

AN ECOLOGICAL STUDY AND THEORETICAL CONSIDERATIONS  
OF BUTTER SOLE (ISOPSETTA ISOLEPIS) POPULATION IN HECATE STRAIT

by

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ABSTRACT

The ecology of the Hecate Strait population of butter sole (Isopsetta isolepis (Lockington)) is studied to facilitate a better understanding of the fluctuations in abundance and to permit a more optimal utilization of the stock. The reaction of the population to varying degrees of exploitation and natural mortality rates is analysed for steady and fluctuating recruitment using Ricker's model. The magnitude of error inherent in the models used for the theoretical studies of exploited populations is also examined by subjecting a hypothetical population in a steady state to various mortality and growth rates. This is done both for a continuous fishery and after appropriate modifications in Beverton's model for a seasonal fishery as well.

Butter sole population spawning in Skidegate Inlet is confined to the Hecate Strait bank. The species show depth stratification, the young ones being found in shallower waters. Although the population exhibits seasonal movements between shallow and deeper waters, a north-south migration is limited mostly to the spawning population. Sexual differences in the time of onset of maturity and migratory pattern are also observed. No association between butter sole and related species of flatfish is noted. A study of the discreteness of the Hecate Strait population suggests that this area is inhabited by a single self-contained stock. Growth studies of butter sole indicate that there are annual, seasonal, regional and sexual differences. The average growth of butter sole belonging to a strong year class seems to be influenced by intra-specific competition, even though a tendency in later years to compensate for the initial difference in growth is also exhibited. The survival rate of butter sole above six years is relatively low.

A comparison of the relative abundance of young butter sole taken in the 1952-1954 samples from along the Graham Island coast with the success and age composition of the fishery which existed from 1958-1960

when these year classes became fully exploitable, indicates that fluctuations in the butter sole population are mainly due to variations in early survival rate.

Yield isopleths and equilibrium yield curves indicate that the maximum equilibrium yield will be obtained when the age of exploitation is 4.83 years or greater only when  $F$  is higher than 1.8. The fishing mortality operates for only a short time each year while natural mortality is continuous, and a change in the latter therefore influences the yield and biomass more than a similar change in the fishing mortality. A higher increase in the natural mortality with age results, under fluctuating recruitment, in greater deviations in yield and biomass. As the older age groups now contribute less to the population, the effects of fluctuations in abundance of the entering year class on the stock become more pronounced.

There is little difference in the yield per recruit ( $Y_w/R$ ) estimates from Beverton's or Ricker's model for a hypothetical population under various situations, provided Ricker's model makes use of an exponential average of the biomass during each time period. The slight difference observed is due to the manner of depicting the growth pattern. Due to seasonal differences in growth rate,  $Y_w/R$  estimate from Beverton's model need not be more accurate than from Ricker's model.

A heavier exploitation of the butter sole population is warranted on the basis of the theoretical studies, provided the heavier exploitation does not decrease the number of fertilized eggs by over-exploiting the males that are more abundant on the spawning grounds. Due to sexual differences in the population parameters and the migratory and recruitment patterns, the two sexes may be treated in further studies, as a special case of two competing populations exploited simultaneously.



## Abstract

The ecology of the Hecate Strait population of butter sole (Isopsetta isolepis (Lockington)) is studied to facilitate a better understanding of the fluctuations in abundance and to permit a more optimal utilisation of the stock. The reaction of the population to varying degrees of exploitation and natural mortality rates is analysed for steady and fluctuating recruitment using Ricker's model. The magnitude of error inherent in the models used for the theoretical studies of exploited populations is also examined by subjecting a hypothetical population in a steady state to various mortality and growth rates. This is done both for a continuous fishery and after appropriate modifications in Beverton's model for a seasonal fishery as well.

Butter sole population spawning in Skidegate Inlet is confined to the Hecate Strait bank. The species show depth stratification, the young ones being found in shallower waters. Although the population exhibits seasonal movements between shallow and deeper waters, a north-south migration is limited mostly to the spawning population. Sexual differences in the time of onset of maturity and migratory pattern are also observed. No association between butter sole and related species of flatfish is noted. A study of the discreteness of the Hecate Strait population suggests that this area is inhabited by a single self-contained stock. Growth studies of butter sole indicate that there are annual, seasonal, regional and sexual differences. The average growth of butter sole belonging to a strong year class seems to be influenced by intra-specific competition, even though a tendency in later years to compensate for the initial difference in growth is also exhibited. The survival rate of butter sole above six years is relatively low.

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## I. Introduction

The Hecate Strait population of butter sole (Isopsetta isolepis (Lockington)) has been exploited on its spawning grounds during the winter months each year since 1943. Catch statistics have been maintained by the Nanaimo Station of the Fisheries Research Board of Canada since the inception of the fishery. During the spawning season a large part of the spawning population is concentrated in a very limited area in Skidegate Inlet (Figure 1) and hence is easily accessible to the commercial gear. The productive Hecate Strait area is inhabited by other closely related groundfish such as halibut (Hippoglossus stenolepis Schmidt), lemon sole (Parophrys vetulus Gerard), rock sole (Lepidopsetta bilineata (Ayres)) and sand sole (Psettichthys melanostictus Girard). Several other species including the Pacific cod (Gadus macrocephalus Tilesius) are also of commercial importance. The ecological relationship and fluctuations in abundance of these species have been analysed by Ketchen (1956, 1961) and others. Butter sole landings have shown considerable annual fluctuations. This may be attributed partly to the yearly variation in fishing pressure and partly to changes in the availability and abundance of the population. However as a result of the small size of the fishery and its relatively low commercial importance, the dynamics of the population of I. isolepis has not, until the present time, been studied in any detail. Very little information was available on the distribution and movements of the population or its growth and survival rates. The discreteness of the butter sole stock and its relative abundance and inter-relations with other flatfish were not understood either. Hence this study of the ecology of I. isolepis and the possible responses of the population to various fishing and natural mortality rates under steady and fluctuating recruitment is undertaken to provide a better understanding of the population in relation to its environment.

Theoretical studies of fish population are done by constructing mathematical models of the system. The indispensable role of models in population problems is emphasised by Beverton and Holt (1957). Their use in understanding the dynamics of the stock is also indicated by Moran (1954) who points out that even an inadequate model which does not represent the system completely often separates the important and unimportant factors in a particular situation and thus aids in a better understanding of the system. When studying fish populations the two basic kinds of analytical models used to relate yield and biomass to mortality rates, growth rates and gear characteristics are those of Beverton and Holt (1957) and Ricker (1958). Both these models attempt to measure the main population variables and incorporate them into the models, but as yet no studies on the magnitude of error involved due to the manner of representing the system by the two conceptual models are found in the literature. In addition, since the butter sole fishery is highly seasonal, Beverton's model cannot be applied without appropriate modifications. Hence before studying the butter sole population the two models were applied to a hypothetical population in a steady state to test their applicability to a variety of situations. These situations included cases when the fishery was either continuous or seasonal. The age and rate of exploitation were varied as were the natural mortality rates and growth rates. The applicability of the two models was studied by comparing the yield per recruit estimated by them. The choice of a mathematical model for studying the butter sole population is based on this analysis.

## II. Materials and methods.

Considerable amounts of data collected by the Fisheries Research Board of Canada, Nanaimo, were used during this study. Part of the data were collected from trawl hauls taken from the Hecate Strait area during February and July, 1961. Commercial samples taken during February, 1962 were also used. The areas sampled are shown in Figure 1.

Movements of butter sole. Studies on the depth distribution and seasonal movements of butter sole were based on the size and age composition of butter sole in the trawl hauls taken during 1954 and 1961 from several localities in Hecate Strait (Figures 4 and 5). The nature of the spawning migration was determined from the size composition in the catches from Skidegate Inlet collected during 1961 and 1962 and from Butterworth ground during 1962. The age composition of butter sole in the samples collected by the special sampling survey during January 1953 was useful in studying differences in the spawning migration of the two sexes.

Abundance of butter sole and related species of flatfish. Data collected on the catch composition of species of flatfish during the trawl survey of Hecate Strait in the summer months of 1952-1954 and the otolith samples collected from the fishery during 1958-1960 were used in studying abundance and association of butter sole and related species in the area.

Discreteness of the stock. Meristic counts were taken from 194 specimens collected from Hecate Strait during July 1961 and February 1962 and 95 specimens from the U.S. coast sampled during February, 1962.

Studies on growth. To study the growth of butter sole, over 1000 otoliths were collected from sampling areas 1, 2, 3, 4 and 6. Of these 762 otoliths from areas 1 to 4 were read for back calculations because the



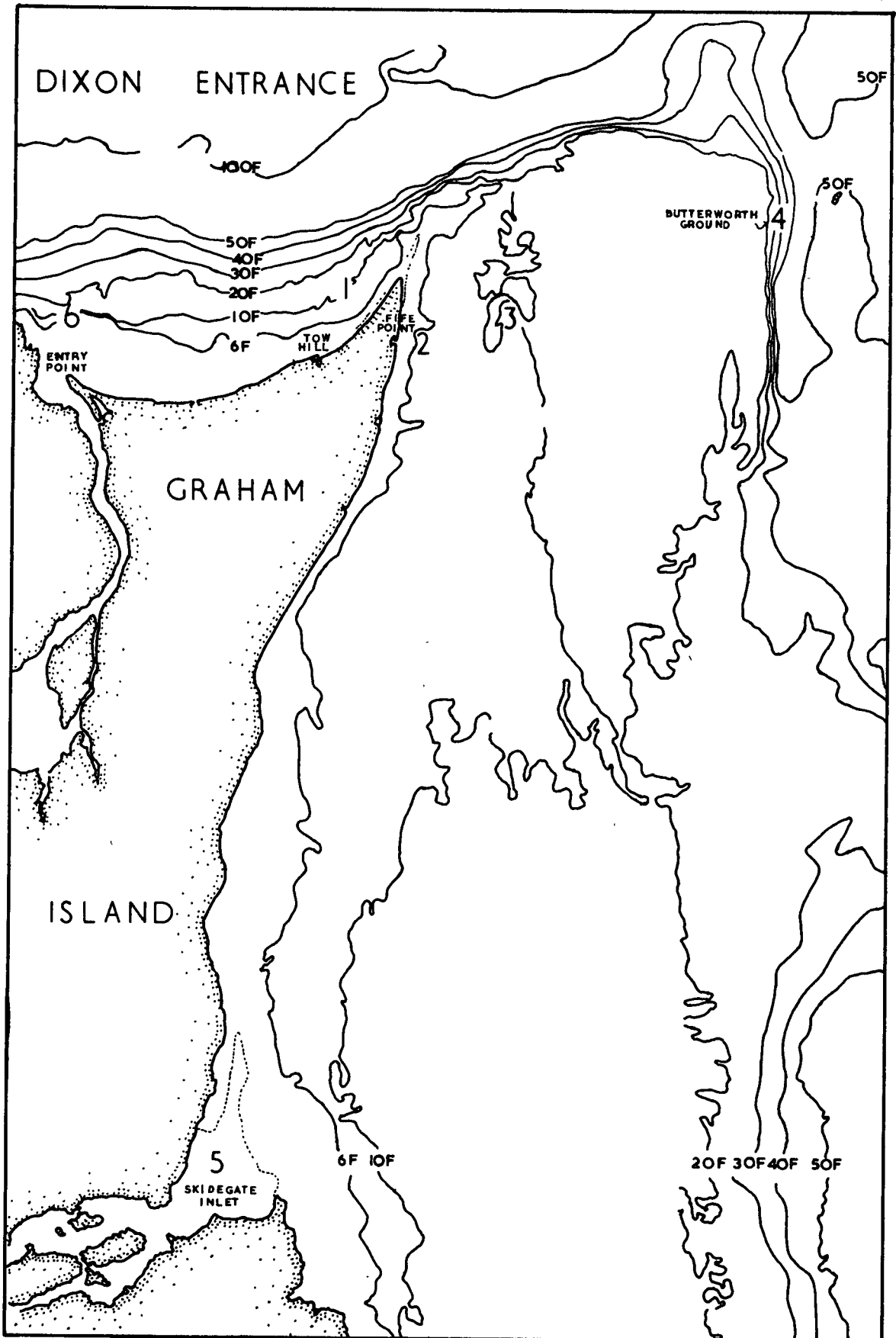


Figure 1. Map of Hecate Strait showing the general sampling localities numbered 1 to 6.

remainder of the otoliths were:- from the wrong side of the head (right side); had indistinct demarcation of the opaque and hyaline zones to be measured accurately; or had to be rejected due to inadequate sampling of the catch for otoliths. To facilitate back calculation a total of 1113 measurements from samples collected during 1960 and 1961 summer hauls were used to establish otolith radius - body length relationship. To check the back calculated lengths from otoliths, modal lengths in the length frequency distribution and the time of formation of opaque and hyaline zones were also studied. Length measurements of 946 females in the July 1961 samples were used to dissect the length frequency distribution by the probability paper method (Harding 1949, Cassie 1950, 1954). The time of formation of opaque and hyaline zones was determined from 2101 otoliths taken from July 1961 trawl hauls and from the commercial samples collected during 1958-1960. Weights of 324 ungutted specimens were taken during February 1961 and of 536 specimens during July 1961 to study the length-weight relationship.

Survival rate. Estimates of survival rate were based on the data on age composition of butter sole in the commercial sample collected during 1951, 1954 and 1955 and by the special sampling survey during January 1953.

Studies on fluctuations of butter sole population. Catch and effort data on butter sole collected for the period 1945-1962 were used to examine the trend in the yearly landings. A mesh selection experiment conducted during February 1961 used 1.5", 3.4", 3.5" and 5.2" mesh cod-ends. The 1.5" and 5.2" mesh cod-ends were of cotton, the 3.4" mesh cod-end was of manila thread and the 3.5" mesh cod-end of drumline. To verify the results from mesh selection experiment the length and girth measurements of 319 fish were taken to obtain the length-girth relationship of butter sole. Data collected on young butter sole along Graham Island coast during 1952-1954

trawl survey and the age composition and landings for the years 1958-1960 were also utilized to study the abundance.

The trawl survey by the Biological Station during 1952-1954 was conducted using small meshed (1.5") shrimp trawl. During July 1961 a small meshed shrimp trawl was used in sampling areas 1, 2, and 3. In sampling area 4 a trawl having a 4" mesh with a small meshed cod-end cover was used. A total of 21 useful hauls were made from the sampling areas (Figure 5). Of these, with the exception of two hauls in area 1 and one in area 2, the entire catch was taken for estimates of length composition. In area 1 sampling was necessary due to heavy catches. The otoliths were taken from all of the specimens in 11 of the hauls. Of the remaining 10 hauls, otoliths from seven hauls were not used for reading since the catch was not adequately sampled. Otoliths from commercial catches were collected at random by the sampler from a box of butter sole taken at random from a boat.

### III. Aspects of the life history of butter sole.

#### 1. Introduction

Isopsetta isolepis is a flatfish belonging to the family Pleuronectidae. The accepted common name (Bailey et al 1960) for the species is butter sole although Roedel (1953) gives the name scaly-fin sole to the species. Butter sole is known by other local names such as Bellingham sole and Skidegate sole. Since development of asymmetry during metamorphosis is characteristic of all flatfishes, the skull and other structures exhibit remarkable asymmetry as a result of distortion and displacement. All members of the family pleuronectidae are dextral so that the topographically dorsal side of the metamorphosed fish represents the original right side of the symmetrical larva. According to Roedel (1953) in butter sole the lateral line curves upward over the pectoral fin and has a dorsal branch. The maxillary extends beyond the anterior half of the lower eye. Scales are rough on the eyed side and number 90 or fewer along the lateral line. The species is easily recognized in fresh condition by the yellow and green blotches on the eyed side and bright lemon colour on the tips of the dorsal and anal fins. Clemens and Wilby (1961) state that butter sole is known to occur from Southern California to Southeastern Alaska. They were also recorded in recent samples collected along Aleutian Islands (Wilimovsky - personal communication). Examination of the stomach contents indicate that butter sole feed on polychaetes, bivalves, prawns and crabs, cirripedes, young sand dollars, certain species of fishes and species of algae.

#### 2. Confines of the butter sole population spawning in Skidegate Inlet.

(a) Hecate Strait habitat. The following description of the Hecate Strait habitat is partly based on the account given by Ketchen (1956) and partly on the accounts by Barber (1957 and 1958). The continental shelf off the west coast of Canada is narrow and in many places shelves very rapidly seaward.

Off the main coast of British Columbia there are three shallow banks (Figure 2), each separated from the other by waters deeper than 50 fathoms. The Hecate Strait bank which is the largest of the three is an extension of the Queen Charlotte Islands and the 50 fathom contour encloses an area of approximately 4550 square miles. This bank is well isolated in the north by the deep water of Dixon Entrance and in the south and southeastern side by the Queen Charlotte Sound. Hecate Strait bank is connected to the shoal areas along the mainland only on its northeastern side by waters shallower than 50 fathoms. The depth contours of the Hecate Strait bank are given in Figure 3. The gradient between 20 and 50 fathom contour is sharp on the north and northeastern sides but is more gradual in other regions. The upper region of the bank has considerable areas of smooth sand. In central and lower regions the bottom is very rough and contains gravel, shale, hard sand and branacles. On the edge of the bank the composition of the bottom changes to soft sand and mud.

Barber (1957) has shown that there is a cyclic alternation of summer and winter deep water. The strong southeast winds during winter cause an accumulation of surface water along the coast of British Columbia displacing the cold deep water offshore. The deep winter water is thus relatively warmer and less saline than the deep summer water. Weak southeast winds during summer cause the accumulated surface waters to move offshore enabling the return of the deeper waters. Barber (1958) has also shown that associated with this alternation of water masses there is a seasonal variation in the oxygen content of deep water, reaching lowest values during summer (Figure 2).

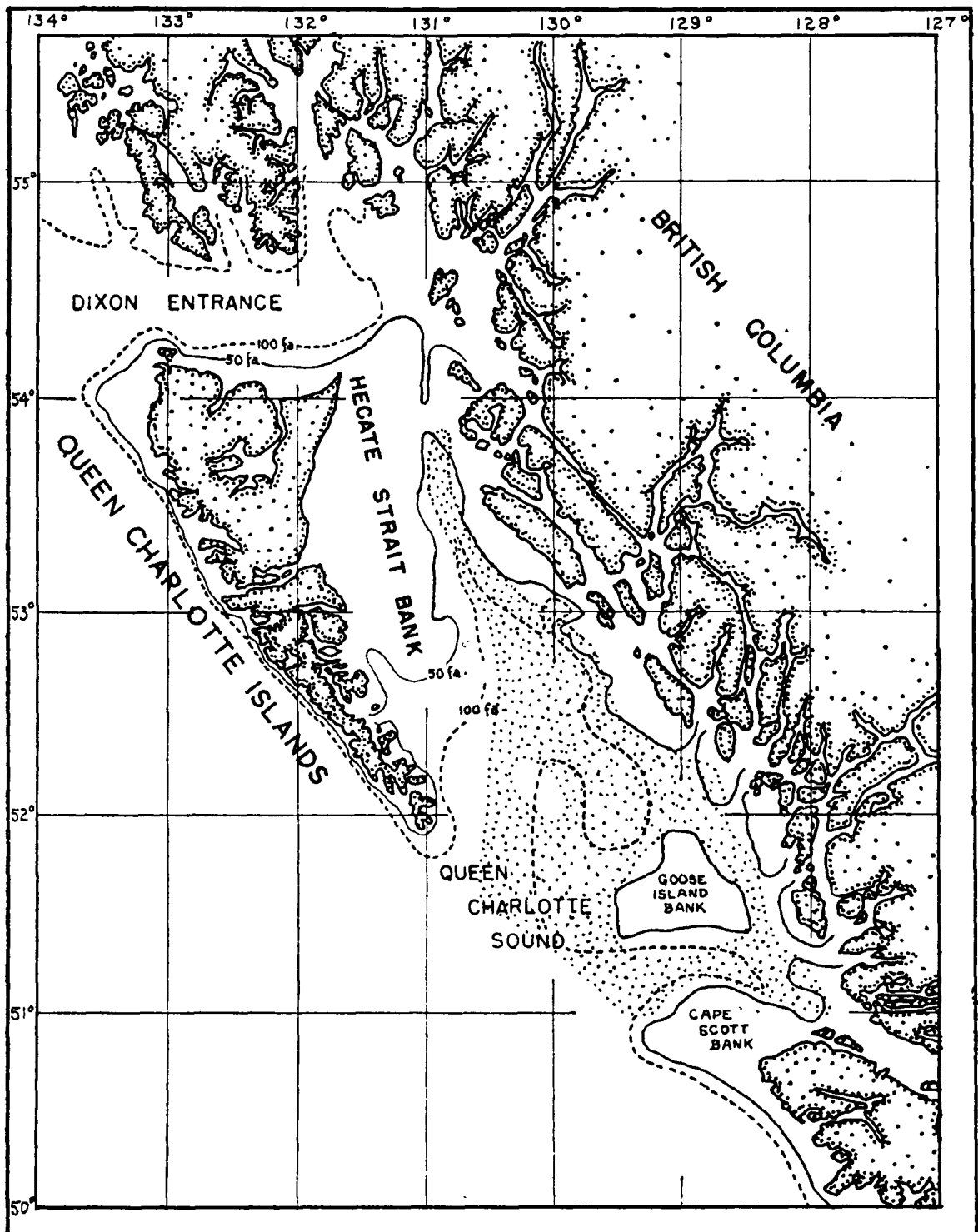


Figure 2. Map of the north coast of British Columbia showing the three shallow banks off the main coast. The dotted region represents the area where the bottom water has oxygen less than 3 mg/l. during the summer months of 1954 and 1955 (adopted from Barber 1958 and Ketchen 1961, slightly modified).

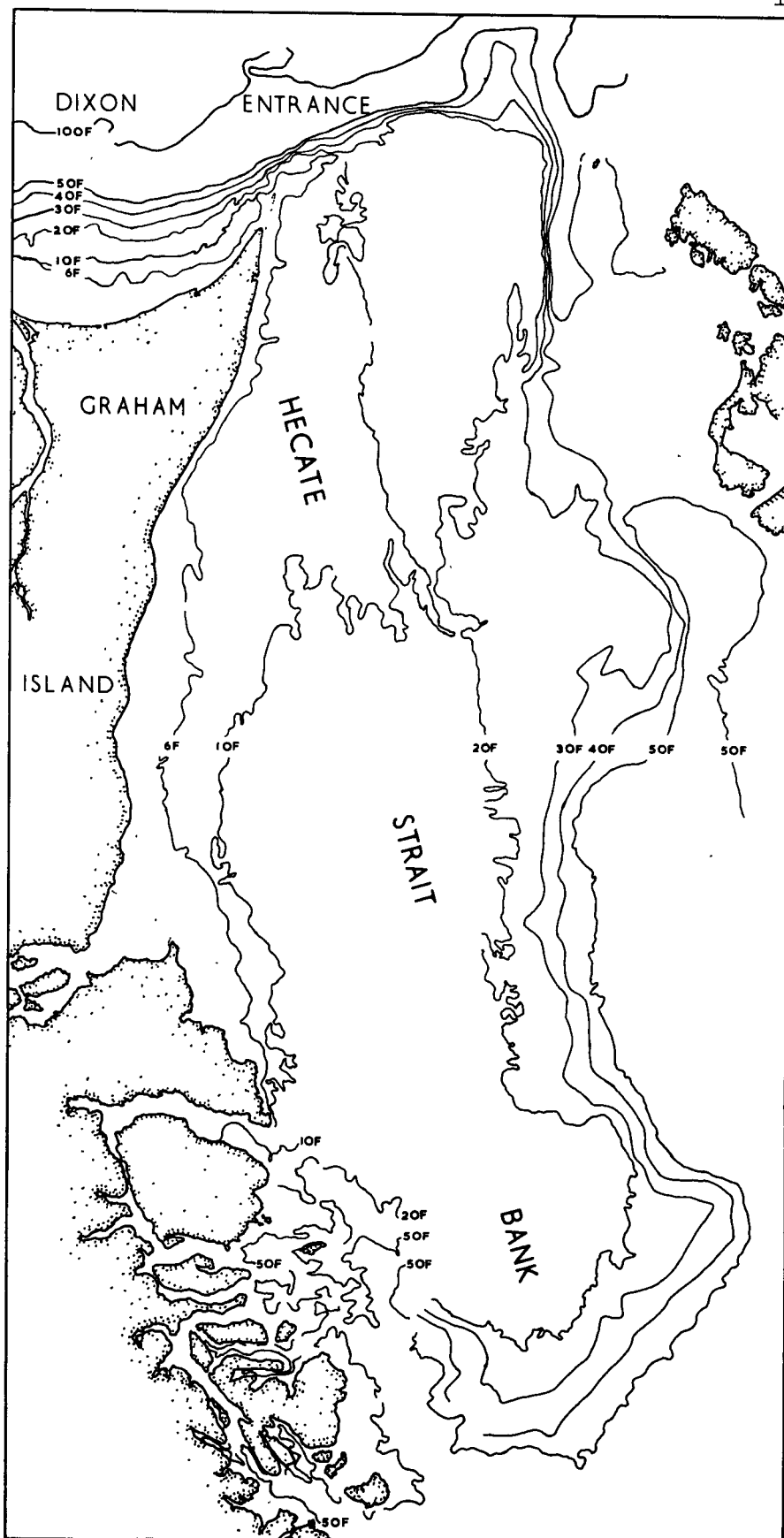


Figure 3. Depth contours of the Hecate Strait bank.

(b) Pattern of distribution of butter sole in Hecate Strait.

The range of the butter sole population inhabiting the Hecate Strait area is examined by studying the distribution, movements, factors limiting distribution and its relation to other species in the area. Unpublished reports on the Hecate Strait trawling surveys conducted during 1953 and 1954 recorded heavy catches of butter sole between Fife Point and Butterworth ground. The area 3 off Fife Point (Figure 1) supported a summer fishery during 1945 and 1946. Butter sole occur only in small numbers on the central and lower regions and along the edge of the Hecate Strait bank. No butter sole were represented in the 5 half-hour trawls made along the edge during July 1961 at a depth of 15-22 fathoms. They were found again between 28 and 33 fathoms but were absent in the single haul made at 62 fathoms.

Ketchen (1956) observed that young lemon sole inhabiting Hecate Strait were distributed nearer the Graham Island shore and older and larger specimens progressively away from the shore in deeper waters. Length frequency distribution of butter sole in the 1954 hauls from Hecate Strait is presented in Table I. The results of the  $X^2$  analysis of the data for hauls grouped approximately at 5 mile intervals from Fife Point (Figure 4) are presented in Table II. The length and age frequency distributions of butter sole collected during 1961 (Figure 5) are given in Table III and Figures 6 and 7. A  $X^2$  analysis of the length frequency distribution of the Butterworth and Fife Point samples is presented in Table IV.

The size distribution of butter sole in the 1954 samples indicated that butter sole in the 9-12 cm. length group were dominant in samples along the Graham Island coast (Haul-group I) and butter sole less than 20 cm. length made up over 97% of the entire catch. The length frequency distribution of butter sole in haul-groups II-V showed significant difference and gave a



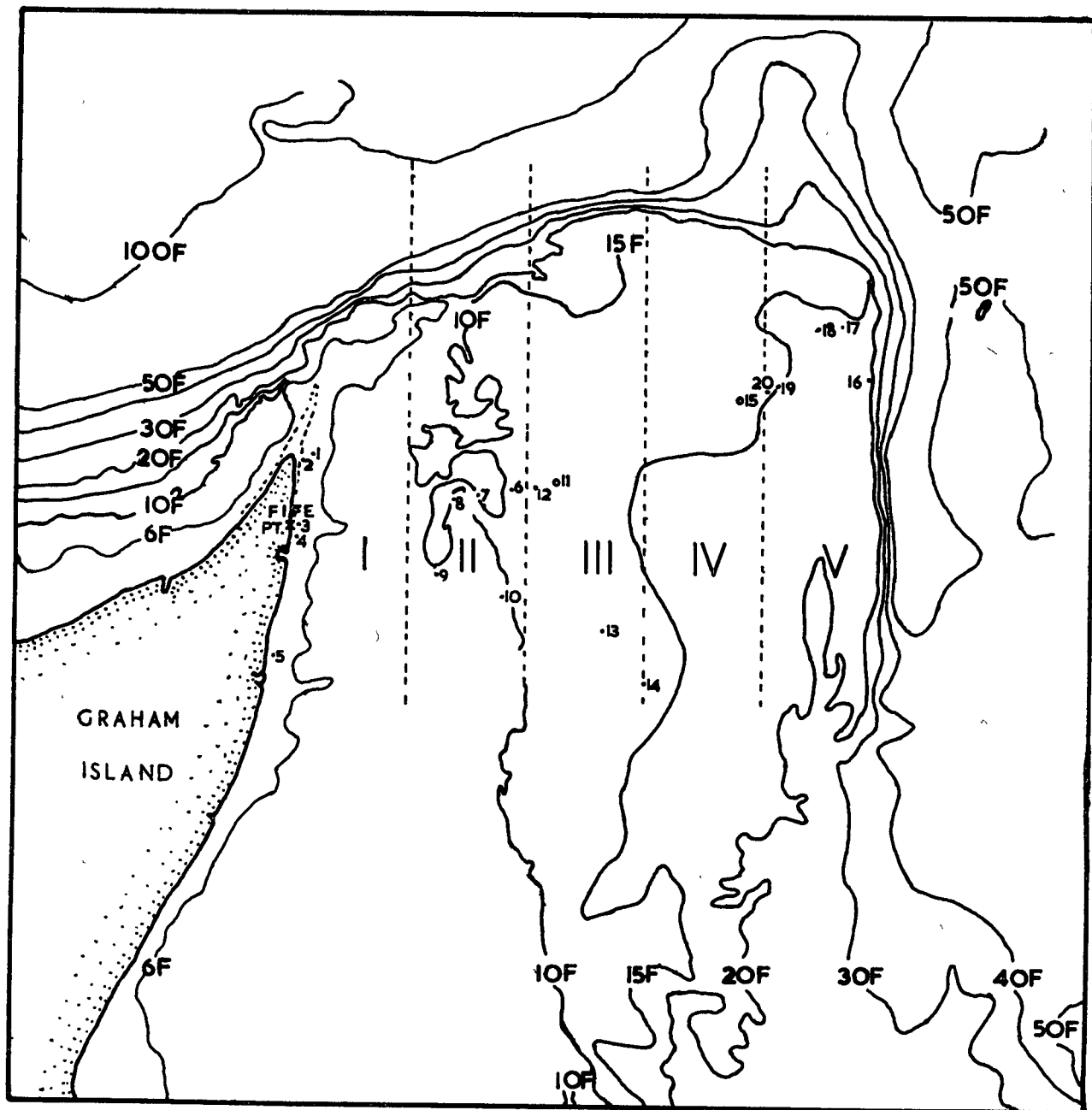


Figure 4. Northern part of the Hecate Strait bank showing the sampling positions in 1954. Positions 11 and 15 are approximate. The dotted lines are drawn approximately at 5 mile intervals from Fife Point to indicate the 5 haul-groups.

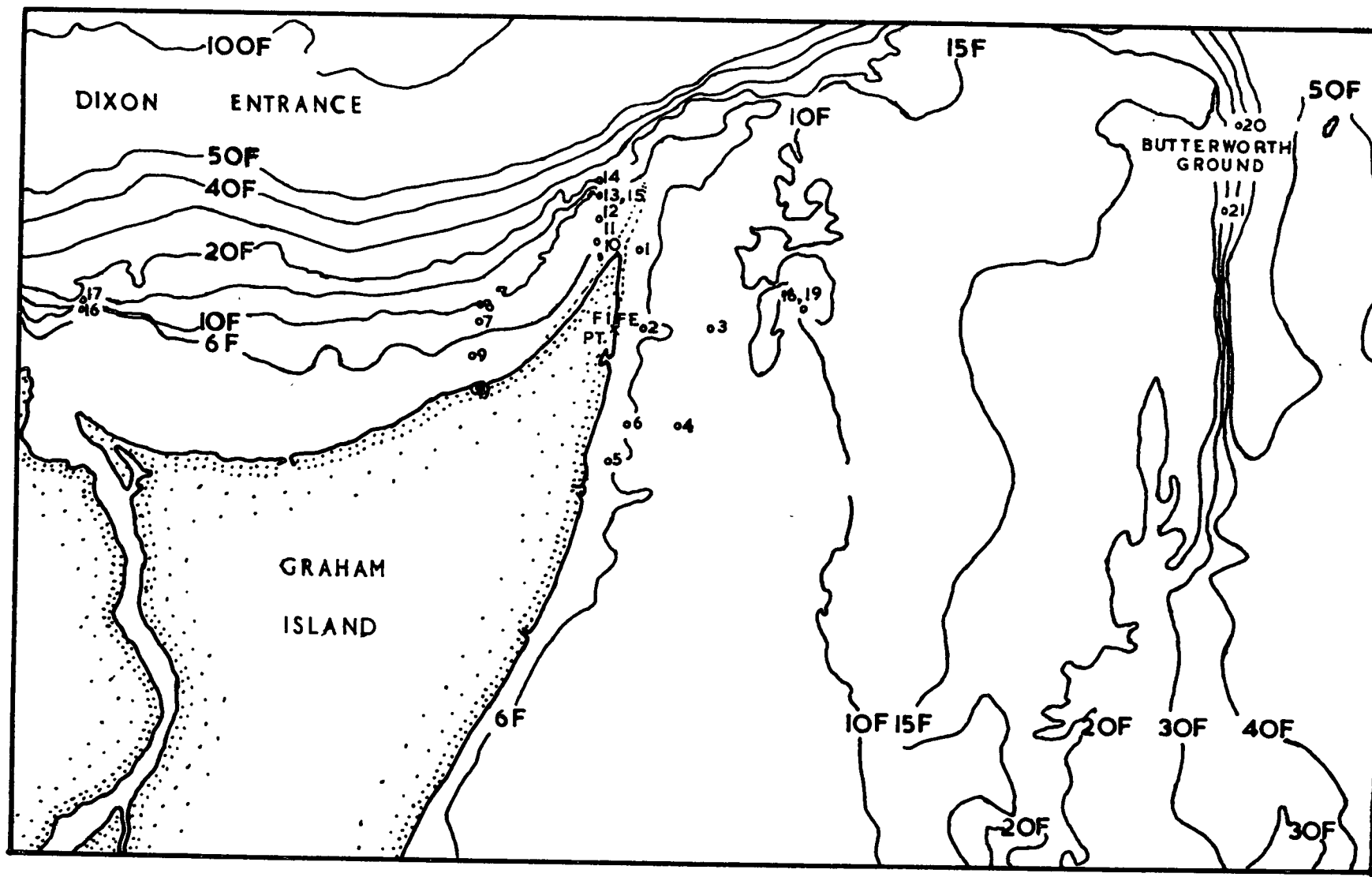


Figure 5. Northern part of the Hecate Strait bank showing the approximate sampling positions in 1961.

Table I. Per cent size composition of butter sole in the 1954 trawl hauls taken from northern Hecate Strait using 1.5" mesh cod-end. The sampling positions are given in Figure 4.

Haul-group	I. (0 to 5 miles from Fife Point) - Haul Nos. 1 - 5	II. (5 to 10 miles from Fife Point) - Haul Nos. 6 - 10	III. (10 to 15 miles from Fife Point) - Haul Nos. 11 - 14	IV. (15 to 20 miles from Fife Point) - Haul No. 15	V. (20 miles to edge of the Bank) - Haul Nos. 16 - 20
Length in cms.	Per-cent Sub-total	Per-cent Sub-total	Per-cent Sub-total	Per-cent Sub-total	Per-cent Sub-total
5	1.32				
6	0				
7	1.32	0.42			
8	2.63	2.40		1.09	
9	9.21	4.95	3.75	0.54	0.43
10	28.95	4.81	2.14	0.54	0.72
11	19.74	2.69	1.79	0	0.51
12	13.16	1.13	0.89	0	0.43
13	3.95	0.99	0.71	0	0.51
14	0	1.98	1.43	1.09	1.95
15	2.63	3.82	1.07	1.09	2.03
16	1.32	2.69	2.14	0.54	0.58
17	6.58	3.39	1.79	3.26	2.17
18	2.63	6.08	0.54	5.43	3.04
19	3.95 97.39	4.95 40.30	2.14 18.39	3.80 17.38	4.56 16.93
20	0	3.68	2.86	2.17	3.11
21	1.32	2.83	2.32	4.35	2.97
22	0	3.96	4.29	3.26	4.78
23	0	3.68	2.32	2.17	5.14
24	1.32	5.09	5.54	6.52	6.58
25		3.96	4.82	5.98	6.37
26		3.39	3.21	3.80	6.08
27		3.25	3.93	2.72	3.91
28		2.69	3.21	1.63	3.69
29	2.64	1.98 34.51	2.14 34.64	2.17 34.77	3.76 46.39
30		2.12	2.68	3.26	3.04
31		1.56	3.75	2.17	3.55
32		1.70	3.39	4.89	4.34
33		3.68	6.61	4.35	5.86
34		4.95	7.32	9.78	4.41
35		3.82	6.43	8.70	5.21
36		3.68	5.71	4.35	4.85
37		2.40	4.11	4.89	2.17
38		0.57	3.04	3.26	1.74
39		0.42	1.07	1.63	0.87
40		0.28	2.32	0.54	0.14
41			0		0.29
42			0		0.07
43		25.18	0.54 46.97	47.82	36.54
Total	100	100	100	100	100
N	76	707	560	552	1382

Table II.  $\chi^2$  analysis of the percent size composition of butter sole in different haul groups given in Table I.

Haul group	II	III	IV	V		
Length group (cms.)	(5-10 miles from Fife Point)	(10-15 miles from Fife Point)	(15-20 miles from Fife Point)	(20 miles to edge of the Bank)	Total	$\chi^2$
0-19	40.30	18.39	17.38	16.93	93.00	28.11
20-29	34.51	34.64	34.77	46.39	150.31	
29+	25.18	46.97	47.82	36.54	156.51	
Total	99.99	100.00	99.97	99.86	399.82	
N	707.0	560.0	552.0	1382.0		

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Table III. Per cent size and age composition of butter sole in 1961 trawl hauls taken from Northern Hecate Strait. The approximate sampling positions are given in Figure 5.

General area	East coast of Graham Island		8 miles off Fife Point		Butterworth ground			East coast of Graham Island		8 miles off Fife Point		Butterworth ground	
Haul No. & depth	1 to 6 2 to 8 f		18 to 19 10 to 12 f		20 to 21 32 to 34 f			1 to 6 2 to 8 f		18 to 19 10 to 12 f		20 to 21 32 to 34 f	
Length (cms.)	Per-cent	Sub-total	Per-cent	Sub-total	Per-cent	Sub-total	Age	Percent		Percent		Percent	
9	1.24		0.57				I+	58.50		0.57		0	
10	12.44		0										
11	21.66		0				II+	38.59		14.28		6.56	
12	13.69		1.14										
13	7.47		2.28		1.00		III+	2.49		23.43		14.14	
14	6.22		5.71		0								
15	8.71		0.57		1.51		IV+	0		10.28		11.62	
16	4.98		3.43		1.00								
17	5.39		1.14		2.01		V+	0		21.71		15.15	
18	7.47		4.57		1.00								
19	3.32	92.09	4.57	23.98	0.05	6.57	VI+	0.41		24.00		29.80	
20	4.15		6.28		2.51								
21	2.07		4.57		4.02		VII+			4.57		15.66	
22	0		6.28		5.02								
23	0.83		4.00		3.01		VIII+			1.14		5.55	
24	0.41		3.43		6.03								
25			5.14		5.02		IX+					1.51	
26			5.14		5.02								
27			11.42		5.53								
28			5.14		6.03								
29		7.46	3.43	54.83	5.53	47.72							
30			2.86		8.04								
31			4.00		4.02								
32			2.86		11.56								
33	0.41		2.86		5.53								
34			5.71		3.01								
35			1.14		5.53								
36			1.71		4.52								
37					0.05								
38					2.01								
39					1.00								
40		0.41		21.14		45.27							
Total		100		100		100		100		100		100	
N		241		175		199		241		175		198	

Table IV.  $\chi^2$  analysis of the percent size composition of butter sole from Hecate Strait in the 1961 sample given in Table III.

