

INTERNATIONAL PACIFIC HALIBUT COMMISSION

**ESTABLISHED BY A CONVENTION BETWEEN
CANADA AND THE UNITED STATES OF AMERICA**

Scientific Report No. 66

**Relation Of Fecundity To Long-Term Changes
In Growth, Abundance and Recruitment**

by

Cyreis C. Schmitt

and

Bernard E. Skud

SEATTLE, WASHINGTON

1978

The International Pacific Halibut Commission has three publications: Annual Reports, Scientific Reports, and Technical Reports. Until 1969, only one series was published. The numbering of the original series has been continued with the Scientific Reports.

Commissioners

NEILS M. EVENS	FRANCIS W. MILLERD
WILLIAM S. GILBERT	ROBERT W. SCHONING
CLIFFORD R. LEVELTON	PETER C. WALLIN

Director

BERNARD EINAR SKUD

INTERNATIONAL PACIFIC HALIBUT COMMISSION
P.O. Box 5009, UNIVERSITY STATION
SEATTLE, WASHINGTON 98105, U.S.A.

Relation Of Fecundity To Long-Term Changes In Growth, Abundance and Recruitment

by
Cyreis C. Schmitt
and
Bernard E. Skud

Contents

Abstract	4
Introduction	5
Fecundity	6
Fecundity-At-Age	7
Fecundity-At-Size	8
Maturity	11
Population Fecundity	12
Relation to Spawning Stock	12
Relation to Recruitment	14
Discussion	17
Summary and Conclusions	19
Dedication and Acknowledgments	20
Literature Cited	21
Appendix I. Treatment of Ovaries	25
Appendix II. Fecundity of Left and Right Ovaries	27
Appendix III. Fecundity and Ovary Weight	28
Appendix IV. Comparisons among Spawning Grounds	30

ABSTRACT

Abundance of Pacific halibut (*Hippoglossus stenolepis*) as indicated by cohort analysis, has declined since the 1940's. This decline has been accompanied by a compensatory increase in the rate of growth. To determine whether this change in growth rate has affected fecundity and age of maturity, we compared estimates from data collected in the 1920's and 1970's. The results show that the relationships between fecundity and length and weight have changed only slightly, but the fecundity of fish at the same age in the 1970's was more than twice that in the 1920's. Further, the age of 50% maturity of females in Area 3 apparently has decreased from 12 to 11 years since the 1950's. A decrease also occurred in Area 2 but was less than half a year.

The changes in growth rate, fecundity and age of maturity evidently are in response to the decline in abundance. Population fecundity increased consistently from 1935 to 1955, but declined thereafter and was as low in the 1970's as it was in 1935; whereas the abundance of juveniles has declined since the 1940's. These trends indicate that factors other than population fecundity, possibly viability of eggs or survival of larvae and juveniles, are affecting abundance. Recruitment was inversely related to population fecundity before 1955, but paralleled it thereafter, possibly an indication of a density-dependent relation. Changes in the growth rate indicate that food is a limiting factor and that abundance, more so than biomass, determines the availability of food. Changes in the abundance of halibut and the competition for food are suggested as the causes for the perpetual increase in growth.

Relation Of Fecundity To Long-Term Changes In Growth, Abundance and Recruitment

by

Cyreis C. Schmitt

and

Bernard E. Skud

INTRODUCTION

Fecundity has been estimated for many species, but data spanning more than fifty years and including information on growth and abundance are rarely available. Fecundity of Pacific halibut (*Hippoglossus stenolepis*) was estimated from ovaries collected in 1915, 1927, and 1973. Thompson (1917) indicated that fecundity increased with size, but he did not examine the relationship of fecundity to age. Kolloen (Ms)¹ extended Thompson's work and described the increase in fecundity with fish length, weight, and age in the 1920's. Since the 1940's, the abundance in numbers of halibut has declined (Hoag and McNaughton 1978) and the growth rate has increased markedly (IPHC 1954; Southward 1967; Bell and St-Pierre 1970). Our study was undertaken in 1973 to determine whether fecundity has increased with growth and whether the age or size of maturity has changed.

