK  = 1

MAXMINSIZE          = 0.001
MAXMINSIZETIME      = 300
MINMINSIZE          = 0.001
MAXLITFOODPROD      = 1
MAXLITFOODTIME      = 120
MINLITFOODPROD      = 1
LITFOODPEAKWIDTHK   = 1
MAXLITAVSIZETIME    = 300
MINLITAVSIZE        = 4
MAXLITAVSIZE        = 4
LITAVSIZEPEAKWIDTHK = 1
LITTMAXSPRED        = 2
LITTMINSPRED        = 2
LITTMAXSPREDTIME    = 300
LITSPREDPEAKWIDTHK  = 1

MAXPELFOODPROD      = 1
MAXPELFOODTIME      = 300
MINPELFOODPROD      = 1
PELFOODPEAKWIDTHK   = 1
PELMAXAVSIZETIME    = 300
MINPELAVSIZE        = .3
MAXPELAVSIZE        = .3
PELAVSIZEPEAKWIDTHK = 1
PELMAXSPRED         = 1.2
PELMINSPRED         = 1.2
PELMAXSPREDTIME     = 300
PELSPREDPEAKWIDTHK  = 1

STARVK              = 1
MOV                 = -0.00004
TROUTPREDK          = 10000
ACUITY              = 0.023
BULLY$              ="N"
```

```
        BULLYPREDK          = 0.01
        MATURE              = -0.0003
        GOTO 00850 if DATAFLAG$<>"Y"

00480 INPUT  "enter time interval<10> ";TIMEINTERVAL%
        TIMEINTERVAL% = 10 IF TIMEINTERVAL% = 0
        INPUT  "STOP AFTER ? YEAR <3600> ";STOPDATE
        STOPDATE = 3600 IF STOPDATE = 0
        INPUT "START PRINTING SUMMARY DATA AT END OF YEAR ? <1> ";STARTSUMMARYDATA
        STARTSUMMARYDATA = 1 IF STARTSUMMARYDATA = 0
        INPUT "Do you want to change Lakes Yes/No<No> ";A$
        a$ = left(edit$(a$,-1%),1%)
        goto  00485 if a$ <>"Y"
        INPUT  "ENTER MEAN LITTORAL DEPTH <5> ";LITTDEPTH
        LITTDEPTH = 5 IF LITTDEPTH = 0
        INPUT "ENTER MEAN PELAGIC DEPTH <110> ";PELDEPTH
        PELDEPTH = 110 IF PELDEPTH = 0
        INPUT  "ENTER LITTORAL/PELAGIC RATIO <0.05> ";LITPELRATIO
        LITPELRATIO = 0.05 IF LITPELRATIO = 0
        INPUT "ENTER SECCHI DEPTH IN METRES <15> ";SECCHIDEPTH
        SECCHIDEPTH = 15 IF SECCHIDEPTH = 0
        INPUT "ENTER MAXIMUM LITTORAL TEMPERATURE <20> ";MAXLITTEMP
        MAXLITTEMP = 20 IF MAXLITTEMP = 0
        INPUT "ENTER DAYS AFTER OCTOBER 1 WHEN THIS OCCURS <130> ";MAXTEMPTIME
        MAXTEMPTIME = 130 IF MAXTEMPTIME = 0
        INPUT "ENTER MAXIMUM PELAGIC TEMPERATURE <15> ";MAXPELTEMP
        MAXPELTEMP = 15 IF MAXPELTEMP = 0
        INPUT "ENTER MINIMUM LAKE TEMPERATURE <10> ";MINTEMP
        MINTEMP = 10 IF MINTEMP = 0
00485   input "Do want to change Spawning conditions Yes/No<No> ";A$
        a$ = left(edit$(a$,-1%),1%)
        goto 00490 if a$<>"Y"
        INPUT  "ENTER EGG SURVIVAL  <1.0> ";EGGSURV
        EGGSURV = 1 IF EGGSURV = 0
        INPUT  "ENTER LENGTH OF SPAWNING SEASON <180> ";SPAWNSEASON%
        SPAWNSEASON% = 180 IF SPAWNSEASON% = 0
00490  Input "Do you want to change predator numbers Yes/No<No> ";a$
```

```
        a$ = left(edit$(a$,-1%),1%)
        goto 00500 if a$<>"Y"
        input  "MAXIMIM TROUT NUMBERS/HECTARE <3> ";A$
        MAXTROUTNOS = VAL(A$) IF LEN(A$)<>0
        INPUT  "PEAK TIME FOR TROUT NUMBERS <120> ";A$
        MAXTROUTNOSTIME = VAL(A$) IF LEN(A$)<>0
        INPUT  "MINIMUM TROUT NUMBERS/HECTARE<1> ";A$
        MINTROUTNOS = VAL(A$) IF LEN(A$)<>0
        INPUT "ARE BULLIES PRESENT ? YES/NO<NO> ";A$
        BULLY$ = LEFT(EDIT$(A$,-1%),1%)