Length group (cms.)	8 miles off Fife Point	Butterworth ground	Total	$\chi^2$
0-19	23.98	6.57	30.55	19.18
20-29	54.83	47.72	102.55	
29+	21.14	45.27	66.41	
Total	99.95	99.56	199.51	
N	175	199		

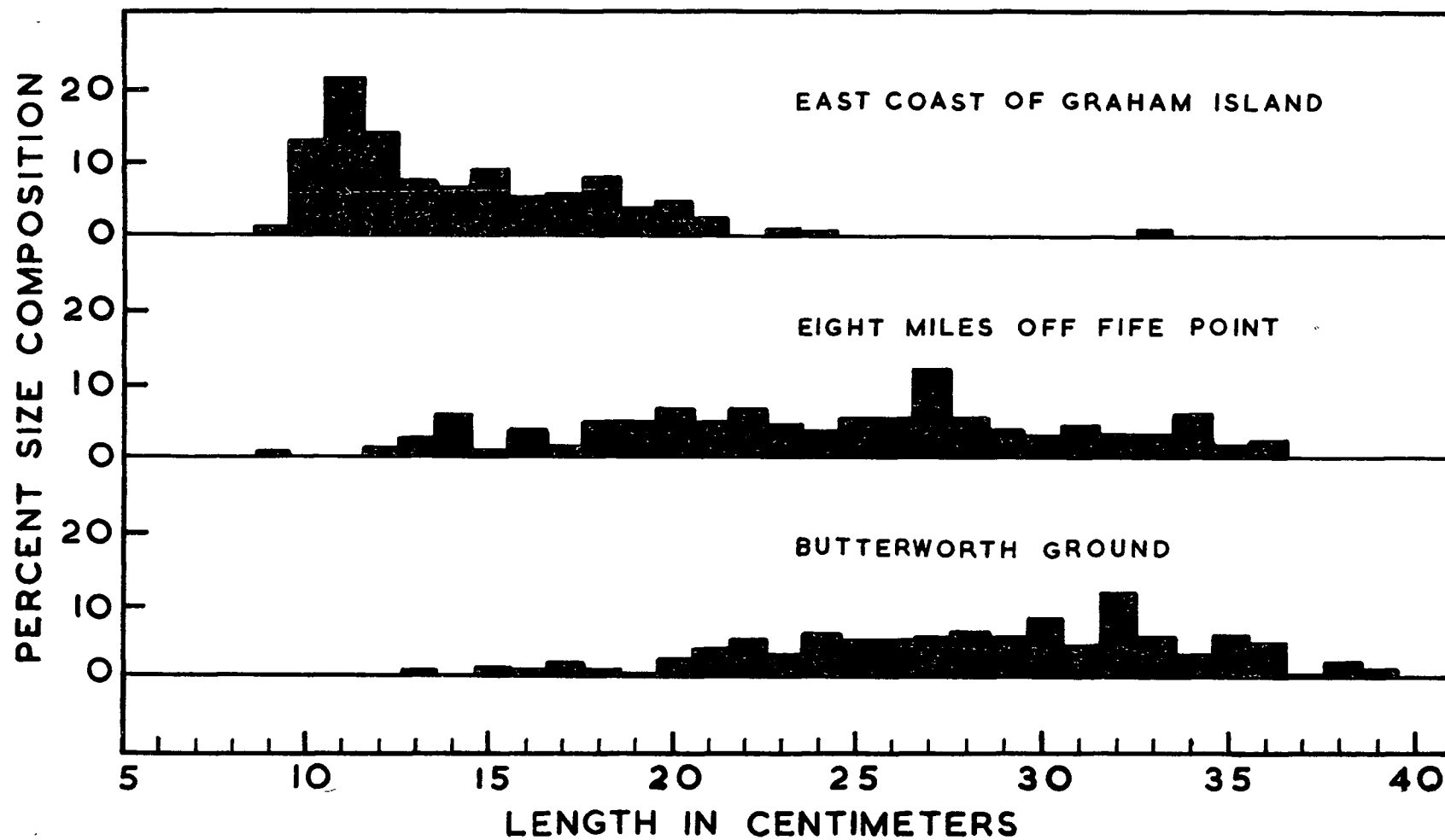


Figure 6. Histogram showing the size frequency distribution of butter sole in the <sup>JULY</sup> 1961 trawl hauls from northern Hecate Strait.

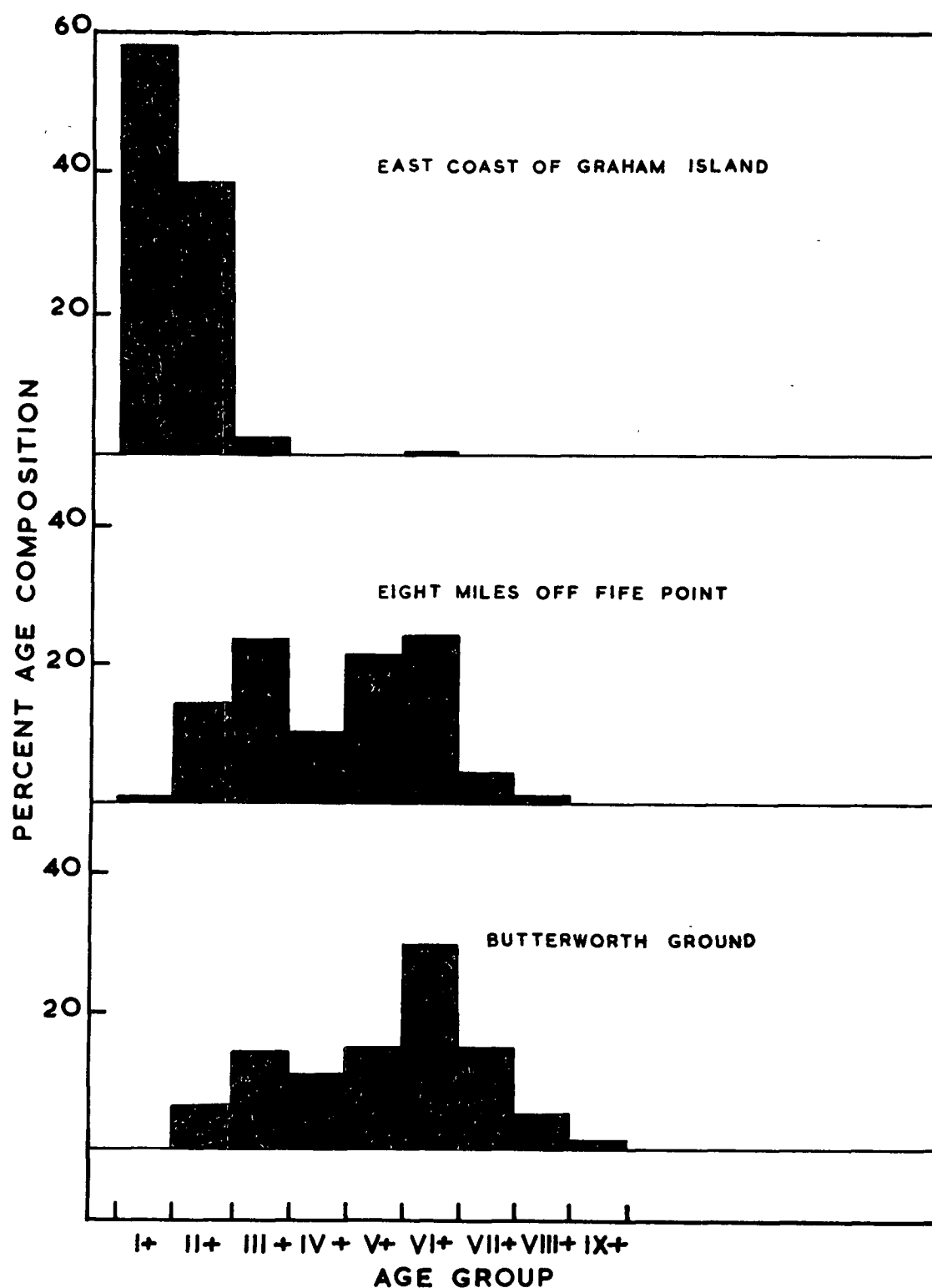


Figure 7. Histogram showing the age frequency distribution of butter sole in the <sup>July</sup> 1961 trawl hauls from northern Hecate Strait.



high  $X^2$  value of 28.11. However a  $X^2$  test did not indicate any significant difference in the size categories of butter sole in haul-groups III to V. While young butter sole less than 20 cm. length exhibit definite depth stratification and are dominant in haul-groups I and II which lie mostly within the 10 fathom belt, no trend in size distribution is seen in the haul-groups III to V. During the summer butter sole occupies the shallow Hecate Strait bank, their main summer feeding ground. Within this area the gradient between 10 and 20 fathoms is very gradual. This may obscure the depth preference of butter sole above 20 cm. length which were dominant in haul groups III to V all lying within the 10-20 fathom belt. The distribution of butter sole in 1961 samples from areas 3 and 4 (Figure 1) at depths of 10-12 and 32-34 fathoms respectively indicated a depth stratification of butter sole with respect to size and age. The  $X^2$  value was significant. The age distribution of butter sole in 1952-1953 samples (Table XXXIX) also showed that butter sole of age 1+ were mainly confined to the east coast of Graham Island.

Butter sole are generally scarce in hauls taken from the shallow water along the Dixon Entrance side of Graham Island. However, heavy catches were obtained in the 1961 summer hauls from this area. Total catch and length frequency distribution of butter sole in the hauls taken from this area are given in Table V and the sampling positions in Figure 5. The dense populations sampled at shallow depths may be local aggregations on good feeding grounds. The other samples taken at different depths in this area however did not indicate a definite depth stratification.

The wide range in the density of butter sole in the 1961 hauls (Tables III and V) suggest their patchy distribution within the Hecate Strait bank.

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Table V. Percent length composition of butter sole in the 1961 trawl hauls taken from Dixon Entrance. Sampling positions are given in Figure 5.

General area	Dixon entrance side of Graham Island								
Haul number and depth	10 4f	11 6f	12 8f	13,15 10f	14 20f	7 8f	8 10f	16 10f	17 15f
Length(cms.)									
10		3.33		1.32					
11		6.66	21.43	13.15					2
12	0.64	10.00	7.14	21.05	19.04				4
13	0	13.33	14.28	25.00	14.29				6
14	1.28	20.00	14.28	23.68	33.33	0.42			2
15	0.64	6.66	14.28	1.32	9.52	0			0
16	1.28	13.33	0	6.58	4.76	0.84			10
17	2.24	10.00	7.14	2.63	0	0.42		7.70	10
18	3.51	3.33	0	2.63	4.76	0.84	0.63	7.70	10
19	3.19	3.33	0	1.32	9.52	1.67	2.50	0	12
20	3.83	3.33	7.14	0	0	3.35	0	0	10
21	5.11	0	7.14	0	0	4.18	0.63	0	10
22	6.34	0	7.14	0	0	2.51	0.63	7.70	2
23	2.87	0		1.32	0	3.76	1.88	0	2
24	4.15	3.33			4.76	4.60	2.50	7.70	4
25	2.87					5.86	4.38	0	6
26	3.51					5.44	2.50	0	2
27	2.55					5.86	5.00	0	2
28	2.87					7.11	6.88	7.70	0
29	5.11					7.11	6.88	7.70	0
30	3.83	3.33				5.86	10.00	7.70	0
31	5.11					7.11	7.50	7.70	2
32	6.34					6.70	14.38	0	0
33	8.31					10.46	10.63	7.70	0
34	11.18					7.11	12.50	14.38	2
35	6.34					5.44	6.25	7.70	0
36	4.15					2.93	1.88	7.70	2
37	0.96					0.42	1.88		
38	0.96						0.63		
39	0.32								
40	0.32								
Total	100	100	100	100	100	100	100	100	100
Sample Size	313	30	14	76	21	239	160	13	50
Total catch	313	30	14	76	21	600	1000 lbs.	13	50

(c) Behaviour and movements of butter sole.

From an examination of trawl catches Alverson (1960) found that all commercially important flatfish in the Pacific northwest area tend to occupy relatively shallow water in summer and deeper water in winter. Tagging experiments conducted by Ketchen (1956) showed that adult lemon sole populations in Hecate Strait exhibit a northward migration in spring and early summer and a southward migration during early fall. On the basis of information provided by trip reports he showed that lemon sole migrate from deeper to shallower waters during late winter. Since heavy concentrations of butter sole occur during summer months in the shallow Hecate Strait flats the tendency to occupy shallower waters in summer seems to be shared as well by butter sole. The presence of a spawning population at depths of 30-35 fathoms in Skidegate Inlet and the occurrence of a large percent of immature females\* along Butterworth ground (Figure 1) at depths less than 50 fathoms suggest that butter sole migrate to deeper waters during winter months. Barber (1957) has postulated that the seasonal movements of the flatfish of the area are in general associated with the cyclic alternation of the water masses in Hecate Strait. It has been suggested that this may be a result of their preference for warmer waters. The seasonal movements of butter sole seem to coincide with this general hypothesis. Nothing is known of the movements of 0+ and 1+ groups of butter sole that occupy the area along Graham Island coast. Young plaice in the North Sea are known to spend their first winter buried in the sand (Wimpenny 1953). Whether this is true of butter sole is not known.

Evidence from Manzer's (1949) tagging experiments in Skidegate Inlet, even though not extensive, indicates that most of the butter sole move

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\* In the February 1962 sample from the Butterworth ground only one of the 45 females examined showed any sign of maturing.

north after spawning in Skidegate Inlet as 11 out of 12 tag recoveries were made north of Skidegate Inlet. The absence of mature females in the sample taken during February 1962 from Butterworth ground (Figure 9) by commercial trawl suggest that only mature specimens show any oriented movement towards the spawning site. A comparison of the size frequency and ovary condition of butter sole in the samples from Butterworth ground and the spawning population in Skidegate Inlet (Figures 8 and 9) also suggest that the non-spawners are non-migrants and that only the spawning population migrates south from northern Hecate Strait to Skidegate Inlet. It is uncertain whether the maturing males in the Butterworth sample would have migrated to Skidegate Inlet as the spawning season progressed. No tag recoveries were made from 550 fish tagged in July 1953 at the northern region of the bank. This may have been due primarily to tagging mortality or to the poor fishery existing in 1954. It could also indicate the presence of other spawning sites in the area. Certainly more convincing evidence on the movements of butter sole can best be obtained by extensive tagging studies.

(d) Spawning migration.

Manzer (1949) attempted to analyse the spawning migration by studying the changes in sex ratio of the commercial sample during the season. He concluded that the males arrive at the spawning site earlier and leave the area earlier than the females. This aspect can be studied only by analysing small meshed trawl hauls taken during the entire spawning season. The length composition of two half-hour trawl hauls (Table VI) taken with a shrimp trawl in the beginning of the fishing season in 1961 show a predominance of males in the sample, the sex ratio being 5.51 : 1. The sampling survey conducted during January 1953 with small meshed trawl hauls in Skidegate Inlet also showed that the sex ratio of the spawning population is predominantly in

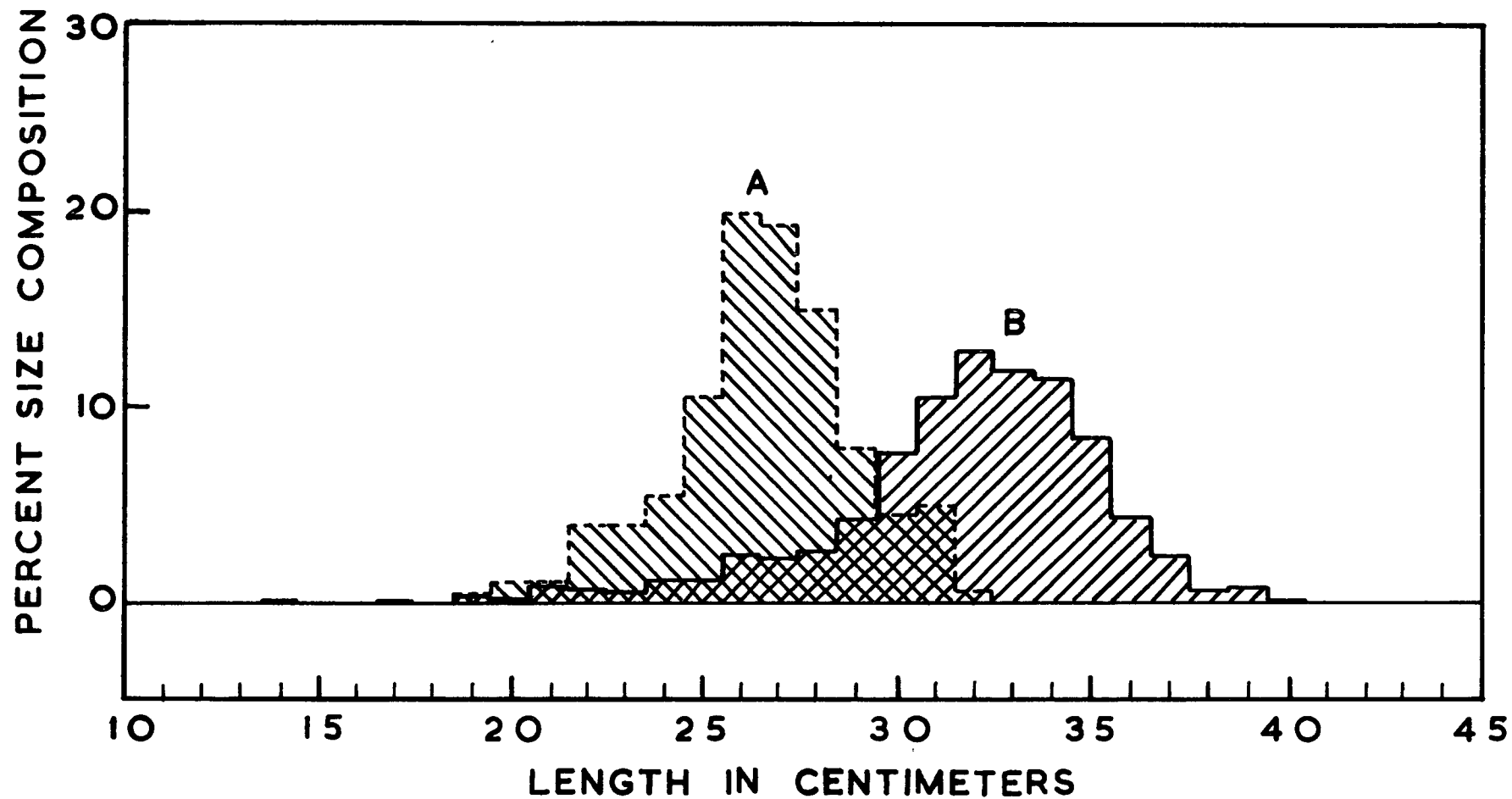


Figure 8. Histogram showing the length frequency distribution of butter sole in samples from Butterworth ground (A) and Skidegate Inlet (B) collected during February 1962 by commercial trawlers.

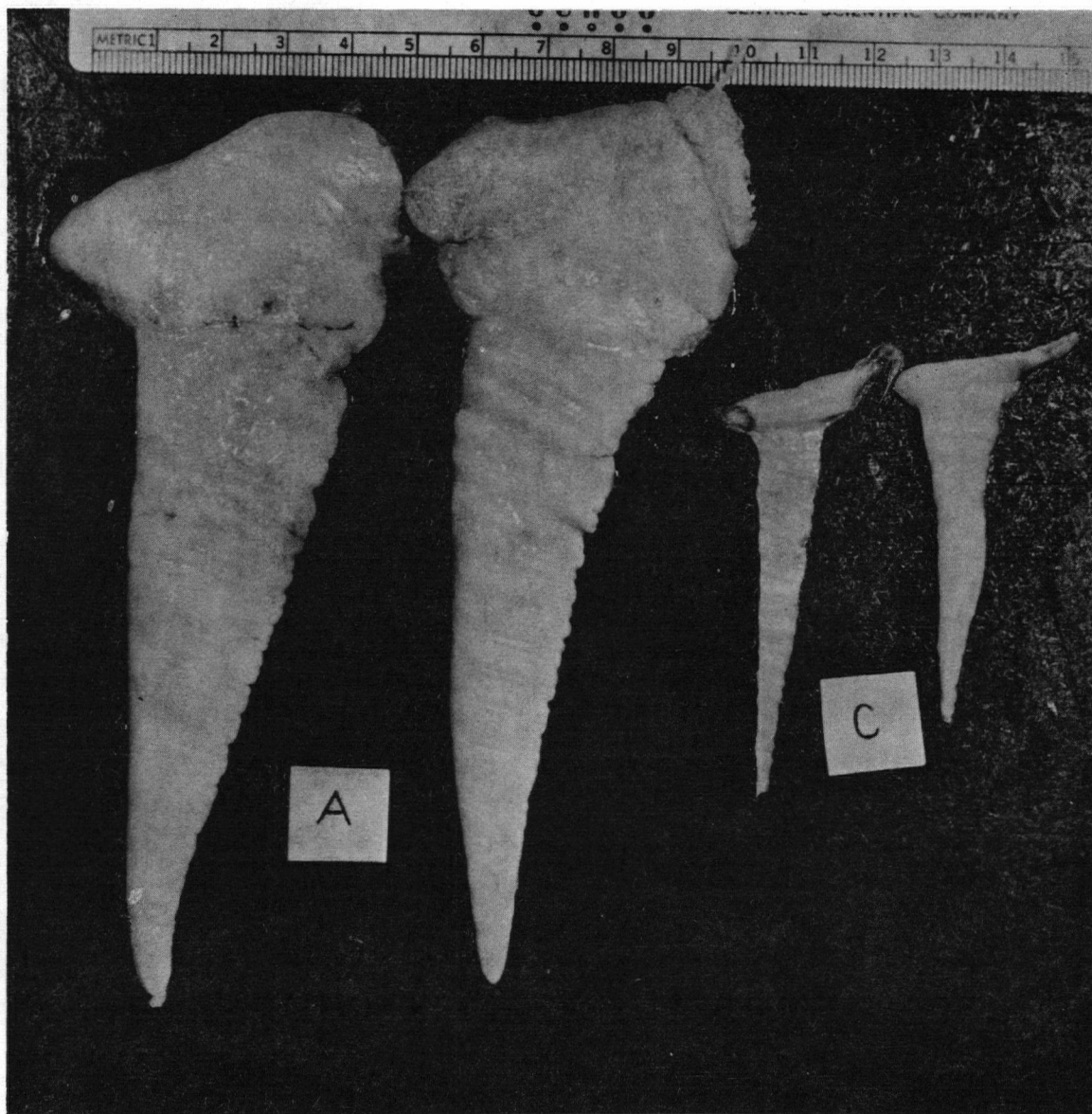


Figure 9. Photograph of the ovaries of butter sole sampled from Skidegate Inlet and Butterworth ground during February 1962; A - mature ovary of butter sole (31cms.) from Skidegate Inlet. C - immature ovary of butter sole (30cms.) from Butterworth ground.

Table VI. Length frequency distribution of male and female butter sole in two half-hour ~~small~~ meshed (1.5") trawl hauls from Skidegate Inlet during February, 1961

Length in cms.	Male	Female
13	1	
14	5	
15	7	
16	9	
17	12	
18	9	1
19	8	
20	2	
21	1	
22	11	
23	3	
24	3	
25	10	
26	15	
27	12	
28	11	
29	10	1
30	14	
31	35	2
32	29	5
33	26	4
34	12	12
35	11	5
36	2	10
37	1	3
38		3
39		1
40		
	259	47

Table VII. Age composition of butter sole in samples taken from Skidegate Inlet during the 1953 sampling survey using 1.5" mesh cod-end.

Age	II	III	IV	V	VI	VII	VIII	IX	X	XI
Male	141	301	1430	1594	1004	902	365	109	14	0
Female	21	11	50	118	305	369	198	61	7	1

favour of males, the sex ratio being 5.14 : 1. The preponderance of males over the females among the spawning population is only partly due to the early arrival of males at the spawning site. Males mature earlier than females and most of the fish migrating to Skidegate Inlet are mature. In the 1953 samples males of age five occurred with the greatest frequency whereas the most frequent age of the females was seven years. From their distribution in the 1953 samples given in Table VII it is evident that young males are much better represented than young females. As suggested for plaice by Wimpenny (1953) male butter sole may be ripe for a longer time and may remain longer at the spawning site. These factors may explain the predominance of males at the spawning site.

(e) Factors limiting the distribution of butter sole in Hecate Strait.

In Hecate Strait butter sole are never caught at depths greater than 50 fathoms. The depth contours of the Hecate Strait area show clearly that the shallow Hecate Strait flat is well isolated by the deep water of Dixon Entrance in the north and Queen Charlotte Sound in the south. Because of the relatively sharp depth gradient around Hecate Strait bank, the depth barriers may be an important limiting factor in the distribution of butter sole. They are known to occur at depths between 55 and 65 fathoms in lower latitudes along the Washington and Oregon coast. This latitudinal difference in depth distribution and the movement to deeper warmer waters during winter also suggest that temperature has an important role in limiting the distribution of butter sole. Since butter sole occur within a narrow depth range in a medium of high oxygen content, the presence of large areas of water of low oxygen content near the bottom during summer, as shown by barber (1958), may also act as a limiting factor.



Another important factor to be considered is the extent to which butter sole are distributed during their pelagic phase. Since no work has been done on the early life history of butter sole it can only be deduced from what is known of related species. Most flatfishes spawn during winter months and in most cases the eggs and larvae are passively drifted by the current until they adopt a benthic habit after metamorphosis. The northerly current of the surface water through Hecate Strait as shown by the drift bottle experiments of Thompson and Van Cleve (1936) may carry the eggs and larvae of butter sole from Skidegate Inlet northward. These larvae on metamorphosis may contribute to the young butter sole population, found mainly in the inshore area along the Graham Island coast north of Skidegate Inlet. The larvae moving into the deep water of Dixon Entrance may perish and not contribute to the Skidegate spawners. My studies on the fluctuations of the butter sole population (Section IV) show that the young butter sole along Graham Island coast are eventually recruited to the spawning population in Skidegate Inlet.

(f) Relative importance of northern Hecate Strait flat as a habitat for flatfish.

The above consideration of the biological and environmental factors limiting the distribution of butter sole suggests that the Hecate Strait bank is the main area of distribution of butter sole spawning in Skidegate Inlet. Since other species of flatfish also occur in the samples the relative importance of the Hecate Strait bank for these species should also be examined. The most frequently occurring species in the samples are butter sole, lemon sole, rock sole and sand sole. The relative abundance and association of these species in the summer hauls taken during 1953-1954 were studied by the rank correlation methods of Kandall (1955). Their use in ecological studies is also discussed by Fager (1957). Since the duration of the hauls used to

take the 1953 samples varied they were first weighted to conform to a standard 15 minute trawl haul.

The results of the analysis of dominance and relative abundance are given in Tables VIII and IX. Table VIII shows that the order of dominance of flatfishes in the area is butter sole > rock sole > lemon sole > sand sole. In 1953 this was statistically significant at the 0.05 level and in 1954 at the 0.01 level. From the rank values the dominance of butter sole over the others in the area is very conspicuous. This can further be seen from the results of analysis of relative abundance taking two species at a time (Table IX). The relative abundance of the four species in the 1953 and 1954 samples is represented in Figure 10, which illustrates that butter sole is more dominant in the northern part of Hecate Strait bank.

The abundance of young flatfishes along the Graham Island coast is examined later (Tables XXXVII and XXXVIII) when the fluctuation in the butter sole population is analysed. The results show that the relative abundance of young flatfishes in this area varies from year to year. This may be due to two reasons. Firstly the Graham Island coast may be the chief nursery ground for the young butter sole, lemon sole and sand sole, as no one species is particularly dominant in the catches. Ketchen (1956) has shown that this area is the main nursery ground for lemon sole. Secondly variations in the year class strength of these species are better expressed in the samples because only young ones occupy this area.

(g) Inter-relationships among species of flatfish

The analysis of relative abundance (Tables VIII and IX) has shown that the dominant species of flatfish over the northern Hecate Strait bank is butter sole. Since lemon sole, rock sole and sand sole are represented in this area by individuals of approximately the same size range as butter sole,

Table VIII. Analysis of dominance of butter sole in the 1953 and 1954 samples from the northern Hecate Strait bank. W = coefficient of concordance. P = probability of getting the observed W by chance.

	1953				1954			
	$\Sigma$ rank	Deviation <sup>2</sup>	W	P	$\Sigma$ rank	Deviation <sup>2</sup>	W	P
Butter sole	19	100	0.255	< 0.05	14	182.25	0.415	< 0.01
Lemon sole	33	16			32	20.25		
Rock sole	27	4			30	6.25		
Sand sole	37	64			34	42.25		
No. of replicates	12				11			
	Mean =	S =			Mean =	S =		
	29	184			27.5	251		

Table IX. Analysis of relative abundance of butter sole, lemon sole, rock sole and sand sole in the 1953 and 1954 samples from the northern Hecate Strait bank.

	1953					1954				
	Respective $\Sigma$ rank	t	P	N		Respective $\Sigma$ rank	t	P	N	
Butter sole x Lemon sole	185.5 279.5	1.95	0.027	15		112.0 239.0	3.26	.0005	13	
Butter sole x Rock sole	147.5 203.5	1.44	0.076	13		247.0 281.0	0.64	0.26	16	
Butter sole x Sand sole	81.0 173.0	3.05	0.001	11		118.0 233.0	2.95	0.002	13	
Lemon sole x Rock sole	187.5 163.5	0.615	0.27	13		160.5 139.5	0.61	0.27	12	
Lemon sole x Sand sole	111.0 142.0	1.02	0.15	11		151.0 149.0	0.06	0.48	12	
Rock sole x Sand sole	85.0 168.0	2.725	0.003	11		145.5 205.5	1.54	0.06	13	

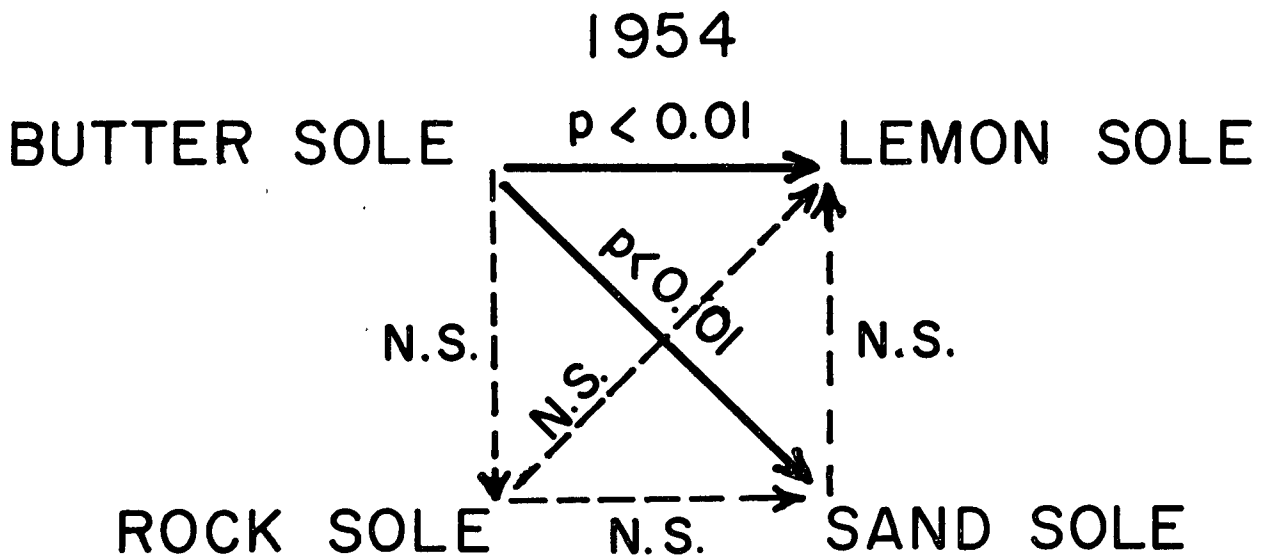
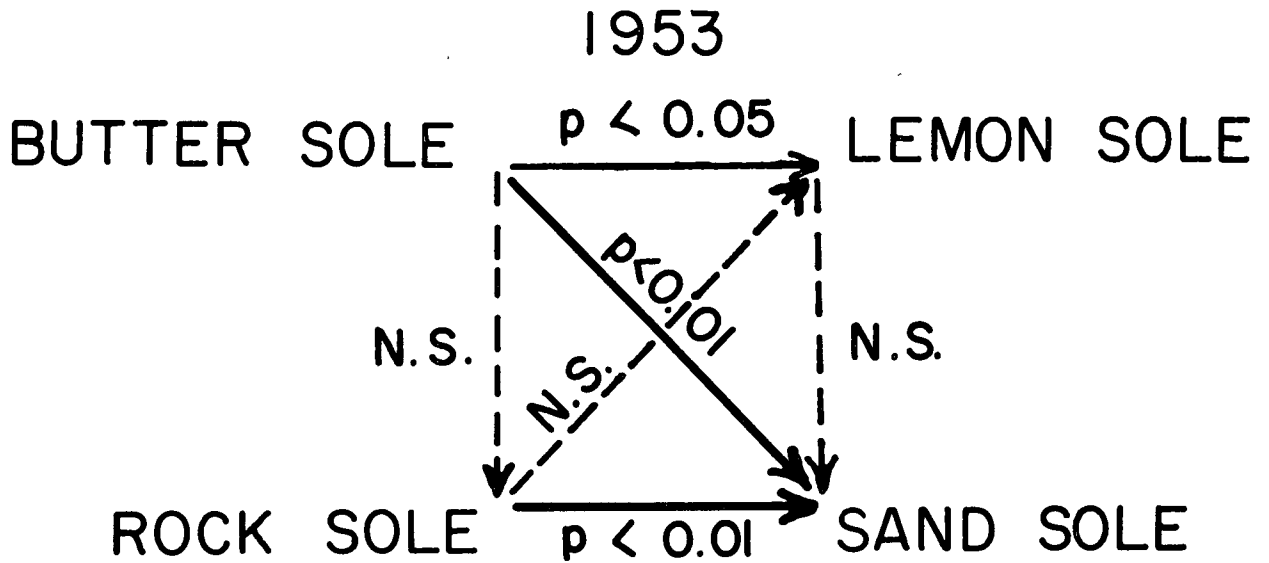


Figure 10. Relative abundance of four species of flatfish in the 1953 and 1954 samples from the northern Hecate Strait.

the 1953 and 1954 samples taken from this area were analysed to see whether the species exhibit any negative or positive association. This might indicate, for example, whether interspecific competition has any significant role in controlling the abundance of these groundfishes. The results of rank correlation analysis are given in Tables X and XI. Neither the results from the inshore area along Graham Island nor the main bank indicated any strong association between the species. The only significant correlation values observed were between butter sole and sand sole and between butter sole and lemon sole. This was not consistent for all the years examined.

#### (h) Conclusion

The analysis of distribution, abundance and movements of butter sole on the Hecate Strait bank indicates that (1) There is a general depth-stratification according to size and age groups with the young ones being restricted to inshore areas along the Graham Island coast (2) Within Hecate Strait a summer migration to shallower waters and a winter migration to deeper waters occur. A north-south migration is shown only by the spawning population. (3) The sex ratio of the spawning population is influenced by sexual differences in the onset of maturity and spawning migration. (4) The population spawning in Skidegate Inlet is mainly confined to Hecate Strait both during the larval and adult phases because of the physical conditions of the area and the existence of a depth barrier. The temperature and oxygen content may also function as limiting factors. (5) There is no active inter-specific association of the flatfish in the area during the post-pelagic phase.

### 3. Discreteness of the Hecate Strait population of butter sole.

The identity of self contained stocks is analysed by examining the

Table X. The association of young butter sole, lemon sole and sand sole along the Graham Island coast as indicated by the rank correlation test.

Year	Butter sole - lemon sole	Butter sole - sand sole	Lemon sole - sand sole
1952	$\tau = 0.9888$ P = 0 N = 10	$\tau = 0.1363$ P = 0.66 N = 10	$\tau = 0.0733$ P = 0.82 N = 11
1953	$\tau = -0.257$ P = 0.31 N = 11	$\tau = 0.0224$ P = 1.0 N = 10	$\tau = 0.4944$ P = 0.058 N = 10
1954	$\tau = 0.60$ P = 0.234 N = 5	$\tau = 0.738$ P = 0.067 N = 5	$\tau = 0.527$ P = 0.17 N = 5

Table XI. The association of butter sole, lemon sole, rock sole and sand sole from the Hecate Strait flat. As indicated by the rank correlation test.

Year	Butter sole- lemon sole	Butter sole- rock sole	Butter sole- sand sole	Lemon sole- rock sole	Lemon sole- sand sole	Rock sole- sand sole
1953	$\tau = 0.4444$ P = 0.0254 N = 15	$\tau = -0.234$ P = 0.30 N = 13	$\tau = 0.679$ P = 0.005 N = 11	$\tau = -0.1558$ P = 0.429 N = 13	$\tau = 0.2076$ P = 0.43 N = 11	$\tau = -0.1321$ P = 0.64 N = 11
1954	$\tau = 0.3225$ P = 0.14 N = 13	$\tau = -0.3025$ P = 0.11 N = 16	$\tau = 0.1161$ P = 0.62 N = 13	$\tau = 0.1212$ P = 0.61 N = 12	$\tau = 0.0153$ P = 1.0 N = 12	$\tau = -0.245$ P = 0.27 N = 13

possibility of effective interchange between populations during larval and adult phases of the life history. This is done by analysing the areas inhabited by butter sole for their ability to maintain an independent stock; and by comparing the biological characters such as the size composition, gonad condition and morphological features of the samples collected from different areas. The nearest known spawning population besides the Skidegate spawners is along the Washington coast. The two populations being separated by approximately 600 miles make the possibility of intermingling by passive drift during the early developmental stages remote. Ketchen (1956) states that lemon sole larvae could cover a distance of 150 - 370 miles assuming that the pelagic phase lasts from six to ten weeks. The factors limiting the distribution of butter sole will also tend to maintain the discreteness of the two stocks so that there is little mixing of the adult populations by active migration. The question remains whether the Hecate Strait population of butter sole is a single self-contained stock. By means of tagging experiments Ketchen and Forrester (1955) showed the existence of local, self-contained resident stocks of lemon sole in the Strait of Georgia distinct from a migratory stock entering the strait from offshore during the summer. He also postulated that local populations of lemon sole in the inlets along the B.C. coast may be self-contained and distinct from the lemon sole population found along the edge of the Hecate Strait bank. Butter sole occur along the edge of the bank throughout the year even when the spawners congregate in Skidegate Inlet during winter. It is not known whether there are other spawning sites in Hecate Strait that maintain more spawning populations, however, spawning was successful during the cold years, 1949 and 1950, when butter sole were absent from Skidegate Inlet. This is evident from the success of the 1956 and 1957 fisheries in Skidegate Inlet (Table XXXI).

Since no additional spawning sites were indicated either by the 1953 survey or by the commercial trawlers engaged in fishing in the area, spawning on a large scale outside Skidegate Inlet may occur only during years when environmental conditions prevent their entry into Skidegate Inlet.

Parish (1956) has pointed out that an area must possess certain features if it is to maintain an independent self-contained stock. It must be suitable for reproduction and growth and it should possess a current system that does not carry the early pelagic stages beyond its boundaries. The current system in Hecate Strait appears favourable for the distribution of the early developmental stages of butter sole from Skidegate Inlet to their nursery ground along the Graham Island coast. Manzer's tagging study (1949) and the analysis of abundance of butter sole from the northern part of Hecate Strait indicate that this area is the main summer feeding ground. The Hecate Strait habitat is thus adequate to maintain a self-contained population. The current pattern in Hecate Strait and the proximity of the deep Dixon Entrance make the Butterworth ground an unfavourable spawning area. There is considerable indirect evidence to support the theory that there is a single self-contained stock of butter sole on the Hecate Strait bank. First there was a dominance of 6+ butter sole in the 1961 summer hauls taken in the northern part of Hecate Strait (Table XXV), this was followed by a successful fishery for spawning adults in Skidegate Inlet (Table XXXI). In comparison at spawning time there is a very large percentage of immature females on the Butterworth ground. This evidence when coupled with length frequencies of commercial samples taken from these areas (Figure 8) and the above analysis of the movements of butter sole also lend support to this theory.



(a) Evidence from meristic study.

Since no tagging studies were done to ascertain the existence of independent self-contained populations, meristic counts were taken on butter sole from different areas to examine whether they show significant differences. Four samples were collected from the Hecate Strait area and one sample each from the Washington and Oregon coasts. Regarding size composition, the populations sampled from Hecate Strait during summer and winter were not homogeneous. The summer samples were from the nursery ground and consisted of both adults and juveniles, while the winter sample from Skidegate Inlet represented the spawning population. The winter sample from Butterworth ground, judging from the condition of the gonads, includes mostly non-spawners of the season. The winter samples from the Washington and Oregon coasts again represent only the adult spawners. Sampling was not uniform since the gear used during summer was small meshed while the samples during the winter, with the exception of that from the Oregon coast, were taken from commercial catches.

Three characters selected for counts were dorsal fin rays, anal fin rays and lateral line pores from the base of the pectoral fin to the tip of the anal fin because, below subspecific levels, significant differences between isolated populations are more easily detected among these, the most variable characters. The analysis is restricted to one sex only to avoid the complication of any sexual differences. The results are given in Tables XII to XVI.

In spite of the deficiencies in sampling, a clear difference in the dorsal and anal fin ray counts was observed between the samples taken from Hecate Strait and the samples from the Washington and Oregon coasts. Since the samples collected during the winter of 1962 from Skidegate Inlet and the United States coast were of mature specimens, their differences in fin ray

Table XII. Details of the meristic counts of butter sole in the samples from Hecate Strait, and the U.S. coast.