Generally, fecundity of fishes increases with an increase in growth rate. For example, Le Cren (1958), de Veen (1970 and 1976), and Martin (1966 and 1970) reported that an increase in growth rate was accompanied by an increase in fecundity of perch (*Perca fluviatilis* L.), sole (*Solea solea* L.), and lake trout (*Salvelinus namaycush*), respectively. Bagenal (1966) concluded that populations of faster-growing plaice (*Pleuronectes platessa* L.) produced more eggs. The relationship between maturity and growth rate is more complex than that between fecundity and growth. Many authors (Alm 1959; Woodhead 1960; Nikolskii 1969; and others) have indicated that early maturity generally is associated with a faster growth rate. However, Martin (1966 and 1970) indicated that the age of maturity for trout was later and the size at maturity was larger following an increase in growth rate. After nearly 80 years in which the relationship between length and maturity of sole remained constant, de Veen (1970 and 1976) reported that growth rate and fecundity increased; however, a corresponding increase in size at maturity was not observed until 5 years later, and the age of maturity did not change. Le Cren (1958) stated that maturity of perch was associated with both size and age and its relationship to growth rate was obscure.

Apparently, the relationship between fecundity and stock abundance differs among species. Bagenal (1966 and 1973), Kipling and Frost (1969), and Nikolskii (1969) suggested that fecundity could act as a density-dependent mechanism in the regulation of population size; whereas de Veen (1976) and Le Cren (1958) indicated

¹ "Egg production in the Pacific halibut (*Hippoglossus hippoglossus*) correlated with length, weight, and age" by Lawrence N. Kolloen, Master of Science Thesis, University of Washington, Seattle, 1934, 115 p.

that no direct correlation was evident between stock abundance and fecundity of sole and perch, respectively. Several authors have examined the relation of stock size to recruitment of halibut. Thompson and Bell (1934) and Thompson and Van Cleve (1936) suggested that the number of mature halibut affects recruitment of young into the fishery; whereas Fukuda (1962) and Cushing (1971) indicated that recruitment was independent of stock size.

The purposes of this study were to estimate the age and size of maturity in 1973; to compare these data with those from 1915 and 1927; and to determine the relationships among fecundity, length, weight, and age. We utilized trends in growth, fecundity, maturity, and abundance since the 1930's to examine the relation of total egg production to resulting recruitment. Detailed descriptions of the treatments of samples and preliminary analyses of fecundity data that are not germane to the discussion of changes in fecundity relationships are presented in the appendices. The locations of spawning grounds and the regulatory areas referenced in this report are depicted in Figure 1.

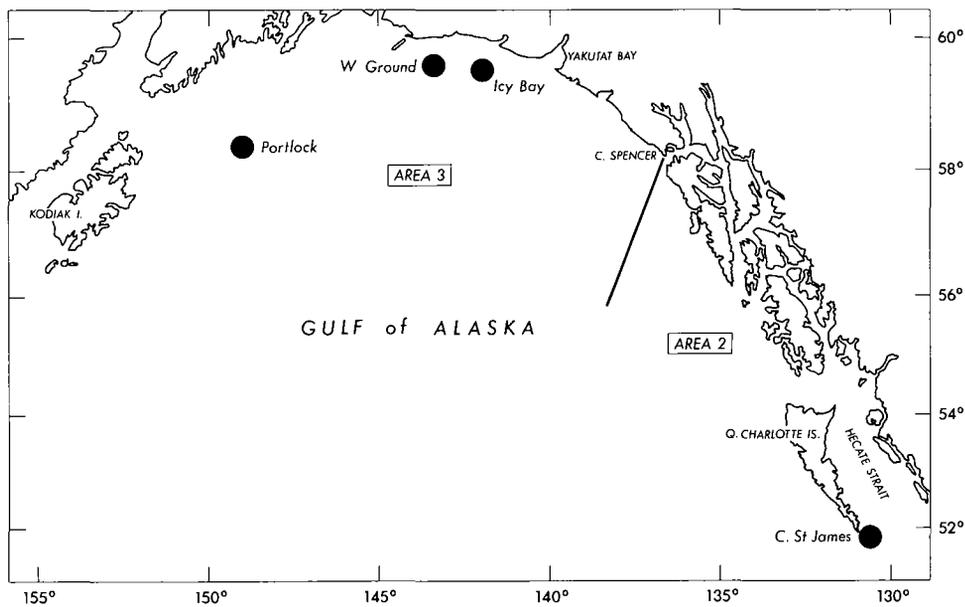


Figure 1. Sampling locations and regulatory areas.