00500  Input "Do you want to change Littoral feeding conditions Yes/No<No> ";a$
        A$ = LEFT(EDIT$(A$,-1%),1%)
        GOTO 00510 IF A$<>"Y"
        INPUT  "ENTER MAX RESOURCE <5> ";A$
        MAXLITFOODPROD = VAL(A$) IF LEN(A$)<>0
        INPUT  "PEAK TIME FOR LITTORAL FOOD <120> ";A$
        MAXLITFOODTIME = VAL(A$) IF LEN(A$)<>0
        INPUT  "MIN FOOD RESOURCE <.2> ";A$
        MINLITFOODPROD = VAL(A$) IF LEN(A$)<>0
        INPUT "MAX AVERAGE SIZE OF LITTORAL PREY SIZE  <15> ";A$
        MAXLITAVSIZE = VAL(A$) IF LEN(A$)<>0
        INPUT  "PEAK TIME FOR LARGE PREY <330>";A$
        MAXLITAVSIZETIME = VAL(A$) IF LEN(A$)<>0
        INPUT "MIN AVERAGE SIZE OF LITTORAL PREY  <5> ";A$
        MINLITAVSIZE = VAL(A$) IF LEN(A$)<>0
00510  Input "Do you want to change Pelagic feeding conditions Yes/No<No> ";a$
        A$ = LEFT(EDIT$(A$,-1%),1%)
        GOTO 850 IF A$<>"Y"
        INPUT  "ENTER MAX RESOURCE <5> ";A$
        MAXPELFOODPROD  = VAL(A$) IF LEN(A$)<>0
        INPUT  "PEAK TIME FOR PELAGIC FOOD <330> ";A$
        MAXPELFOODTIME  = VAL(A$) IF LEN(A$)<>0
        INPUT  "MIN FOOD RESOURCE <1> ";A$
        MINPELFOODPROD = VAL(A$) IF LEN(A$)<>0
        INPUT "MAX AVERAGE SIZE OF PELAGIC PREY  <1.0> ";A$
        MAXPELAVSIZE  = VAL(A$) IF LEN(A$)<>0
```

```
        INPUT  "PEAK TIME FOR LARGE PREY <330> ";A$
        PELMAXAVSIZETIME  = VAL(A$) IF LEN(A$)<>0
        INPUT "MIN AVERAGE SIZE OF  PELAGIC PREY  <0.1> ";A$
        MINPELAVSIZE  = VAL(A$) IF LEN(A$)<>0
00850   DIM PELFREQ(MAX%)
        DIM LITFREQ(MAX%)
        DIM SPAWNERS(360)
        DIM LITTBIOMASS(360)
        DIM PELBIOMASS(360)
        DIM LITTROUTFOOD(360)
        DIM PELTROUTFOOD(360)
        DIM LITTROUT(360)
        DIM PELTROUT(360)
        DIM FREQ(MAX%)
        DIM LITEATEN(MAX%)
        DIM PELEATEN(MAX%)
        KMIN% = 2%
        KMAX% = MAX%
        DIM RQDDAY%(36%),RQDYR%(10%)
        LASTYR%=(STOPDATE/360)-2
        DAY      = 1
        YDAY     = 360/TIMEINTERVAL%
        YYDAY    = (360-TIMEINTERVAL%)/TIMEINTERVAL%
        LITTROUTFOOD(YDAY)  = 100
        LITTROUTFOOD(YYDAY) = 100
        PELTROUTFOOD(YDAY)  = 100
        PELTROUTFOOD(YYDAY) = 100
00940 linput"Do you want to specify dates for intermediate print of Frequencies  Yes/No<No> ";a$
        a$= left(edit$(a$,-1%),1%)
        goto 00958 if a$<>"Y"
00943   linput"Enter Required day(s) (as  nnn,nn,nn) ";a$
        goto 00940 if a$=""
        k%,j%=0%
00945   i%= instr(j%,a$,',')
        i%= len(a$)+1% if i% = 0%
        k% = k%+1%
        rqdday%(k%)=val(seg$(a$,j%,i%-1%))
```