		Hecate Strait				Wash. coast	Oregon coast
		summer		winter		winter	winter
		Hecate Strait bank	Butterworth ground	Skidgate Inlet	Butterworth ground	8-10 miles SW to WSW off Quillayute	Between Umatilla and mouth of River Lapush
Dorsal fin ray count	Mean	86.35	85.86	86.08	86.94	88.18	88.16
	Range	80-92	80-92	81-92	82-92	82-95	85-92
	St. error	0.419	0.390	0.322	0.300	0.358	0.282
	Sample size	49	44	50	51	50	45
Anal fin ray count	Mean	66.47	66.19	65.84	66.14	67.48	67.13
	Range	61-72	62-71	57-70	61-69	62-72	59-71
	St. error	0.333	0.267	0.289	0.246	0.309	0.289
	Sample size	45	42	50	50	50	45
Lateral line pores	Mean	75.45	75.32	75.40	75.60	75.92	75.16
	Range	71-80	70-79	71-80	70-81	72-80	71-82
	St. error	0.285	0.297	0.251	0.290	0.264	0.344
	Sample size	42	41	50	50	49	43

Table XIII. t-values and their probability levels obtained from a comparison of dorsal and anal fin ray counts in the samples from Skidegate Inlet and the U.S. coast collected during February, 1962.

	Skidegate Inlet			
	Dorsal fin ray		Anal fin ray	
	t	p	t	p
Washington coast	4.36	<0.001	3.87	<0.001
Oregon coast	4.86	<0.001	3.16	<0.005

Table XIV. Analysis of variance on the dorsal fin ray counts within the samples from Hecate Strait.

Source	D.F.	S.S.	M.S.	F.
Total	193	1214.6		1.724
Means	3	32.19	10.73	N.S.
Residual	190	1182.41	6.22	

Table XV. Analysis of variance on the anal fin ray counts within the samples from Hecate Strait.

Source	D.F.	S.S.	M.S.	F
Total	186	707.9		0.83
Means	3	9.48	3.161	N.S.
Residual	183	698.42	3.816	

Table XVI. Analysis of variance on the number of lateral line pores within the samples from Hecate Strait.

Source	D.F.	S.S.	M.S.	F
Total	182	647.3		0.186
Means	3	2.011	0.67	N.S.
Residual	179	645.29	3.60	

counts were examined separately (Table XIII). The results showed highly significant differences between the Skidegate Inlet population and those from the United States coast. No significant differences were observed in the meristic counts of butter sole from the Washington and Oregon coasts. It is not known whether they belong to the same population or represent two spawning populations.

Tables XIV to XVI give the results of analysis of variance for samples taken within Hecate Strait. No significant variance ratio was observed for any of the three characters examined. However, a t-test indicates that the difference in the mean values of dorsal fin ray counts in the samples from Butterworth ground during the summer and winter is significant at the 5% level with a t-value of 2.198 for 93 df. This difference is interpreted here as an artifact partly due to the fact that the Butterworth ground samples were taken from commercial catches during the winter and from small meshed trawl hauls during the summer and partly due to seasonal variation in the size composition of butter sole in this area. Lindsey (1962) discusses the bias introduced in sampling as a result of the existence of a correlation between meristic count and size of fish from the same brood. In spite of sampling variability and possible differences between slow and fast growers, the highly significant differences in meristic counts observed between the Hecate Strait population and those along the United States coast seem to be the result of genuine environmental differences of the areas inhabited by the respective populations.

#### (b) Conclusion

On the basis of meristic studies and other biological factors discussed above, the weight of evidence favours the view that there is a single self-contained stock in Hecate Strait which is distinct from those along the Washington and Oregon coasts.

#### 4. Aspects of the population characteristics of butter sole.

##### (a) Age and growth of butter sole.

Because of its importance as a population variable the pattern and rate of growth of butter sole was studied in considerable detail. In this study the opaque and hyaline zones of otoliths were interpreted as being annular. A large amount of literature is available on the use of hard parts of fish in growth studies. Besides Graham (1929) and Van Oosten (1929) who reviewed the literature, Hickling (1933), Rollefson (1935), Hile (1941), Saetersdal (1953), Trout (1958) and others, have made valuable contributions. Otoliths of butter sole have fairly well defined opaque and hyaline zones which can, with the exception of older specimens, be read easily (Figure 11).

The otoliths sampled for age and growth studies were grouped at one cm. intervals of fish length and preserved in a mixture of equal parts water and glycerine. A few thymol crystals were added to the mixture to prevent the formation of moulds. Reading the otoliths\* from specimens above 35 cm. is more difficult than those from younger ones. For the back calculation of fish lengths the otolith radius can be measured from the nucleus to the end of the hyaline zones along a chosen axis. Radii along two axes (Figure 11) of 194 otoliths from a length range of 15 to 38 cm. were measured. Variations in the otolith radius measurements along the two axes were found on the average

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\* For reading, the otoliths were kept on the medial or sulcal side and the opaque and hyaline zones were examined against an illuminated black dish using 9x magnification. Most of the readings were done in a 2% solution of papain, a proteolytic enzyme from the papaya tree. Since butter sole spawn during February and March, the end of each winter season is taken to mark the end of one year. In determining the age it is found that best results are obtained if the reading is first done on females starting from the youngest specimen.

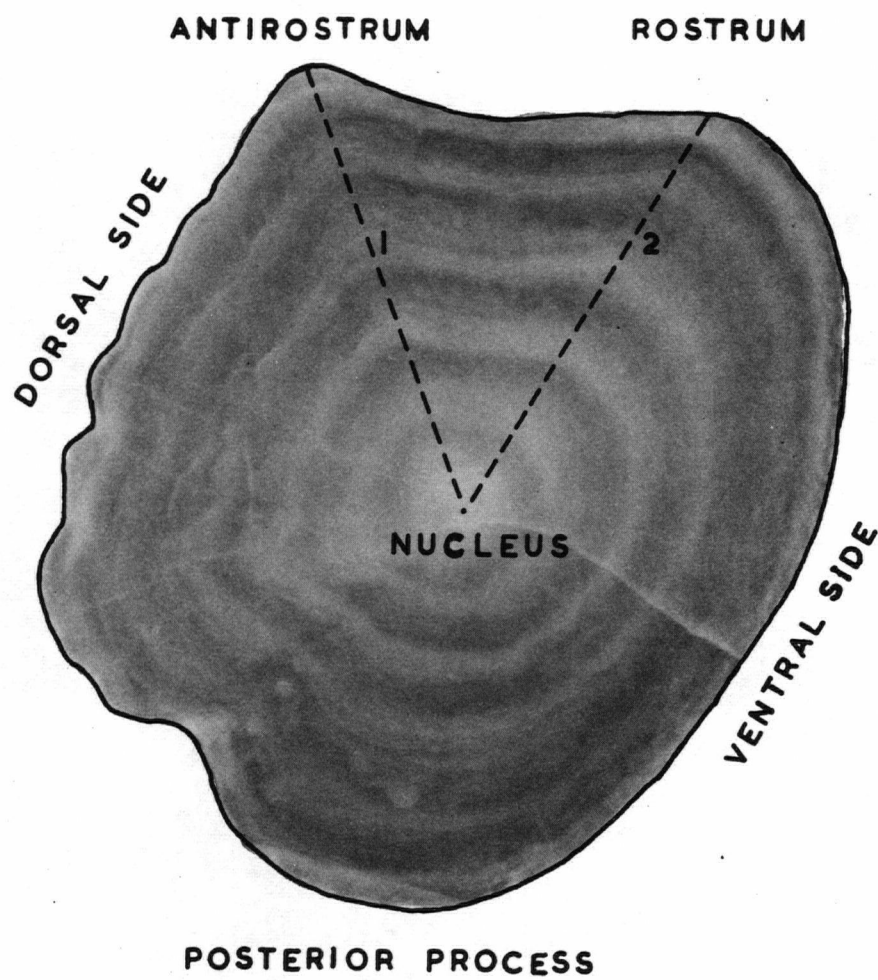


Figure 11. Photograph of the butter sole otolith showing hyaline and opaque zones.

to be of the same magnitude. The axis from the nucleus to the rostrum was chosen to measure the zones since it was along this radius that the most zones could be distinguished at the outer edge of the older otoliths. The measurements were made using a one cm. eyepiece micrometer which had been graduated into 100 divisions.

To facilitate back calculations the otolith radius-body length relationship was determined. Back calculation was based on the assumption that the intercept or the time <sup>of</sup> first formation of the otolith was constant and that any deviation of individual points from the calculated regression line was due to variability in the slope. To obtain a weighted mean back calculated length at different ages, back calculations obtained from different age groups were weighted according to the estimated numbers of these age groups in the catches from sampling localities 1 and 4 shown in Figure 1. Since regional differences in the density of the population and in growth rate were noticed this procedure would increase the accuracy of the estimated length at various ages.

(i) Body length-otolith radius relationship.

Since the relationship between body length and otolith radius varies widely between different species an accurate estimate of this relationship is important to avoid errors in back calculations. The estimated relationships for male and female butter sole are given in Figure 12. The body length-otolith radius relation for the male was found to be

$$\text{Length (cms.)} = 0.7944R - 0.70$$

and for the female

$$\text{Length (cms.)} = 0.09 + 0.7594R.$$

The results of the analysis of covariance for these two regression lines are presented in Table XVII.

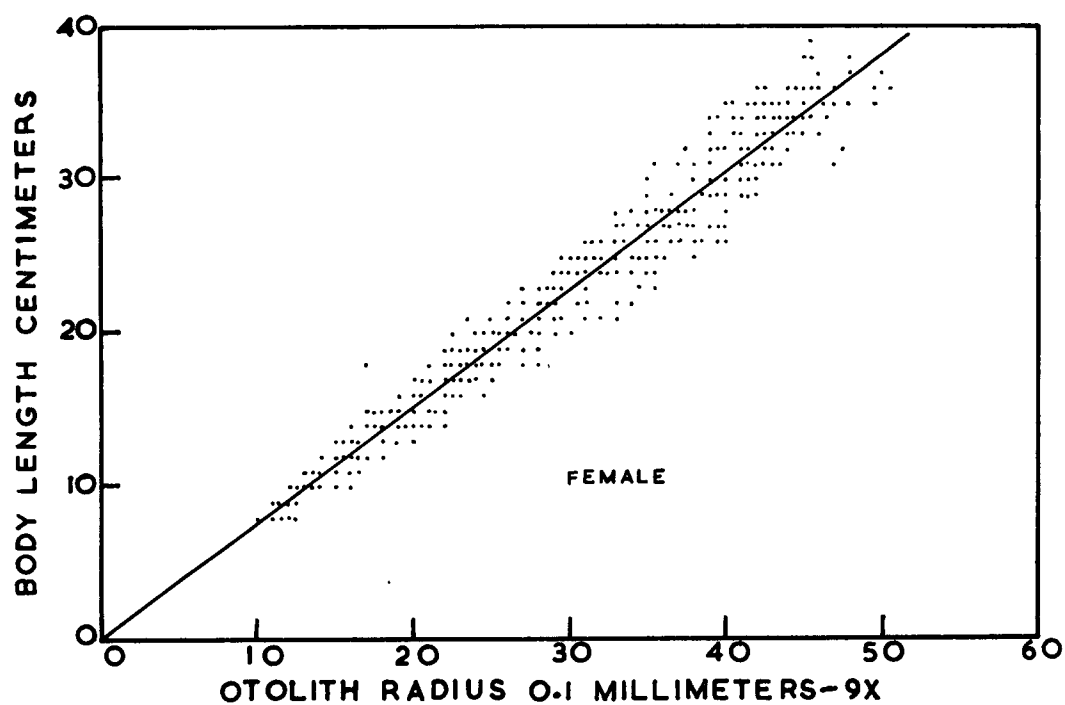
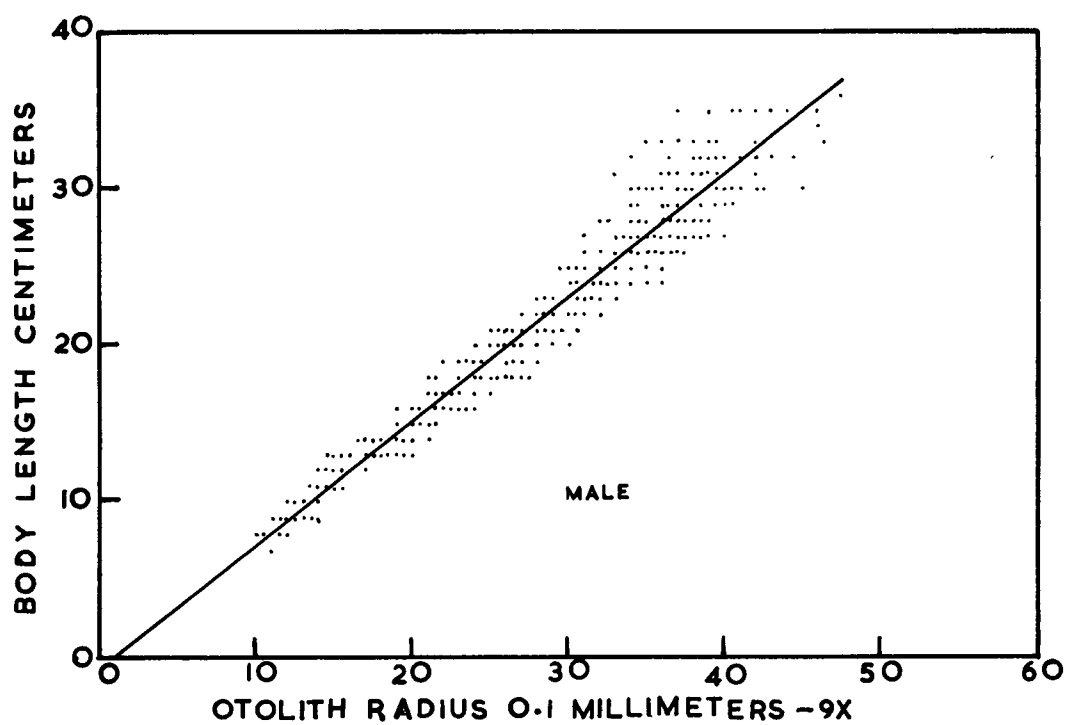


Figure 12. Body length - otolith radius relationship of butter sole.



Within the length range examined, the body length-otolith radius relationship is linear. Only the otoliths from the small meshed trawl hauls collected during 1961 were used for back calculation. If material from earlier periods had been included it may have increased the variability, as suggested by Southward (1962) for halibut. Long periods of preservation may also increase the variability. The significant variance ratio for the regression coefficients suggests that the body length-otolith radius relationship for the two sexes is different. Since the power of the covariance analysis is very high with such a large number of degrees of freedom even a slight difference in the two slopes may appear as significant. Nevertheless back calculation of lengths from otoliths was done separately for the two sexes using the respective regression lines.

(ii) Validity of otolith reading.

The reliability of the age readings from scales and otoliths have been studied for many species of fishes. References include Hile (1941), Jensen and Clark (1958), Saetersdal (1953, 1958), Frost and Kippling (1959), Bratberg (1956) and others. Most of these authors found that the regular formation of zones in the hard parts permitted reliable estimates of the fish's age. In the case of an otolith the opaque zone is generally laid down during the summer and the hyaline zone during the winter. However, Muller (1958) has noted a reversal in the timing of the zone formation in certain populations of Lota lota (Linnaeus). In butter sole the reliability of otolith reading is tested (a) by studying the timing of the zone formation (Figure 3) and (b) by comparing the estimated lengths at different ages with that determined by analysing the length frequency distribution by the probability paper method as described by Harding (1949) and Cassie (1950, 1954). The length measurements of 946 females in the July 1961 samples were

used for this purpose (Figure 14). The results are given in Tables XVIII and XIX.

In the summer a great proportion of the otoliths possess an opaque zone at the edge (Figure 13). As the winter progresses this proportion dwindles rapidly and the number of otoliths with hyaline edges increases. The slight discrepancy in the April sample may be due to inadequate sample size. This observation supports the view that the zones are laid annually, the opaque zone during summer and the hyaline zone during winter. The close identity of the lengths at different ages estimated from otoliths with the various modal lengths obtained by dissecting the length frequency data for the females (Table XIX) lends further support to the reliability of the otoliths in age determination. This study has, however, some limitations. There is a certain amount of personal bias introduced in determining the nature of the zone at the edge of the older otoliths. Also the estimation of modal lengths of the older age groups from the length frequency is subjected to errors due to the greater overlap of age groups, the insufficient number of class intervals between means and bias in sampling. As an example in the 1961 samples from the Hecate Strait bank, older age groups dominated the relatively heavy catches in area 1. This may have affected the estimation of the modal lengths of the older age groups. Hence the similarity of the estimated modal lengths obtained by the probability paper method and by back calculation may be partly due to chance. However, such errors are minimal in the estimates of modal lengths for the first three age groups.

(iii) Growth rate of butter sole.

The lengths at various ages, estimated by reading otoliths sampled from the spawning population, are entered in Tables XX and XXI. The back calculated

46.  
Table XVII. Body length - otolith radius relationship:- analysis of covariance among sexes to test the homogeneity of the regression coefficients.

Source of Variation	Residual S.S.	df.	M.S.	F.
Common	2714.69	1110		
Within sexes	2681.07	1109	2.4176	13.9060
Reg.coef.	33.62	1	33.6200	

Table XVIII. Estimated percent of otoliths with opaque or hyaline zones at the edge in the July 1961 and 1958-1960 winter samples.

	Number examined	Opaque edge	Hyaline edge	uncertain
1961 July	348	87.35	6.61	6.03
1958-'60				
January	138	60.87	36.96	2.17
February	982	41.55	44.91	13.54
March	576	25.52	60.76	13.71
April	57	33.33	50.88	15.79

Table XIX. Comparison of mean back calculated lengths at different ages from otoliths and the estimated modal lengths obtained from the length frequency distribution of female butter sole in the sample collected during July 1961.

Age group	I+	II+	III+	IV+	V+	VI+	VII+
From otolith (unweighted)	11.89	16.97	21.97	25.34	28.26	31.73	34.45
From otolith (weighted)	11.95	17.22	22.54	25.95	29.82	31.70	35.67
From length frequency (unweighted)	11.95	17.10	21.66	24.70	28.00	31.66	34.30

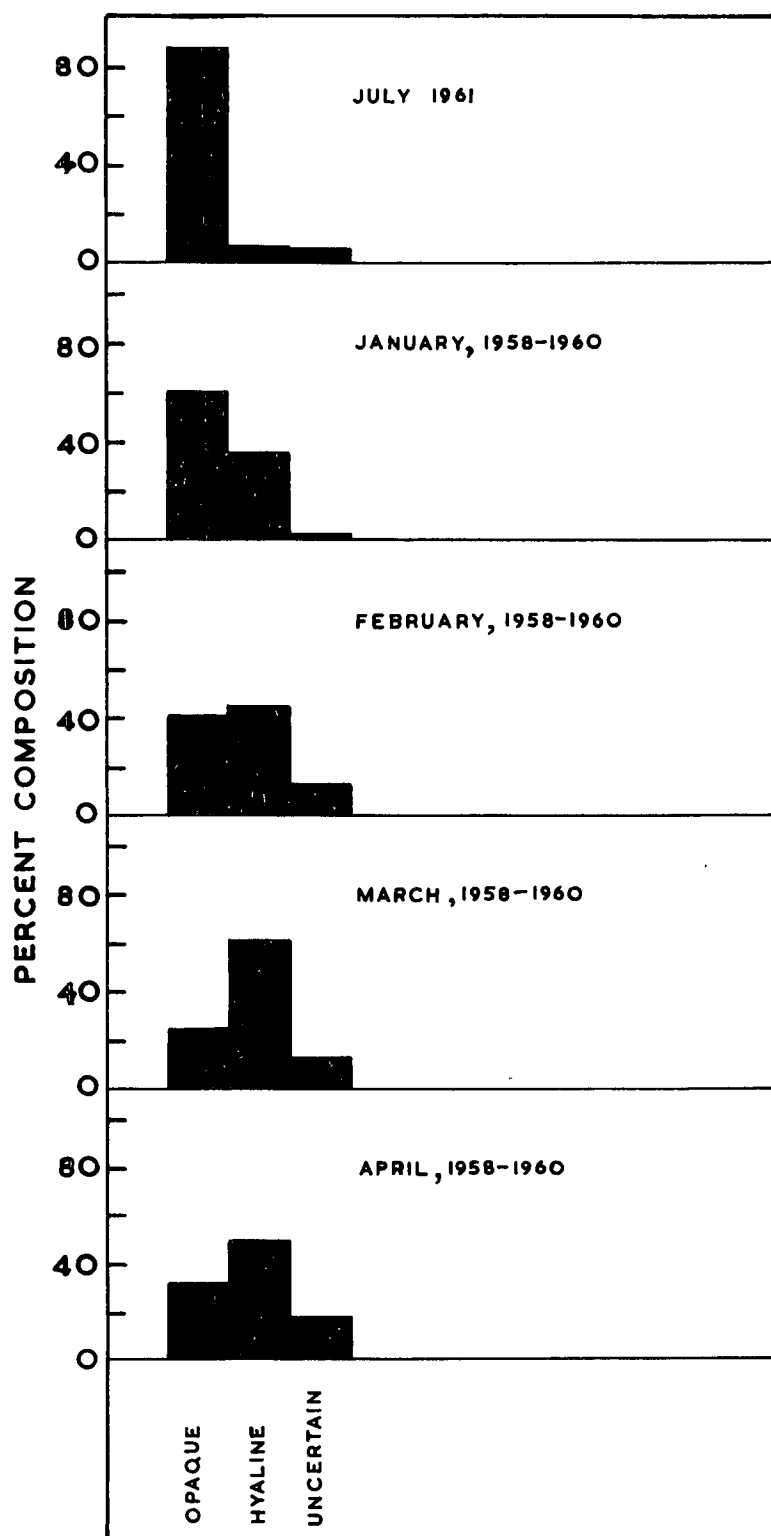


Figure 13. Percent of butter sole otoliths in the sample with opaque, hyaline or uncertain edges.

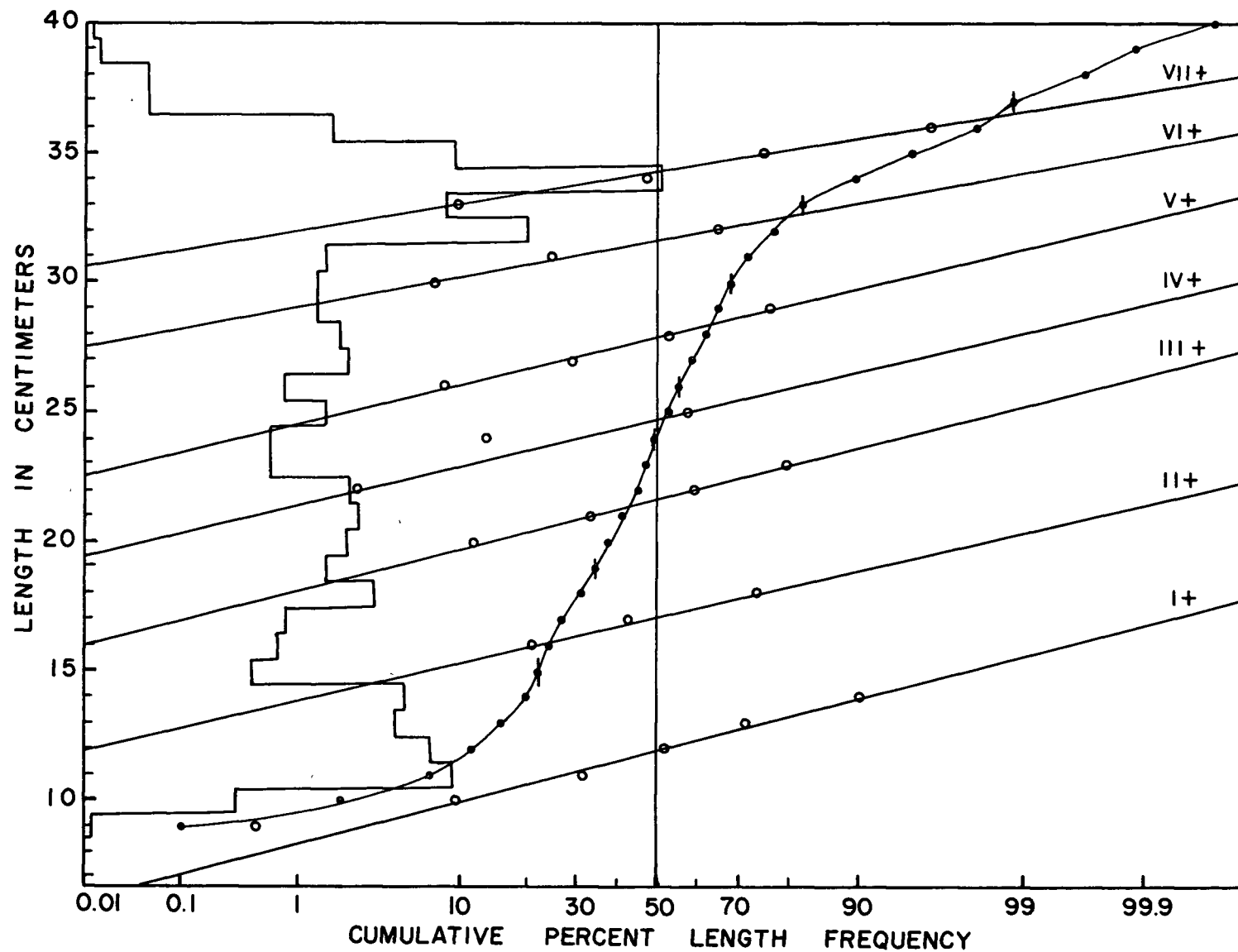


Figure 14. Dissected length frequency distributions of female butter sole by the probability paper method into modal length groups.

lengths given in Table XXII were determined from otoliths taken from both juveniles and adults. In obtaining mean lengths equal weights are assigned to each back calculated length from different age groups irrespective of the sample size. Because of the yearly variations in growth rate a weighted mean based on the sample size of each age group cannot be estimated. Since the number of age groups from which the mean back calculated length at the end of each year of life is obtained progressively decreases, the estimated mean lengths are influenced more and more by errors in back calculated lengths. In Table XXII the back calculated length of 11+ females is based on one otolith from a slow growing fish. This single specimen considerably reduces the estimated mean lengths of the ages greater than seven. The lack of adequate samples for the older age groups and yearly variations in growth rate may thus influence the accuracy of the estimated lengths of older ages. Because of this the lengths for higher ages were obtained by fitting a Wal-ford plot to the mean lengths up to age six for females and age seven for males. The Wal-ford graph drawn for the butter sole data is given in Figure 15. The estimated growth together with the maximum length ( $L_{\infty}$ ) and K or the rate of deceleration in growth increments obtained from the Wal-ford plot are entered in Table XXIII. The growth curves for the two sexes are drawn in Figure 16.

Comparison of the back calculated lengths and the lengths estimated by reading otoliths sampled from the spawning population.

The age estimated by reading otoliths from the spawning population is subject to errors because the early year classes will be represented in the sample only by those maturing faster. As shown in Table XIX the maximum growth increments occur between ages 4 and 5. The mean lengths for older age groups do not seem to be representative. This may partly be due to decreasing

Table XX. Mean lengths of butter sole at various ages estimated by reading otoliths sampled from the spawning population during January 1953, using a small meshed shrimp trawl.

Age	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Male	-	13.90	18.3	21.4	27.1	30.9	32.9	33.8	33.5	34.8	-
Female	-	13.90	17.2	21.9	30.2	34.3	35.3	36.2	36.8	39.4	35.0

Table XXI. Mean lengths of female butter at various ages estimated by reading otoliths from commercial catches for the period 1958-1960.

Age	V	VI	VII	VIII	IX	X	XI
	32.90	34.43	35.61	36.80	37.68	37.81	39.5

Table XXII. Weighted back calculated lengths at the end of each year of life of 316 males and 446 females collected during July 1961.

Sex	Age at capture	Length (cms.) at capture	No. of fish	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Male	I+	11.07	31	5.97										
	II+	16.94	54	5.65	13.02									
	III+	21.86	54	6.23	13.38	19.58								
	IV+	26.06	29	6.05	13.55	19.88	24.26							
	V+	28.39	47	6.20	12.89	18.90	23.76	26.79						
	VI+	30.04	75	5.89	12.16	18.07	22.95	26.51	28.81					
	VII+	32.16	18	6.02	12.56	18.84	23.71	26.83	28.92	31.10				
	VIII+	33.06	7	5.76	11.63	17.65	22.70	26.30	28.85	31.19	32.41			
	IX+	35.00	1	6.62	13.95	18.52	22.19	24.93	27.68	30.42	32.25	33.63		
			Mean	6.04	12.89	18.78	23.26	26.27	28.56	30.90	32.33	33.63		
Female	I+	11.95	44	6.81										
	II+	17.22	103	6.22	13.01									
	III+	22.54	79	6.49	13.96	20.12								
	IV+	25.95	38	6.48	13.24	19.66	24.05							
	V+	29.82	53	6.56	13.02	19.12	24.45	28.09						
	VI+	31.70	78	6.44	12.55	18.74	23.73	27.65	30.40					
	VII+	35.67	31	6.88	14.68	21.29	26.63	30.00	33.01	34.80				
	VIII+	35.17	13	6.58	13.24	18.89	24.12	27.49	30.76	32.38	34.16			
	IX+	35.84	6	6.08	13.56	19.08	24.56	28.91	32.05	33.77	34.85	34.92		
	XI+	37.00	1	6.00	14.12	20.02	23.71	25.93	29.25	30.73	32.20	33.31	34.79	35.89
			Mean	6.45	13.49	19.61	24.46	28.01	31.09	32.92	33.74	34.11	34.79	35.89
			Increment	7.04	6.12	4.85	3.55	3.08	1.83	0.82	0.37	0.68	1.10	



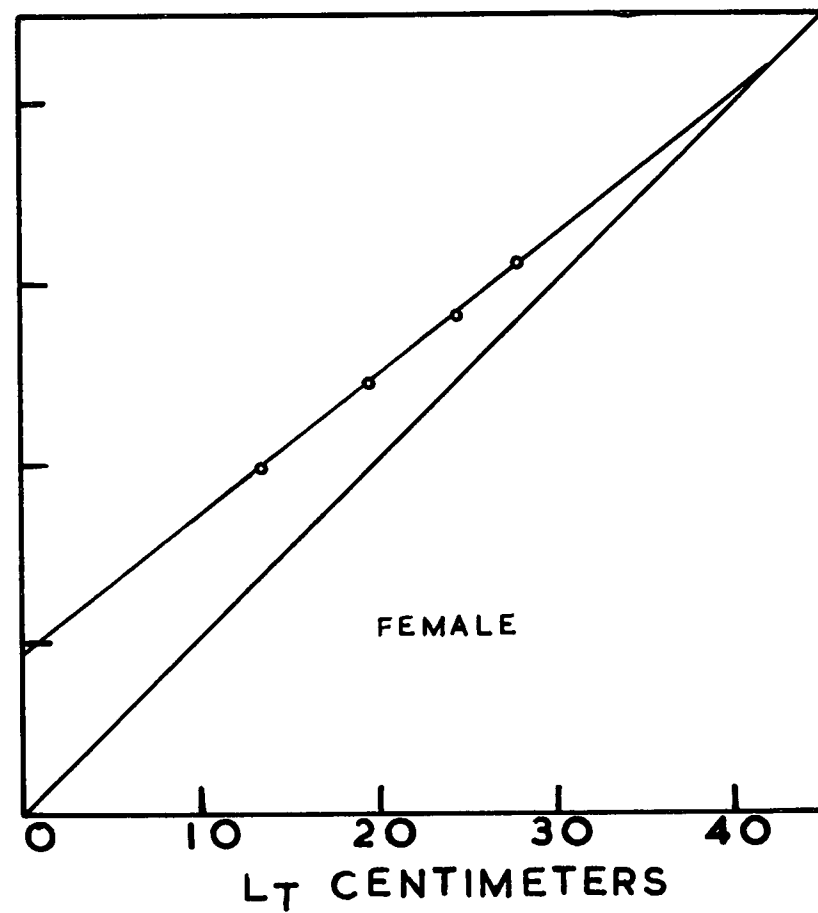
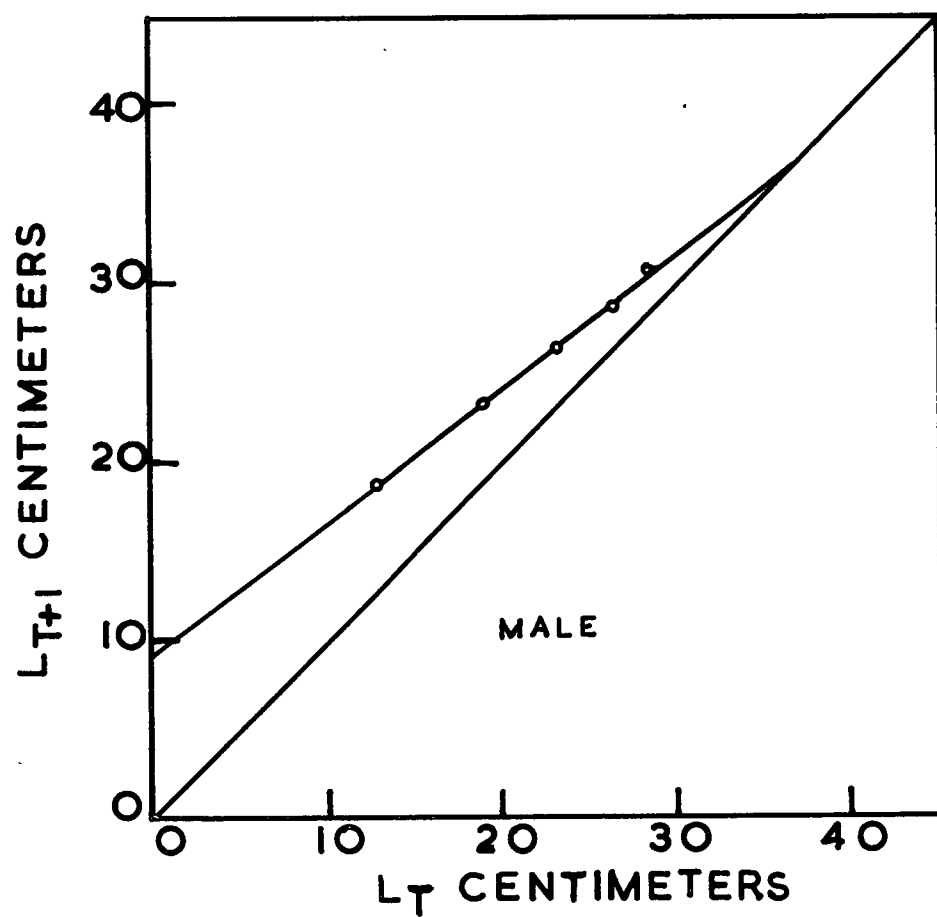


Figure 15. Wal-ford plot of the back calculated lengths of butter sole.

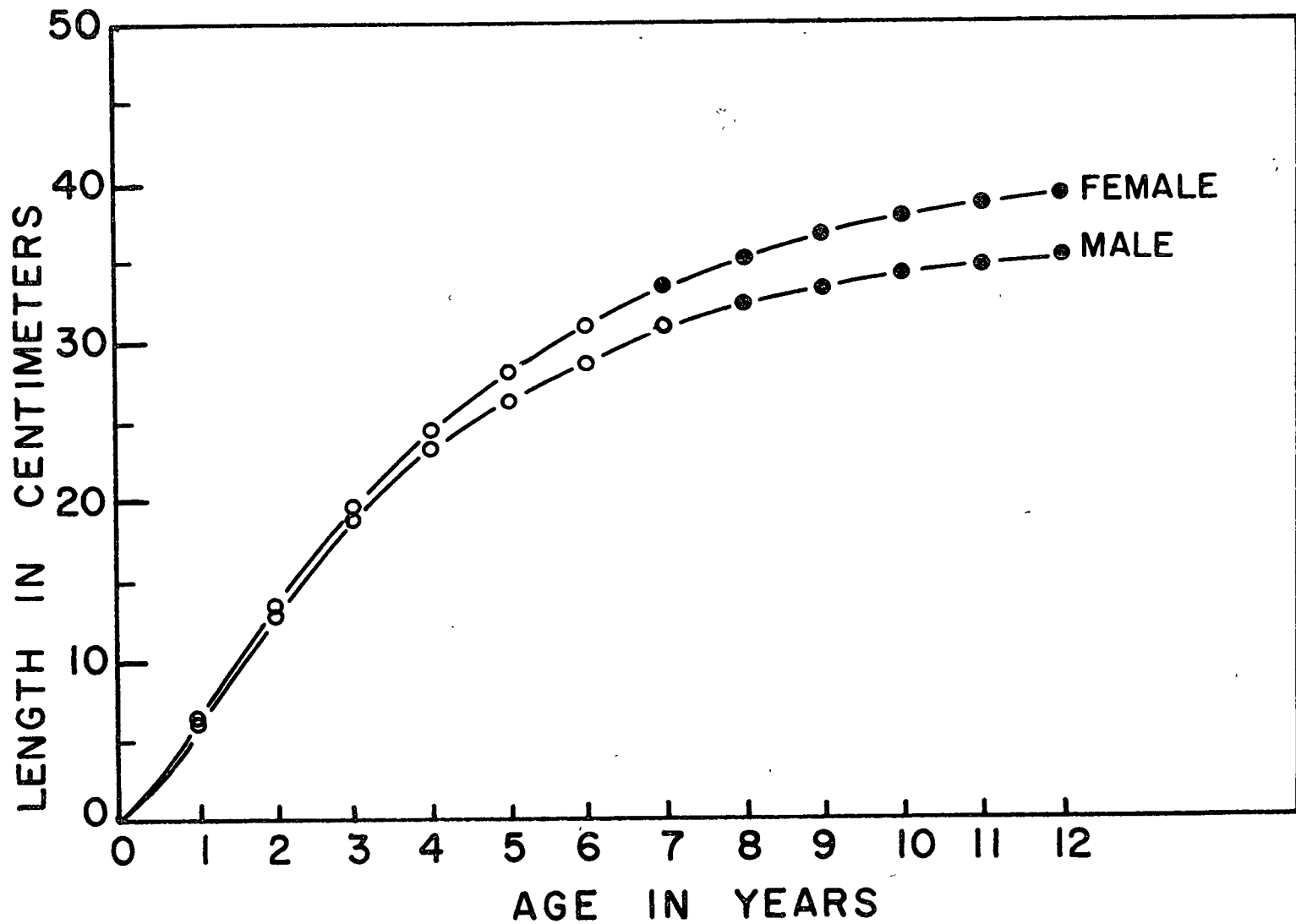


Fig. 16. Growth curve of butter sole. Solid points are the theoretical lengths estimated from the Wal-ford plot.

accuracy of aging older otoliths and partly to their inadequate representation in the sample. The growth rates of females were estimated from the commercial sample collected during 1958-1960 (Table XXI) and are influenced by market selection as well as gear selection. Because of this, the estimated lengths of 5 and 6 year olds in particular, are considerably higher than would be representative of the general stock. Hart (1948) has discussed the effect of gear and market selection on the accuracy of the growth rate estimates made by reading otoliths from the commercial butter sole catch. Since the sample for the back calculated lengths are from the nursery ground and the early age groups are adequately represented, the back calculated lengths (Table XXII) provide a more reliable estimate for the early ages. However, as mentioned earlier, even here the sample is not adequate for the older age groups. Hence the theoretical growth rates entered in Table XXIII are obtained from the Wal-ford plot.

#### Yearly variations in growth rate.

Errors in the back calculated lengths may arise for various reasons, such as the use of an incorrect body length-otolith radius relationship, bias in the sample due to selective fishing of faster growing fish and a higher mortality rate of the faster growing fish. They result in the occurrence of Lee's phenomenon or a progressive decrease in the calculated lengths from successively older otoliths. This aspect has been discussed recently by Parrish (1956), Jones (1958) and Taylor (1958). The back calculated lengths in Table XXII do not show any indication of Lee's phenomenon. Errors from selective fishing may not be significant since fishing takes place primarily, on the small section of the population over seven years of age. Within the length range examined the linear relationship between body length and otolith radius seems to be reliable. The back calculated lengths

thus provide not only reasonably accurate estimates of growth but also information on its variations. The yearly variation in growth from the means of 3+ to 8+ year olds is given in Table XXIV and Figure 17. Figure 17 shows appreciable differences in growth rate which are partly explained by the relative brood strength, though factors such as changes in the abundance of food, temperature and other environmental factors may also be involved. The 1953 year class represented by the 8+ fish in the 1961 summer sample contributed heavily to the 1960 fishery as seven year old fish. The analysis of the relative abundance of the 1953 year class (Section IV) suggests that the 1953 spawning produced a moderately strong year class. Similarly, judging from the abundance of 6+ year olds in the July 1961 sample (Table XXV), the 1955 spawning may also have been successful. Thus the slow growth rate of the 6+ and 8+ fish in the July 1961 sample (Figure 17) may partly be due to intraspecific competition. The growth rate of 7+ butter sole is above average though this is not evident in the males. Since the 1961 fishery was not successful it is presumed that 1954 was a poor brood year. The growth of 4+ year olds is also above average though this trend is seen only among males. This age group is poorly represented in the 1961 sample (Table XXV) suggesting that spawning in 1957 was not successful. The association between the growth rate and the relative brood strength suggests the role of intra-specific competition as one of the factors controlling yearly variations in the growth rate of butter sole.

It is also evident from Figure 17 that the per cent deviation of lengths from the mean gradually decreases as the fish get older. Thus if the growth rate is slow initially (6+ and 8+) it is compensated for in later years by faster growth. The reverse also seems to be true. The 7+ females show a higher growth rate in the beginning but the per cent deviation from the mean

Table XXIII. The mean length of butter sole at the end of each year's life. The lengths at ages above 6 years for females and 7 years for males were obtained from the Wal-ford plot.

Age	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	$L_{\infty}$	K
Male	6.04	12.89	18.78	23.26	26.27	28.56	30.90	32.31	33.37	34.17	34.78	35.24	36.64	0.2814
Female	6.45	13.49	19.61	24.46	28.01	31.09	33.38	35.18	36.59	37.69	38.56	39.24	41.71	0.2437

Table XXIV. Percent deviation of the back calculated lengths from the mean for age groups III+ to VIII+ given in Table XXII. Values up to fourth decimal place are retained in calculating percent deviation.

Age in years				I	II	III	IV	V	VI	VII	VIII
Male: Mean length(cms.)				6.04	12.89	18.78	23.26	26.27	28.56	30.90	32.31
Sex	Year Class	Age at capture	Length at capture (cms.)								
Male	1958	III+	21.86	3.07	3.80	4.27					
	1957	IV+	26.06	0.13	5.09	5.89	4.29				
	1956	V+	28.39	2.55	-0.02	0.65	2.14	1.96			
	1955	VI+	30.04	-2.53	-5.65	-3.76	-1.34	0.89	0.84		
	1954	VII+	32.16	-0.32	-2.60	0.33	1.92	2.14	1.25	0.63	
	1953	VIII+	33.06	-4.72	-9.82	-5.99	-2.40	0.09	1.00	0.93	0.32
Female: Mean length(cms.)				6.45	13.49	19.61	24.46	28.01	31.09	33.38	35.18
Female	1958	III+	22.54	0.53	3.52	2.58					
	1957	IV+	25.95	0.41	-1.79	0.21	-1.71				
	1956	V+	29.82	1.69	-3.50	-2.53	-0.06	0.28			
	1955	VI+	31.70	-0.21	-6.96	-4.47	-3.00	-1.30	-2.23		
	1954	VII+	35.67	6.60	8.88	8.55	8.85	7.09	6.16	4.25	
	1953	VIII+	35.17	1.93	-1.86	-3.70	-1.39	-1.85	-1.09	-3.01	-2.91

Table XXV. Estimated age composition of butter sole in the samples taken from northern Hecate Strait during July 1961.

I	II	III	IV	V	VI	VII	VIII	IX	X	XI
154	249	390	312	469	860	346	134	66	0	1

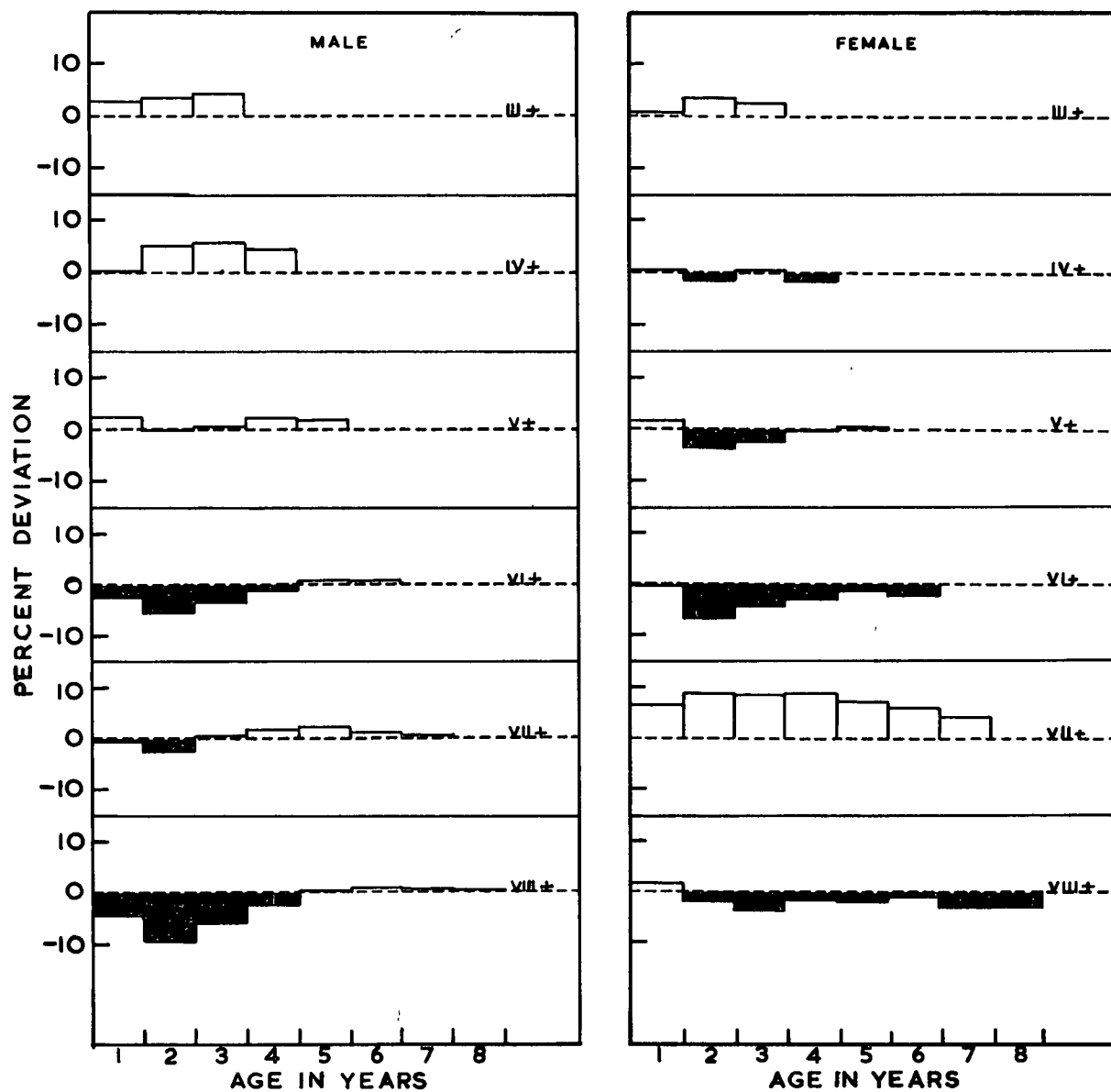


Figure 17. Percent deviation of the back calculated lengths from the mean at different years for age groups III+ to VIII+ in the July 1961 samples.

gradually decreases in later years. Such changes in the growth pattern of a year class may be observed if the species possesses an asymptotic length which they tend to attain. Since the Wal-ford plots (Figure 15) of butter sole data beyond two years of age are close to a straight line the species may be said to possess an asymptotic length. Figure 17 also shows that most often the per cent deviation of the growth rate from the mean is maximum during the second year. This may be expected since an inflection to deceleration in growth rate occurs around two years of age. These changes in the growth pattern of a year class compared to the mean growth rate of the butter sole population may thus be described by means of its growth curve and the asymptotic length. Hence even though the growth rate may be influenced by environmental factors, it seems reasonable to assume that butter sole possesses a characteristic growth pattern. Unless there is a long term change in the growth of butter sole, these deviations in the growth rate of a year class may be ignored in theoretical studies as they are compensated for in later years. The year classes examined above, especially those with an initial slow growth, attain their normal mean size at the end of four or five years which is before they are fully recruited to the fishery.

#### Seasonal differences in growth rate.

The samples taken between July 14 and 23, 1961 were used to calculate the mean growth increment up to July for each of the age groups I+ to VI+. These increments and the proportions of the mean annual increments that they represent are given in Table XXVI. 1+ and 2+ butter sole have already completed a greater proportion of one year's increment by July. Percy (1962) also observed the same phenomenon in an estuarine population of winter flounder Pseudopleuronectes americanus (Walbaum). 3+ and older butter soles appear to be more uniform in their growth. If it is assumed that most of the year's

growth occurs after the beginning of April, then the 3+ and older age groups complete approximately 50% of the year's growth in four months. This estimate, however, is influenced by yearly variations in the growth rate. Further confirmation is required and can be obtained only by studying the seasonal growth over a period of several years. Seasonal growth could not be estimated for age groups above six years since inadequate representation of older age groups in the sample has biased the estimated mean lengths of females above six years and males above seven years.

#### Regional differences in growth rate.

In his study on juvenile winter flounders of the Mystic River estuary in eastern Connecticut, Percy (1962) observed regional differences in the growth rates of the same population as a result of the larger fish moving farther into the shoals. Table XXVII gives the estimated growth of butter sole from different sampling areas (Figure 1) within Hecate Strait. Samples from area 2 have mostly 1+ and 2+ old butter sole and therefore are not considered here. Striking differences in the estimated growth rates are observed in different areas. Minimum growth rates are found in the sample off Fife Point in sampling area 3 (Figure 1). The sample from area 1 exhibits maximum growth. When one considers the existence of a summer fishery off Fife Point during 1945 and 1946 and the abundance of butter sole in the sample collected during 1953 and 1954, the presence of slow growing butter sole in the 1961 sample suggest that the area off Fife Point is no longer preferred by the species. Short term fluctuations in the habitat suitability within the shallow flats can be brought about as a result of constant wind and wave action. There is also an abundance of sand dollars in the samples collected from this area during recent years. Dendraster excentricus (Eschscholtz) and Echinarachnius parma (Lamark) are both found in the area. The present



Table XXVI. Percent growth increment up to July of butter sole of various age groups in the 1961 sample. Values up to fourth decimal place are retained in calculating percent deviation.

	Age group	I+	II+	III+	IV+	V+	VI+
Male	Mean Increment	6.85	5.89	4.48	3.01	2.29	2.34
	Increment up to July	5.11	3.92	2.28	1.81	1.61	1.23
	% Increment	74.54	66.52	50.92	59.97	70.06	52.75
Female	Mean Increment	7.04	6.12	4.85	3.55	3.08	
	Increment up to July	5.14	4.20	2.42	1.91	1.73	
	% Increment	73.14	68.62	49.82	53.80	56.28	

Table XXVII. Back calculated lengths at various ages calculated from otolith samples collected from different regions of Hecate Strait during July 1961.

Sex	Area sampled (Figure 1)	No. of otoliths	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Male	Dixon Entrance (1)	116	6.22	13.16	18.99	23.41	26.36	28.56	30.90	32.30	33.63		
	Off Fife Point (3)	80	5.34	11.35	16.96	22.13	25.75	28.68	30.69	33.75			
	Butterworth Ground (4)	65	5.84	11.90	17.70	22.14	25.69	28.92	31.14				
Female	Dixon Entrance (1)	155	6.53	13.64	19.77	24.64	28.44	31.20	33.00	33.71	34.11	34.79	35.89
	Off Fife Point (3)	87	6.13	12.05	17.98	22.93	27.31	31.00	33.29				
	Butterworth Ground (4)	110	6.52	12.83	18.59	23.09	26.76	30.27	32.74	35.27			

Table XXVIII. Length-Weight Relationship. Covariance analysis to test the homogeneity of the regression coefficients.

Source	Residual S.S.	D.F.	M.S.	F
Common	1.88423	855		
Error	1.85816	852	0.00218	
Reg. Coef. for sexes	0.01089	1	0.01089	5.00
Reg. Coef. for seasons	0.00121	1	0.00121	0.55
Sex-season Interaction	0.01397	1	0.01397	6.41

evidence, however, is too scanty to assert that the Hecate Strait bank forms a "mobile habitat" for butter sole within which short term alterations in the habitat suitability of the sub-areas may be brought about by waves and perhaps fluctuations in the abundance of other bottom organisms. The data also suggest a segregation of fast and slow growers in their summer feeding grounds.

Sampling area 1 had a dense population of butter sole with a maximum growth rate while the areas 3 and 4 are sparsely populated and appear to have poorer growth rates. It is not known whether this is due to a possible tendency of the faster growing ones to move together.

#### Sexual differences in growth rate.

The growth curves of males and females indicated in Figure 12 show that females grow faster than males. It is also evident that the females reach the maximum or asymptotic length at a slower rate than the males and hence exhibit higher growth rates at older ages than the males.

#### Length-Weight relationship of butter sole.

The length-weight relationships of male and female butter sole by season are:

$$\begin{aligned} \text{Male (summer)} : \text{Weight (gms)} &= 0.009260L \text{ (cms)}^{3.023} \\ \text{Male (winter)} : \text{Weight (gms)} &= 0.007236L \text{ (cms)}^{3.103} \\ \text{Female (summer)} : \text{Weight (gms)} &= 0.007344L \text{ (cms)}^{3.094} \\ \text{Female (winter)} : \text{Weight (gms)} &= 0.027896L \text{ (cms)}^{2.746} \end{aligned}$$

The length-weight relationship for the two sexes is shown in Figure 18 and the results of the covariance analysis are given in Table XXVIII. The low exponential value of 2.746 for the females collected during February, 1961 is probably due to sampling error associated with the narrow length range of the fish in the sample. Hennemuth (1959) observed a similar situation for skipjack tuna. This could not be avoided since the spawning population sampled

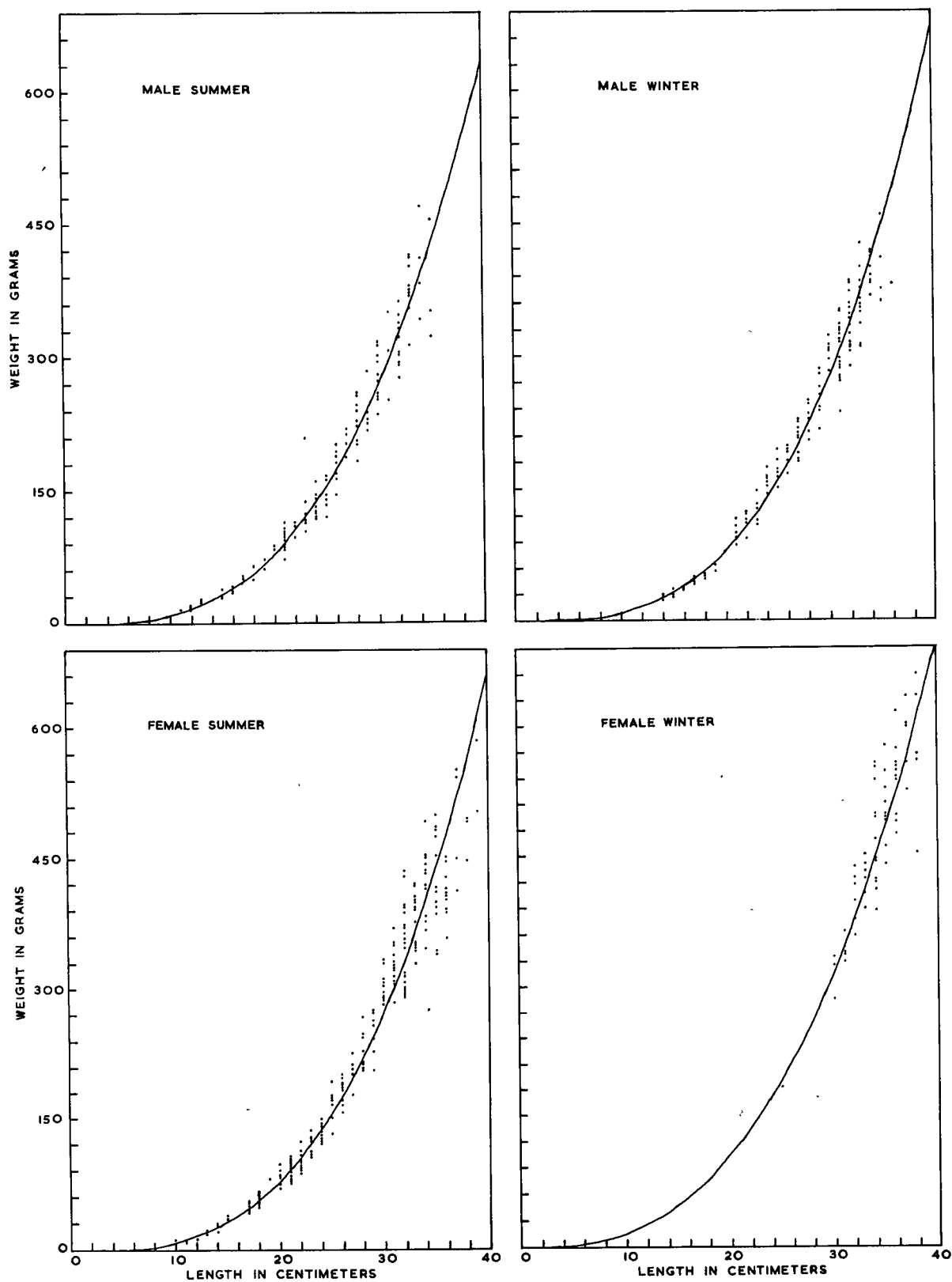


Figure 18. Length-weight relationship of butter sole.

contained only larger length groups. The rest of the exponential values in the length-weight relationship for the sexes by season are greater than 3. The covariance analysis (Table 28) shows that the regression coefficients of the two sexes differ significantly. The high variance ratio for the interaction between season and sex shows that the difference within season in females is greater than in males.

(b) Survival rate.

As Beverton and Holt (1956a) have indicated, the estimation of mortality rates from age composition and effort data depends on certain assumptions and hence is subject to considerable error. Since butter sole of seven or more years of age are fully recruited and are adequately sampled by the commercial gear\* the age composition data for these age groups were used to estimate the annual survival rate. These estimates may also be biased to a certain extent due to variations in year class strength and difficulties in 'aging' otoliths. The results for the two sexes are given in Table XXIX.

The mortality rates are found to be higher for the males in all the years examined. This phenomenon, also observed by Hart (1948), may be due to higher natural mortality and/or fishing mortality. If the males remain on the spawning ground longer than the females a higher fishing mortality for the males may be expected. Since there was no fishing during 1949 and 1950, and the fishing intensity during the period 1953-1955 was quite low (Table XXXI), the higher mortality estimate for males may be due to a higher natural mortality rate. Mortality rates also show an increase with

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\* The commercial gear uses codend with a mesh size ranging from four to five inches. From length-girth relationship (Section IV) their 50% retention point would be less than the length of 7 year old fish.

Table XXIX. Instantaneous and annual total mortality rates of butter sole estimated from the age composition data.

Z = Instantaneous total mortality rate; a = Annual total mortality rate.

Age Interval	Male							
	1951		1953		1954		1955	
	Z	a	Z	a	Z	a	Z	a
VII-VIII	1.129	0.677	0.905	0.596	1.866	0.845	1.523	0.782
VIII-IX	1.830	0.840	1.209	0.702	1.609	0.800	1.749	0.826
IX-X	1.735	0.824	2.052	0.872	-	-	2.079	0.875
	Female							
	Z	a	Z	a	Z	a	Z	a
VII-VIII	0.693	0.500	0.623	0.464	0.472	0.376	0.972	0.622
VIII-IX	1.128	0.676	1.177	0.692	1.668	0.811	1.409	0.756
IX-X	1.959	0.859	2.165	0.885	-	-	1.299	0.727

age. Since butter sole above six years are equally vulnerable to the gear the increasing mortality rates are perhaps largely due to an increase in the natural mortality rate with age. The separation of total mortality into its component parts requires a reliable estimate of the fishing intensity and usually involves the assumption that natural mortality is constant with respect to age. The assumption of constant natural mortality is not valid for butter sole. An accurate estimate of the fishing intensity could not be made either (see Section IV), hence fishing and natural mortality rates were not separated. An estimate of the natural mortality rate for the early year classes could have been attempted from the age composition of the samples taken in 1953 by small meshed trawl hauls from the spawning population if the per cent in each year class that would have matured in the succeeding spawning season could have been estimated. An examination of the sample collected in July 1961 showed that this could not be done as the gonads had not yet started maturing. The total mortality rates estimated in Table XXIX are largely due to the natural mortality rates because, as previously mentioned, the fishing intensity was rather low for the years examined. Since the total mortality rates are high, butter sole seven years and above are presumably subjected to high natural mortality rates. This is also suggested by the relatively high value of  $K$ , the rate of deceleration in growth increments. In their discussions, Beverton and Holt (1959) and Holt (1962) have pointed out that natural mortality and  $K$  are positively correlated.

(c) Conclusion.

1. Zones in the otolith of butter sole are found to be reliable indicators of age. The back calculations of fish length based on the body length-otolith radius relationship are therefore used in tracing the growth history of the species.

2. The growth pattern of butter sole over two years of age is adequately described by the Von Bertalanffy growth curve; even though seasonal differences in the growth rate are superimposed on it.
3. A year class with an initial slower or faster growth shows a tendency in later years to attain the mean values estimated for the population.
4. Growth rates show differences with respect to year, season, region and sex.
5. The length-weight relationship based on ungutted specimens show seasonal and sexual differences.
6. The natural mortality rate beyond seven years of age is relatively high and is found to increase with age.

#### IV Fluctuations in the abundance of the butter sole population

##### 1. Introduction

Extreme fluctuations in abundance are usually associated with pelagic fishes although they occur in varying degrees in all exploited populations. Sette(1961) records a year class of western Atlantic mackerel which was 15,000 times as large as the smallest year class recorded. Clarke and Marr (1955) mention a 720-fold difference between the smallest and largest recorded year classes of Pacific sardine. Groundfishes also exhibit considerable variation in abundance (Hjort 1914, 1926, Ketchen 1956, Saville 1959, Beverton 1962 and others), but they are less extensive than those of pelagic fishes. Fluctuations in the butter sole population were studied to examine the possibility of predicting their magnitude. This provides a means of studying their influence on the population biomass and yield.

##### 2. Examination of the butter sole fishery

###### (a) Age of full exploitation

When studying the fluctuations of a fish population, a knowledge of the age at which the fish is fully exploited permits a comparison of the strength of a year class during its pre- and post- exploitation phases. It also enables one to estimate the influence of the year class on the total yield. In addition, such knowledge is of use in examining whether the existing age of exploitation is the most desirable from the point of view of optimum fishing. Consequently, an analysis of the selectivity of the trawl mesh was carried out for butter sole.

###### (i) Mesh selection experiment

The selectivity of a gear is the change in the ratio of the abundance of different size groups in the catch to that of the population fished. Buchanan-Wollaston (1927) showed that, depending on the size of the cod-end



mesh, all the fish below a certain length can escape through the mesh, while above a certain length all the fish encountered by the gear are captured. Within the intermediate length or the "selection range" the efficiency of the gear increases with increase in the length of the fish. The curve obtained by plotting the per cent retained against the length is the "selection ogive" of the cod-end mesh. Wollaston first pointed out that the selection ogive approximates a "normal ogive" and it gives the proportion of fish entering the cod-end that are retained, i.e. the chance of a fish of that size being captured. This was later confirmed by the mesh selection experiments of various workers such as Graham (1954), Margetts (1955), Gulland (1955) and Davis (Graham 1956).

The method adopted for estimating the mesh selection of butter sole by commercial trawlers was to make two consecutive hauls of 30 minutes duration with 1.5", 3.4", 3.5" and 5.2" cod-end meshes. In estimating the per cent retained by the commercial trawler, the catch of the 5.2" cod-end was compared with that of the 1.5" mesh. The length-frequency distribution of the catch with 1.5" mesh was adjusted by using the catches of the 3.4" and 3.5" mesh to obtain an accurate estimate of the size composition of the population. The procedure is illustrated in Table XXX. Only the size groups beyond the full retention point of the 3.5" cod-end mesh as estimated from the length-girth relationship were considered for weighting. A comparison of the length-frequency distribution of butter sole in the catches of the 1.5" and 3.5" cod-end meshes (Table XXX) indicated that size groups 24 cms. and above could be used for weighting. The absence of fish below 24 cms. in the catches of the 3.5" cod-end mesh may have been caused by their absence in the population fished. Because the 3.4" mesh fished a denser population, as shown by the catch (Table XXX), the estimation of the adjusted size frequency

of the population was not done with respect to the mean catch of the three nets. Instead the size frequency of the catch with 1.5" cod-end mesh was corrected. Adjustment for the 3.5" mesh would yield a very similar result since the total catch of 1.5" and 3.5" cod-ends were of the same magnitude.

Cod-ends of the same material were not available for the above experiment. While the catches of the 3.4" and 3.5" meshes were used for weighting, the possible effect of the different materials on the selective properties of the cod-ends may not have influenced the calculations since the minimum size group considered lies beyond the full retention point of the 3.5" cod-end.

The results of the mesh selection experiment are given in Table XXX. The estimated per cent of butter sole retained at each length up to 38 cm. by the 5.2" mesh is shown in Figure 19. The 50% selection length was found to be 31.5 cm. The value sigma (6), measuring the spread of the selection ogive, on the assumption that the selection ogive has the same properties as a normal ogive, was found to be 1.04 cm.

The discrepancies observed beyond the full retention point in Figure 19 can be expected in such alternate haul experiments due to the movement of shoals of fish about the ground or variations in the populations fished (Graham 1956). Margetts (1955), who used the same method, observed even greater discrepancies in mesh selection experiments on sole. Hence the individual hauls should be of sufficient duration to minimize these errors (Graham 1956). The population should also be of moderate density (Wollaston 1927). Otherwise the cod-end may become clogged, preventing the escape of small fish. Both these conditions were met in the present study. However, hauls were taken over a period of about 48 hours and thus resulted in increased sampling variability. This could be offset only by taking more hauls with each cod-end. Certain trends may also be present in the ratios

Table XXX. Length frequency distribution of butter sole above 24 cm. caught in two hauls with each cod-end and the estimation of the percentage retained by the 5.2" mesh in an alternate haul experiment.

Length (cms.)	Size composition of butter sole above 24 cms. in hauls using different cod-end meshes			Total	Weighted percent $\frac{\text{Total}}{1079} \times 100$	Adjusted frequency with 1.5" mesh. (Weighted % x 2.37)	Catch of 5.2" mesh cod end	% retained by 5.2" mesh compared to that of 1.5" mesh
	1.5"	3.4"	3.5"					
24	3	12	4	19	1.761	4	0	0
25	10	57	11	78	7.228	17	0	0
26	15	39	15	69	6.390	15	1	6.66
27	12	69	14	95	8.804	21	1	4.76
28	11	36	10	57	5.282	13	1	7.69
29	11	34	9	54	5.004	12	1	8.25
30	14	38	19	71	6.580	16	2	12.50
31	37	42	21	100	9.268	22	11	50.0
32	34	76	40	150	13.901	33	17	51.51
33	30	60	32	122	11.306	27	29	107.40
34	24	62	30	116	10.750	25	12	48.0
35	16	23	21	60	5.561	13	9	69.23
36	12	26	9	47	4.356	10	5	50.0
37	4	14	6	24	2.224	5	3	60.0
38	3	5	2	10	0.926	2	2	100.0
39	1	3	2	6	0.556	1	0	0
40	0	0	1	1	0.093	0	1	-
Total	237	596	246	1079	100.0	236	95	

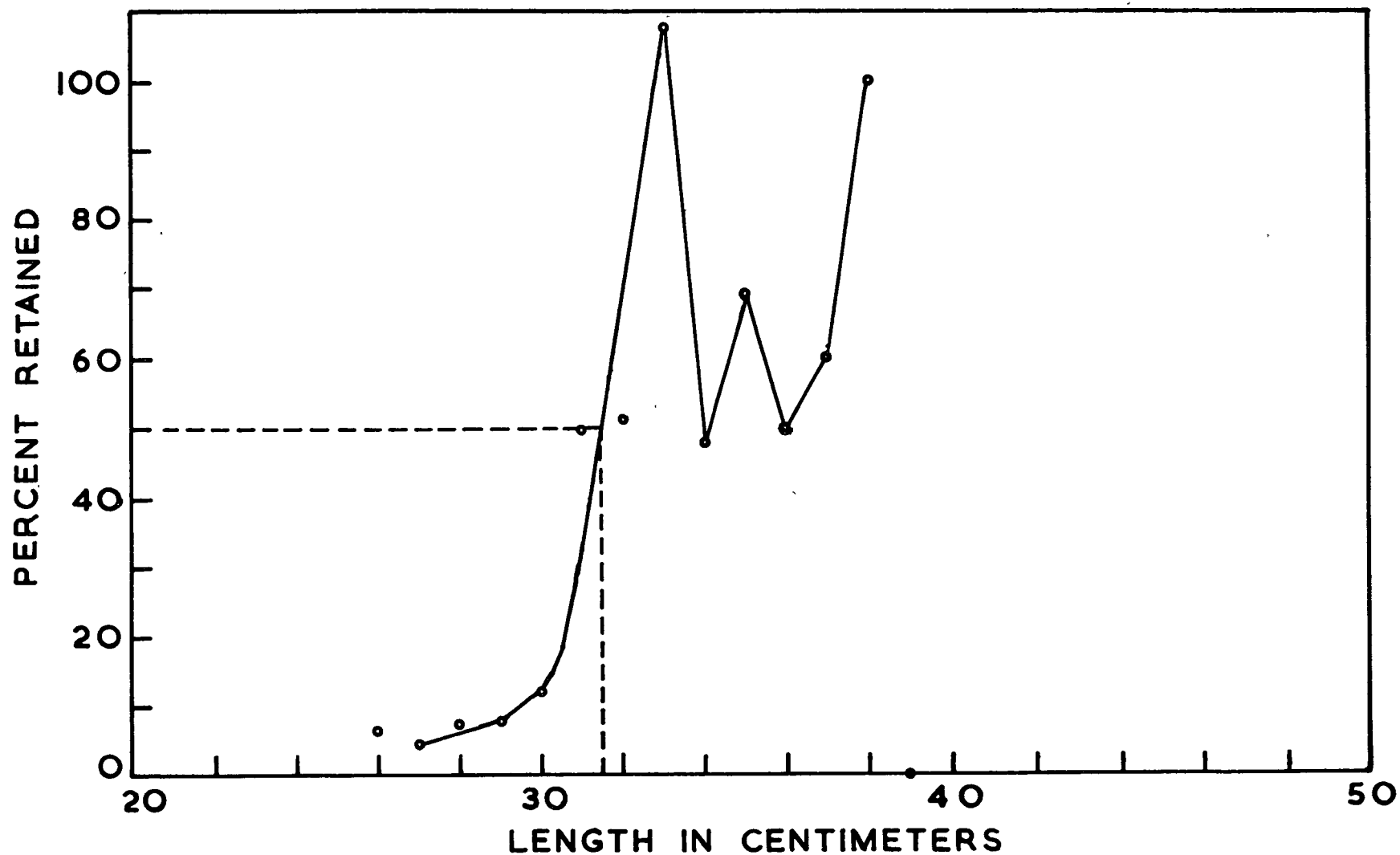


Figure 19. Percentage of butter sole retained at each length by 5.2" cod-end mesh. (Alternate hauls). The dotted line indicates the 50% release length.

retained by the cod-end. Beverton and Holt (1957) found that with increase in mesh size the ratios retained by the cod-end were greater than unity due to an increase in fishing power with increase in mesh size. They also observed with the 72.2 mm. and 113.0 mm. meshes that the observed ratios above the 100% retention point not only attained values greater than unity but they gradually decreased linearly with an increase in the size of the fish. No such trends were observed in butter sole. Although an increase in mesh size may result in an increase in the fishing power this is not evident in the data. This may be partly due to the small number of length groups beyond the full retention point and partly to the insufficient number of hauls with the 5.2" cod-end. Hence, no adjustments for the fishing power were made when estimating the selection ogive of the 5.2" mesh. The length frequency distributions of the 3.4" and 3.5" cod-end meshes also show no such trend. The reliability of the estimated 50% selection point is further verified by comparing the internal perimeter of the cod-end and the girth of the fish corresponding to the 50% retention length as determined from the length-girth relationship.

(ii) Length-girth relationship

If fish grow isometrically the length and girth will be proportionally related so that the average mesh size and the 50% release length will be proportional (Beverton and Holt 1956b). Thus, by using a length-girth relationship the 50% selection point of any cod-end mesh can be determined. This could be used to check the validity of the mesh selection experiment. Such studies have been done by Lucas et al (1954), Margetts (1954) and Gulland (1955). Graham (1954) has pointed out the usefulness of such studies because of random and systematic errors of mesh selection experiments.

Length and girth measurements for 319 freshly caught butter sole were taken on the research vessel, A.P. Knight, during February, 1961. The girth measurement was taken at the widest part of fish with a measuring noose, tightened to such a degree as would permit the fish to be pulled from it when gentle pressure was applied. Margetts (1954) has defined this measurement as the constricted girth. Figure 20 illustrates the length-girth relationship of butter sole. The fitted regression line shows the relationship:

$$\text{girth(cms)} = 0.9486 \text{ length(cms)} - 3.409$$

The internal circumference of the 5.23" mesh is 10.46". The estimated girth of fish at the 50% release length of the 5.23" mesh is 26.47 cms. or 10.42". The analysis is based on two hauls only so the close similarity between the estimated girth of the fish at 50% length and the internal circumference of the corresponding cod-end may be due to random and systematic errors. Nevertheless the similarity of the two values indicates that the length-girth relationship of butter sole could be used to check the validity of the estimated 50% release length from the selection ogive. The estimated 50% release lengths for the 3.4" and 3.5" meshes are 21.80 and 22.34 cms. respectively. These estimates, however, could not be verified by mesh selection experiments. The minimum size group represented in the catch of the 3.5" cod-end mesh is 24 cms. This may be due to the size composition of the population fished. A similar situation occurs with the 3.4" cod-end mesh when none of the length groups below the 50% retention point, as estimated from the length-girth relationship, are represented (Appendix I). If the 20 and 21 cm. groups are as scarce in the spawning population as indicated by the catch of the 1.5" mesh (Appendix I) then they probably represent the tail-ends of two adjacent modal groups. This may

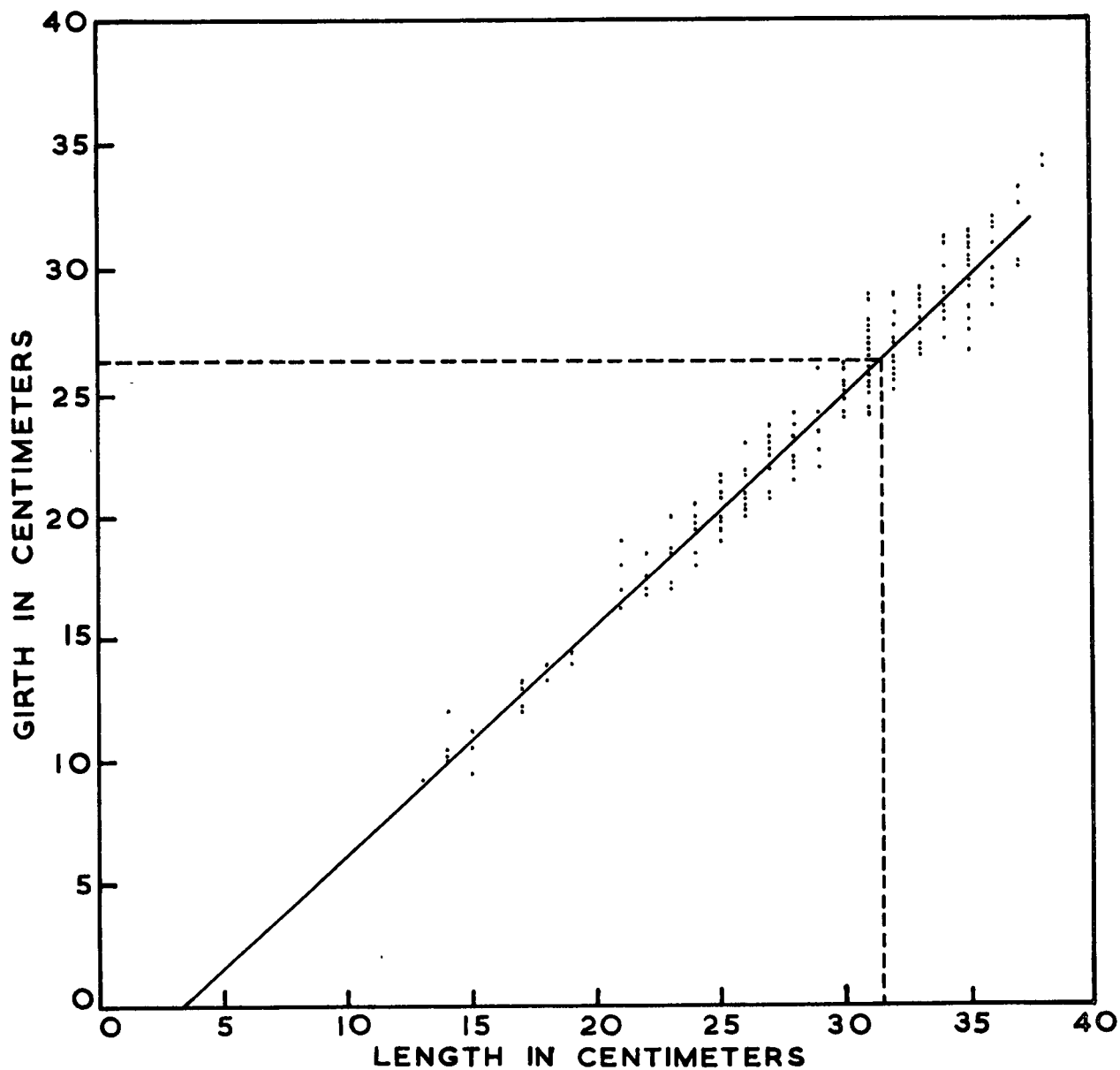


Figure 20. Length-girth relationship of butter sole. The dotted line indicates 50% release length for the 5.23" cod-end mesh.

partly explain the absence of length groups below 22 cms. in the catch of the 3.4" mesh cod-end.

(b) Variations in butter sole landings

The butter sole fishery depends on the spawning population that migrates to the eastern part of Skidegate Inlet and is thus highly localized. Fishing is very seasonal and lasts only for about two months of the year. Since 1953 the peak fishing season has shifted to February-March. The magnitude of the fishery compared to that for other ground fishes of Hecate Strait is quite small. Butter sole is used for human consumption and for mink feed, but there is relatively little demand for it. For this reason, and because of the favourable economic position of the fishermen, the population is exploited only if it is sufficiently abundant at the spawning site to bring a reasonable profit to the fishermen. However, it does afford a sheltered fishery when fishing in Hecate Strait is undependable (Hart 1948).

The estimated butter sole landings for 1945-1962 are given in Table XXXI. Except for 1945 and 1946, when there was also a summer fishery in Hecate Strait, the catches came entirely from the spawning population in Skidegate Inlet. Sporadic catches from statistical area 4 (Figure 21) were not included in these estimates. Since 1953 the butter sole landed were used partly as food fish and partly as mink feed. In addition to gear selection, the fish destined for human consumption are further selected to meet the market requirements. The mink feed landings of butter sole include those not selected for the market plus the entire landings of boats operating for mink feed alone.