```
        j% = i%+1%
        goto 00945 unless j%>len(a$)
        numdr% = k%
00950   linput"Enter Required years(s) (as  n,n,nn  or  n:n) ";a$
        goto 00950 if a$=""
        k%,j% = 0%
        rn% =  instr(0%,a$,':')
        if rn%<>0% then
            rmin% = val(left (a$,rn%-1%))
            rmax% = val(right(a$,rn%+1%))
            rqdyr%(j%) = j% for j% = rmin% to rmax%
            k% = k%+1% for j% = rmin% to rmax%
            goto 00957
00955   i%= instr(j%,a$,',')
        i%= len(a$)+1% if i% = 0%
        k% = k%+1%
        rqdyr%(k%)=val(seg$(a$,j%,i%-1%))
        j% = i%+1%
        goto 00955 unless j%>len(a$)
00957   numpyr% = k%
00958   print"Do you want to change range of lengths shown? (3-";max%;
        linput")  Yes/No<no> ";a$
        a$= left(edit$(a$,-1%),1%)
        goto 00960 if a$<>"Y"
        input"Start length frequency display at length? <3> ";kmin%
        kmin% = 3% if kmin%=0%
        print"Finish frequency display at length? <";max%;
        input "> ";kmax%
        kmax% = max% if kmax%=0%
00960   PRINT #1,"MEAN LITTORAL DEPTH                                  =   ";LITTDEPTH
        PRINT #1,"MEAN PELAGIC DEPTH                                   =   ";PELDEPTH
        PRINT #1,"MAXIMUM LITTORAL TEMPERATURE                         =   ";MAXLITTEMP
        PRINT #1,"MAXIMUM PELAGIC TEMPERATURE                          =   ";MAXPELTEMP
        PRINT #1,"MAXIMUM TEMPERATURE OCCURS ";MAXTEMPTIME;" DAYS AFTER OCTOBER 1"
        PRINT #1,"MINIMUM TEMPERATURE                                  =   ";MINTEMP
        PRINT #1,"RATIO OF LITTORAL TO PELAGIC HABITAT                 =   ";LITPELRATIO
        PRINT #1,"SECCHI DEPTH (metres)                                =   ";SECCHIDEPTH
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PRINT #1," "
PRINT #1,"LENGTH OF SPAWNING SEASON (DAYS)                      =   ";SPAWNSEASON%
PRINT #1,"EGG SURVIVAL                                          =   ";EGGSURV
PRINT #1," "
PRINT #1,"MAXIMUM TROUT NUMBERS PER HECTARE                     =   ";MAXTROUTNOS
PRINT #1,"MINIMUM TROUT NUMBERS PER HECTARE                     =   ";MINTROUTNOS
PRINT #1,"PEAK TROUT ABUNDANCE OCCURS ";MAXTROUTNOSTIME;" DAYS AFTER OCTOBER 1"
PRINT #1,"PEAK BREADTH CONSTANT FOR TROUT ABUNDANCE             =   ";TROUTNOSPEAKWIDTHK
PRINT #1," "
PRINT #1,"  ARE  BULLIES  PRESENT ?                                 ";BULLY$
PRINT #1," "
PRINT #1,"MAXIMUM DAILY LITTORAL FOOD PRODUCTION (WET WEIGHT)  =   ";MAXLITFOODPROD
PRINT #1,"PEAK LITTORAL FOOD PRODUCTION OCCURS ";MAXLITFOODTIME;" DAYS AFTER OCTOBER 1"
PRINT #1,"MINIMUM DAILY LITTORAL FOOD PRODUCTION (WET WEIGHT)  =   ";MINLITFOODPROD
PRINT #1,"PEAK BREADTH CONSTANT FOR LITTORAL FOOD PRODUCTION    =   ";LITFOODPEAKWIDTHK
PRINT #1," "
PRINT #1,"MAXIMUM LOWER PREY SIZE LIMIT                         =   ";MAXMINSIZE
PRINT #1,"MAXIMUM LOWER LIMIT OCCURS ";MAXMINSIZETIME;"DAYS AFTER OCTOBER 1"
PRINT #1,"MINIMUM LOWER PREY SIZE LIMIT                         =   ";MINMINSIZE
PRINT #1," "
PRINT #1,"MAXIMUM AVERAGE SIZE OF LITTORAL PREY                 =   ";MAXLITAVSIZE
PRINT #1,"MINIMUM AVERAGE SIZE OF LITTORAL PREY                 =   ";MINLITAVSIZE
PRINT #1,"MAXIMUM AVERAGE SIZE OCCURS ";MAXLITAVSIZETIME;" DAYS AFTER OCTOBER 1"
PRINT #1,"PEAK BREADTH CONST. FOR AVGE SIZE OF LITTORAL PREY    =   ";LITAVSIZEPEAKWIDTHK
PRINT #1," "
PRINT #1,"MAX. SHAPE CONST. FOR LITTORAL PREY SIZE DISTRIBUT'N =   ";LITTMAXSPRED
PRINT #1,"PEAK TIME FOR MAX. LITTORAL SHAPE CONSTANT            =   ";LITTMAXSPREDTIME
PRINT #1,"MIN. SHAPE CONST. FOR LITTORAL PREY SIZE DISTRIBUT'N =   ";LITTMINSPRED
PRINT #1,"PEAK BREADTH CONST. FOR LITT. PREY SIZE SHAPE TERM    =   ";LITSPREDPEAKWIDTHK
PRINT #1," "
PRINT #1,"MAXIMUM DAILY PELAGIC FOOD PRODUCTION (WET WEIGHT)   =   ";MAXPELFOODPROD
PRINT #1,"PEAK PELAGIC FOOD PRODUCTION OCCURS ";MAXPELFOODTIME;" DAYS AFTER OCTOBER 1"
PRINT #1,"MINIMUM DAILY PELAGIC FOOD PRODUCTION (WET WEIGHT)   =   ";MINPELFOODPROD
PRINT #1,"PEAK BREADTH CONST. PELAGIC FOOD PRODUCTION           =   ";PELFOODPEAKWIDTHK
PRINT #1," "
PRINT #1,"MAXIMUM AVERAGE SIZE OF PELAGIC PREY                  =   ";MAXPELAVSIZE
PRINT #1,"MINIMUM AVERAGE SIZE OF PELAGIC PREY                  =   ";MINPELAVSIZE
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        PRINT #1,"MAXIMUM AVERAGE SIZE OCCURS ";PELMAXAVSIZETIME;" DAYS AFTER OCTOBER 1"
        PRINT #1,"PEAK BREADTH CONST. FOR AVGE. SIZE OF PELAGIC PREY   =   ";PELAVSIZEPEAKWIDTHK
        PRINT #1," "
        PRINT #1,"MAX. SHAPE CONST. FOR PELAGIC PREY SIZE DISTRIBUTION =   ";PELMAXSPRED
        PRINT #1,"PEAK TIME FOR MAX. PELAGIC SHAPE CONSTANT            =   ";PELMAXSPREDTIME
        PRINT #1,"MIN. SHAPE CONST. FOR PELAGIC PREY SIZE DISTRIBUTION =   ";PELMINSPRED
        PRINT #1,"PEAK BREADTH CONST. FOR PELAGIC PREY SIZE SHAPE TERM =   ";PELSPREDPEAKWIDTHK
        PRINT #1," "
        PRINT #1," "
        PRINT #1,"TROUT PREDATION CONSTANT                             =   ";TROUTPREDK
        PRINT #1,"BULLY PREDATION CONSTANT                             =   ";BULLYPREDK IF BULLY$ = "Y"
        PRINT #1,"TIME DEPENDENT STARVATION SURVIVAL CONSTANT          =   ";STARVK
        PRINT #1,"MOVEMENT   CONSTANT                                  =   ";MOVE
        PRINT #1,"MATURATION  CONSTANT                               =   ";MATURE
        PRINT #1," "

00970 FOR L% = 2 TO MAX%
        PELFREQ(L%)  = 0.1
        LITFREQ(L%)  = 1
00980 NEXT L%

        HAB$="P"