Catch figures show considerable annual variations (Figure 22). In addition to changes in the density of the spawning population, the changes in the fishing effort also influence the yearly landings. The demand immediately



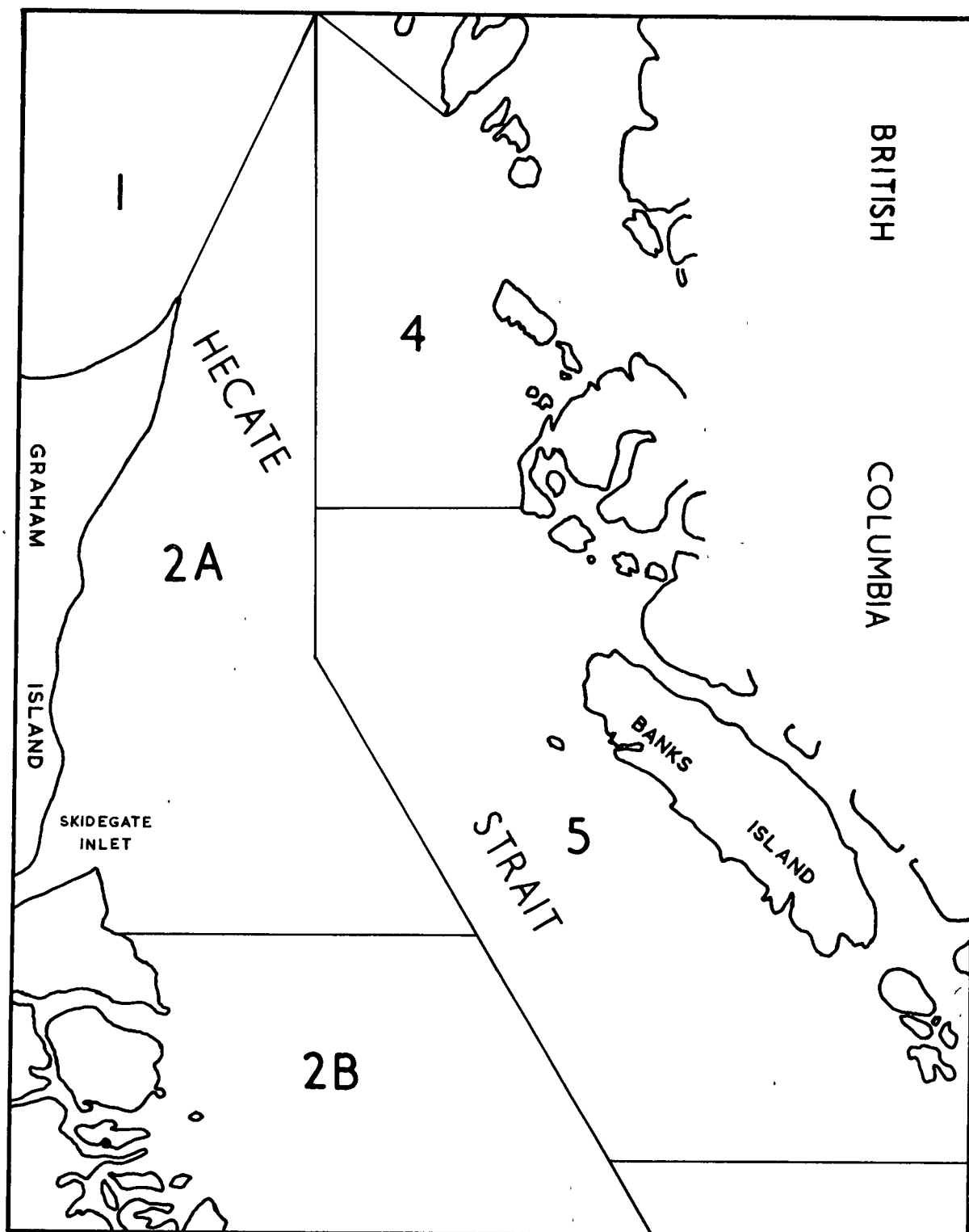


Figure 21. Map showing the statistical areas of Hecate Strait in the neighbourhood of Skidegate Inlet.

Table XXXI. Landings of butter sole from Skidegate Inlet and the estimated catch per unit effort for vessels of 30-59 ton range. The landings for 1945-1950 are corrected for the difference between log book total and Department record.

Year	Food fish (pounds)	Total catch- (Food and mink) (pounds)	Catch per day for boats fishing for food alone (pounds)	Catch per day for boats fishing both for food and mink (pounds) and mink alone
1945	1,542,856.0	-	16,899.0	-
1946	1,715,605.0	-	11,866.0	-
1947	271,533.0	-	3,523.0	-
1948	649,032.0	-	9,782.0	-
1949	18,890.0	-	10,494.0	-
1950	1,545.0	-	1,717.0	-
1951	1,838,128.0	-	28,761.0	-
1952	3,708,232.0	-	10,902.0	-
1953	224,052.0	393,052.0	10,113.0	26,222.0
1954	181,430.0	201,930.0	11,560.0	15,804.0
1955	470,339.0	727,803.0	8,400.0	7,997.0
1956	716,244.0	1,419,085.0	5,764.0	12,859.0
1957	1,291,579.0	1,436,936.0	10,166.0	10,814.0
1958	499,642.0	960,170.0	12,680.0	22,966.0
1959	212,902.0	449,494.0	10,495.0	14,532.0
1960	93,857.0	1,252,840.0	4,481.0	13,973.0
1961	15,846.0	543,177.0	-	7,297.0
1962	41,549.0	1,394,937.0	-	13,806.0

Table XXXII. Estimation of the fishing power of 'single' gear taking 'double' gear as the standard.

Year	Tonnage class	Catch in pounds per day		Fishing power of single gear	Number of trips made by the tonnage class	Weighted geometric mean
		Single gear	Double gear			
1946	40-49	5547.3	6758.5	0.8207	9	0.8955
1951	40-49	27218.0	31175.0	0.8730	10	
1952	20-29	8203.8	8524.7	0.9623	14	
1952	30-39	8615.1	9676.38	0.8903	28	
1952	40-49	9234.55	14925.19	0.6187	16	
1952	50-59	14587.95	9104.23	1.6023	9	
1957	30-39	8796.2	9272.8	0.9486	13	
1957	30-39	8796.2	9723.94	0.9046	13	

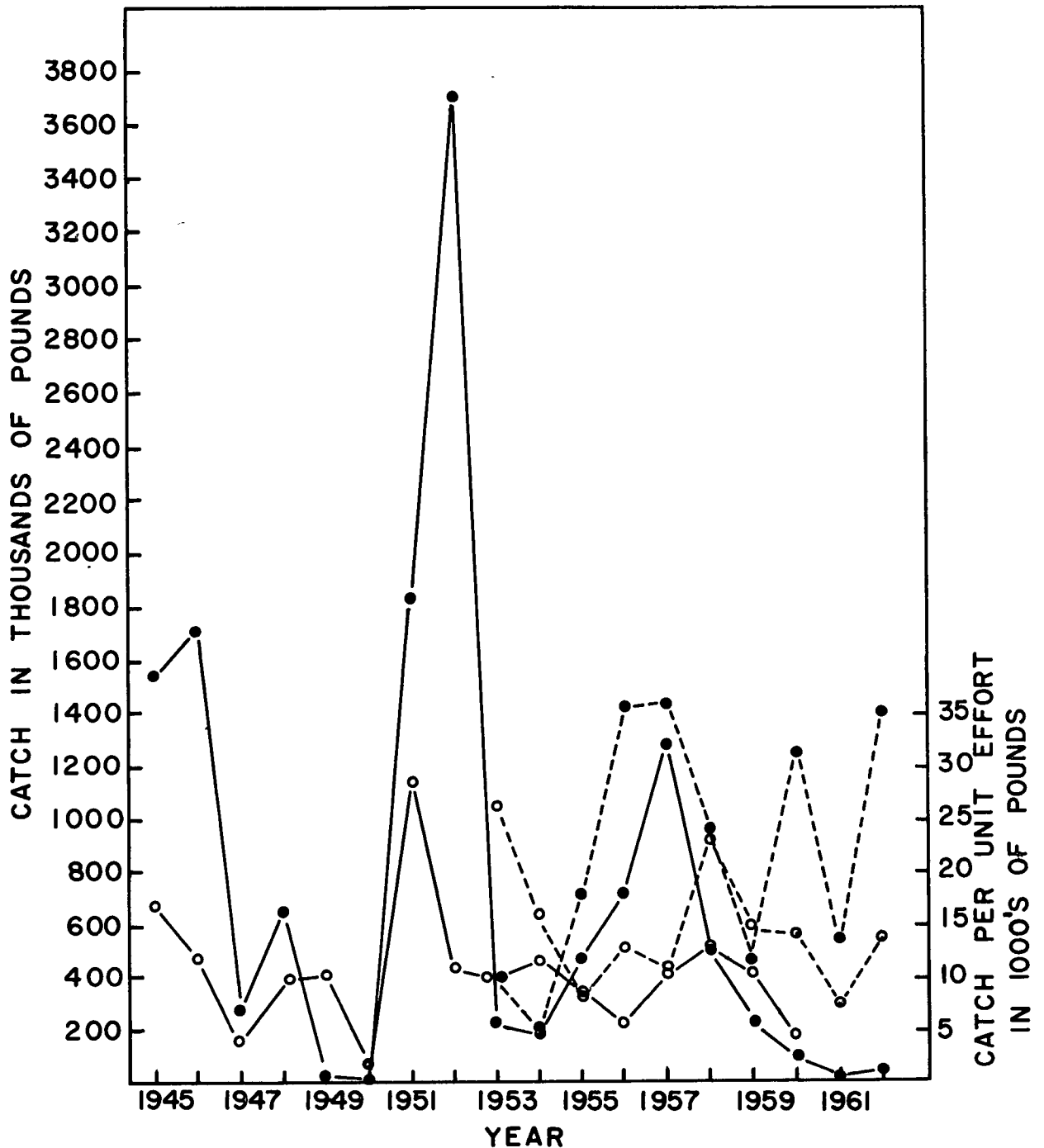


Figure 22. Butter sole landings and catch per unit effort for the period 1945-1962. —●— Food fish landings, ---●--- Total landings (food and mink), —○— Catch per day of boats fishing for food alone, ---○--- Catch per day of boats fishing for mink feed alone and both for mink feed and food. Data from Table XXXI.

after the second World War supported a summer fishery in 1945 and 1946. The fishery was also particularly heavy during 1952. Separate food and mink feed categories in the landings made since 1953 introduce further variations in the catch figures. The number of boats engaged in fishing for food, for mink feed, or for both, may vary in different years. Hence the use of catch figures as an index of abundance may be biased by year to year variations in the fishing intensity and the demand for the food and mink feed items of the landings. The possibility of studying variations in the density of the spawning population by estimating the catch per unit effort is therefore examined.

(i) Estimation of the catch per unit effort

A reliable estimate of the catch per unit effort can serve as a valuable index of abundance when the effect of fishing and the fluctuations of a population are being studied. An accurate estimate of the fishing intensity is a prerequisite for the calculation of catch per unit effort. A constant improvement in gear and a gradual increase in tonnage of vessels are two conspicuous features in the fishery. 'Single' gear where the trawl is towed with one cable is better adapted for small vessels. 'Double' gear is towed with two cables. Ketchen (1951) found that, at normal towing speed, the spread of the American style trawling gear ('double' gear) is about 1.4 times that of the 'single' gear. The assessment of the performance of trawlers by Ketchen and Thomson (No date) also indicates that the fishing power increases with tonnage. Gulland's (1956) extensive analysis of the fishing power of English trawlers also confirms this conclusion. As the average size of the Canadian trawlers increased, more 'double' gear was used by the fishermen. To the butter sole fishery, these changes are only incidental since such changes are associated with the more important trawl fisheries of the area.

However, such changes in the fishing power have to be accounted for by standardizing the fishing effort.

#### Relation of fishing power to tonnage

The catch data from 1958 to 1962 permit a reliable estimate of the fishing power for vessels equipped with 'double' gear and operating for mink feed alone and for both mink feed and food. The catch per hour for individual trips was calculated for all boats. Taking the catch per hour of one boat as the standard, the relative fishing power of all boats was calculated taking care to see that such comparisons of catch per unit effort were made of boats fishing, as far as possible, at the same time as the standard vessel. In addition to such direct comparisons, a number of indirect estimates of the fishing power of vessels were also made using the chain link method described by Beverton and Holt (1957). Thus the catch per hour of one boat was linked to that of the standard vessel through a varying number of catch per hour estimates of other vessels. For example, if  $t_{c_n}$  is the catch per hour of a boat represented by the suffix on its right side, and the time of fishing by the suffix on the left, then

$$\frac{i^c_x}{i^c_m} \times \frac{j^c_m}{j^c_d} \times \frac{l^c_d}{l^c_b} \times \frac{k^c_b}{k^c_f} \times \frac{o^c_f}{o^c_{\text{standard vessel}}}$$

would be one estimate of the fishing power of vessel X.

The regression analysis of fishing power on tonnage was based on a total of 897 estimates. The data were at first transformed by taking the square root of the fishing power. The relation of fishing power to tonnage is given in Figure 23 along with the confidence belt of  $\mu_Y$  for any X. The estimated relationship is

$$\sqrt{\text{Fishing power}} = 0.7820 + 0.0085 \text{ Tonnage}$$

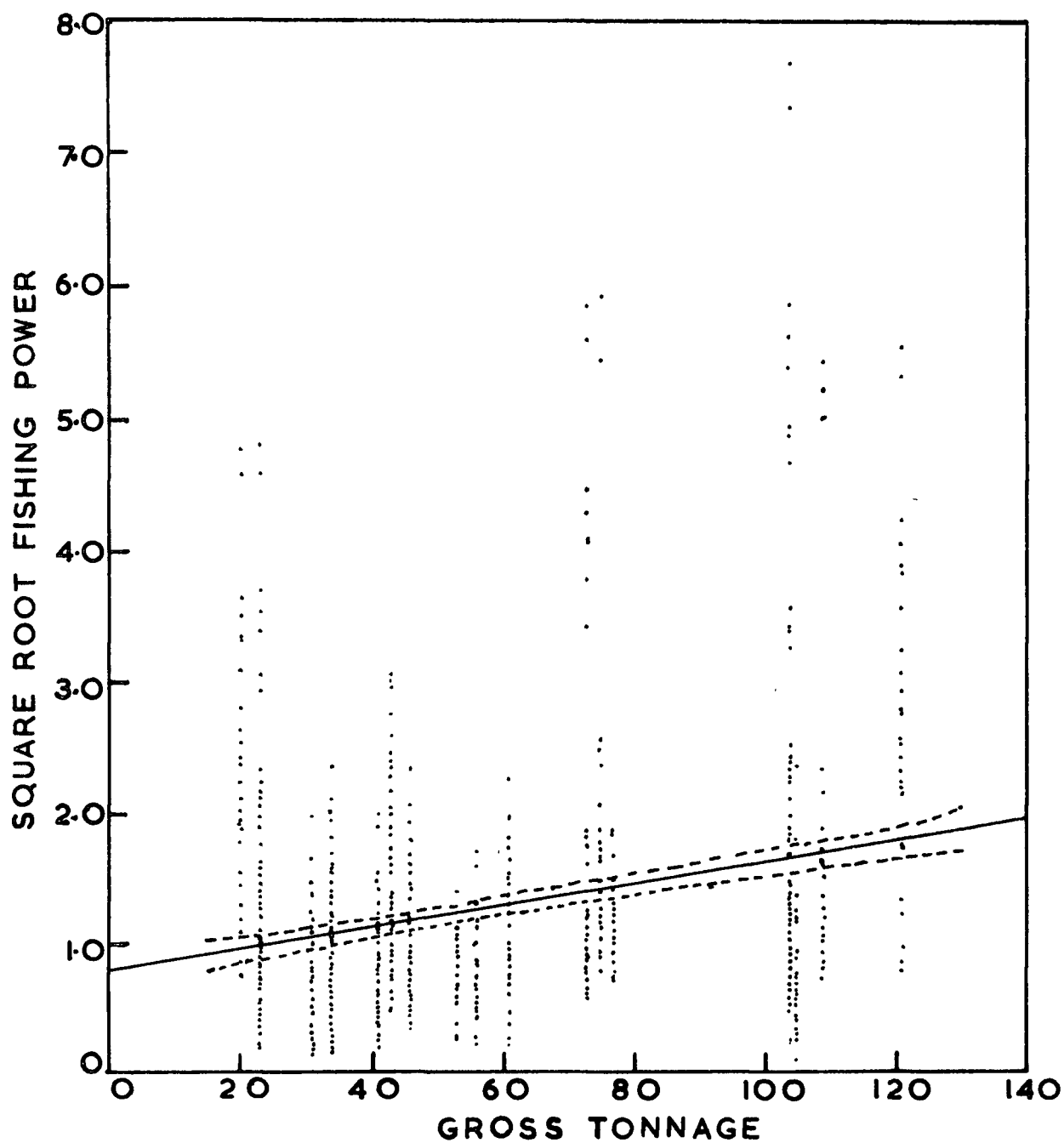


Figure 23. Relation of fishing power and gross tonnage of vessels equipped with 'double' gear engaged in the butter sole fishery during the period 1958-1962.

The sample standard deviation of  $\hat{Y}$  calculated for drawing the confidence belt is

$$S_{\hat{y}} = \sqrt{0.0009936 + 0.000001108(x - \bar{x})^2}.$$

The slope is significant with a t-value of 6.55 for 895 degrees of freedom. Figure 23 shows considerable scatter even in the transformed data. Some of the factors that could contribute to the variability are the differences in the ages of the vessels, the ability of the skippers and in the distribution, density and migratory patterns of butter sole within the spawning ground. Since only two boats equipped with 'single' gear fished during the period 1958-1962, the relation of fishing power to tonnage of vessels using 'single' gear was not studied for that period.

In estimating the mean catch per unit effort adjustments for the increase in fishing power with tonnage were not based on the above relationship. Accurate effort data in terms of actual number of hours fished were available only from 1957. Hence the catch per unit effort had to be calculated taking each day as a unit. Furthermore, with the exception of one boat in 1955, vessels above 60 tons did not appear regularly in the fishery until 1958. Since vessels in the 30-59 ton range were well represented, the standardization of fishing effort was done for vessels within this range.

Standardization of fishing effort and the catch per unit effort for the 30-59 ton classes.

In comparing the efficiency of 'single' and 'double' gear or of the tonnage classes, the data used were restricted to the period when the different units compared were represented in the effort data. The catch per day was taken as a unit since the effort data did not permit the choice of a smaller unit. The efficiency of the 'single' gear was adjusted by taking a weighted geometric mean of the relative fishing power (Table XXXII),

using the number of trips made by the respective tonnage class for the weighting. Taking 'double' gear as the standard, the estimated fishing power of 'single' gear was found to be 0.8955.

After adjusting the fishing power of 'single' gear, differences in the efficiency of tonnage classes were tested for the 30-59 ton range (Tables XXXII to XXXVI). The efficiency of any two tonnage classes was tested by analysis of variance treating each pair of data as a separate block (Table XXXIII). Since the landings contained only one category until 1952, the monthly estimations of the catch per day pertained only to food fish. Since 1953 the catch per day for the tonnage classes was calculated, wherever possible, both for food fish and for total landings. This procedure increased the number of blocks compared.

The results are given in Tables XXXIV to XXXVI. The analysis shows no significant difference in the efficiency of the tonnage classes within the 30-59 ton range. This is to be expected when one considers the varying abilities of the skippers and the variations introduced by the migratory pattern. The small tonnage range and the short fishing season also contribute. Extreme localization of the fishery makes the species vulnerable to any gear. The number of boats in each tonnage class available for the estimation of catch per day was not large. This was particularly so since 1953 because after this date boats could operate for either food fish or mink feed. In addition, some boats took fish for both purposes. This increases the sources of error in the data. A separate analysis of the catch per day of boats operating for food fish alone and for boats operating for mink feed alone, or for both, may not increase the accuracy of the data because the division of the 30-59 tonnage range into the three groups further reduces the number of boats in each category. Such an analysis is not worth attempting when the low variance



Table XXXIII. Estimated catch per day of 30-39, 40-49 and 50-59 ton classes.

Tonnage class	30-39	40-49	50-59
1945 J	18476.0	18863.04	-
F	8040.0	13852.90	-
1946 J	7040.03	5791.20	6250.0
F	8933.55	8333.30	6250.0
1947 J	-	2307.70	1785.71
F	2783.70	2000.0	2142.80
1948 J	9305.04	3000.0	-
F	6319.13	11695.0	-
1951 J	26295.0	22330.0	26664.0
F	23458.0	30625.0	33578.0
1952 J	8353.80	14006.70	10035.40
F	10337.20	12092.30	11797.60
1953 J	-	1666.60	9000.0
1955 J	12166.30	5511.75	8224.25
F	8213.60	10160.0	9329.66
1956 J	4000.60	4188.70	3191.20
F	4170.40	8707.30	9360.30
J	-	8266.07	6929.26
F	6314.70	11435.0	-
M	1193.74	17834.28	7415.30
M	10914.0	31691.14	18573.90
A	16287.20	44000.0	12892.70
1957 J	9197.80	2448.70	-
F	9601.65	8255.80	9894.90
F	10365.30	9836.80	13235.13
M	9366.50	11746.0	33427.10
1958 F	16451.80	8836.53	11878.80
F	-	12123.40	30861.60
M	3325.0	17267.50	17142.50
M	-	22168.70	35646.50
1959 F	26063.0	6826.88	-
M	15943.70	5176.78	5204.0
M	-	10998.80	16086.60
1960 F	-	12255.0	4480.60
F	-	22880.0	3269.25
M	-	18607.10	13689.0

Table XXXIV. Analysis of variance of the log catch per day of 30-39 and 40-49 ton classes.

Source of Variation	D.F.	Sum of Sq.	Mean Sq.	Variance ratio
Total	53	5.1699	0.0975	0.0837 N.S.
Months	26	3.0831	1.1858	
Tonnage classes	1	0.0067	0.0067	
Error	26	2.0800	0.0800	

Table XXXV. Analysis of variance of the log catch per day of 40-49 and 50-59 ton classes.

Source of Variation	D.F.	Sum of Sq.	Mean Sq.	Variance ratio
Total	57	6.7081	0.1176	0.0947 N.S.
Months	28	5.4326	0.1940	
Tonnage classes	1	0.0043	0.0043	
Error	28	1.2712	0.0454	

Table XXXVI. Analysis of variance of the log catch per day of 30-39 and 50-59 ton classes.

Source of Variation	D.F.	Sum of Sq.	Mean Sq.	Variance ratio
Total	39	3.9171	1.0043	1.596 N.S.
Months	19	2.9191	0.1536	
Tonnage classes	1	0.0773	0.0773	
Error	19	0.9206	0.0484	

ratio is considered. Thus in estimating the catch per unit effort for the 30-59 tonnage class adjustments were made only for vessels using 'single' gear. The estimated catch per unit effort of butter sole for the years 1945-1962 is entered in Table XXXI and Figure 22.

(ii) Catch per unit effort as an index of abundance

An examination of the catch per unit effort does not suggest that it could be used as an index of abundance. In 1949 butter sole were almost absent in Skidegate Inlet. After the heaviest recorded fishery in 1952, the fishery in 1953 was poor. It was to be expected, from the numerical strength of the 1952 year class appearing as 1+ fish in the 1953 sample (Table XXXIX), that the density of the 1959 spawning population would be below average. This was later substantiated by the total landings (Table XXXI) and age composition of the 1959 commercial catch (Table XL). The estimated catch per unit effort for these years is comparatively high. Catch per day may not be as sensitive a unit as catch per hour for expressing the index of abundance. Variations in the catches as a result of the migratory behaviour affecting the distribution and density of the population could be minimized if a large number of boats were available for the estimation of the mean catch per unit effort. The short fishing season, the small size of the fishery, and the relatively low demand for the species, allow only a small number of vessels to operate in any one season. The estimates of the catch per unit effort were made from fewer boats since 1953, because after this the total effort was divided between boats operating for food fish alone, for mink feed or for both. The secondary selection of food fish by fishermen may vary considerably from year to year depending on the demand. In poor years fishing may be restricted to the period of highest density. Variation in the density of the spawning population is thus not adequately expressed by the catch per unit effort.

However, catch per hour would be a more accurate index of abundance. Because of the relatively low demand for the fish and the favourable economic position of the fishermen, the total landings cannot be expected to indicate more than the general trend in the abundance. This could be partially verified for the years 1958-1960 by comparing the relative abundance of the 1951-1953 year classes in the 1952-1954 samples and their contribution to the 1958-1960 fishery. This aspect is dealt with below where the fluctuation of the butter sole population is considered.

### (c) Conclusion

1. The 50% selection length of the 5.2" mesh was found to be at 31.5 cms. with a sigma (6) value of 1.04 cms. Because of the random and systematic errors in the mesh selection experiment the 50% retention length of 5.2" mesh was also verified by studying the length-girth relationship.

(2) Butter sole landings show considerable year to year fluctuations. The estimated catch per day was not found to be a sensitive index of the abundance of the spawning population in Skidegate Inlet.

### 3. Analysis of fluctuations in the butter sole population

The factors controlling the availability of the butter sole population in Skidegate Inlet are not understood. Butter sole were almost totally absent in Skidegate Inlet during 1949 and 1950. There are suggestions that the temperature of the bottom water influences the availability of butter sole. Barber (1957) has shown for Hecate Strait that the southeast winds in winter cause a displacement of the deep cold water by warmer, less saline surface water. He records that the southeast winds were very weak in January 1950. The alterations in the migratory course of the 1950 spawning population and the resulting absence of a fishery in Skidegate Inlet may thus be due to a lack of sufficient mixing. The low surface temperature during 1949 and

1950 may also have prevented their entry across the shallow sill at the entrance of Skidegate Inlet. Simpson (1953) has also shown that the North Sea cod and plaice avoid very cold water in the winter and thus change their migratory route during unfavourable years. Flemming and Laevastu (1956) point out that fishes are more sensitive to temperature changes during the spawning season. Bull's (1952) experiments indicate that teleosts can respond to changes as small as  $0.03^{\circ}\text{C}$  in temperature,  $0.02\%$  in salinity and  $0.05$  p.H.

(a) Method adopted in analysing changes in abundance

Buckmann (1930) points out that the peculiar depth distribution of bottom fishes makes precise sampling difficult for a study of the relative abundance of year classes in the nursery ground. Hence a reliable estimate of the catch per unit effort cannot easily be obtained. Besides, it measures only the abundance of the whole population and not the individual year classes. If sampling is not proportional the age composition of the sample will not be representative of the population. It is possible that an average year class, which shows up very strongly when compared with a series of poor year classes, may be mistaken for a strong year class. However, the limited range of the Hecate Strait population of butter sole facilitates their sampling. Estimates of the catch per unit effort from the commercial sample in conjunction with the age composition of the market sample can be used to study abundance, but this does not permit prediction of the success of the fishery. In this study the abundance of young butter sole in the small-meshed trawl hauls taken along the Graham Island coast during 1952-1954 was analysed. This was done by studying the order of dominance and relative abundance of butter sole and the related species, lemon sole, rock sole and sand sole, by means of the ranking technique. This analysis was interpreted after a consideration of the relative strengths of the 1+ and 2+ butter sole in the 1952-1954 samples.

Since these fish were old enough to be fully exploited by the 1958 to 1960 fishery, its success and the age composition of the commercial catch were also considered. Because the length frequency distribution of the age groups in the 1952-1954 sample show very little overlap, they could be separated easily and accurately. Hence no refined techniques for dissecting the length frequency were used. Since the durations of the hauls, especially during 1952, were not steady, the catch from each haul was weighted to 20 minutes duration.

(b) Results

The results of the dominance and relative abundance analysis are given in Tables XXXVII and XXXVIII. For the year 1952, the order of dominance in the sample was lemon sole > sand sole > butter sole, significant at the 0.05 level. The order of dominance for 1953, significant at the 0.01 level, was sand sole > lemon sole > butter sole. The order of dominance for 1954 was lemon sole > butter sole > sand sole, but it is not statistically significant. The results of the relative abundance analysis are presented in Figure 24 (data from Table XXXVIII). The figure shows the same order of abundance among the species as indicated by the analysis of dominance for the two years. In 1952 no one species was found to be particularly more abundant than the other two, however, in 1953 sand sole was significantly more abundant than butter sole. There was not enough samples in 1954 to permit the analysis of relative abundance.

In the above analysis, the abundance of young sand sole and lemon sole also influences the results, since the Graham Island coast is the main nursery ground for these species. Ranking techniques can be used to study the relative abundance of young butter sole alone over a period of years. Because of the lack of sufficient data, a consideration of the age composition of

Table XXXVII. Analysis of dominance of butter sole in the 1953 and 1954 samples from the Graham Island coast. Low rank values indicate numerical superiority of the species in the sample. The grouping procedure eliminates rock sole from the Graham Island coast since they are present in less than half the number of samples.

	1952				1953				1954			
	$\Sigma$ rank	S	W	P	$\Sigma$ rank	S	W	P	$\Sigma$ rank	S	W	P
Butter sole	26	67.1	0.34	< 0.05	28	128.0	0.64	< 0.01	14.5	12.7	0.19	N.S.
Lemon sole	14.5				20				9.5			
Sand sole	21.5				12				12.5			
No. of replicates	10				10				6			
Mean	20.7				20.0				12.2			

Table XXXVIII. Analysis of relative abundance of young butter sole, lemon sole and sand sole along the Graham Island coast during 1952 and 1953.

	1952					1953				
	Number of rep- licates	Respective $\Sigma$ rank	t	p		Number of rep- licates	Respective $\Sigma$ rank	t	p	
Butter sole x Lemon sole	10	124.0 86.0	1.44	0.0750		11	150 101	1.54	0.0618	
Butter sole x Sand sole	10	123.0 87.0	1.36	0.0869		10	149 61	3.33	0.0004	
Lemon sole x Sand sole	10	111.5 141.5	0.96	0.1676		10	123 87	1.36	0.0869	



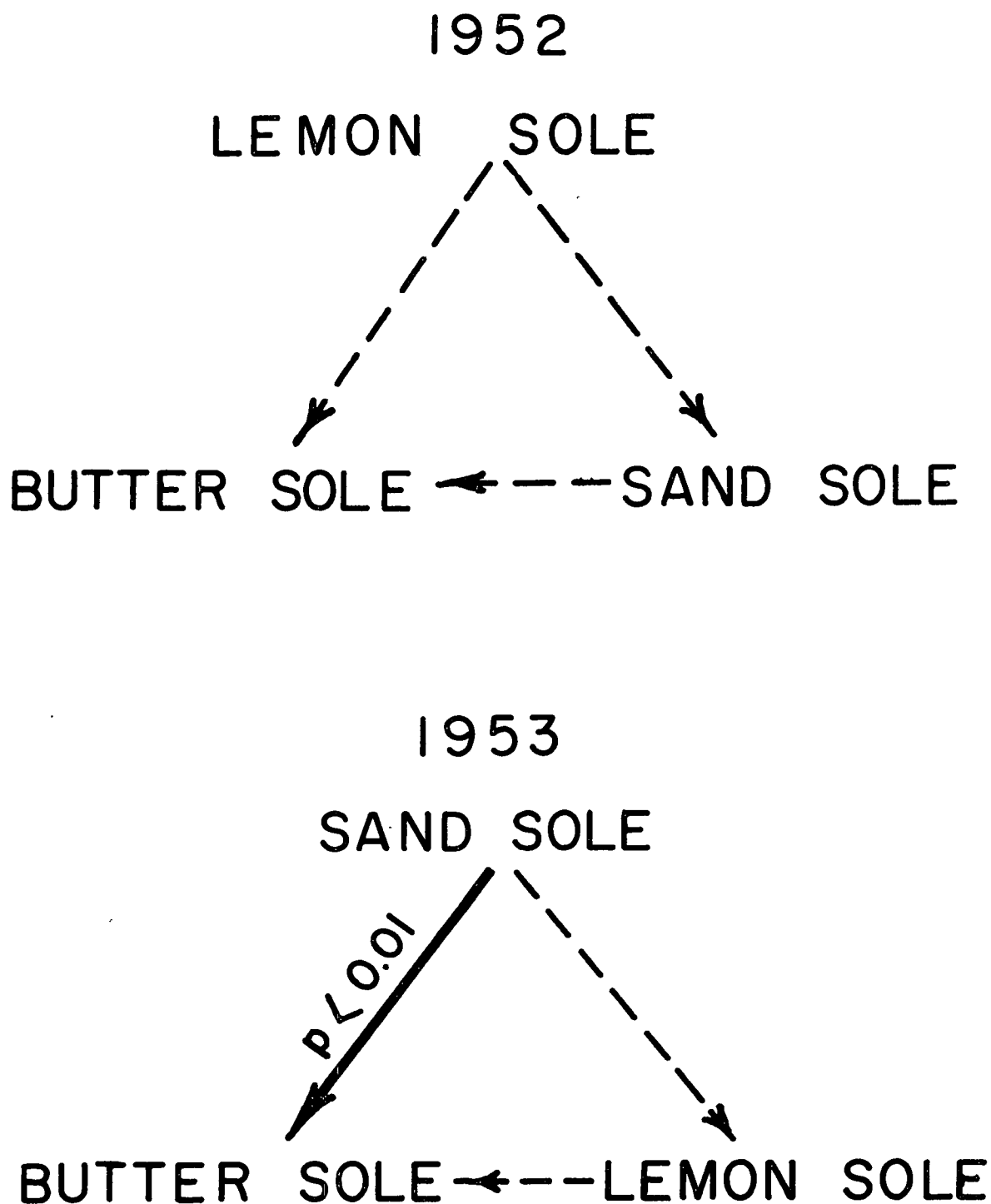


Figure 24. Relative abundance of the three species of flatfish in the samples from the Graham Island coast collected during 1952 and 1953. The species to which arrow is indicated is less abundant. Dotted lines indicate that the difference is not statistically significant.

butter sole in these samples helps in the interpretation of the above analysis. Table XXXIX indicates clearly that butter sole of age 1+ and 2+ are poorly represented in 1953 compared to 1952. The scarcity of 1+ butter sole in 1953 is at least partly due to the poor 1952 year class which in turn may be a result of the heavy fishery in 1952. Since seven year olds contribute heavily to the fishery, one would expect better fisheries in 1958 and 1960 than in 1959. This is supported by the catch figures for these years even though unselected mink feed forms a considerable portion of the landings and hence the younger age classes would also contribute part of the catch. A comparison of the age composition of the commercial catches (Table XL) with the abundance of 1+ fish in the 1952-1954 samples also supports the above contention. The adequacy of the food sample as compared with the unselected mink feed sample was examined by analysing the age composition of the food and mink feed samples for 1960 (Table XL). This analysis showed that the selection by the fisherman over and above the gear selection does not influence the number of females of age seven or older. The moderate abundance of 1+ and 2+ butter sole in the 1952 summer hauls is reflected in the equal representation of seven and eight year olds in the 1958 catches. In 1959 six, seven and eight year olds occurred at approximately the same frequency and together they formed the major proportion of the relatively poor fishery. Because of the weakness of the 1952 year class the six and eight year olds formed a proportionately larger share of the catch than is the case in normal years. The abundance of the 1953 year class and the scarcity of the 1952 year class in the 1954 samples are similarly reflected in the high percentage of seven year olds and poor representation of eight year olds in the 1960 landings. Thus the estimates of abundance of young butter sole belonging to different year classes could be substantiated six

Table XXXIX. The abundance of I+, II+ and > II+ age groups of butter sole taken in the small meshed (1.5") trawl hauls along the Graham Island coast during 1952-1954. The values in brackets are the corrected estimates made by adjusting the hauls to a standard 20 minutes.

Duration of haul	Unsteady - less than 20 minutes			20 minutes			20 minutes			
Sample Number		1952			1953			1954		
		I+	II+	>II+	I+	II+	>II+	I+	II+	>II+
1	Age groups not separated	25 Nos.- 10to25 cms.(50)			6	4	4	3	0	0
2		39 Nos. mostly I+ (52)			4	1	1	2	0	0
3		26 Nos. mostly II+ (52)			2	0	1	17(43)	3(8)	2(5)
4		7(18)	0	0	3	2	0	0	1	1*
5		2(5)	0	0	0	0	1	14	6	2
6		10(20)	3(6)	1(2)	0	0	6	24	2	1
7		3(6)	2(4)	0	2	2	12			
8		14(16)	6(7)	4(5)	1	3	90			
9		7(8)	4(5)	2(2)	1(1)	2(2)	1(1)			
10		1(2)	3(6)	3(6)	0	0	2			
11					0	8(16)	7(14)			
Mean		6.29 (10.71)	2.57 (4.00)	1.43 (2.14)	1.73 (1.73)	2.00 (2.73)	11.36 (12.00)	10.00 (14.33)	2.00 (2.83)	1.00 (1.50)

\*net badly torn

Table XL. Age frequency distribution of female butter sole in the commercial catches taken during 1958-1960.

	Age	5	6	7	8	9	10	11	Total
1958 Food sample	Number	8	80	170	187	92	19	2	558
	Percent	1.43	14.34	30.47	33.51	16.49	3.40	0.36	100
1959 Food sample	Number	14	180	166	154	44	9	-	567
	Percent	2.47	31.74	29.27	27.16	7.76	1.59	-	100
1960 Food sample	Number	5	71	119	53	10	7	-	265
	Percent	1.88	26.79	44.90	20.0	3.77	2.64	-	100
1960 Mink-feed sample	Number	11	111	147	44	14	5	-	332
	Percent	3.31	33.43	44.27	13.25	4.21	1.50	-	100

years later when these fish became exploitable. It then appears that the fluctuations in abundance are determined during the early life history and once a benthic habit has been adopted the year class strength remains relatively stable.

This analysis also establishes that the area along the Graham Island coast is the major nursery ground for young butter sole. Thus if a reliable estimate of the year class strength can be made from this area, then it is possible to predict the success of the fishery that depends on these year classes. The relative abundance analysis performed by the ranking technique cannot be used to measure the magnitude of abundance. It can only detect significant changes in abundance. Since most of the young butter sole are distributed along the Graham Island coast, a density index can be determined by taking a sufficient number of samples from this area each year. From this a relative index of the abundance of the year classes can be estimated by using the chain-link method. These results could be used in studying changes in biomass and yield. Since butter sole is restricted largely to the northern part of Hecate Strait during summer, estimates of the abundance of young year classes along the Graham Island coast can be checked in subsequent years by taking samples from northern Hecate Strait. The abundance of 6+ fish in the July, 1961, samples from this area (Table XXV) and the successful fishery in 1962 (Table XXXI) also indicate the usefulness of butter sole samples from Hecate Strait.

### (c) Conclusion

(1) The above study based on an examination of (a) dominance and relative abundance of young butter sole in the nursery ground in relation to other species of flatfishes (b) variations in the numerical strength of butter sole of age 1+ in the 1952-1954 samples (c) the success and age composition

of the commercial catches when these year classes become exploitable indicates that fluctuations in the butter sole population are largely determined during the early period of their life history.

(2) Their abundance tends to remain relatively stable once they adopt a benthic habit.

(3) The estimation of the year class strength in samples from the Graham Island coast is a reliable index of abundance for studying changes in biomass and yield. The validity of these estimates could also be checked in subsequent years with samples from northern Hecate Strait.

## V Theoretical yield study of the butter sole population

### 1. Introduction

Theoretical studies of animal populations are done by means of analogues and/or models. The most complete of the main types of conceptual models are those of Beverton and Holt (1957) and Ricker (1958). The latter model was chosen for studying the butter sole population as it describes adequately the characteristics peculiar to this population and can be used when the population parameters are not constant. The adequacy of Ricker's model compared to Beverton's was examined for a hypothetical population in a steady state exposed to a continuous and seasonal fishery under different growth and mortality rates and with different ages of exploitation.

Using Ricker's model the following aspects of the butter sole population were studied:

- (a) changes in the mean biomass of the spawning population and yield under steady state with changes in fishing and natural mortality rates and age of exploitation.
- (b) variation in the mean biomass and yield when the recruitment varies i.e. when the assumption of steady state is released.

### 2. Procedure

Before using Ricker's model for studying the butter sole population, the yield per recruit estimates for a hypothetical population using both Ricker's and Beverton's models were compared to examine the magnitude of error. After assuming that Bertalanffy's growth equation describes the growth pattern of this population, the growth rate was altered by changing the value of  $K$ , the rate of deceleration in growth increments, while maintaining  $T_0$  and  $L_\infty$  constant although more often a change in  $K$  is accompanied by changes in  $T_0$  and  $L_\infty$ . The population is also assumed to

exhibit isometric growth. The two models were then applied to the data both for a continuous and seasonal fishery<sup>\*</sup>. In using Ricker's model to study changes in yield and biomass of the spawning population of butter sole the average weight of stock during time  $t$  may be estimated by taking the arithmetic mean or the exponential average. When studying the magnitude of error, the yield per recruit estimates from both cases were compared with the results obtained from Beverton's equation.

The present theoretical study of the butter sole population makes use of the biological information given in Sections III and IV above. A weighted growth curve is estimated based on the sex ratio of males and females in each age group in the 1953 sampling survey (Table VII)<sup>\*\*</sup>. Since fish of seven years and above are beyond the selection range of the gear and recruitment is complete, one weighting factor found by estimating the geometric mean of the sex ratio is used beyond this age. Each year was divided into the following intervals: April to July, August to January and February to March. This was done because it was known that approximately 50% of the year's growth occurred by the end of July and it was assumed that little growth would occur during the peak spawning season in February and March. Butter sole exhibit seasonal differences in growth and their availability to the fishery is highly seasonal, being limited to the peak spawning season. Under these

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<sup>\*</sup>Computer programmes for Ricker's and Beverton's equations are available at the Institute of Fisheries, University of British Columbia.

<sup>\*\*</sup>Back calculated lengths used in theoretical studies were obtained using the regression line of otolith radius (Y) on length (X) even though it should be based on the regression line of length (Y) on otolith radius (X) since the sum of squares of deviation has to be based on the dependent variable or the variable to be predicted. The estimated lengths in Table XXIII are based on the correct regression line. However, there is very little difference in the two estimates especially for five years and above.



conditions "knife edge" selection by the gear cannot be assumed since fishing takes place on a population consisting of 1.83, 2.83, etc. year old fish. Hence to study the effect of a change in mesh size or 50% retention age ( $T_p$ ) on yield, the proportion of fish of different ages retained within the selection range of the gear is first estimated assuming that the selection ogive resembles a normal ogive. The calculated sigma ( $\sigma$ ) value of 1.04 cms., which measures the spread of the selection ogive of the 5.2" mesh, is used for this purpose. The respective fishing mortality rate is obtained using this proportion. To study the effect of varying recruitment on the yield and biomass an index of abundance for the entering year class is introduced in Ricker's model. This index is obtained from the yearly landings as they indicate the possible range of fluctuations in the year class strength.

There are certain limitations in the present analysis which could be overcome only by acquiring more detailed knowledge of the ecological life history of the population. They are: (a) The data on the seasonal differences in the growth rate are not extensive and the division of the year into three time intervals to fit the yearly differences in the growth rate may be subject to error. (b) The length-weight relationship used in the present study is estimated from ungutted specimens and ignores the sexual and seasonal differences in weight as a result of differences in the gonad condition. (c) The exact recruitment pattern to the spawning ground is not studied. Hence an arbitrary age of 4.83 years is chosen to represent the age of entry to the exploitable phase. This value is chosen because it is assumed to be a close approximation of the actual age of recruitment and the net increase in weight at this age is not too low for studying the effect of various mortality rates. (d) The mortality rates appear to increase with age. Since the total mortality could not be separated into its component

parts, the most likely theoretical values had to be chosen to represent the natural mortality rate ( $M$ ). A preliminary plot of the total mortality rate against age beyond seven years suggests a linear increase in the total mortality with age and since all fish above seven years are equally liable to be captured by the gear the natural mortality would also appear to increase linearly with age. Hence the two selected natural mortality rates were each made to increase, in steps of 0.2 and 0.4 respectively, at the end of each year beginning at the age of six. (e) The index of year class strength was estimated from the total landings as data available were not extensive enough to measure the actual brood strength over a period of years. (f) Even though it is likely that the spread of the selection curve may increase with increase in mesh size, the proportion of different ages retained within the selection range of different mesh sizes is estimated on the assumption that this is constant for all meshes. This aspect can be studied only by extensive mesh selection experiments.

### 3. Results

#### (a) Comparison of the yield per recruit values obtained from Beverton's and Ricker's models for a hypothetical population.

The yield per recruit ( $Y_W/R$ ) estimates using Beverton's and Ricker's models for different mortality rates and age of exploitation ( $T_p$ ) using different growth rates having a  $K$  value of 0.05128 and 0.17327 respectively are given in Tables XLI and XLII and in the form of yield isopleths in Figures 25 and 26. The average weight of stock during time  $t$  as estimated by Ricker's model is obtained by taking the arithmetic mean. The percent deviation of  $Y_W/R$  estimates obtained by Ricker's method from those obtained by Beverton's are entered in Table XLIII and Figures 27 and 28 and show that the difference in the two estimates increases with increase in age of

Table XII.  $Y_W/R$  estimations in grams by the methods of Beverton and Ricker (arith. mean) for a hypothetical population under steady state subject to a continuous fishery. Data (1)  $K = 0.05128$ ,  $W_\infty = 2930.3$  gms. ;  $T_0 = 0$  ;  $T_p = 1$  ;  $T_A = 21$  years.  
 $T_p$  = First age of full exploitation or 50% retention age.

Natural Mortality (M)	M = 0.2										M = 0.6									
Fishing Mortality (F)	F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8		F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8	
$Y_W/R$ by the respective methods for various $T_p$ values	Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.		Bev. Rick.	
$T_p = 1$	13.89	13.88	5.33	5.30	2.85	2.80	1.90	1.84	1.43	1.38	1.78	1.77	1.71	1.68	1.36	1.31	1.11	1.07	0.95	0.93
$T_p = 6$	25.78	25.78	25.28	25.67	23.76	25.06	22.87	25.58	22.32	26.90	1.14	1.16	1.93	2.03	2.21	2.47	2.35	2.83	2.43	3.19
$T_p = 11$	23.95	24.06	30.40	31.36	31.24	33.86	31.50	36.55	31.62	39.79	0.19	0.19	0.34	0.37	0.41	0.48	0.45	0.57	0.47	0.65
$T_p = 16$	13.43	13.52	21.54	22.39	23.43	25.69	24.10	28.38	24.44	31.28	0.02	0.02	0.03	0.04	0.04	0.05	0.05	0.06	0.05	0.07

Table XLII.  $Y_W/R$  estimations in grams by the methods of Beverton and Ricker (arith. mean) for a hypothetical population under steady state subject to a continuous fishery.

Data(2)  $K = 0.17327$ ;  $W_\infty = 2930.3$  gms. ;  $T_0 = 0$  ;  $T_p = 1$  ;  $T_\infty = 21$  years.

$T_p$  = First age of full exploitation or 50 percent retention age.

Natural Mortality (M)	M = 0.2										M = 0.6									
Fishing Mortality (F)	F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8		F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8	
$Y_W/R$ by the respective methods for various $T_p$ values	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.
$T_p = 1$	172.16	171.71	101.44	100.26	65.21	63.63	47.88	46.25	38.33	37.04	33.81	33.42	39.13	38.18	34.20	33.04	29.81	28.81	26.58	26.10
$T_p = 6$	236.75	237.33	293.47	301.01	299.37	321.41	299.78	343.43	299.21	370.98	13.24	13.58	24.31	26.10	28.98	33.20	31.50	39.05	33.05	44.75
$T_p = 11$	139.90	141.13	201.46	210.08	217.92	240.12	225.40	266.99	229.65	295.88	1.23	1.28	2.39	2.64	2.95	3.49	3.27	4.21	3.48	4.91
$T_p = 16$	54.51	55.13	91.55	96.02	102.46	113.86	107.22	128.33	109.92	143.29	0.08	0.08	0.15	0.17	0.19	0.23	0.21	0.28	0.23	0.32

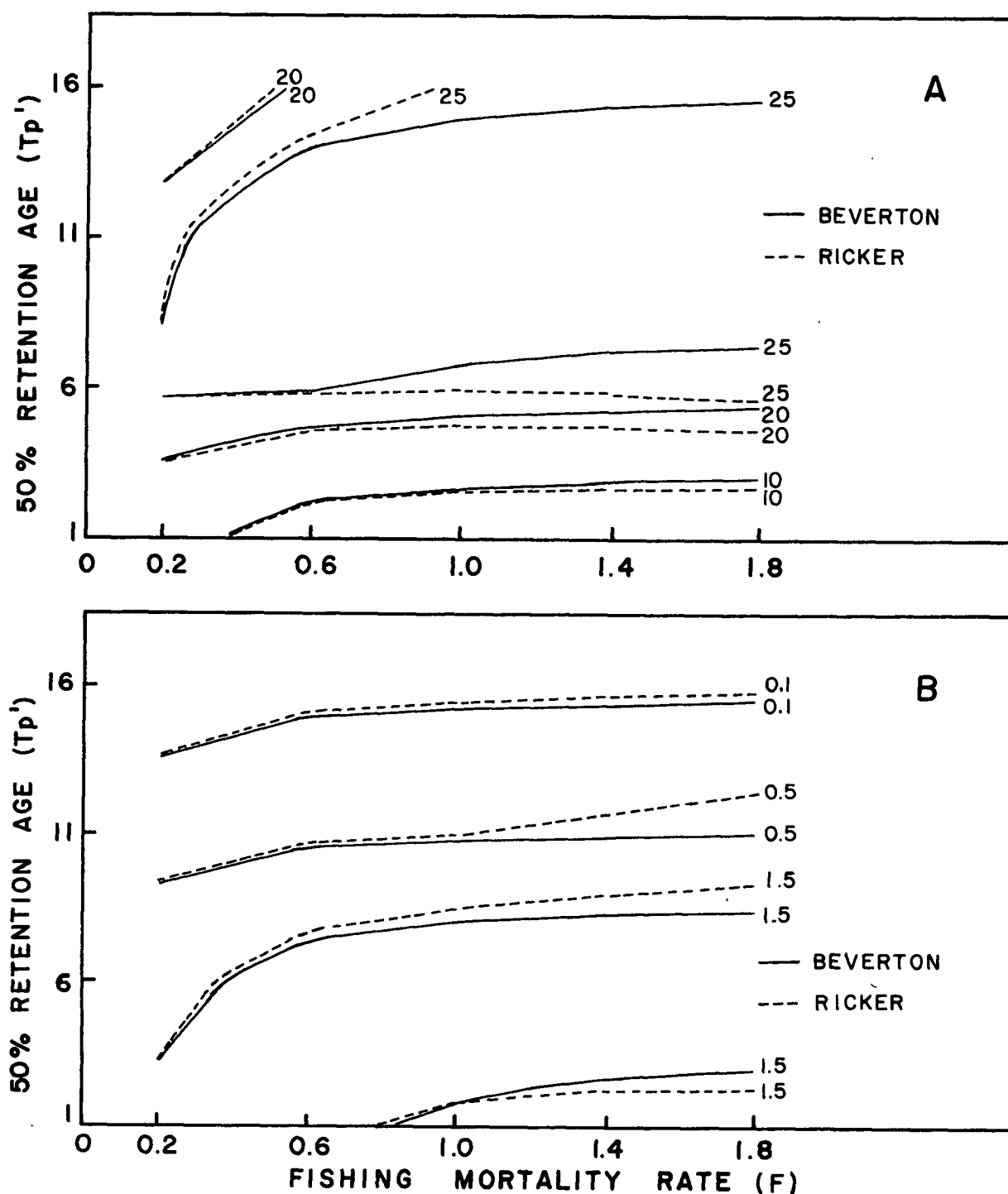


Figure 25. Comparison of the yield isopleths for a hypothetical population obtained from Beverton's and Ricker's (arith.mean) models.  $Y_W/R$  estimates for  $M = 0.6$  are rounded at the 4th decimal place for drawing yield isopleths. (A):  $K = 0.05128$ ,  $M = 0.2$ ; (B):  $K = 0.05128$ ,  $M = 0.6$ . Data from Table XLI.

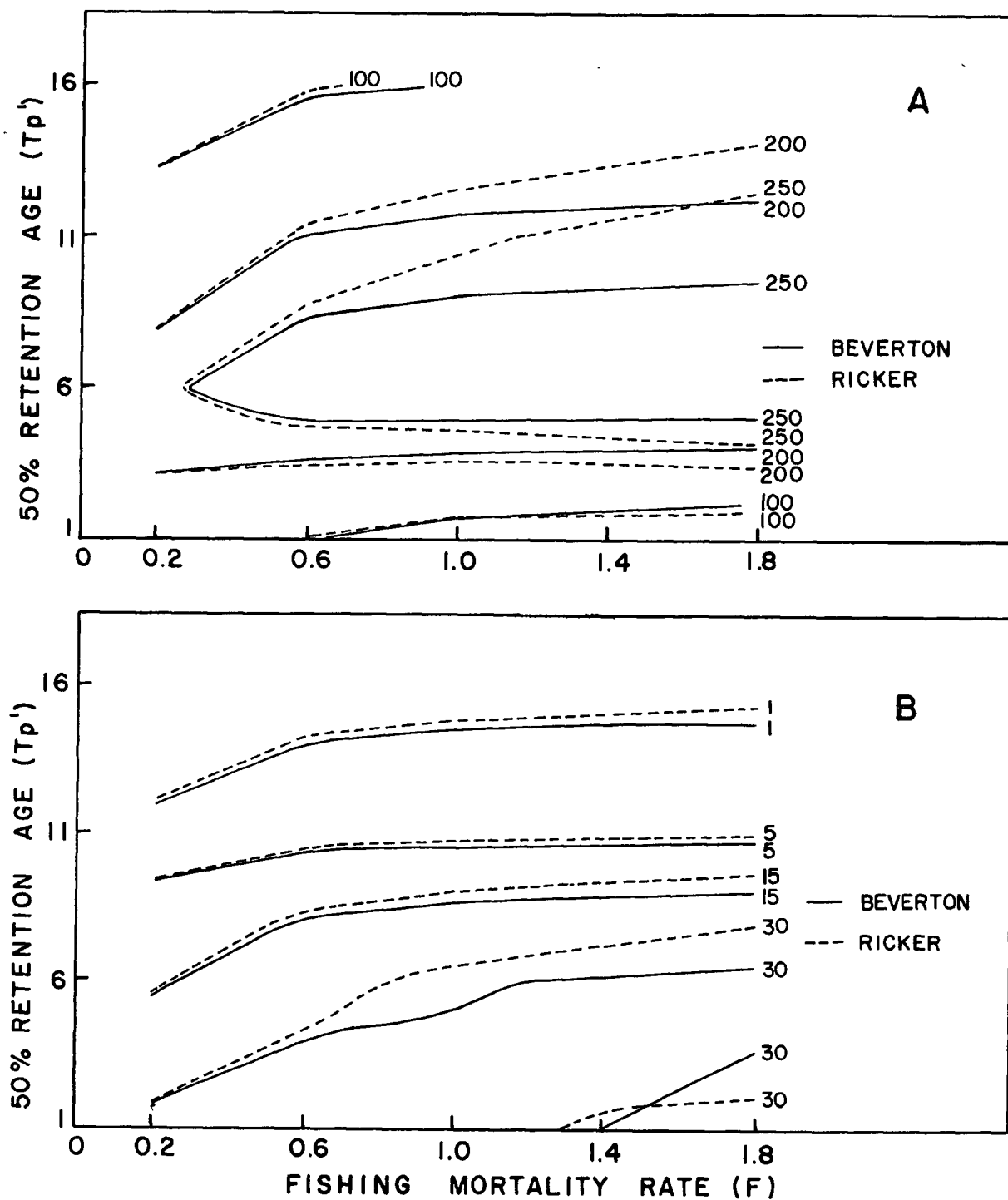


Figure 26. Comparison of the yield isopleths for a hypothetical population obtained from Beverton's and Ricker's (arith.mean) models.  $Y_W/R$  estimates for  $M = 0.6$  are rounded at the 4th decimal place for drawing yield isopleths. (A):  $K = 0.17327$ ,  $M = 0.2$ . (B):  $K = 0.17327$ ,  $M = 0.6$ . Data from Table XLII.

Table XLIII. Percent deviation of  $Y_w/R$  estimated by Ricker's method (arith. mean) from that of Beverton for the different values of  $K$ ,  $M$ ,  $F$  and  $T_p$ . Data from Tables XLI and XLII.  $Y_w/R$  values for  $M$  of 0.2 are rounded to the 2nd decimal place in calculating the % deviation, and for  $M$  of 0.6 the values are rounded to the 4th decimal place.

K = 0.05128 ; $W_\infty$ = 2930.3 gms. ; $T_0$ = 0 ; $T_p$ = 1 ; $t_\lambda$ = 21 years.										
Natural Mortality (M)	M = 0.2					M = 0.6				
Fishing Mortality (F)	F = 0.2	F = 0.6	F = 1.0	F = 1.4	F = 1.8	F = 0.2	F = 0.6	F = 1.0	F = 1.4	F = 1.8
$T_p$ = 1	-0.072	-0.563	-1.754	-3.158	-3.497	-0.677	-1.850	-3.018	-3.495	-2.616
$T_p$ = 6	0	1.543	5.471	11.850	20.520	1.546	5.472	11.841	20.470	31.254
$T_p$ = 11	0.459	3.158	8.387	16.03	25.840	3.104	8.373	16.011	25.834	37.605
$T_p$ = 16	0.670	3.946	9.646	17.759	27.987	3.202	8.524	16.171	26.018	37.740
K = 0.17327 ; $W_\infty$ = 2930.3 gm. ; $t_0$ = 0 ; $t_p$ = 1 ; $t_\lambda$ = 21 years										
$T_p$ = 1	-0.261	-1.163	-2.423	-3.404	-3.366	-1.164	-2.426	-3.392	-3.193	-1.777
$T_p$ = 6	0.245	2.569	7.362	14.561	23.986	2.569	7.360	14.561	23.988	35.403
$T_p$ = 11	0.879	4.279	10.187	18.452	28.840	4.277	10.176	18.448	28.837	41.095
$T_p$ = 16	1.137	4.883	11.126	19.688	30.358	4.891	11.091	19.701	30.342	42.870

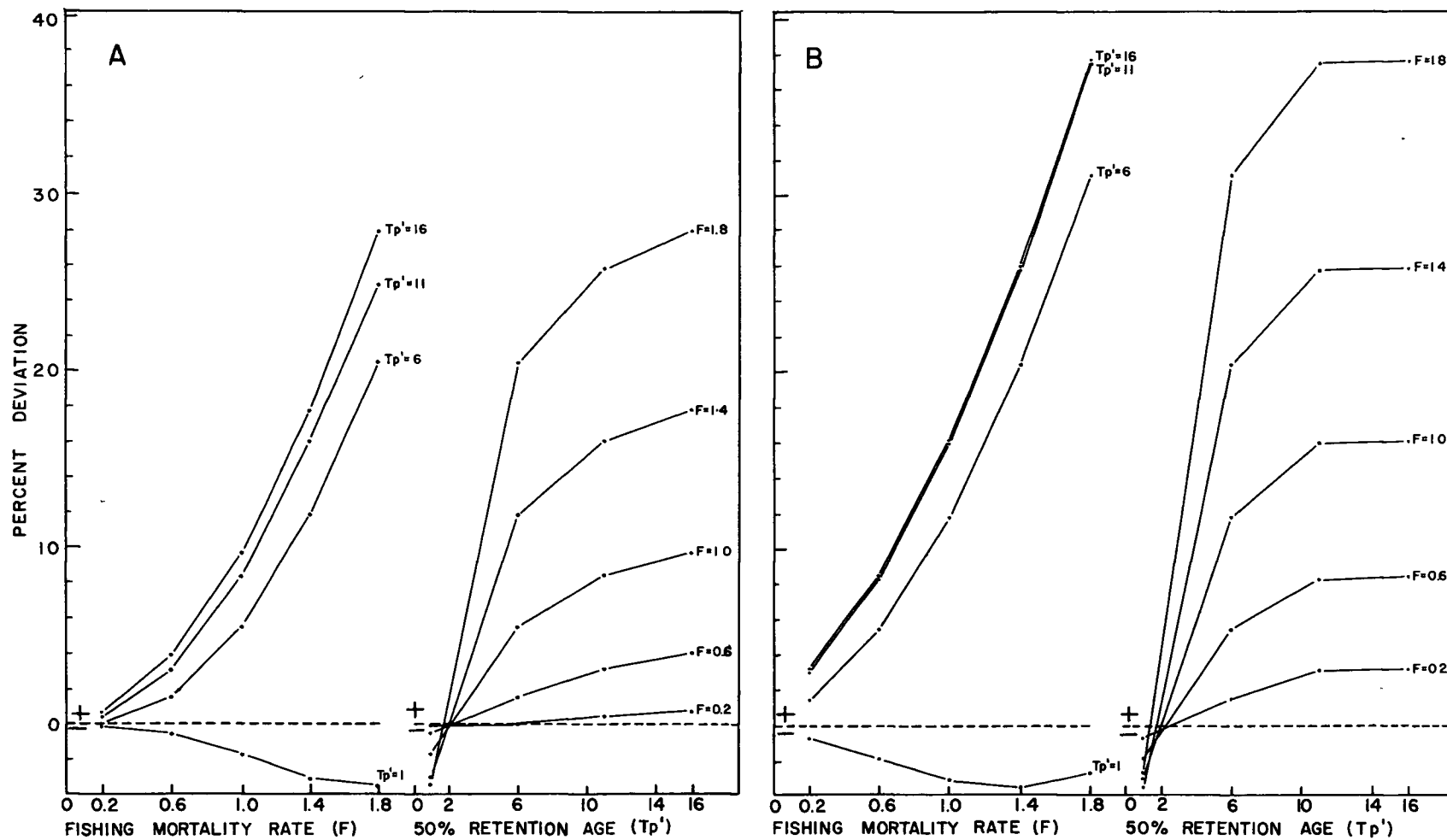


Figure 27. Percent deviation of  $Y_w/R$  estimated by Ricker's method (arith. mean) from that of Beverton showing the trend for various fishing mortality rates and ages of exploitation. (A)  $K = 0.05128$ ,  $M = 0.2$ ; (B)  $K = 0.05128$ ,  $M = 0.6$ . Data from Table XLIII.



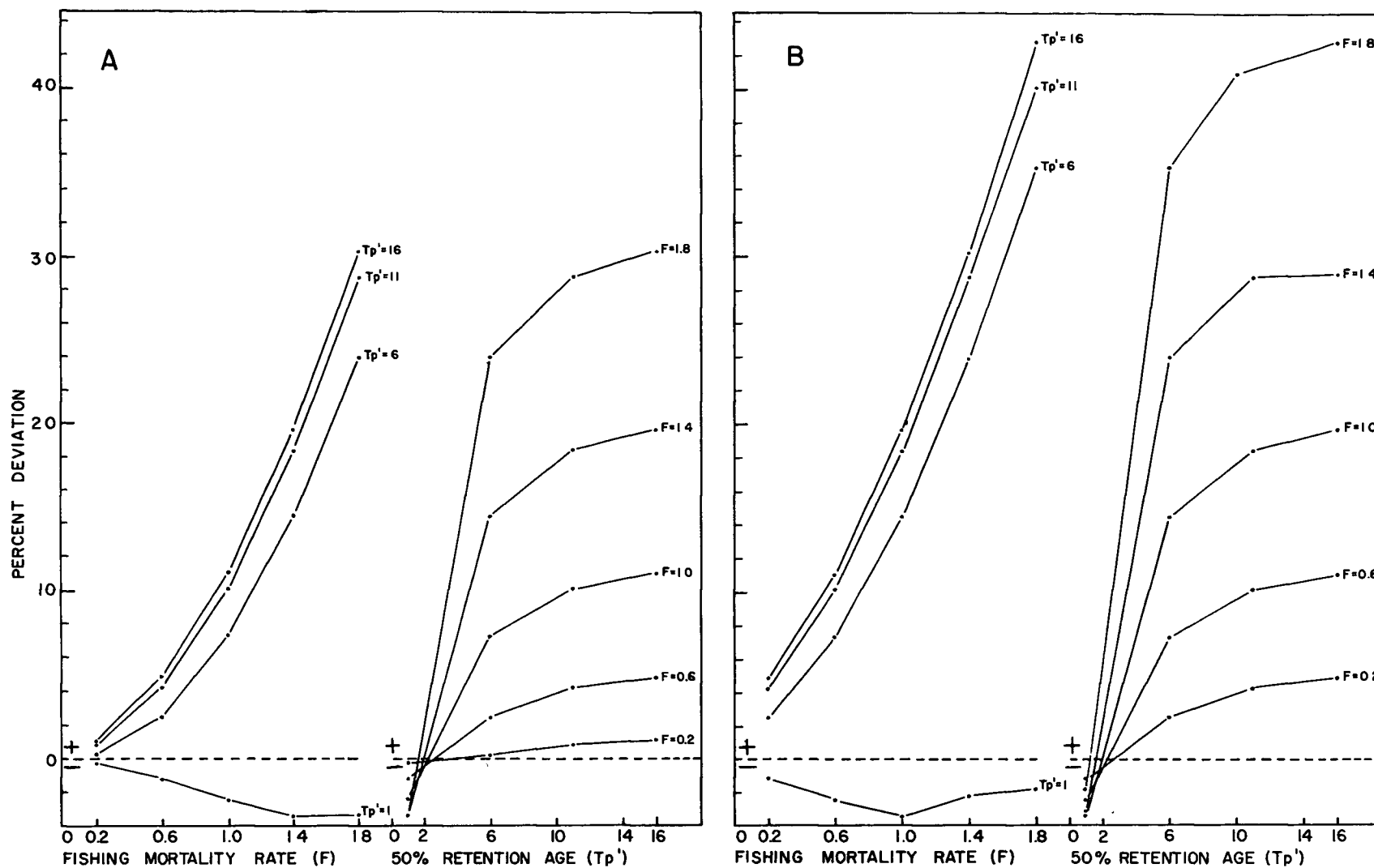


Figure 28. Percent deviation of  $Y_W/R$  estimated by Ricker's method (arith.mean) from that of Beverton showing the trend for various fishing mortality rates and ages of exploitation. (A)  $K = 0.17327$ ,  $M = 0.2$ ; (B)  $K = 0.17327$ ,  $M = 0.6$ . Data from Table XLIII.

exploitation. This difference also increases with increase in growth rate, natural mortality rate and fishing mortality rate. Hence a maximum difference of 42.8% is observed in the table for a combination of the highest values of  $T_p$ ,  $K$  and total mortality. The figures also indicate that for this population a sharp increase in the per cent deviation occurs at a  $T_p$  of six years.

Another comparison of the  $Y_W/R$  values obtained by the two methods is presented in Table XLIV. In this case the average weight of stock during time  $t$ , as determined by Ricker's method, is obtained by taking the exponential average. The per cent deviation of the two sets of values is given in Table XLV and Figure 29. By using the exponential average in Ricker's model, the difference in the  $Y_W/R$  estimates by the two methods has decreased considerably. Figure 29 shows that the difference between the two estimates decreases with increase in the age of exploitation. A slight increase in the per cent deviation with increase in mortality rates is also noticed although its magnitude is negligible at higher  $T_p$  values. The maximum per cent deviation in the above example is observed when the value of  $T_p$  is one.

All estimations in the above tables were for a continuous fishery. The  $Y_W/R$  values for a seasonal fishery as estimated by the methods of Ricker, using both the arithmetic mean and exponential average as the average weight of stock during time  $t$ , and that of Beverton, are given in Table XLVI. Their per cent deviations from those of Beverton are presented in Table XLVII and Figure 30. It is evident from a comparison of Table XLVII with Tables XLIII and XLIV or Figure 30 with Figures 27-29 that when the fishing season is reduced, the per cent deviation in the  $Y_W/R$  values is very slight even when Ricker's model makes use of an arithmetic mean for an estimate of the average weight of stock. When an exponential average is used the difference

Table XLIV.  $Y_W/R$  estimations in grams by the methods of Beverton and Ricker (exp.av.) for a hypothetical population under steady state subject to a continuous fishery.

Data (2).  $K = 0.17327$  ;  $W_\infty = 2930.3$  gms. ;  $T_0 = 0$  ;  $T_p = 1$  ;  $T_\lambda = 21$  years.

$T_p$  = First age of full exploitation or 50% retention age.

Natural Mortality (M)	M = 0.2										M = 0.6									
Fishing Mortality (F)	F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8		F = 0.2		F = 0.6		F = 1.0		F = 1.4		F = 1.8	
$Y_W/R$ by the respective methods for various $T_p$ values	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.	Bev.	Rick.
$T_p = 1$	172.16	169.91	101.44	98.25	65.21	61.95	47.88	44.71	38.33	35.29	33.81	32.75	39.13	37.17	34.20	31.93	29.81	27.45	26.58	24.21
$T_p = 6$	236.75	236.05	293.47	292.30	299.37	298.03	299.78	298.37	299.21	297.79	13.24	13.19	24.31	24.20	28.98	28.84	31.50	31.35	33.05	32.90
$T_p = 11$	139.90	139.78	201.46	201.24	217.92	217.66	225.40	225.13	229.65	229.38	1.23	1.23	2.39	2.39	2.95	2.95	3.27	3.27	3.48	3.48
$T_p = 16$	54.51	54.49	91.55	91.52	102.46	102.42	107.22	107.18	109.92	109.88	0.08	0.08	0.15	0.15	0.19	0.19	0.21	0.21	0.23	0.23

Table XLV. Percent deviation of  $Y_W/R$  estimated by Ricker's method from that of Beverton for the different values of  $M$ ,  $F$  and  $T_p$ , given in Table XLIV.  $Y_W/R$  estimates for  $M$  of 0.2 are rounded to the 2nd decimal place in calculating % deviation and for  $M$  of 0.6 the values are rounded to the 4th decimal place.

K = 0.17327, $W_{\infty}$ = 2930.3 gms. ; $T_0$ = 0 ; $T_p$ = 1 ; $T_A$ = 21 years										
Natural Mortality (M)	M = 0.2					M = 0.6				
Fishing Mortality (F)	0.2	0.6	1.0	1.4	1.8	0.2	0.6	1.0	1.4	1.8
$T_p$ = 1	-1.307	-3.145	-4.999	-6.495	-7.931	-3.140	-4.995	-6.6215	-7.928	-8.914
$T_p$ = 6	-0.296	-0.399	-0.448	-0.470	-0.475	-0.402	-0.448	-0.469	-0.476	-0.475
$T_p$ = 11	-0.086	-0.109	-0.119	-0.120	-0.118	-0.114	-0.117	-0.122	-0.119	-0.121
$T_p$ = 16	-0.037	-0.033	-0.039	-0.037	-0.036	-0.040	-0.066	0	-0.047	-0.044

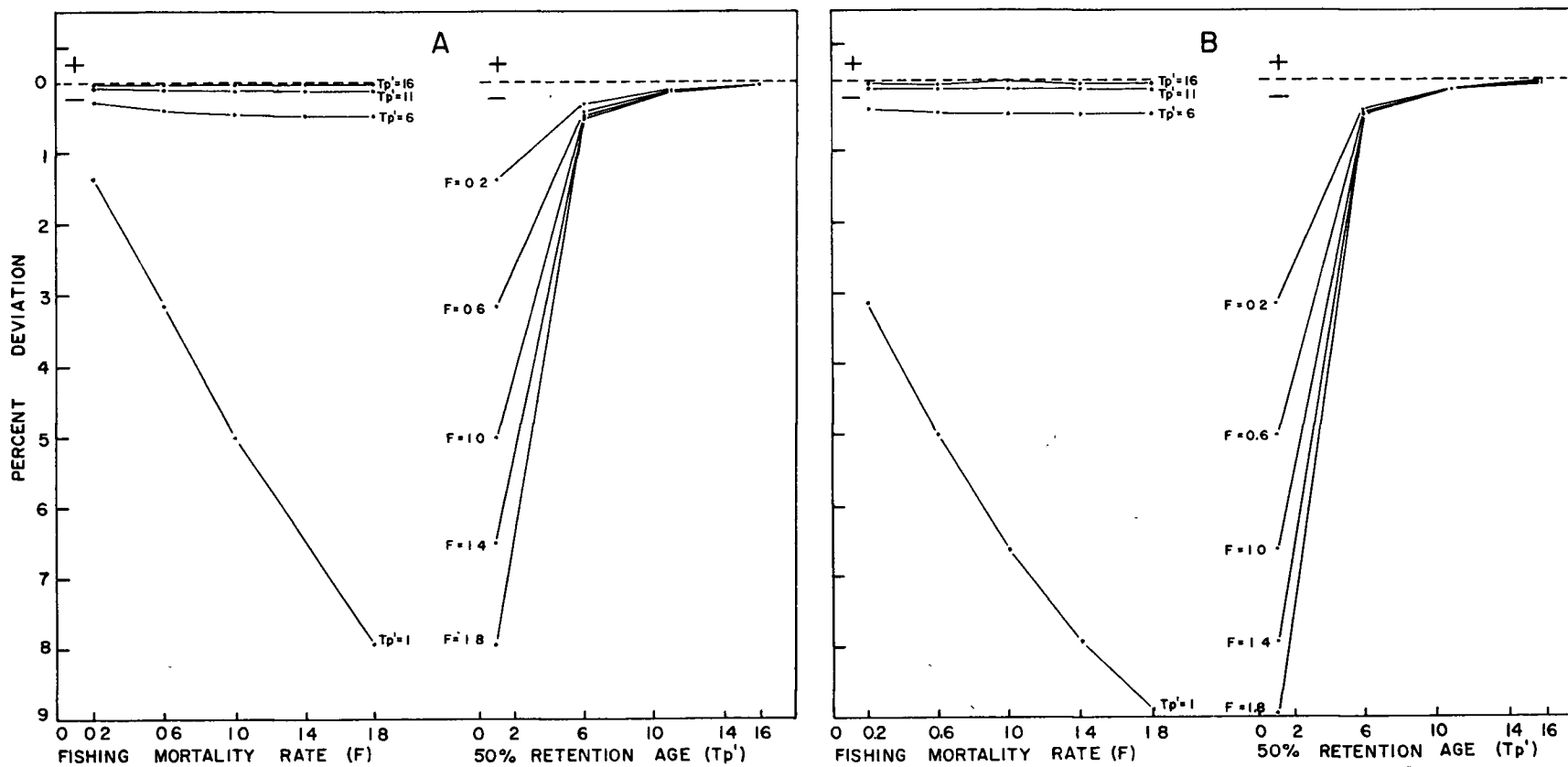


Figure 29. Percent deviation of  $Y_W/R$  estimated by Ricker's method (exp.av.) from that of Beverton showing the trend for various fishing mortality rates and ages of exploitation. (A)  $K = 0.17327$ ,  $M = 0.2$ ; (B)  $K = 0.17327$ ,  $M = 0.6$ . Data from Table XLV.

Table XLVI.  $Y_W/R$  estimations in grams by the methods of Beverton and Ricker for a hypothetical population under steady state subject to a seasonal fishery.

$T_p$  = First age of full exploitation or 50% retention age

K = 0.17327; $W_\infty$ = 2930.3 gms. ; $T_0$ = 0 ; $T_\lambda$ = 21 years ; M = 0.2																
Fishing Mortality (M)		0.2			0.6			1.0			1.4			1.8		
$Y_W/R$ by the respective methods for various $T_p$ values.		Bev.	Rick.1 (arith. mean)	Rick.2 (exp. av.)	Bev.	Rick.1 (arith. mean)	Rick.2 (exp. av.)	Bev.	Rick.1 (arith. mean)	Rick.2 (exp. av.)	Bev.	Rick.1 (arith. mean)	Rick.2 (exp. av.)	Bev.	Rick.1 (arith. mean)	Rick.2 (exp. av.)
Fishing season 0.25 year	$T_p = 1$	114.56	114.56	114.51	164.78	164.96	164.67	150.71	151.15	150.57	127.86	128.59	127.69	107.24	108.25	107.06
	$T_p = 6$	109.42	109.46	109.42	214.74	215.19	214.72	257.19	258.57	257.16	276.50	279.31	276.46	286.11	290.85	286.06
	$T_p = 11$	57.33	57.36	57.33	126.10	126.46	126.10	162.70	163.79	162.70	184.02	186.25	184.02	197.51	201.31	197.51
	$T_p = 16$	19.30	19.32	19.31	47.63	47.78	47.63	66.48	66.96	66.49	79.28	80.30	79.28	88.14	89.92	88.15
Fishing season 0.5 year	$T_p = 1$	157.56	157.56	157.19	144.30	144.48	143.63	104.11	104.52	103.34	77.26	77.90	76.47	60.05	60.92	59.25
	$T_p = 6$	173.35	173.50	173.24	267.98	269.93	267.76	289.23	294.90	288.95	295.52	306.82	295.21	297.47	316.25	297.14
	$T_p = 11$	95.76	95.98	95.75	171.94	173.83	171.91	199.58	204.79	199.53	212.97	223.12	212.92	220.75	237.42	220.70
	$T_p = 16$	34.20	34.30	34.20	72.01	72.90	72.01	89.79	92.34	89.79	98.98	104.01	98.98	104.25	112.53	104.24

Table XLVII. Percent deviation of  $Y_W/R$  values obtained by Ricker's methods 1 and 2 from that of Beverton for a seasonal fishery as estimated from Table XLVI. Values up to 4th decimal place are retained in calculating % deviation.

K = 0.17327; $W_{\infty}$ = 2930.3 gms, ; $T_0$ = 0 ; $T_A$ = 21 years; $M$ = 0.2											
Fishing Mortality		0.2		0.6		1.0		1.4		1.8	
	$T_p$	Rick.1	Rick.2	Rick.1	Rick.2	Rick.1	Rick.2	Rick.1	Rick.2	Rick.1	Rick.2
Fishing sea- son 0.25 year.	1	0.016	-0.040	0.108	-0.066	0.294	-0.095	0.571	-0.129	0.941	-0.165
	6	0.033	-0.007	0.208	-0.010	0.535	-0.013	1.016	-0.015	1.657	-0.017
	11	0.063	0.001	0.285	0.0007	0.669	0.0002	1.217	-0.0003	1.927	-0.0007
	16	0.078	0.005	0.316	0.005	0.720	0.005	1.288	0.005	2.020	0.005
Fishing sea- son 0.5 year.	1	0.001	-0.234	0.126	-0.464	.393	-0.737	0.825	-1.032	1.455	-1.337
	6	0.090	-0.061	0.725	-0.083	1.962	-0.097	3.825	-0.108	6.312	0.112
	11	0.230	-0.016	1.100	-0.020	2.614	-0.022	4.768	-0.024	7.549	0.025
	16	0.289	-0.002	1.238	-0.002	2.839	-0.003	5.082	-0.003	7.950	0.003

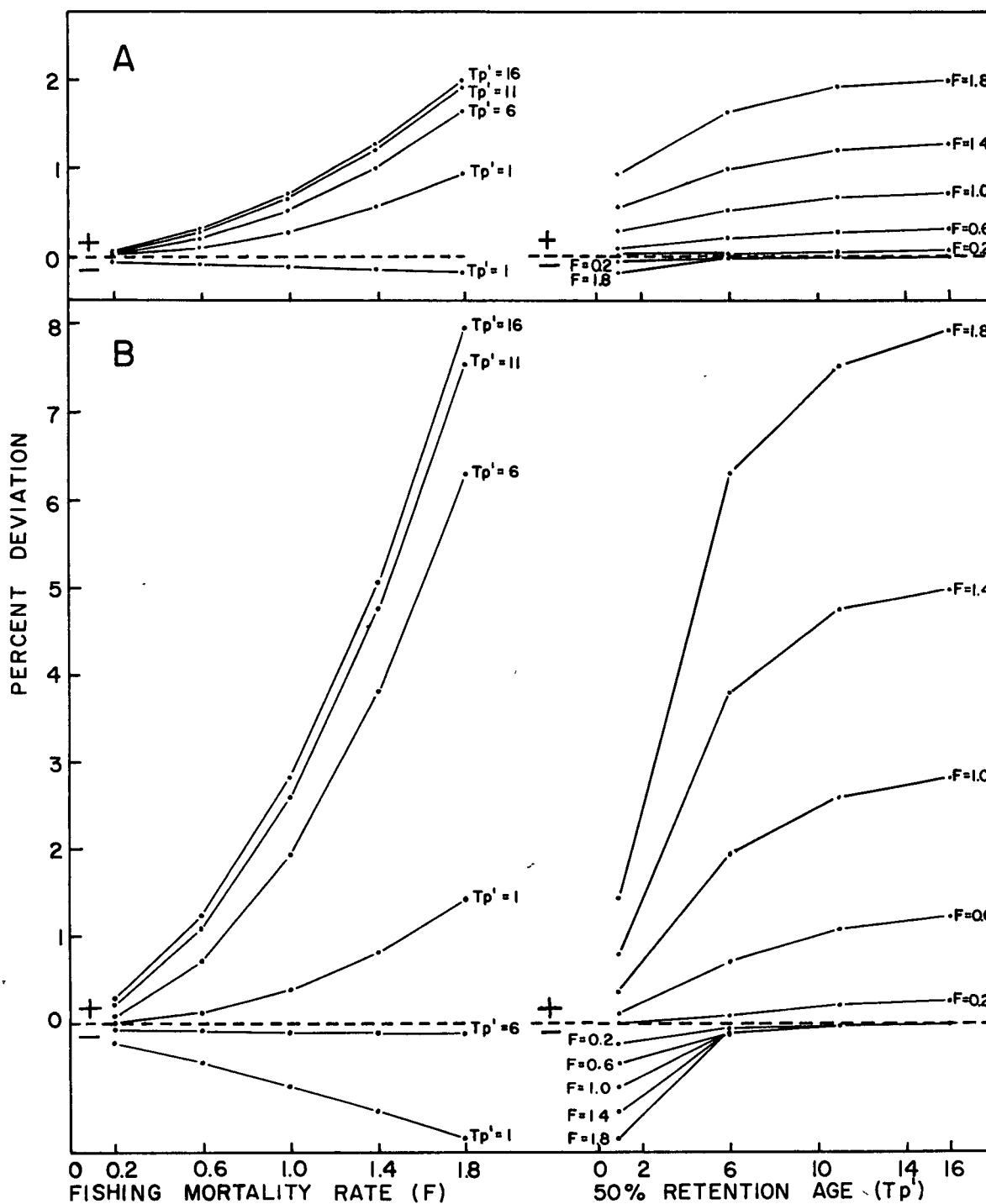


Figure 30. Percent deviation of  $Y_W/R$  estimated by Ricker's methods 1 and 2 from that of Beverton for a seasonal fishery. The lines of negative deviation are for values from Ricker's method using exponential average.  
 (A) Duration of fishing season = 0.25 year. (B) Duration of fishing season = 0.5 year. Data from Table XLVII.



in the  $Y_W/R$  estimations by the methods of Beverton and Ricker for a seasonal fishery becomes extremely small.