01040 IF HAB$ = "P" THEN
        HAB$             = "L"
        DEPTH            = LITTDEPTH
        MAXFOODTIME      = MAXLITFOODTIME
        MAXFOODPROD      = MAXLITFOODPROD
        MINFOODPROD      = MINLITFOODPROD
        FOODPEAKWIDTHK   = LITFOODPEAKWIDTHK
        MINAVSIZE        = MINLITAVSIZE
        MAXAVSIZE        = MAXLITAVSIZE
        MAXAVSIZETIME    = MAXLITAVSIZETIME
        AVSIZEPEAKWIDTHK = LITAVSIZEPEAKWIDTHK
        MAXSPRED         = LITTMAXSPRED
        MINSPRED         = LITTMINSPRED
        MAXSPREDTIME     = LITTMAXSPREDTIME
```

```
        SPREDPEAKWIDTHK  = LITSPREDPEAKWIDTHK
        DAYNOW%          = DAYNOW%+TIMEINTERVAL%
    ELSE
        HAB$             = "P"
        DEPTH            = PELDEPTH
        MAXFOODTIME      = MAXPELFOODTIME
        MAXFOODPROD      = MAXPELFOODPROD
        MINFOODPROD      = MINPELFOODPROD
        FOODPEAKWIDTHK   = PELFOODPEAKWIDTHK
        MINAVSIZE        = MINPELAVSIZE
        MAXAVSIZE        = MAXPELAVSIZE
        MAXAVSIZETIME    = PELMAXAVSIZETIME
        AVSIZEPEAKWIDTHK = PELAVSIZEPEAKWIDTHK
        MAXSPRED         = PELMAXSPRED
        MINSPRED         = PELMINSPRED
        MAXSPREDTIME     = PELMAXSPREDTIME
        SPREDPEAKWIDTHK  = PELSPREDPEAKWIDTHK
        GOTO 1500

01270  SEASMOVE  = (SIN((DAYNOW%-60)*2*PI/360)+1.2)^2.5

          FOR L% = 2 TO max%

01340  IF L% < 25 THEN
             PELFREQ(L%) = PELFREQ(L%)+LITPELRATIO*LITFREQ(L%)
             LITFREQ(L%) = 0
       ELSE
            R05          = EXP(MOV*SEASMOVE*((0.036*L%)^12)*TIMEINTERVAL%)
            R07          = 1-R05
            LEAVINGPEL   = PELFREQ(L%)*R07
            LEAVINGLITT  = LITFREQ(L%)*R05
            COMETOPEL    = LEAVINGLITT*LITPELRATIO
            COMETOLITT   = LEAVINGPEL/LITPELRATIO
            LITT         = LITFREQ(L%)-LEAVINGLITT+COMETOLITT
            PEL          = PELFREQ(L%)-LEAVINGPEL+COMETOPEL
            LITFREQ(L%)  = LITT
            LITFREQ(L%)  = 0 IF LITT < 1E-06
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            PELFREQ(L%)  = PEL
            PELFREQ(L%)  = 0 IF PEL  < 1E-06

01490   NEXT L%



01500  FOR L% = 2 TO max%

        IF HAB$ = "L" THEN
          FREQ(L%)      = LITFREQ(L%)
        ELSE
          FREQ(L%)      = PELFREQ(L%)

01600   FREQ(L%)        = 0 IF FREQ(L%) < 1.E-06
        NEXT L%

        DAY         = DAYNOW%/TIMEINTERVAL%
        YDAY        = DAY-1
        YDAY        = (360/TIMEINTERVAL%) IF YDAY < 1
        YYDAY       = YDAY-1
        INTSPAWNERS = 0
       IF HAB$ = "L" AND DAYNOW% <= SPAWNSEASON% THEN
                EGGS           = 0
                INTSPAWNERS    = 0
                SEASMATURE     = (SIN((DAYNOW%-70)*2*PI/360)+2.0)
          FOR L% = 34 TO max%
                RIPE           = 1-EXP(SEASMATURE*MATURE*((0.026*L%)^12)*TIMEINTERVAL%)
                EGGS           = EGGS+(L%^3.59*.000784*(FREQ(L%)*RIPE*0.5))
                INTSPAWNERS    = INTSPAWNERS+(RIPE*FREQ(L%))
                SPAWNMORT      = 1-(1/(1+(0.00525*DAYNOW%*(L-33))))
                FREQ(L%)       = FREQ(L%)-(FREQ(L%)*RIPE*SPAWNMORT)
                FREQ(L%)       = 0 IF FREQ(L%) < 1E-06
          NEXT L%
                LIVEGGS        = EGGSURV*EGGS

                SPAWNERS(DAY) = INTSPAWNERS/TIMEINTERVAL%
```

```
02000   SEASAVSIZE   = 1+COS((DAYNOW%-MAXAVSIZETIME)*2*PI/360)
        AVSIZE       = MINAVSIZE+(SEASAVSIZE*((MAXAVSIZE-MINAVSIZE)^(AVSIZEPEAKWIDTHK))/2)^AVSIZEPEAKWIDTHK
        SEASMINSIZE  = 1+COS((DAYNOW%-MAXMINSIZETIME)*2*PI/360)
        MINSIZE      = MINMINSIZE+(SEASMINSIZE*(MAXMINSIZE-MINMINSIZE)/2)
        SEASPRED     = 1+COS((DAYNOW%-MAXSPREDTIME)*2*PI/360)
        SHAPEK       = MINSPRED+(SEASPRED*((MAXSPRED-MINSPRED)^(1/SPREDPEAKWIDTHK))/2)^SPREDPEAKWIDTHK
        PEAK         = AVSIZE/(((SHAPEK-1)/SHAPEK)^(1/SHAPEK))
        SEASFOODPROD = 1+COS((DAYNOW%-MAXFOODTIME)*2*PI/360)
        FOOD         = 100*(MINFOODPROD+(SEASFOODPROD*((MAXFOODPROD-MINFOODPROD)^(1/FOODPEAKWIDTHK))/2)^FOODPEAKWIDTHK)

02010 IF HAB$ = "L" THEN
        MAT LITFREQ  = ZER
      ELSE
        MAT PELFREQ  = ZER
02020   TOTEATEN     = 0
        TOTAVAILABLE = 0
        MINLENGTH%   = 0

          FOR L% = 2% TO max%
        MAXLENGTH% = L% IF FREQ(L%)>0
        MINLENGTH% = L% IF FREQ(L%)>0 AND MINLENGTH% = 0
          NEXT L%


02030   FOR L% = MINLENGTH% TO MAXLENGTH%
         GOTO 2870 IF FREQ(L%) = 0
         FOODINTAKE  = 0
         COMPETITORS = 0
         M% = L%
         M% = L%+1% IF L% < MAXLENGTH%
02040    M% = M%+1% IF M% < MAXLENGTH%
         GOTO 2040 IF FREQ(M%) = 0
         LOWA         = 0.001*L%^1.6
         K%           = INTEGER(1+((LOWA/0.00742)^(1/1.69)))
```

```
         K%          = MINLENGTH% IF K% < MINLENGTH%
02050    K%          = K%+1% IF FREQ(K%) = 0
         GOTO 2050 IF FREQ(K%) = 0
         GOTO 2870 IF K% >= MAXLENGTH%
         J%          = K%
         COMPETITORS = COMPETITORS + FREQ(K%)
02060    J%          = J%+1%
         COMPETITORS = COMPETITORS + FREQ(J%)
         GOTO 2060 IF J% < L%
         UDL         = 0.00742*L%^1.69
        !  PRINT "DAY = ";DAYNOW%; "L = ";L%; " K = ";K%;"M = ";M%; "  COMPETITORS = ";COMPETITORS

02070    UDK         = 0.00742*K%^1.69
         LDM         = 0.001*M%^1.6
        IF UDK < LDM THEN
           UPPA = UDK
        ELSE
           UPPA = LDM
02080    UPPA = UDL IF LDM < UPPA
         GOTO 2100 IF UPPA > LOWA

        IF UDK > LDM THEN
           UPPA = UDK
        ELSE
           UPPA = LDM
02090    UPPA = UDL IF UPPA <= LOWA

02100    LOLIM       = LOWA - MINSIZE
         LOLIM       = 0 IF LOLIM < 0
         UPLIM       = UPPA - MINSIZE
         UPLIM       = 0 IF UPLIM < 0
         SSLOWA      = 1-EXP(-((LOLIM/PEAK)^SHAPEK))
         SSUPPA      = 1-EXP(-((UPLIM/PEAK)^SHAPEK))
         AREA        = SSUPPA-SSLOWA
         FOODINTAKE = FOODINTAKE+((FOOD*AREA)/COMPETITORS)
         LOWA       = UPPA
         GOTO 2500 IF UPPA = UDL
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         GOTO 2210 IF UDK  = LDM
         GOTO 2240 IF UPPA = LDM
         COMPETITORS = COMPETITORS - FREQ(K%)
         COMPETITORS = FREQ(L%) IF COMPETITORS <= 0
02200    K%          = K%+1% IF K% < MAXLENGTH%
         GOTO 2200 IF FREQ(K%) = 0
         GOTO 2070
02210    COMPETITORS = COMPETITORS + FREQ(M%) - FREQ(K%)
02220    K%          = K%+1% IF K% < MAXLENGTH%
         GOTO 2220 IF FREQ(K%) = 0
02230    M%          = M%+1% IF M% < MAXLENGTH%
         GOTO 2230 IF FREQ(M%) = 0
         GOTO 2070
02240    COMPETITORS = COMPETITORS + FREQ(M%)
02250    M%          = M%+1% IF M% < MAXLENGTH%
         GOTO 2250 IF FREQ(M%) = 0
         GOTO 2070

02500   WEIGHT       = 1.316E-07*L%^4.053
        TOTAVAILABLE = TOTAVAILABLE + (FOODINTAKE*FREQ(L%))
        FOODINTAKE   = (0.25*WEIGHT) IF FOODINTAKE > (0.25*WEIGHT)
        TOTEATEN     = TOTEATEN + (FOODINTAKE*FREQ(L%))
        METAB        = 0.05+((1+COS((DAYNOW%-140)*2*PI/360))*0.025)  !Range .05 to .1
        MET          = WEIGHT*METAB
        DAILYGROWTH  = FOODINTAKE-MET
        GOTO 2650   IF  DAILYGROWTH < 0
                SLONEWW            = WEIGHT+TIMEINTERVAL%*0.5*DAILYGROWTH
                AVGNEWW            = WEIGHT+TIMEINTERVAL%*DAILYGROWTH
                FASTNEWW           = WEIGHT+TIMEINTERVAL%*1.5*DAILYGROWTH
                SLOWL%             = INTEGER((SLONEWW/1.316E-07)^(1/4.053)+0.5)
                SLOWL%             = MAX% IF SLOWL% > MAX%
                AVGEL%             = INTEGER((AVGNEWW/1.316E-07)^(1/4.053)+0.5)
                AVGEL%             = MAX% IF AVGEL% > MAX%
                FASTL%             = INTEGER((FASTNEWW/1.316E-07)^(1/4.053)+0.5)
                FASTL%             = MAX% IF FASTL% > MAX%
                GOTO 2810
02650     IF DAILYGROWTH < 0 THEN
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                DEFICIT       = DAILYGROWTH/WEIGHT
                STARVSURV     = EXP(DEFICIT*TIMEINTERVAL%*STARVK)
                FREQ(L%)      = FREQ(L%)*STARVSURV
               PRINT "HAB =";HAB$;"   L =";L%;"   DEFICIT = ";DEFICIT;"   STARVATION SURVIVAL= ";STARVSURV IF STARVSURV > 1
          IF HAB$  = "L" THEN
                LITFREQ(L%)  = LITFREQ(L%)+FREQ(L%)
          ELSE
                PELFREQ(L%)  = PELFREQ(L%)+FREQ(L%)
02795         GOTO 2870
02810         IF HAB$="L" THEN
                LITFREQ(SLOWL%)  = LITFREQ(SLOWL%)+0.2*FREQ(L%)
                LITFREQ(AVGEL%)  = LITFREQ(AVGEL%)+0.6*FREQ(L%)
                LITFREQ(FASTL%)  = LITFREQ(FASTL%)+0.2*FREQ(L%)
             ELSE
                PELFREQ(SLOWL%)  = PELFREQ(SLOWL%)+0.2*FREQ(L%)
                PELFREQ(AVGEL%)  = PELFREQ(AVGEL%)+0.6*FREQ(L%)
                PELFREQ(FASTL%)  = PELFREQ(FASTL%)+0.2*FREQ(L%)