The hypothetical population under consideration is assumed to be in a steady state with constant growth, recruitment and mortality rates. Since a theoretical set of data are used for studying the magnitude of error, the difference in the yield per recruit estimations from different models as a result of discrepancies in the data is minimal. Hence any such difference would arise only from the manner of representing the data by the model. For purposes of comparison,  $Y_W/R$  estimations from Beverton's equation are taken as the standard since the mathematical treatment of the data is more elegant. The  $Y_W/R$  estimations made by Ricker's method for various mortality rates, growth rates and age of exploitation vary considerably from those of Beverton when the average weight of the stock is obtained by taking the arithmetic mean. By using an exponential average the per cent deviation is made negligibly small. Ricker (1958) suggests that an arithmetic mean may be a better average than the exponential. However, when the model assumes exponential growth and mortality rates within each time interval, an accurate estimate of the average weight of stock for the time  $t$  is given only by an exponential average. Under these conditions the use of an arithmetic mean results in an over estimation of the yield and thus introduces an error in the calculation. The magnitude of the error in the  $Y_W/R$  values would depend on the difference in the estimates of mean biomass at the beginning of each exploitable age, the values of the growth and mortality rates and the duration of the time  $t$ . The steepness of the exponential curve describing the change in the biomass during time  $t$  depends on the value assumed by growth and mortality rates. With low growth or mortality rates, the exponential curve approaches a straight line so that there is little difference in the two

estimates of the mean biomass and hence the estimates of yield will also be similar. Thus the per cent deviation in the  $Y_W/R$  values in Table XLIII shows a continuous increase with increase in  $T_p$ , values, mortality rates and  $K$  values when an arithmetic mean is used. The error is less when the fishing season is reduced (Table XLVII). The arithmetic mean can be used only if the biomass is a linear function of time. A comparison of the  $Y_W/R$  estimates by Ricker's model, using an arithmetic mean, and those obtained by Beverton's method is found to be either an over or an under-estimate. If the weight of stock is on the average decreasing, then use of an arithmetic mean overestimates the yield. On the other hand if the stock is increasing then it may, depending on the curve describing the change in biomass, under-estimate the yield. Hence at the optimum  $T_p$ , when the changes in biomass due to growth and mortality balance each other, the  $Y_W/R$  estimate from Ricker's model using an arithmetic mean would be an over-estimate compared to Beverton's even for the smallest fishing mortality rate. The assumption of exponential growth and mortality rates for each time interval should mean that the biomass is an exponential function of time. Hence the per cent deviation of the  $Y_W/R$  values estimated by Ricker's model using an exponential average from those of Beverton is very much less, although the  $Y_W/R$  is now found to be always less than that obtained by Beverton's model. However, the slight difference observed in the two estimates is mainly due to the manner of representing the growth pattern in the two models.

The chief drawback in Beverton's equation is the complexity assumed by the model when the parameters are not constant. In the present study, in order to calculate one  $Y_W/R$  value for a seasonal fishery, changes involved in modifying Beverton's equation for a seasonal fishery maintaining all other parameters constant alone makes the equation over twenty times more time

consuming. When the exploitable phase lasts twenty years with one short fishing season, the yield for each season is calculated in exactly the same manner as it is for a continuous fishery. In addition, the number of recruits at the beginning of each season has to be calculated separately. If growth is also seasonal and fish do not grow isometrically, the appropriate modifications involve complex numerical integration. Ricker's equation, on the other hand, accommodates changes in growth and mortality rates with no modifications in the original method. When one considers (a) the complexity assumed by Beverton's model under these circumstances (b) the simple calculations required in Ricker's method and flexibility with which it accommodates changes in growth and mortality rates (c) the variability inherent in the biological data and (d) almost identical results from the two equations, Ricker's model may be preferred for studying the changes in yield and biomass when growth and mortality rates are not constant or when the fish do not grow isometrically.

(b) Changes in the yield and biomass of the butter sole population

The reaction of the butter sole population to varying degrees of exploitation at different ages and mortality rates is examined for fish above 4.83 years of age, although the recruitment to the spawning ground is not complete at this age as seen from Table VII. The mesh size of 50% retention must have a perimeter much less than the girth of fish 4.83 years in order to account for the recruitment pattern. Since this pattern is not known precisely, changes in the biomass and yield are examined assuming that fish above 4.83 years of age represent a post-recruit phase of the population. The individual or simultaneous effect of a change in the fishing mortality rates and the age of exploitation (i.e. the 50% retention age) on the biomass is presented in the form of an isopleth diagram in Figure 31. With increase

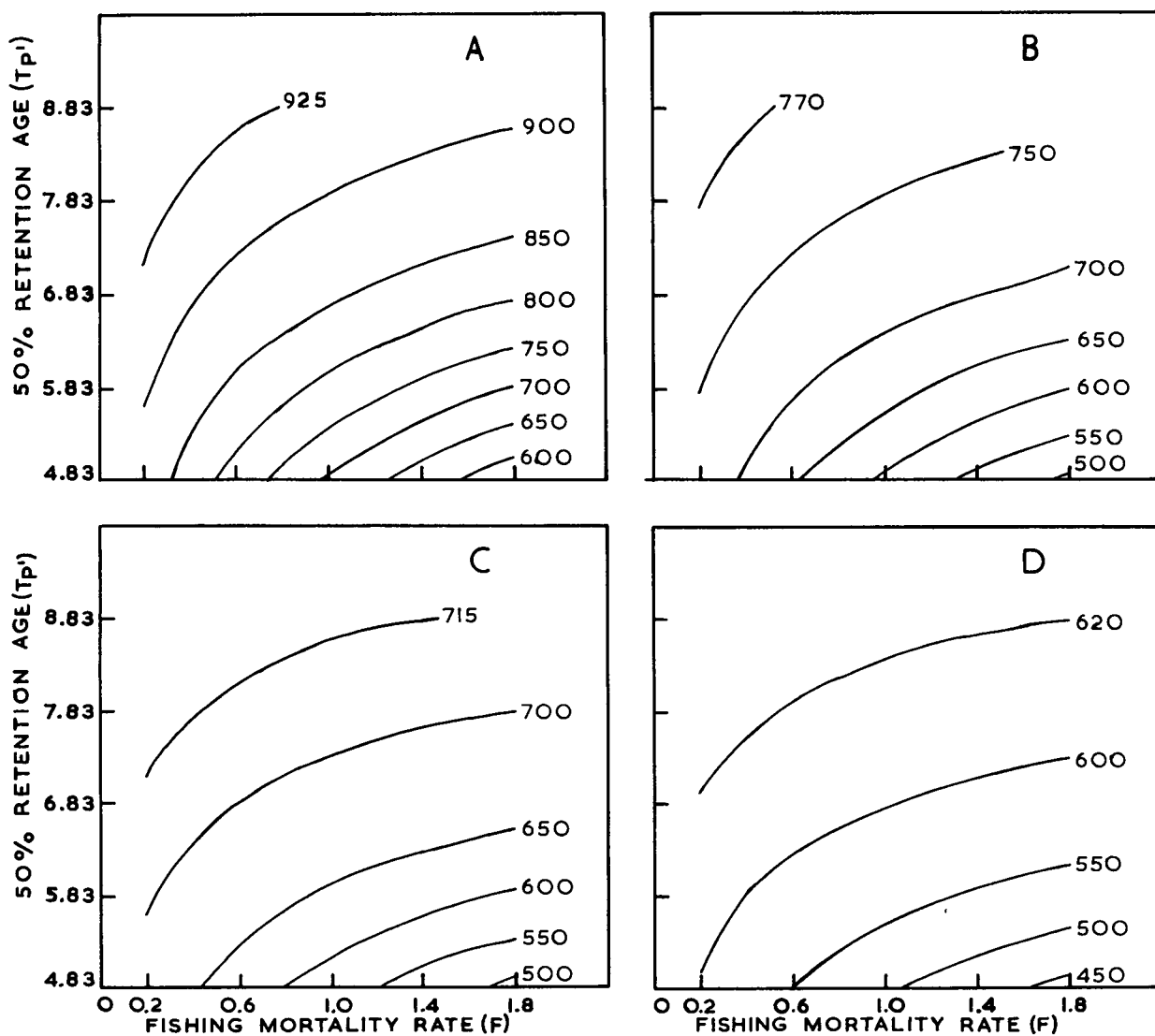


Figure 31. Butter sole: Isopleth diagram for biomass per recruit for the post-recruit phase. (A)  $M = 0.1$ ,  $\Delta M = 0.2$ . (B)  $M = 0.2$ ,  $\Delta M = 0.2$ . (C)  $M = 0.1$ ,  $\Delta M = 0.4$ . (D)  $M = 0.2$ ,  $\Delta M = 0.4$ .

in the age of exploitation, the mean biomass of the spawning population increases. Increase in the natural and fishing mortality rates reduces the biomass of the post-recruit phase. However, the relative effect of a change in the two mortality rates on the biomass are very different (Figure 32). When the initial natural mortality rate is 0.1 (Figure 32A), a change in the fishing mortality rate from 0.2 to 0.6 reduces the mean biomass per recruit from 880.77 gms to 778.55 gms. A change in the natural mortality rate from 0.1 to 0.2 (Figure 32B) reduces it from 880.77 to 732.39 gms. The effect of a change in the fishing mortality rate is not felt in the biomass as much as a change in the natural mortality rate. This is because fishing is highly seasonal and operates at a time when the growth rate is at its minimum, whereas natural mortality operates throughout the year. A relatively high fishing mortality rate is required to significantly lower the mean biomass. Since the vulnerability or catchability of the fish to the gear is fairly high, a high fishing mortality rate can be generated during the spawning season and thus bring about an appreciable dent in the population.

The effects on the yield of changing the age of exploitation for four sets of natural mortality rates are given in Figure 33. If the age of exploitation is very low, a low fishing mortality would result in higher yield since more young fish with faster growth rates are left to realize their growth potentialities. With increase in the age of exploitation, the fishing mortality rate that would give the maximum yield also increases. Finally, at the age when the increase due to growth and the decrease in numbers from natural mortality balance each other, an infinitely high fishing mortality rate is required to obtain the potential yield as designated by Holt (1958). The weight of a year's brood is maximum at this age. The equilibrium yield curves presented in Figure 33 have their modes at ages less

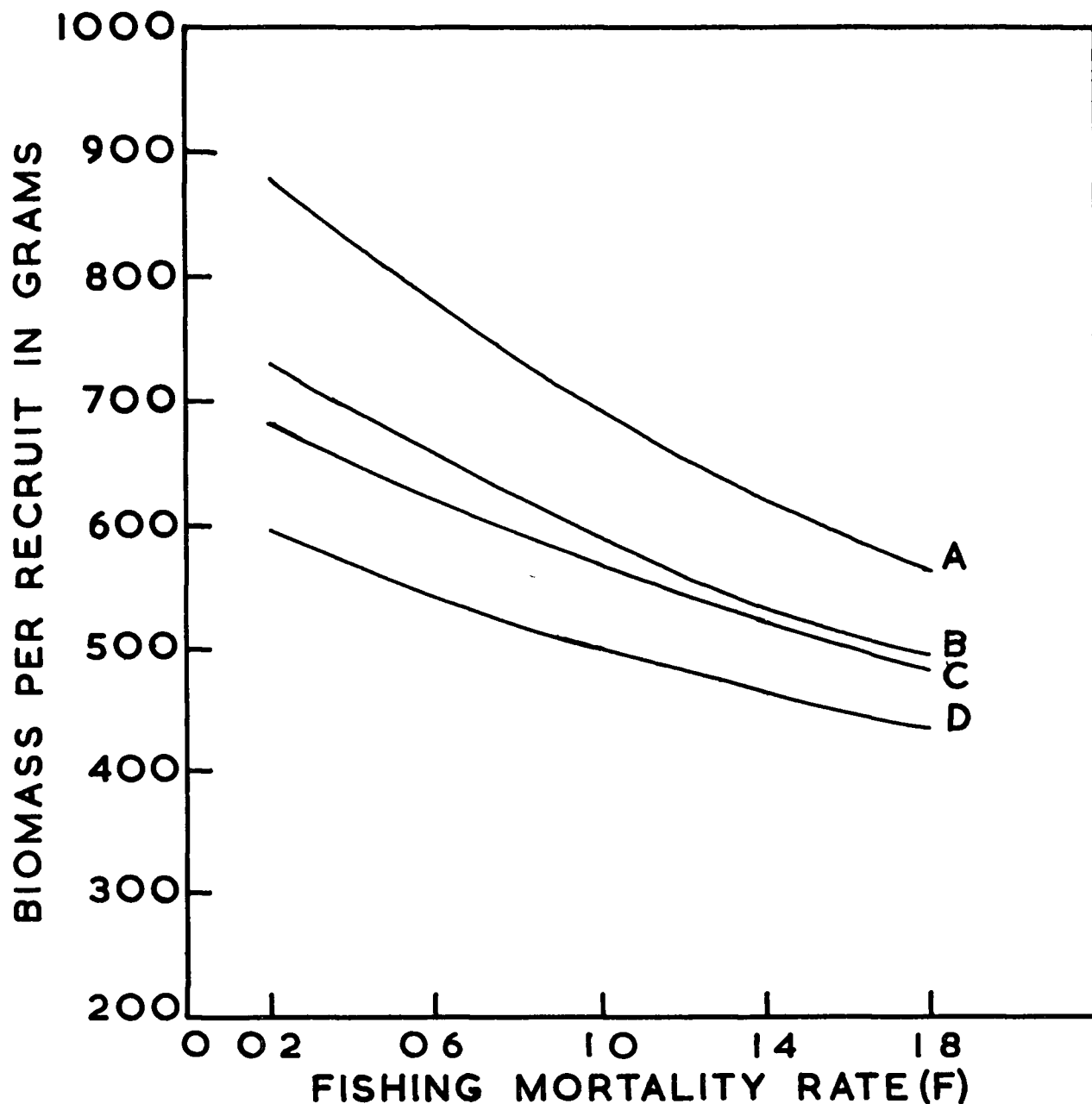


Figure 32. Butter sole: Changes in the biomass per recruit for different fishing and natural mortality rates when  $T_p$  is 4.83 years. (A)  $M = 0.1, \Delta M = 0.2$ . (B)  $M = 0.2, \Delta M = 0.2$ . (C)  $M = 0.1, \Delta M = 0.4$ . (D)  $M = 0.2, \Delta M = 0.4$ .

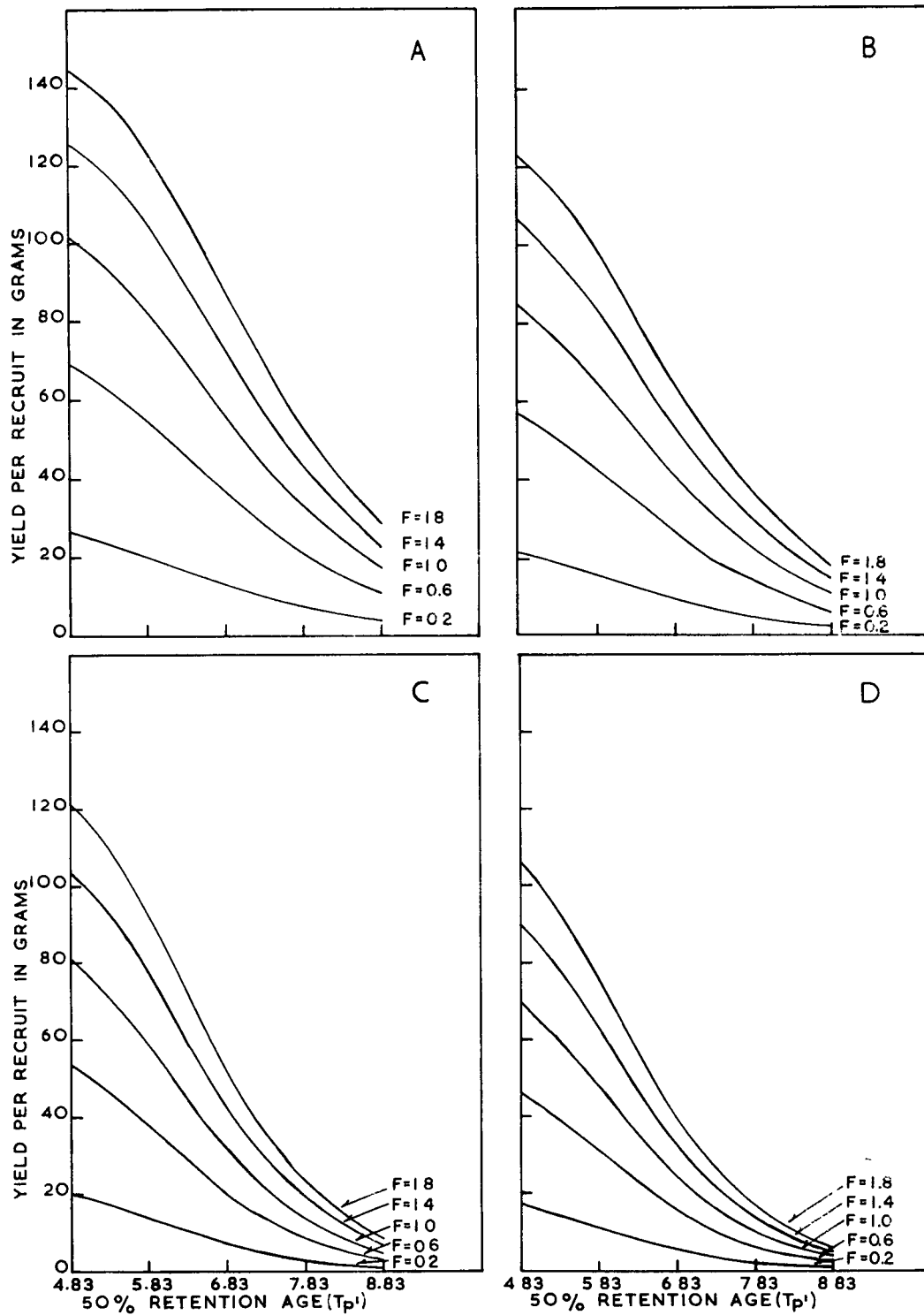


Figure 33. Butter sole: Equilibrium yield curves for various sets of natural mortality rates. (A)  $M = 0.1$ ,  $\Delta M = 0.2$ . (B)  $M = 0.2$ ,  $\Delta M = 0.2$ . (C)  $M = 0.1$ ,  $\Delta M = 0.4$ . (D)  $M = 0.2$ ,  $\Delta M = 0.4$ .

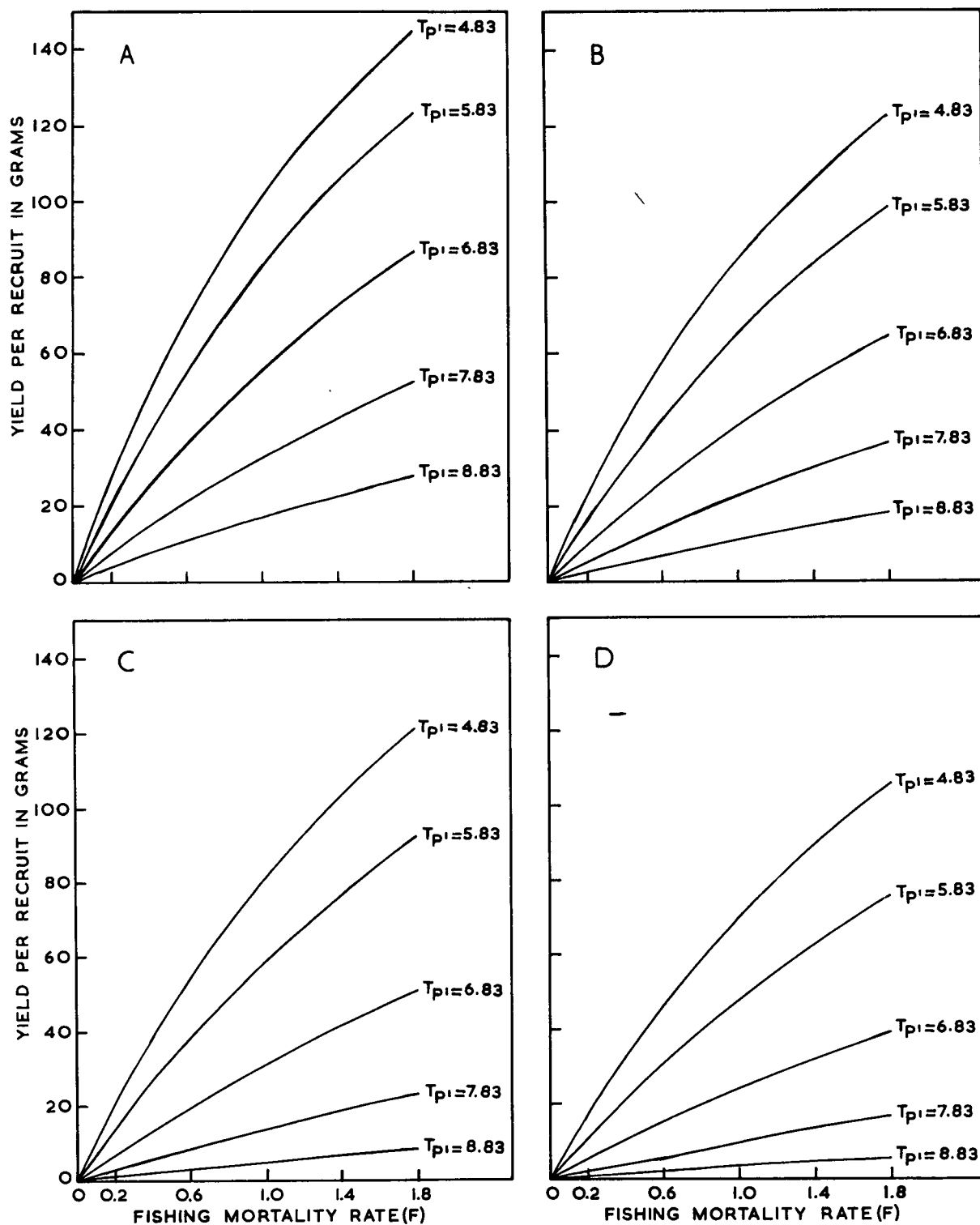


Figure 34. Butter sole: Equilibrium yield curves for various sets of natural mortality rates. (A)  $M = 0.1, \Delta M = 0.2$ . (B)  $M = 0.2, \Delta M = 0.2$ . (C)  $M = 0.1, \Delta M = 0.4$ . (D)  $M = 0.2, \Delta M = 0.4$ .



than 4.83 years for all the fishing mortality rates examined. Since the age of first exploitation is fairly high the equilibrium yield curves plotted in Figure 34 do not attain the maximum at the fishing mortality rates examined. Above the optimum age of exploitation the population biomass is decreasing since the biomass lost because of natural mortality is no longer fully compensated for by growth. Hence beyond this age an increase in the fishing mortality rate always increases the yield however, the same yield can be realized at a lower fishing mortality rate if the age of exploitation is below the optimum age.

The curve which maximizes the sustained yield for a given fishing mortality rate by adjusting the age of exploitation is defined as the eumetric yield curve by Beverton and Holt (1956b). They define the eumetric fishing curve as the "curve defining the relationship between the fishing mortality and the  $T_p$ , needed to produce a eumetric yield curve". The eumetric fishing curve can be drawn by joining the modes of the contours of yield per recruit drawn in a yield isopleth diagram. The highest yield per recruit values for a given fishing mortality lie along this line flanked on either side by lesser yield per recruit values.

The yield isopleth diagrams for butter sole presented in Figure 35 permit an analysis of the effect of a simultaneous change in the fishing mortality and the age of exploitation. The eumetric fishing curve cannot be drawn even when the initial natural mortality rate is as low as 0.1, since the modes of the contours of yield per recruit lie below the age of 4.83 years. This is also seen from the equilibrium yield curves in Figures 33 and 34 which have their modes at ages less than 4.83 years for all the fishing mortality rates examined. Hence the maximum yield for a fishing mortality rate less than 1.8 is obtained only below this age. For this reason the fishing mortality rate

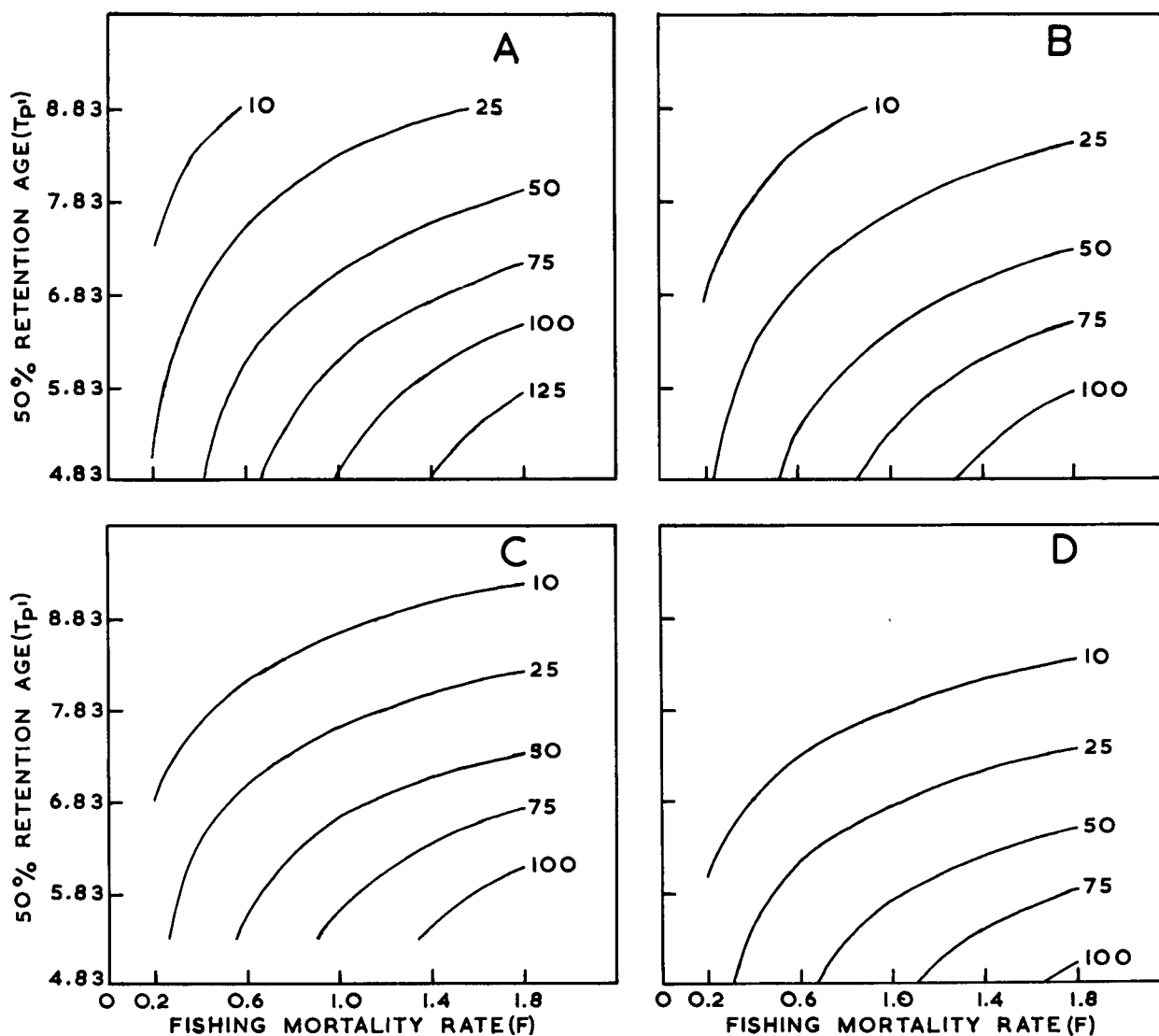


Figure 35. Butter sole: Yield isopleth diagrams when different mortality rates are operating showing the yield for different ages of exploitation and fishing mortality rates. (A)  $M = 0.1$ ,  $\Delta M = 0.2$ . (B)  $M = 0.2$ ,  $\Delta M = 0.2$ . (C)  $M = 0.1$ ,  $\Delta M = 0.4$ . (D)  $M = 0.2$ ,  $\Delta M = 0.4$ .

that would result in the maximum sustained yield when the age of exploitation is 4.83 is well above 1.8. It should, however, be noted that as the fishing season lasts only two months or 0.17 year the effective fishing mortality is only  $1.8 \times 0.17$  or 0.306. However, because the population is highly vulnerable to the gear a higher fishing mortality may be generated.

The isopleth diagrams drawn by Beverton and Holt (1957) for North Sea populations of plaice and haddock in a steady state assume that (a) recruitment is independent of the size of the spawning stock (b) the growth pattern conforms to Bertalanffy's equation and (c) that fishing and natural mortalities are continuous and constant for all ages. There are significant seasonal differences in the growth of butter sole even if the growth pattern is described by Bertalanffy's equation. Natural mortality also varies with age. Since the butter sole fishery is highly seasonal, changes in the biomass and yield per recruit with changes in the mortality rates and age of exploitation are estimated in relation to the spawning population on which the fishery exists. With respect to the spawning population, the greatest biomass per recruit is attained at 5.83 years for all the natural mortality rates studied (Figure 36) even if the greatest weight of a year's brood may not be attained at this age (Figure 36A). Since the availability of butter sole to the fishery is highest during the spawning season, the possibility of increasing the yield by moving the fishing season to a period when the weight of stock is greatest is not considered. In addition, this increase in the biomass of a year class above 5.83 years is observed only for the lowest natural mortality rate chosen and even then it is very slight (Figure 36A).

(c) Effects of fluctuating recruitment on the biomass and yield

In the above analysis of the reaction of the butter sole population to varying mortality rates and ages of exploitation it is assumed that the

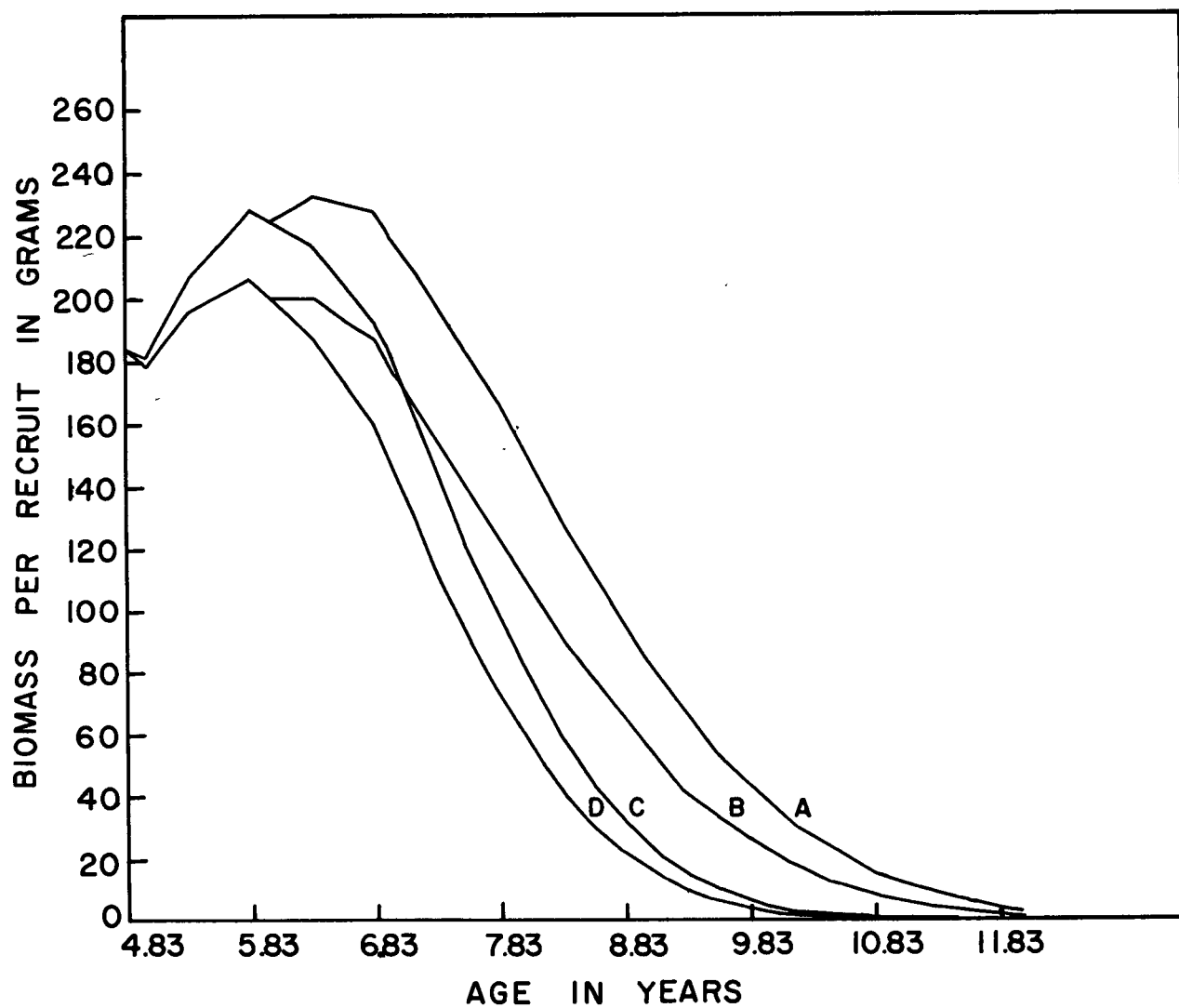


Figure 36. Butter sole: Changes in the biomass per recruit at different ages when no fishing mortality is operating. (A)  $M = 0.1, \Delta M = 0.2$ . (B)  $M = 0.2, \Delta M = 0.2$ . (C)  $M = 0.1, \Delta M = 0.4$ . (D)  $M = 0.2, \Delta M = 0.4$ .

population parameters are constant from year to year. Although the factors controlling fluctuations in the butter sole population are not known, evidence is presented in Section IV which suggests that they are largely determined during the early stages of the life history and that an index of year class strength can be obtained by sampling young butter sole along the Graham Island coast. The results of an analysis of the changes in biomass and yield using an index of abundance based on the yearly landings are presented in Table XLVIII and Figure 37. Since the entering year class is subjected to fluctuations, the age composition also varies from year to year and no relationship between the size of the biomass of the post-recruit phase and yield can be arrived at unless the fluctuations occur in a definite pattern. In Figure 37A the mean biomass for the post-recruit phase during year  $N + 1$  is very close to that of a steady state population, but it resulted in a yield considerably higher than that for the steady state. During the next year both the biomass and yield remain close to the base line. As long as the fishing mortality rate is steady, the effect of different mortality rates on the yield and biomass is very similar. However, this is not the case when the natural mortality rate increases at different rates. A comparison of the Figures 37A and 37C or 37B and 37D shows that fluctuations in the biomass and yield are much greater when the mortality rate increases in steps of 0.4 instead of 0.2 for the fish over six years of age. This is expected since the older year classes now contribute less to the size of the stock and to the yield so that fluctuations of the entering year classes are not as well dampened as before. In general the seven year old fish are best represented in the fishery, followed by six and eight year olds. Changes in the biomass and yield can be traced if an accurate estimate of the year class strength can be obtained. The effect of a change in the age of exploitation ( $T_p$ ) from 5.83 years to 6.33 years is higher when the natural mortality rate

Table XIVIII. Butter sole. The changes in biomass (post-recruit phase) and yield in grams under fluctuating recruitment in six successive years (N to N+5) compared to yield and biomass under steady state conditions. The age of recruitment is 4.83 years. The two sets of natural mortality rates increase in steps of 0.2 and 0.4 respectively at the end of each year beginning from 6 years of age. Fishing mortality operates during the last 0.17 year for each age class.

Natural mort.rate(M)		M = 0.1, $\Delta M = 0.2$ from 6 years								M = 0.1, $\Delta M = 0.4$ from 6 years							
50% retent'n age( $T_p$ )		5.83 years				6.33 years				5.83 years				6.33 years			
Fishing mort.rate(F)		F=0.2		F=0.6		F=0.2		F=0.6		F=0.2		F=0.6		F=0.2		F=0.6	
Age group	Index of abundance	Biomass	Yield	Biomass	Yield	Biomass	Yield	Biomass	Yield	Biomass	Yield	Biomass	Yield	Biomass	Yield	Biomass	Yield
0.83	1.40	892.66	18.66	829.15	50.50	901.51	14.32	832.68	38.85	686.88	12.82	651.90	35.83	684.79	8.40	666.89	23.65
1.83	0.57	801.87	19.08	737.79	50.94	810.50	16.75	760.89	43.48	591.90	12.21	563.61	33.21	597.06	9.67	577.96	27.34
2.83	1.25	896.08	18.59	826.68	49.58	905.83	14.79	852.89	39.54	664.27	11.58	629.10	32.14	670.20	7.72	645.46	21.37
3.83	0.45	903.57	20.57	836.13	54.81	914.56	18.84	866.26	51.33	696.62	12.83	658.03	35.03	704.24	11.09	679.38	30.90
4.83	0.96	995.37	23.78	936.01	64.71	1005.25	20.21	963.21	55.96	825.13	16.87	793.87	46.90	832.26	13.36	813.87	37.77
5.83	1.44		21.92		60.06		16.89		46.67		16.25		45.85		11.29		32.26
6.83	1.42																
7.83	0.73																
8.83	0.20	904.21*	20.30*	840.82*	54.72*	913.60*	16.88*	866.28*	46.05*	703.11*	13.60*	671.52*	37.77*	709.20*	10.18*	688.57*	28.61*
9.83	0.39																
10.83	3.70																
11.83	1.84																

\* The respective biomass and yield per recruit values under steady state.

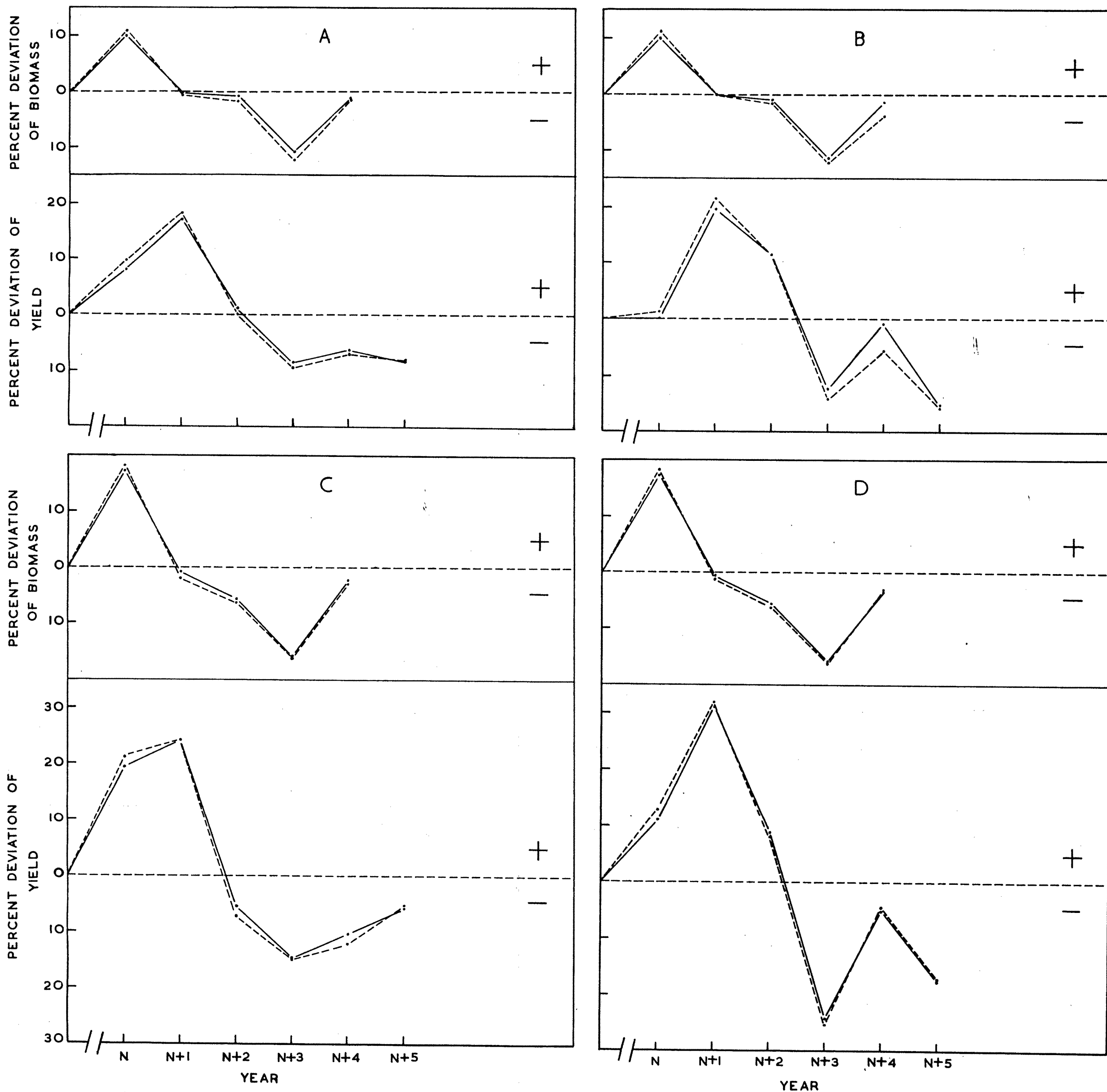


FIGURE 37. BUTTER SOLE: PERCENT DEVIATION IN YIELD AND BIOMASS (POST-RECRUIT PHASE) UNDER FLUCTUATING RECRUITMENT FOR DIFFERENT AGES OF EXPLOITATION AND MORTALITY RATES. (A):  $T_p=5.83$  YEARS,  $M=0.1$ ,  $\Delta M=0.2$ , —  $F=0.2$ , ----  $F=0.6$ . (B):  $T_p=6.33$  YEARS,  $M=0.1$ ,  $\Delta M=0.2$ , —  $F=0.2$ , ----  $F=0.6$ . (C):  $T_p=5.83$  YEARS,  $M=0.1$ ,  $\Delta M=0.4$ , —  $F=0.2$ , ----  $F=0.6$ . (D):  $T_p=6.33$  YEARS,  $M=0.1$ ,  $\Delta M=0.4$ , —  $F=0.2$ , ----  $F=0.6$ .

increases in steps of 0.4 (Figure 37D).