02870 NEXT L%

02880     !    PRINT "HAB = ";HAB$;" FOOD =";FOOD;"  TOTEATEN = ";TOTEATEN; "  AMOUNT AVAILABLE = ";TOTAVAILABLE

02900   GOTO 3050 IF HAB$   = "P"
        GOTO 3000 IF BULLY$ = "N"
        FOR L% = 2% TO MAX%
           BULLYPREDSURV = EXP(BULLYPREDK*TIMEINTERVAL%*LOG(1-.25*.9^L%))
           LITFREQ(L%)   = LITFREQ(L%)*BULLYPREDSURV
           LITFREQ(L%)   = 0 IF LITFREQ(L%) < 1E-06
        NEXT L%
03000   SEASTROUTNOS   = COS((DAYNOW%-MAXTROUTNOSTIME)*2*PI/360)+1
        TROUTDENSITY   = (MINTROUTNOS+(SEASTROUTNOS*((MAXTROUTNOS-MINTROUTNOS)^(1/TROUTNOSPEAKWIDTHK))/2))^TROUTNOSPEAKWIDTHK
        PELAREA        = 1/LITPELRATIO
        TROUTNUMBERS   = TROUTDENSITY*(1+PELAREA)
        ARRIVALS        = TROUTNUMBERS-((LITTROUT(YDAY)*LITPELRATIO)+PELTROUT(YDAY))
        ARRIVALS        = 0 IF ARRIVALS < 0
        GOTO 03200 IF TROUTNUMBERS = 0
        SEASTEMP       = 1+COS((DAYNOW%-MAXTEMPTIME)*2*PI/360)
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      LITTEMP          = MINTEMP+((SEASTEMP*(MAXLITTEMP-MINTEMP)/2))
      PELTEMP          = MINTEMP+((SEASTEMP*(MAXPELTEMP-MINTEMP)/2))
      LITPREF          = EXP(-((((LITTEMP^2)-225)^2)/1E05))
      PELPREF          = EXP(-((((PELTEMP^2)-225)^2)/1E05))

03010 TROUTFOOD        = 0

      FOR L% = 2 TO MAX%
         APPARENTSIZE = (2*((L%*0.0119*L%^1.59)/PI)^0.5)/10  !Centimetres
         LITRANGEVISIBLE = (0.01*APPARENTSIZE)/ACUITY  !Metres
         LITRANGEVISIBLE = SECCHIDEPTH IF LITRANGEVISIBLE > SECCHIDEPTH
         LITVOLSEARCHED  = (4/3)*PI*LITRANGEVISIBLE^3 IF LITRANGEVISIBLE <= (0.5*LITTDEPTH)
         LITVOLSEARCHED  = PI*LITTDEPTH*LITRANGEVISIBLE^2 IF LITRANGEVISIBLE > (0.5*LITTDEPTH)
         LITCHOICE       = LITCHOICE+(LITVOLSEARCHED*LITFREQ(L%))

         PELRANGEVISIBLE = (0.01*APPARENTSIZE)/ACUITY  !Metres
         PELRANGEVISIBLE = SECCHIDEPTH IF PELRANGEVISIBLE > SECCHIDEPTH
         PELVOLSEARCHED  = (4/3)*PI*PELRANGEVISIBLE^3 IF PELRANGEVISIBLE <= (0.5*PELDEPTH)
         PELVOLSEARCHED  = PI*PELDEPTH*PELRANGEVISIBLE^2 IF PELRANGEVISIBLE > (0.5*PELDEPTH)
         PELCHOICE       = PELCHOICE+(PELVOLSEARCHED*PELFREQ(L%))
       NEXT L%

       LITCONSUMPTION  = (LITTROUTFOOD(YDAY)+LITTROUTFOOD(YYDAY))/2
       PELCONSUMPTION  = (PELTROUTFOOD(YDAY)+PELTROUTFOOD(YYDAY))/2

       LITABUNDANCE    = (0.01*PELCONSUMPTION)+(LITCONSUMPTION*LITPREF)
       PELABUNDANCE    = (0.01*LITCONSUMPTION)+(PELCONSUMPTION*PELPREF)
       TOTABUNDANCE    = LITABUNDANCE+(PELABUNDANCE/LITPELRATIO)
       GOTO 3030 IF TOTABUNDANCE = 0

03020  LITTROUT(DAY)   = TROUTNUMBERS*LITABUNDANCE/TOTABUNDANCE      !N.Ha
       PELTROUT(DAY)   = TROUTNUMBERS*PELABUNDANCE/TOTABUNDANCE      !N.Ha