(d) Conclusion

1. The version of Ricker's model that makes use of an exponential average as the weight of stock during time  $t$  is more accurate than the one using the arithmetic mean. Compared to Beverton's model, Ricker's equation is equally accurate for studying changes in the yield and biomass of an exploited population, especially when the variability inherent in the biological data is considered. It is more flexible and easily accommodates seasonal changes in growth and mortality without increasing the complexity of the model.
2. Using Ricker's model changes in the butter sole population and yield are studied for varying mortality rates and age of exploitation. Results are presented in the form of isopleths and equilibrium yield curves. The present study is confined to the spawning season since the fishery depends on the spawning population and the availability of butter sole is not as high at other times.
3. Since fishing is highly seasonal, a change in the natural mortality rate exerts a greater influence on the biomass than a similar change in the fishing mortality rate. An increase in the age of exploitation increases the mean biomass while an increase in the mortality rates decreases it.
4. As the age of recruitment is fairly high the fishing mortality rate that results in maximum yield is higher than 1.8. Hence the yield per recruit contours in the yield isopleth diagram do not have their modes at the fishing intensities examined. Therefore the initial slope of the eumetric fishing curve is absent in the isopleth diagram drawn for the spawning population above 4.83 years.
5. When the strength of the entering year class varies from year to year, the relationship between the size of the biomass and yield is less precise.



Under steady state conditions with a given age of exploitation and given mortality rates, the biomass and yield are always constant. When the natural mortality rate increases in steps of 0.4 instead of 0.2 beyond six years of age the older year classes contribute less to the size of the stock. Consequently, deviations in biomass and yield become more pronounced since the fluctuations of the entering year classes are less dampened by the older age groups of the population.

## VI. Discussion

### 1. Ecology of the butter sole population

Fluctuations in abundance of fish populations are due to variations in the biotic and abiotic factors of the environment. While certain populations are comparatively steady, others, especially the pelagic species such as sardine and mackerel, show extreme fluctuations. Populations often exhibit changes in the reproductive output, growth and mortality rates as a result of such fluctuations. Wynne-Edwards (1962) discusses the self-regulatory mechanisms of populations. He also points out that the homeostatic adaptations of populations are recognized in developing the modern theory of exploitation of fish populations. This is evident both in Russel's (1931) exposition of the idea of rational fishing and in subsequent works by Graham (1935), Schaefer (1954), Beverton and Holt (1957) and others. Despite the various views that exist to explain fluctuations in abundance, this problem can be understood only by studying the ecological life history of the species as outlined by Gill (1910) and recently by Koster (1955).

The butter sole that spawn in Skidegate Inlet are inhabitants of the Hecate Strait flat. Trawling surveys indicate that they are more abundant on the northern part of the bank. There seems to be a latitudinal difference in the depth distribution of the species. Generally, fish of the Hecate Strait population are not found at depths greater than 50 fathoms, although on the Washington and Oregon coast they are found at depths between 55 and 65 fathoms. Examination of the factors limiting their distribution suggests that the population spawning in Skidegate Inlet does not extend its range beyond the Hecate Strait bank either during the larval or adult phases. Analysis of the length composition of butter sole (Tables I-V) in the 1954

and 1961 samples indicates a depth stratification according to size and age groups. The young ones are restricted to the inshore area along the Graham Island coast while the larger and older ones occur progressively farther away from this area. Two factors which tend to obscure this depth distribution pointed out in Section III are: (a) The shallow Hecate Strait bank forms the main summer feeding ground for butter sole. They are found in shallower waters during summer and deeper waters during winter and (b) the change from the 10 to 20 fathom contour is very gradual compared to the gradient between the 20 and 50 fathom contours. Hence the  $\chi^2$  value for 1954 samples lying in this belt (haul-groups III to V) is not significant which suggests no depth stratification of butter sole within this area. However, the length composition in samples collected from areas 1 and 2, especially area 1, consist mainly of young butter sole. A north-south migration is exhibited only by the spawning population. This is shown by the length composition data of butter sole collected from the spawning ground in Skidegate Inlet and from Butterworth ground (Figure 8). Sexual differences in the onset of maturity and spawning migration are evident in the size composition and sex ratio of the spawning population (Tables VI and VII). Similarity in the relative abundance of young butter sole along the Graham Island coast during 1952-1954 and in the success and age composition of the fishery in Skidegate Inlet when these year classes reach an exploitable age (Section IV) suggests that the Graham Island coast is the chief nursery ground for the young butter sole that will later spawn in Skidegate Inlet.

A study of the interspecific association of butter sole and related species of flatfish inhabiting the same general area indicates no strong positive or negative association between these species. Hence no definite conclusion can be made with respect to the degree of inter-specific association

that might exist between these species. No sizable coastal populations which could mix with the Skidegate spawners in their summer feeding ground are known to exist. The analysis of homogeneity of the Hecate Strait population of butter sole (Section III) also does not suggest the possibility of more than one self-contained stock in the area. This aids considerably in the interpretation of growth data of butter sole collected from the Hecate Strait bank.

The growth of butter sole above ~~two~~ years of age is described by Von Bertalanffy's growth curve although seasonal differences in the growth rates are superimposed on it. Males grow slower than females. Growth rates estimated for different year classes indicate annual differences which are partly explained by intra-specific competition. If the initial growth is above or below average, a tendency to compensate for this difference in later years is also observed. Regional difference in the growth rates of butter sole (Table XXVII) and the relative abundance in these areas (Tables III and V) suggest variations in habitat suitability and segregation of the fast and slow growers. Examination of the survival rate indicates a relatively high natural mortality rate that increases with age. It is also found to be higher for the males.

Because the population migrates to Skidegate Inlet for spawning during the winter months their availability to the commercial gear increases sharply during this period, supporting a highly localized and seasonal winter fishery. Butter sole of seven years and above contribute the greater portion of the landings. Hence only a small section of the population is exploited. This is due to two things: (a) they are recruited to the spawning ground relatively late (Tables VI and VII) and (b) the demand for butter sole as food fish compared to related species of flatfish is low,

resulting in considerable secondary selection by the fishermen. Only recently more and more unselected catches have been landed as mink feed and hence the younger fish, particularly the males of less than seven years of age, have been better represented. Landings show considerable fluctuation as a result of changes in demand and fluctuations in the size of the spawning stock. An examination of the relative abundance of young butter sole along the Graham Island coast and the success and age composition of the fishery in Skidegate Inlet six years later indicate that fluctuations in abundance are largely determined during the early period of the life history. Hence estimations of year class strength from samples taken on the Graham Island coast are a reliable index of abundance that can be checked in subsequent years with Hecate Strait samples.

Since the information collected on the ecological life history of the population is limited, only certain general conclusions are drawn from the theoretical study of the changes in biomass and yield with changes in the mortality rates and abundance. Fishing mortality is highly seasonal, hence its effect on the biomass is less noticeable than a change in the natural mortality rate. However, as the vulnerability of butter sole to the gear during the spawning season is high, a heavy fishing mortality could be generated. The equilibrium yield curves and the  $Y_W/R$  contours of the yield isopleth diagrams were without a mode for all the ages of exploitation and mortality rates examined. Figures 33-35 also indicate that when the age of exploitation ( $T_p$ ) is 4.83 years, the maximum equilibrium yield for all natural mortality rates examined can be obtained only with a fishing mortality rate higher than 1.8.

The relationship between the size of the biomass and yield becomes less precise under fluctuating recruitment. A higher rate of increase of the

natural mortality rate for ages above six years causes greater fluctuations in yield and biomass since fluctuations in recruitment are now less dampened by the older year classes. On the other hand, since the fishing mortality rate is constant for all ages, a change in the fishing mortality rate is not accompanied by a similar deviation in the size of biomass and yield.

Biomass per recruit at different ages constantly decreases beyond 5.83 years for all but one set of natural mortality rates (Figure 36). The highest fishing pressure that is economically feasible may therefore be exerted on this section of the population provided the population maintains a steady state. The heavy fishery in 1952 might have affected the poor 1952 year class. However, there is no direct evidence of the effect of fishing on the strength of the year class. Since the fishery is very localized, heavy trawling removes a considerable number of spawners. It may also decrease the suitability of the spawning ground or destroy significant numbers of eggs. However, there are no signs of the population being overfished at present.

The maximum utilization of the existing mesh regulation, i.e. use of 4" mesh cod-end followed by a heavy fishery, would result in greater exploitation of males than females because of the sex composition of the spawning population arising from sexual differences in the recruitment and migratory patterns. This may eventually alter the sex-ratio of the population. However, since males are in milt for a longer time and appear to remain longer on the spawning ground, the effect of greater exploitation may not be serious until the sex-ratio is altered drastically. The male-female ratio of the spawning population is about 5:1 and the possible effect, if any, of greater exploitation of males can be determined only by harvesting the stock. Beverton and Holt (1957) state that male plaice are in milt for a longer time than females so that there may be an excess of ripe males on the spawning

ground even though males are less abundant. They cite Simpson's remark that in plaice the proportion of unfertilized egg is very small.

## 2. Further Studies

Butter sole exhibit sexual differences in growth, mortality rates, recruitment and migratory patterns. The two sexes may, therefore, be treated as a special case of two competing populations exploited simultaneously. Hence a more detailed study requires information on the above characteristics of the population so that the effects of varying degrees of exploitation on the two sexes can be studied separately.

A knowledge of the recruitment pattern is needed for assessing the biomass of the spawning population, in estimating the stock-recruitment relationship and in arriving at the best exploitation level. A rough estimate of the recruitment can be obtained by estimating the per cent males and females in each age class that would mature in the next spawning season from samples taken from Hecate Strait prior to the spawning migration. An alternative procedure would be to obtain natural mortality rates of the population in the pre-recruit phase from age composition data collected by extensive sampling of the nursery ground. If fluctuations in recruitment are not great, then the per cent of the incompletely recruited age classes can be obtained by expressing their numbers on the spawning ground as a per cent of the first fully recruited age group after adjusting for natural mortality. If recruitment varies considerably then their numbers have to be adjusted first by the reciprocal of the index of abundance for each age class. A mean estimate of the per cent recruitment based on many year's data would give a fairly accurate estimate of the recruitment pattern. A third possible method is by comparing directly the estimated numbers of each age class in the nursery and spawning grounds. A comparison of these different estimates would

confirm the accuracy of the estimated recruitment pattern.

Since the fishery depends on the spawning population, subjected to both immigration and emigration, a knowledge of the migratory pattern is required to avoid bias in the estimates of the biomass and fishing mortality of the spawning population. Very little is known of the migratory pattern. Immigration and emigration may both be a continuous process or, depending on the nature of spawning, emigration may begin later after the spawning season is well advanced. An attempt to either tag the population prior to their spawning migration to obtain data on immigration or to tag the spawning population to study the emigration pattern would be an extensive program. This may not be feasible since the fishery is small and its demand relatively low compared to other species. Ketchen (1953) obtained reliable information on the migration of lemon sole using a modified Delury method by plotting catch per unit effort against cumulative catch and recaptured lemon sole. In applying the method to butter sole the migratory pattern of the two sexes have to be studied separately. The average male-female ratio beyond the post-recruit phase as determined from extensive sampling during 1953 is 2:1. Because this ratio is not influenced by the recruitment pattern, this difference is partly due to variation in the migration of the two sexes.

Various methods of estimating fishing and natural mortality rates are reviewed by Beverton and Holt (1956a, 1957) and Ricker (1958). Beverton and Holt (1956a) have indicated that separation of total mortality rate into fishing and natural mortalities often involves the assumption that natural mortality rate is constant for all ages. However, methods involving catch sampling require considerable yearly changes in the fishing intensity which would result in significant variation in the estimates of total mortality rates. The natural mortality rate of butter sole is fairly high and the



fishing mortality operates for only a short period. The demand for the species is also not high. Hence yearly changes in fishing intensity may not be sufficiently reflected in the total mortality to allow their estimation with accuracy. An accurate estimate of the fishing intensity in terms of the actual number of hours fished is also required, especially since the fishery is small. However, the fishing mortality rate can be estimated by tagging. Manzer's (1949) data on the size distribution of tagged and recaptured butter sole suggest that the tagged fish disperse randomly and hence their behaviour may be similar to the untagged fish. During the fishing season large numbers of fish can be tagged in a short time. Since the fishing season is very short, bias from tag loss and tagging mortality will be small. The fishery is restricted to Skidegate Inlet and the number of boats operating at a time are few, so that the failure to report recovered tags should be at a minimum. Estimation of the mortality of the butter sole population from the ratio of the number recaptured during time  $t$  to the number of tagged fish at large at the beginning of time  $t$  would be a reliable estimate of the fishing mortality for the period. Natural mortality during such short intervals may be small and not cause serious errors in the estimate. However, this estimate may be biased due to immigration and emigration. Hence the Delury method, as used by Ketchen (1953) for studying the migratory pattern can also be used. This method would account for immigration, emigration and natural mortality. One requirement in the Delury type analysis, however, is that the catch per unit effort should decline, due to fishing as the season advances. Once the fishing mortality is estimated, natural mortality may be obtained by subtracting the fishing mortality from the total mortality rate. An estimate of the natural mortality may also be obtained from tagging provided tag loss and tagging

mortality are not serious. There were no recoveries from the 550 fish tagged during July 1953 from Hecate Strait flat. It is not known whether this is due to tagging mortality or to the poor fishery during 1954.

As is the case in the estimation of fishing mortality, tagging offers the best method of estimating the biomass of the spawning population. Various methods such as those of Petersen, Schnabel, Delury or Ketchen's modified version of Delury may be used. The first three estimates involve the assumption that the population is closed, i.e. there is no immigration, emigration or natural mortality.

From the estimate of the biomass and age composition of the spawning population an estimate of the number of fully recruited age groups can be made. Since it is found (Section IV) that the abundance of young butter sole along the Graham Island coast may indicate the success of spawning in Skidegate Inlet, an estimate of their number by adequate sampling will also be useful in studying the stock-recruitment relationship and in predicting the success of the fishery. Even though the number of eggs laid during the spawning season can be estimated from the number of spawning females and mean fecundity, information on the early survival rate cannot be obtained easily.

A study of the effect of differential exploitation of the two sexes due to sexual differences in the population characteristics is useful in understanding the dynamics of the stock. Since it is an exploited population the fishing mortality is an important factor in controlling population abundance through changes in the reproductive potential, growth and mortality rates. However, fluctuations in population abundance can be understood only by studying the effect of the environment as a whole on population parameters during the various stages in the life history. Watt (1956), Wicket (1958) and Wynne-Edwards (1962) have reviewed the effect of some of the environmental

factors on population parameters. The growth rate of butter sole is described by Bertalanffy's growth equation despite seasonal variations in growth rate. In his equation,  $K$  or the rate of deceleration in growth increments is proportional to the catabolic rate. Beverton and Holt (1957) suggest that an increase in temperature affects anabolism and catabolism equally, resulting in a higher  $K$  value. The asymptotic weight is influenced by the availability of suitable food. The growth rates of butter sole belonging to a strong brood year are generally slower in the early years due to intraspecific competition although compensation occurs in later years. In addition to the direct effect of a change in growth on the biomass, variations in the growth rate may influence the reproductive potential and natural mortality rate.

Some of the major contributing factors to the natural mortality are deaths due to predation and competition and the scarcity of suitable food. Unfavourable climatic and physico-chemical factors of the environment, especially during certain critical stages in the life history are also important contributing factors. The natural mortality rate is subject to variation depending on the intensity of these and other mortality factors. A number of studies on the fluctuations in fish populations by Hjort (1914, 1926), Sette (1943, 1961), Murphy (1961) and Beverton (1962) have shown that the greatest fluctuations in population abundance are due to changes in survival rates during the early stages of the life history. Analysis of the fluctuations in butter sole also indicates that fluctuations in the year class strength are due to variations in the early survival rates.

### (3) Use of models in studying the butter sole population

Once the population parameters are estimated the understanding of the population dynamics is facilitated by constructing mathematical models of the

population for various situations. The different types of models used in fish population studies can be classified into empirical, deductive or logical, and inductive or analytical. Empirical models, unlike deductive and inductive models, do not assign any biological meaning to their constants. Deductive and inductive models are conceptual models in that, as Pringle (1960) points out, the properties of the system as a whole are assumed to be derived from the properties of certain known parts. Watt (1956) classified the existing models into four groups depending on the extent of information required in each case. The empirical analysis as done by Royce and Schuck (1954) requires data on the effort and catch by age for a series of years. Their methods have some predictive value provided an estimate of the effort for the year concerned can be obtained in advance. As Watt indicated, since the method does not make use of biological informations this model is not useful for studying optimum exploitation. The models developed by Graham (1935), Schaefer (1954) and others, are largely deductive and are based on the logistic theory of population growth for a limited environment. As pointed out by Beverton and Holt (1957) these models assume that population growth in weight follows a symmetrical sigmoid curve which implies that rate of increase is dependent only on the weight of stock present at any one time and hence independent of the age and size composition of the population. Models by Beverton and Holt (1957) and Ricker (1945, 1958) are analytical since the main population parameters are measured and incorporated into the model. The basic difference between these two models, aside from the manner of representing growth pattern, is that, while Ricker divides the entire fishable life span into a series of discrete periods, Beverton and Holt consider the age distribution as continuous and integrate the rate of change of yield in weight between the limits of the fishable life span. Watt (1956,1959)

proposed a model that would also consider the effect of fluctuating environmental factors. Following Andrewartha and Birch (1954) he divides the environment into four main components such as weather, food, other animals and a place to live. The relationship of the net effect from each of these factors on the population parameters such as recruitment, growth and mortality has to be obtained by regression analysis from data collected for a number of years. The biomass of a year class at time  $t$  is then obtained as the product of the estimated number and mean weight and the productivity ( $P$ ) is the difference between the biomass at the beginning and end of time  $t$ . However, his model cannot be applied until a thorough knowledge of the population in relation to its environment is obtained.

Hence, of the existing models, those of Beverton and Holt and Ricker are the most widely used to study fish populations. Moran (1954) has pointed out that they also represent the two types of model studies of populations which involve multiple age classes by treating the age distribution either as continuous or as discrete units.

Ricker divided the fishable life span into a series of discrete periods whose duration could be adjusted to suit the characteristics of the population. Assuming exponential growth and mortality rates within each time interval, the equation for yield in weight developed by him is

$$Y_W = \sum_{t=T_Y}^{t=T_A} F_t \cdot \bar{W}_t \quad \text{where}$$

$t$  = successive time periods,

$T_Y$  = age of first exploitation,

$T_A$  = maximum exploitable age,

$F_t$  = instantaneous fishing mortality rate during time  $t$ ,

$\bar{W}_t$  = average weight of stock during time  $t$ .

Since the model assumes that the weight of stock during time  $t$  changes exponentially, the exact average weight of stock for this period is obtained by integrating the rate of change in stock between the time limits and dividing it by the time interval.

Hence

$$\bar{W}_t = \frac{\int_{t_0}^{t_1} w_0 e^{(q_t - z_t)t} dt}{t_1 - t_0}$$

or in its integrated form

$$\bar{W}_t = \frac{w_{t_0} (e^{q_t - z_t} - 1)}{\Delta t \cdot (q_t - z_t)}$$

A second, less accurate, method of determining the average weight of stock during time  $t$  is to take the arithmetic mean of the standing crop at the beginning and end of time  $t$ , i.e.,

$$\bar{W}_t = \frac{w_{t_0} + w_{t_0} e^{(q_t - z_t)}}{2}$$

In Beverton's model where the growth pattern is considered to follow Bertalanffy's equation, the rate of change of yield in weight is integrated between the limits of the fishable life span ( $T_A - T_{P'}$ ) for a continuous age distribution, i.e.,

$$Y_W = F \int_{T_{P'}}^{T_A} N_t w_t dt$$

where

$F$  = instantaneous fishing mortality rate,

$N_t$  = number at time  $t$ ,

$W_t$  = weight at time  $t$ .

The equation for yield in weight ( $Y_w$ ) developed by him for a continuous fishery is:

$$Y_w = FR'W_{\infty} \sum_{n=0}^3 \frac{n e^{-nK(T_p - T_0)}}{F + M + nK} \left[ 1 - e^{-(F+M+nK)(T_{\lambda} - T_p)} \right]$$

where

$T_0$  = theoretical age at which fish is of zero length had it been growing according to Bertalanffy's growth equation throughout its life,

$T_p$  = first age of full exploitation\*,

$T_{\lambda}$  = maximum exploitable age,

$K$  = the rate of deceleration in growth increments in Bertalanffy's growth equation,

$n$  = the exponential value in the equation describing the length-weight relationship,

$F$  = instantaneous fishing mortality rate,

$M$  = instantaneous natural mortality rate,

$R'$  = number of recruits ( $R$ ) of the age at which fish become fully exploitable,

and  $W_{\infty}$  = the average maximum attainable weight as determined by Bertalanffy's growth equation.

Since Ricker's equation divides the fishable life span into a series of time periods, population parameters such as growth and mortality rates can vary for each time interval. As he assumes exponential growth and mortality rates during time  $t$ , changes in these parameters with respect to season or age can be easily introduced into the model. Vital statistics of different age groups at different times and conditions, may be estimated from the relationships expressing the effects of density dependent and independent factors on population parameters. These relationships need not directly

\*The authors have shown that this age corresponds approximately to the age of 50% retention by the gear provided the age of recruitment is below the selection range of the gear.

enter the yield equation and hence the simplicity of the original equation can be retained. In Section V, an index of abundance for the entering year class is used to study the effect of varying recruitment on the yield and biomass of butter sole. Hence, in this case, the yield from a year class is given by the equation

$$Y_w = \sum_{t=T_y}^{t=T_A} F_t (\bar{W}_t \cdot I_A) \quad \text{where}$$

$I_A$  = the index of abundance for the respective year class in the population

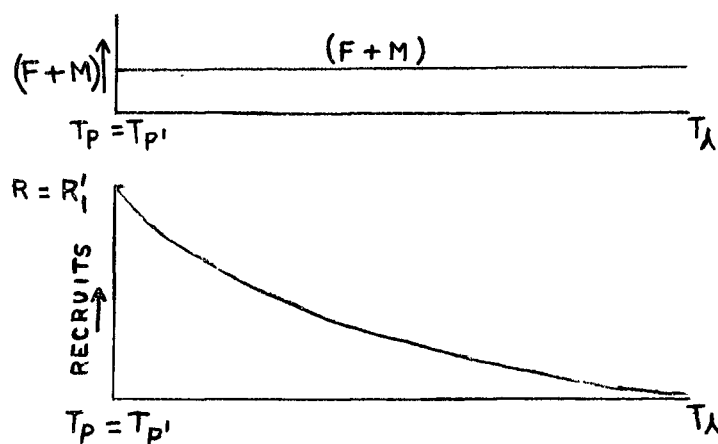
and

$\bar{W}_t$  = the average weight of a normal year class at time  $t$ . Although the factors responsible for variation in recruitment were not understood, it was found (Section IV) that an index of the abundance of year classes could be estimated for butter sole. If recruitment is the only factor subject to variation then, for any year, yield and biomass can be calculated by multiplying the average weight and yield of each age group comprising the population in a steady state by the appropriate index of year class strength. If fishing intensity varies annually, or if growth and natural mortality are not steady within each age group, then the biomass and yield from each year class in the population is calculated separately.

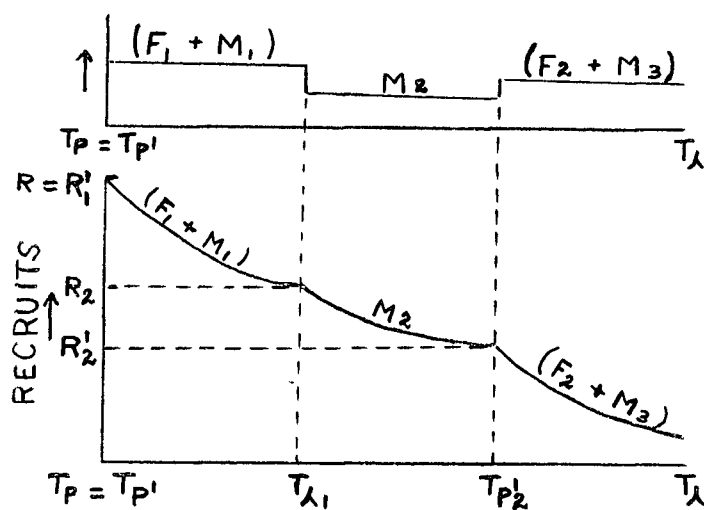
Relationships expressing variations in population parameters enter directly in Beverton's model. To avoid undue complexities, Beverton and Holt consider the effects of variations in population parameters such as recruitment, growth and mortality with respect to age, time and density taking one parameter at a time. The modifications involved in applying Beverton's model to a seasonal fishery may be illustrated as follows. In Beverton's simple yield equation for a continuous fishery, the change in the



number of recruits with respect to  $F$  and  $M$  during the exploitable phase is given by



If the mortality rates are not constant within the exploitable phase, the change in the number of recruits with respect to  $F$  and  $M$  may be shown graphically as



Since  $F$  and  $M$  are not constant, the number of recruits at the beginning of each fishing season has to be estimated before obtaining the yield per recruit for each period. The yield for the first period is given by

$$Y_{W1} = F_1 W_{\infty} R'_1 \sum_{n=0}^3 \frac{n e^{-nK(T_{P1}' - T_0)}}{F_1 + M_1 + nK} \left[ 1 - e^{-(F_1 + M_1 + nK)(T_{A1} - T_{P1}')} \right]$$

To obtain the yield for the second period the number of recruits at the beginning of the second fishing season is calculated as follows. The number of recruits at the end of the first fishing season is

$$R_2 = R'_1 e^{-(F_1 + M_1)(T_{A1} - T_{P1}')}$$

The number of recruits at the beginning of the second fishing season is

$$R'_2 = R'_1 e^{-(F_1 + M_1)(T_{A1} - T_{P1}')} \cdot e^{-M_2(T_{P2}' - T_{A1})}$$

Inserting  $R'_2$  in the yield equation, the yield from the year class for the second fishing season is given by

$$Y_{W2} = F_2 W_{\infty} R'_1 e^{-(F_1 + M_1)(T_{A1} - T_{P1}')} \cdot e^{-M_2(T_{P2}' - T_{A1})} \sum_{n=0}^3 \frac{n e^{-nK(T_{P2}' - T_0)}}{F_2 + M_3 + nK} \left[ 1 - e^{-(F_2 + M_3 + nK)(T_{A2} - T_{P2}')} \right]$$

$(Y_{W1} + Y_{W2})$  is the total contribution from the year class for the exploitable phase. Hence the yield per recruit is obtained by dividing the total yield by the number of recruits at the beginning of the first season, i.e.

$$\frac{Y_W}{R'_1} = \frac{(Y_{W1} + Y_{W2})}{R'_1}$$

If the rate of deceleration in growth increments is different for the two fishing seasons, then the appropriate  $K$  values are used in the equation to obtain the yield during the two periods. The general form of the equation when  $K$ ,  $M$  and/or  $F$  varies within the exploitable phase may be written as

$$\frac{Y_W}{R} = W_\infty \sum_{j=1}^m F_j I_j \left\{ \sum_{n=0}^3 \frac{\gamma_n e^{-nK(T_j - T_0)}}{F_j + M_j + nK} \left[ 1 - e^{-(F_j + M_j + nK)(T_{j+1} - T_j)} \right] \right\}$$

where

$$I_j = \prod_{\ell=1}^{j-1} e^{-(F_\ell + M_\ell)(T_\ell - T_{\ell-1})} \quad \text{for } j \geq 2,$$

$I_j = 1.0$  where  $j = 1$  and  $j$  ranges from 1, 2, 3, .....,  $m$  since the post-recruit phase is divided into  $m$  equal or unequal intervals of any duration each expressed as a fraction of one year.

In the modified Beverton's equation given above, there is an abrupt change in the mortality rate at the end of each time interval. However, by setting the time interval sufficiently short, the model can be used, without losing accuracy, to obtain yield irrespective of the manner in which the mortality factors vary with age or season. Therefore the equations describing these relationships do not enter the model as such. The growth pattern within the exploitable phase may possess one or more stanzas due to physiological or environmental changes, each described by Bertalanffy's growth equation. Beverton and Holt (1957) have indicated that a change in temperature changes the metabolic rate which in turn may alter the rate of deceleration in growth increments ( $K$ ) keeping  $T_0$  and  $W_\infty$  constant. If the availability of food varies, the asymptotic weight also will be influenced. For such cases the equation 9.11 of Beverton and Holt gives the yield for a continuous fishery. If there is a change in  $T_0$  and  $W_\infty$  associated with a change in  $K$  then the equation for yield given above for a seasonal fishery becomes

$$\frac{Y_W}{R} = W_\infty \sum_{j=1}^t F_j I_j \left[ \sum_{n=0}^{\infty} \frac{-\frac{1}{n} e^{-n K_1 (T_j - T_0)}}{F_j + M_j + n K_1} \left\{ 1 - e^{-(F_j + M_j + n K_1)(T_{j+1} - T_j)} \right\} \right] +$$

$$2 W_\infty \sum_{j=t+1}^{\infty} F_j I_j \left[ \sum_{n=0}^{\infty} \frac{-\frac{1}{n} e^{-n K_2 (T_j - T_0)}}{F_j + M_j + n K_2} \left\{ 1 - e^{-(F_j + M_j + n K_2)(T_{j+1} - T_j)} \right\} \right]$$

To sum up, the modifications in Beverton's model involve an estimation of the number of recruits at the beginning of each fishing season. The mortality factors are considered to be constant within each time period and the rate of change of yield in weight is integrated between the limits of each season. The growth pattern is assumed to be described by Bertalanffy's growth equation. The individual fish is also assumed to grow isometrically and hence the exponential value in the equation describing the length-weight relationship is taken to be three.

The yield per recruit estimates obtained from Beverton's and Ricker's models (Section V) were almost identical under all conditions of growth and mortality rates provided the mean standing crop during time  $t$  used in Ricker's equation was the exponential average. Use of the arithmetic mean of biomass implies that the biomass is a linear function of time. As the model assumes exponential growth and mortality rates within each time interval, the arithmetic mean is a less accurate estimate than the exponential average, the magnitude of error depending on the steepness of the exponential curve describing the change in the biomass during time  $t$ . Similarly it is also found that, if the weight of stock is on the average decreasing, then the use of an arithmetic mean overestimates the yield or, if the stock is increasing, then it may, depending on the curve describing the change in biomass, underestimate the yield. Hence, above the optimum  $T_p$ , since the stock is decreasing, the  $Y_W/R$  estimates from Ricker's model using an arithmetic mean

would always be an over-estimate compared to Beverton. Even though the mathematical treatment in Beverton's model is more elegant, the results obtained using his model need not be more accurate. In Beverton's model the growth pattern of the fish is described by Bertalanffy's growth equation. However, seasonal differences in growth are often superimposed on it. These authors have pointed out that if fishing is not continuous then the seasonal differences in growth have also to be taken into account. Considering the flexibility of Ricker's model in accomodating changes in growth, recruitment and mortality rates, this model, using the exponential average for the mean weight of stock during time  $t$ , is preferred for studying the butter sole population.

## VII. Summary

### Aspects of the life history of butter sole

1. The butter sole population spawning in Skidegate Inlet does not extend its range beyond the Hecate Strait bank because of the physical conditions of the area and the presence of a depth barrier. The possible role of temperature and low oxygen content of deep waters as limiting factors affecting distribution is indicated.
2. The species seem to exhibit a latitudinal difference in depth distribution. While no butter sole from the Hecate Strait population were found at depths greater than 50 fathoms, along the United States coast they were caught at depths between 55 and 65 fathoms.
3. The size composition of butter sole in the samples from Hecate Strait suggested a depth stratification. Young butter sole were restricted to the inshore area along the Graham Island coast while the larger and older ones were caught farther offshore.
4. In summer the population migrates to the shallow Hecate Strait bank while in winter it occupies deeper waters.
5. The spawning members of the population exhibit a north-south migration from the Hecate Strait bank to Skidegate Inlet during winter months.
6. Sexual difference in the onset of maturity and migratory pattern influence the sex ratio of the spawning population.
7. Rank correlation analysis did not suggest any inter-specific association between butter sole and related species of flatfish during the post-pelagic phase.
8. Movements, factors limiting distribution and a comparison of the meristic counts of butter sole taken from different areas favour the theory that the Hecate Strait population of butter sole is a single self-contained stock.

9. The body length-otolith radius relationship was found to be linear. The relationship for the two sexes was described by the equation,

$$\text{Male: Length(cms.)} = 0.7944R - 0.70$$

$$\text{Female: Length(cms.)} = 0.09 + 0.7594R$$

10. The otolith zones were laid down annually and were found to be reliable indicators of age.

11. Growth of butter sole beyond two years of age was described adequately by Bertalanffy's growth curve. The asymptotic length ( $L_{\infty}$ ) and the rate of deceleration in growth increments (K) for the two sexes from the Wal-ford plot were:

$$\text{Male: } L_{\infty} = 36.64 \text{ cms. } K = 0.2814$$

$$\text{Female: } L_{\infty} = 41.71 \text{ cms. } K = 0.2437$$

12. Annual differences in growth rate are partly due to intra-specific competition. The population shows a tendency to compensate in later years for any initial differences from the average growth pattern.

13. Butter sole of age 1+ and 2+ seem to complete a greater portion of the year's growth by the end of July while roughly 50 per cent of the year's growth is completed at this time by fish of age 3+ and above. More extensive study on the seasonal differences in growth is necessary.

14. Regional differences in the growth and density of the Hecate Strait population suggest variation in habitat suitability and a tendency of fast and slow growers to segregate.

15. Males were found to grow slower than females.

16. Length-weight relationships for the two sexes based on ungutted specimens were:

$$\text{Male (summer) : weight (gms.)} = 0.009260L(\text{cms.})^{3.023}$$

$$\text{Male (winter) : weight (gms.)} = 0.007236L(\text{cms.})^{3.103}$$

$$\text{Female(summer)} : \text{weight(gms.)} = 0.007344L(\text{cms.})^{3.094}$$

$$\text{Female(winter)} : \text{weight(gms.)} = 0.027896L(\text{cms.})^{2.746}$$

17. The natural mortality rate beyond seven years of age was relatively high and increased with age. It was also higher for the males.

#### Fluctuations in abundance of the butter sole population

18. The 50% retention length of the 5.2" cod-end mesh as estimated from the mesh selection experiment was 31.5 cms. with a sigma (6) value, measuring the spread of the selection curve, of 1.04 cms. The reliability of this estimate was verified by comparing the internal perimeter of the cod-end and the girth of the fish corresponding to the 50% release length based on length-girth relationship. The two estimates were nearly identical.

19. The calculated length-girth relationship of butter sole was

$$\text{girth(cms.)} = 0.9846L(\text{cms.}) - 3.409$$

20. The small and highly localized fishery during the winter months depends on the spawning population migrating to Skidegate Inlet. Butter sole is landed both as mink feed and as food fish. Because of the relatively low demand, food fish landings are subjected to secondary selection by fishermen, to meet the market demands.

21. Catch figures show considerable annual variations due to changes in the demand for mink feed and food fish as well as the availability and abundance of butter sole.

22. Catch per unit effort was estimated after standardizing the effort to determine whether it would provide a suitable index of abundance.

23. The estimated relationship of fishing power to tonnage for vessels equipped with 'double' gear was

$$\sqrt{\text{Fishing power}} = 0.7820 + 0.0085 \text{ Tonnage.}$$



The considerable scatter in the estimates of fishing power was partly due to differences in age of vessels and ability of skippers and partly due to the distribution, density and migratory patterns of the butter sole.

24. Due to lack of adequate data the above relationship was not used in estimating the catch per unit effort. Since the majority of vessels belonged to the 30-59 tonnage class the catch per unit effort was obtained from the catch and effort data of vessels within this range. The efficiency of vessels using single gear compared to those equipped with double gear was estimated by taking catch per day as one unit. The fishing power of single gear compared to double gear was found to be 0.8955. Analysis of variance of the fishing power of vessels in the 30-39, 40-49 and 50-59 tonnage classes shows no significant difference. Therefore in standardizing fishing effort the only adjustments made were for vessels equipped with single gear.

25. The estimated catch per unit effort was not found to be a sensitive index of abundance. This may be due to several reasons, including the small number of boats in the fishery and the division of the effort into food and mink feed categories. In poor years, fishing may be restricted to the period of highest density. In addition, catch per day may not be as sensitive a unit as catch per hour, but the latter could not be calculated for lack of data.

26. Study of the relative abundance of young butter sole, lemon sole and sand sole along the Graham Island coast in the samples collected during 1952-1954, indicated that butter sole was less abundant in 1953 than in 1952 and 1954. Their abundance was partly reflected in the age composition and success of the fishery when the young butter sole in the 1952-1954 samples became fully exploitable, suggesting that fluctuations in abundance were large due to variations in early survival rate. The usefulness of the year class strength of young butter sole in samples from the Graham Island coast as an index of

abundance was also suggested.

#### Theoretical yield studies of the butter sole population

27. The magnitude of error involved in using Beverton's or Ricker's model was first examined. Ricker's model assumes exponential growth and mortality rates. Hence the use of an arithmetic mean for the average weight of stock during time  $t$  in his equation introduces an error and results in an over-estimation of the  $Y_W/R$ . The magnitude of error is dependent on the steepness of the curve describing the change in biomass during time  $t$ . Consequently the per cent deviation in the  $Y_W/R$  estimates increases with increase in age of exploitation, mortality rates and rate of deceleration in growth increments.

28. When the arithmetic mean is used the  $Y_W/R$  values from Ricker, compared to those of Beverton, are either over or under-estimates, depending on whether the stock is decreasing or increasing. Above the age of optimum exploitation the stock is decreasing, and the  $Y_W/R$  values, obtained from Ricker's model are always over-estimates.

29. The  $Y_W/R$  estimate from Ricker, using an exponential average, is very slightly less than that of Beverton. However, this difference in the two estimates is greatest at the youngest age of exploitation and decreased with increase in age of exploitation. This difference is largely due to the manner of depicting the growth pattern by the two models.

30. The modified Beverton's equation for a seasonal fishery can accommodate changes in the natural and fishing mortality and in  $K$ , the rate of deceleration in growth increments.

31. In nature, since seasonal differences in growth are superimposed on Bertalanffy's growth curve, the  $Y_W/R$  estimates from Beverton's model need not be more accurate than those of Ricker.

32. Ricker's model can easily be applied to populations when the parameters

vary with age, season or when the fish do not grow isometrically.

33. The information collected on the population characteristics of butter sole was not extensive. Hence only general conclusions were drawn from the theoretical study of the butter sole population. Since the fishing mortality was highly seasonal its effect on the population biomass and yield was less than that of the natural mortality rate.

34. Yield isopleth diagrams and equilibrium yield curves were devoid of a mode and indicated that the maximum equilibrium yield when the age of exploitation was 4.83 years would be obtained only when the fishing mortality rate was higher than 1.8.

35. Under fluctuating recruitment the relationship between biomass and yield is less precise. In the present study the natural mortality was increased in steps beyond six years of age. This is in contrast to the fishing mortality rate which was constant for all ages above the full retention point of the gear. The fluctuations in yield and biomass were considerably greater when the natural mortality rate was increased in steps of 0.4 rather than 0.2. This is because fluctuations in the entering year class were less affected by the older year classes in the fishery. In comparison, an increase in the fishing mortality rate did not result in any appreciable change in the fluctuations of the yield and biomass.

36. There are sexual differences in the population parameters, and the recruitment and migratory patterns. Hence it is suggested that the two sexes be treated separately in any further study of the population.

# VIII Literature cited

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Appendix I. Size composition of butter sole in hauls of cod-ends with different mesh size taken during February 1961 from Skidegate Inlet.

Length group (cms.)	Cod end mesh size			
	1.5"	3.4"	3.5"	5.2"
13	1			
14	5			
15	7			
16	9			
17	12			
18	10			
19	8			
20	2			
21	1			
22	11	9		
23	3	11		
24	3	12	4	
25	10	57	11	
26	15	39	15	1
27	12	69	14	1
28	11	36	10	1
29	11	34	9	1
30	14	38	19	2
31	37	42	21	11
32	34	76	40	17
33	30	60	32	29
34	24	62	30	12
35	16	23	21	9
36	12	26	9	5
37	4	14	6	3
38	3	5	2	2
39	1	3	2	0
40	0	0	1	1
Total	306	616	246	95

Appendix II. Butter sole of age seven years and above in the commercial sample from Skidegate Inlet taken during 1951, 1954, 1955 and during the trawl survey in 1953, used to estimate the total mortality rates.

Age	Male			
	1951	1953	1954	1955
7	328	902	97	211
8	106	365	15	46
9	17	109	3	8
10	3	14	0	1

Age	Female			
	1951	1953	1954	1955
7	482	369	85	238
8	241	198	53	90
9	78	61	10	22
10	11	7	0	6