       LITARRIVALS     = ARRIVALS*LITABUNDANCE/TOTABUNDANCE          !N.Ha
       PELARRIVALS     = ARRIVALS*PELABUNDANCE/TOTABUNDANCE          !N.Ha
       GOTO 3040
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03030   LITTROUT(DAY)    = LITTROUT(YDAY)
        PELTROUT(DAY)    = PELTROUT(YDAY)

03040   LITIMMIGRANTS    = PELTROUT(YDAY)-(PELTROUT(DAY)+PELARRIVALS)
        LITIMMIGRANTS    = 0 IF LITIMMIGRANTS < 0
        PELIMMIGRANTS    = LITTROUT(YDAY)-(LITTROUT(DAY)+LITARRIVALS)*LITPELRATIO
        PELIMMIGRANTS    = 0 IF PELIMMIGRANTS < 0

        SMELTINLITGUT    = (LITTROUTFOOD(YDAY)*LITTROUT(YDAY))+(PELTROUTFOOD(YDAY)*LITIMMIGRANTS)
        NOWLITGUT        = SMELTINLITGUT/LITTROUT(DAY) IF LITTROUT(DAY) > 0
        NOWLITGUT        = 0 IF LITTROUT(DAY) = 0
        AVLITTROUTGUT    = (NOWLITGUT+PREVLITGUT)/2
        PREVLITGUT       = AVLITTROUTGUT
        SMELTINPELGUT    = (PELTROUTFOOD(YDAY)*PELTROUT(YDAY))+(LITTROUTFOOD(YDAY)*PELIMMIGRANTS)
        NOWPELGUT        = SMELTINPELGUT/PELTROUT(DAY) IF PELTROUT(DAY) > 0
        NOWPELGUT        = 0 IF PELTROUT(DAY) = 0
        AVPELTROUTGUT    = (NOWPELGUT+PREVPELGUT)/2
        PREVPELGUT       = AVPELTROUTGUT

03050   TROUTFOOD          = 0
        IF HAB$            = "L" THEN
           DEPTH           = LITTDEPTH
           TROUTNUMBERS    = LITTROUT(DAY)
           CHOICE          = LITCHOICE
           STUDYVOLUME     = 100*LITTDEPTH
           GUT             = AVLITTROUTGUT
        ELSE
           DEPTH           = PELDEPTH
           TROUTNUMBERS    = PELTROUT(DAY)
           CHOICE          = PELCHOICE
           STUDYVOLUME     = 100*PELDEPTH
           GUT             = AVPELTROUTGUT

03060   GOTO 3200 IF CHOICE = 0
        GOTO 3200 IF TROUTNUMBERS = 0
03070   HUNGER           = 1/(1+(0.001*(2^(GUT^0.5))))
        !       PRINT"HAB = ";HAB$;"   GUT =";GUT;"  HUNGER =";HUNGER;"   PREDACTIVITY =";PREDACTIVITY
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03080   FOR L% = 2% TO MAX%
            FREQ(L%)       = LITFREQ(L%) IF HAB$ = "L"
            FREQ(L%)       = PELFREQ(L%) IF HAB$ = "P"
            GOTO 3100 IF FREQ(L%) = 0
            APPARENTSIZE = (2*((L%*0.0119*L%^1.59)/PI)^0.5)/10   ! centimetres
            RANGEVISIBLE = (0.01*APPARENTSIZE)/ACUITY  !Metres
            RANGEVISIBLE = SECCHIDEPTH IF RANGEVISIBLE > SECCHIDEPTH
            VOLSEARCHED  = (4/3)*PI*RANGEVISIBLE^3 IF RANGEVISIBLE <= (0.5*DEPTH)     !Cubic metres
            VOLSEARCHED  = DEPTH*PI*RANGEVISIBLE^2 IF RANGEVISIBLE > (0.5*DEPTH)
            PROPSEEN       = VOLSEARCHED*TROUTNUMBERS*0.01/STUDYVOLUME
            UNIFORMITY   = VOLSEARCHED*FREQ(L%)/CHOICE
            ATTACKED       = PROPSEEN*UNIFORMITY*TIMEINTERVAL%*HUNGER*TROUTPREDK
!               PRINT"L =";L%;" ATTACKED =";ATTACKED;" PROPSEEN =";PROPSEEN;" ENCOUNTERS =";ENCOUNTERS
            ESCAPE           = 1/(1+1E06*0.75^L%)
            EATEN             = ATTACKED-(ATTACKED*ESCAPE)
            EATEN             = 1 IF EATEN > 1
            NOTEATEN       = 1-EATEN
            W                   = 1.316E-07*L%^4.053
            TROUTFOOD     = TROUTFOOD+(W*FREQ(L%)*EATEN)/(TROUTNUMBERS*0.01) !trout per 100 square metres
            IF HAB$ ="L" THEN
             LITEATEN(L%) = FREQ(L%)*EATEN
             LITFREQ(L%)  = FREQ(L%)*NOTEATEN
             LITFREQ(L%)  = 0 IF FREQ(L%) < 1E-06
            ELSE
            PELEATEN(L%)  = FREQ(L%)*EATEN
            PELFREQ(L%)   = FREQ(L%)*NOTEATEN
            PELFREQ(L%)   = 0 IF FREQ(L%) < 1E-06
03100   NEXT L%

03200   IF HAB$ = "L" THEN
           LITTROUTFOOD(DAY) = TROUTFOOD/TIMEINTERVAL%
        ELSE
           PELTROUTFOOD(DAY) = TROUTFOOD/TIMEINTERVAL%
        !   PRINT"LITTROUTFOOD =";LITTROUTFOOD(DAY);"PELTROUTFOOD =";PELTROUTFOOD(DAY)

03300 IF HAB$ = "L" AND DAYNOW% <= SPAWNSEASON% THEN
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      LITFREQ(2%) = 0.2*LIVEGGS+LITFREQ(2%)
      LITFREQ(3%) = 0.6*LIVEGGS+LITFREQ(3%)
      LITFREQ(4%) = 0.2*LIVEGGS+LITFREQ(4%)
03400 GOTO 1040 IF HAB$ = "L"
      LITTBIOMASS(DAY) = 0
      PELBIOMASS(DAY)  = 0
      FOR L% = 2% TO MAX%
        W                = 1.316E-07*L%^4.053
        LITTBIOMASS(DAY) = LITTBIOMASS(DAY)+(W*LITFREQ(L%))
        PELBIOMASS(DAY)  = PELBIOMASS(DAY)+(W*PELFREQ(L%))
      NEXT L%
      LITTBIOMASS(DAY) = LITTBIOMASS(DAY)/100   !Biomass per square metre
      PELBIOMASS(DAY) = PELBIOMASS(DAY)/100     !Biomass per square metre

      pr%=0%  !When true, this is a required day
      py%=0%  !When true, this is a required year

      pr%=1% if DAYNOW% = rqdday%(k%) for k% = 1% to numdr% if numdr%>0%
      py%=1% if (numyr%+1) = rqdyr%(k%) for k% = 1% to numpyr% if numpyr%>0%
      py%=1% if (numyr%+1)=lastyr%
      GOTO 4000  UNLESS  PR%=1% AND PY%=1%
      fmt$= "### 'E #########.### 'E ###.### 'E ########.### 'E ###.###"
      PRINT #1," "
      PRINT #1," "
      PRINT #1," "
      PRINT #1,"                   DAY = ";DAYNOW%;"                  YEAR  = ";(NUMYR%+1%)
      PRINT #1," "
      PRINT #1,"LENGTH     LITTORAL FREQUENCIES                PELAGIC FREQUENCIES"
      PRINT #1," "
      PRINT #1,"                 ALIVE        EATEN                  ALIVE        EATEN"
      FOR K% = kmin% TO kmax%
      PRINT #1 using fmt$,K%,"  ",LITFREQ(k%),"  ",LITEATEN(K%),"          ",PELFREQ(k%),"   ",PELEATEN(K%) IF (LITFREQ(K%)+PELFREQ(K%))
      NEXT K%
04000 ENDYR  = COS(DAYNOW%*2*PI/360)
04010  GOTO 4200 IF ENDYR < 1
      NUMYR% = NUMYR%+1%
      GOTO 4200    IF NUMYR% < STARTSUMMARYDATA
```

```
 PRINT#1,"  "
 PRINT#1,"  "
 PRINT#1,"                              END  OF  YEAR  ";NUMYR%
 PRINT#1,"  "
  fmt2$ = "### 'E ###.# 'E ##.## 'E ##.## 'E ###.# 'E ###.# 'E ##.## 'E ##.##"
  fmt3$ = "### 'E ##.## 'E ##.## 'E ###.# 'E ###.# 'E ##.## 'E ##.##"
 PRINT #1,"                 LITTORAL   PELAGIC   LITTORAL  PELAGIC  LITTORAL  PELAGIC"
 PRINT #1,"DAY  SPAWNERS   BIOMASS   BIOMASS  TROUT GUT TROUT GUT  TROUT     TROUT"
 PRINT #1,"   (n.100m^-2) (g.m^-2)   (g.m^-2)  (g.Tr.D)  (g.Tr.D)  (n.Ha)   (n.Ha)"
     FOR K% = 1% TO 36%
        IF (K%*10%) <= SPAWNSEASON% THEN
 PRINT #1 USING FMT2$,10%*K%,"",SPAWNERS(K%),"  ",LITTBIOMASS(K%),"    " &
  ,PELBIOMASS(K%),"   ",LITTROUTFOOD(K%),"  ",PELTROUTFOOD(K%),"   ",LITTROUT(K%),"   ",PELTROUT(K%)
        ELSE
 PRINT #1 USING FMT3$,10%*K%,"           ",LITTBIOMASS(K%),"    "   &
  ,PELBIOMASS(K%),"   ",LITTROUTFOOD(K%),"  ",PELTROUTFOOD(K%),"   ",LITTROUT(K%),"   ",PELTROUT(K%)
04100   NEXT K%

04200   TOTDAY = TOTDAY+TIMEINTERVAL%
        DAYNOW% = 0 IF DAYNOW% >= 360
        GOTO  01040 IF TOTDAY < STOPDATE
        GOTO 32761
19000   !ERRORS
        if erl = 100 and err = 2 then
                print "Invalid file name"
                print "must be 1-to-9 chrs . 1-to-3 chrs"
                resume 100
19005   resume 00943 if err=52 and erl= 00945
        resume 00950 if err=52 and erl= 00955
        resume 00955 if err=50 and erl= 00955
        PRINT "Err = ";err;"  "+ert$(err)+" @";erl

19008        IF ERR = 51 THEN
                PRINT"NEWW =";NEWW
                PRINT "PEL:"
                resume 32761
```

```
19010       IF ERR = 48 AND ERL = 03070 THEN
                HUNGER = 0
                RESUME 03080
19030   if err = 252 then
                close 1
                ER%=ERL
                resume 20001
19999 on error goto 0 !Something else - abort.

20001! Recover from disk quota overflow...
                open "TT:" for output as file 1%
                print "Disk quota exceeded. Remainder of output to terminal."
                goto 1500 IF ER%=1500
                GOTO 955 IF ER%=955
                GOTO 4010 IF ER%=4010

32760 PRINT"NO MORE SMELT"
32761   CLOSE 1%
32767 end
```

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ERRATA

Page 65, figure 49, top panel. *Boeckella propinqa* should be *Boeckella propinqua*.

All figures illustrating seasonal variations in simulated population parameters. In the third panel, describing seasonal patterns of trout density, the ordinate units, n.Ha, should be n. Ha^{-1}.