FECUNDITY

Thompson (1915) examined ovaries of Pacific halibut collected throughout the year and concluded that spawning occurred from the middle of December to the middle of May. He and Kolloen (op. cit.) also described egg development within the ovary and reported that spawning by each female could last for several months. Ovaries for estimating fecundity were collected during November and early December, immediately prior to spawning.

Fecundity was estimated for females caught off Icy Bay in 1915, on Portlock and "W" Grounds in 1927, and "W" Grounds and Cape St. James in 1973. The

treatment of ovaries differed in each of the years and is described in Appendix I. As shown in Appendix II, the number of eggs in the left ovary often was greater than the number of eggs in the corresponding right ovary. Because relatively few counts were made from right ovaries, all fecundity estimates were calculated by doubling the number of eggs in the left ovary. As a result, fecundity is overestimated, but the difference is small and the comparability among samples is maintained.

Thompson (1917) indicated that fecundity increased with size for 12 females collected off Icy Bay, Alaska in 1915. He recorded standard lengths and collected otoliths for age determination. However, he could not assess the effect of age independently of size because the number of samples was small. Thompson did not determine fecundity relationships, but his data were incorporated in Kolloen's analyses.

Kolloen (op. cit.) studied the relation of fecundity to fish length, weight, and age from ovaries that had been collected during the winter of 1927. His analyses were based on 60 mature females, 40 from Portlock Bank in November and 20 from "W" Grounds in December. The data included fork length, gross weight (eviscerated, head-on), ovary weight and age of the fish. To ensure that females had not already spawned, he excluded all ovaries containing translucent eggs (see Appendix I). Generally, the number of eggs produced (F) increased with the length (L), weight (W), and age (A) of the fish, and Kolloen defined these relationships by the method of least squares: $F=0.5183 L^{3.627}$, $F=6.189 W^{1.175}$, and $F=292.37 A^{2.484}$. His analyses included the data from Thompson's study. (Apparently, Kolloen was unaware that Thompson measured standard lengths rather than fork lengths, thereby introducing an error.) Kolloen noted a large variation in the egg counts for fish of the same age, and the relation between fecundity and age was more variable than for length or weight. To reduce the variability, Kolloen averaged fecundity estimates for each two years of age. From these averages, he concluded that the relationship between fecundity and age could be expressed by a straight line and estimated that $F=115,814 A - 1,031,115$. However, we considered the power function more definitive and used it in our comparisons. As shown in Appendix IV, the fecundity relationships at Portlock Bank and "W" Grounds were not significantly different and, thus, the 1927 data were combined for comparison with data collected in 1973.

The relationships between fecundity and length, weight, and age were estimated from ovaries collected in 1973 from 27 females taken off Cape St. James in November and from 29 females at "W" Grounds in early December. Fork length, gross weight, and ovary weight were recorded. Otoliths were collected for subsequent age determination. The fecundity relationships among spawning grounds differed (Appendix IV), and therefore, only data from "W" Grounds are compared with 1927 data.

Fecundity-At-Age

Comparability of age readings is critical to a comparison of fecundity-age relationships. Otoliths collected for the fecundity study in 1927 were available for reexamination. The ages were redetermined and did not differ significantly from the original 1927 age readings (paired *t* test). The otoliths from the 12 females in Thompson's 1915 data were not available, but ages were redetermined for 437 other otoliths he had aged. Results of a paired *t* test indicated that the two readings were significantly different at the 5% level; hence, his age readings

for the 12 females were not considered comparable to the 1927 and 1973 data and were excluded from our analysis.

The 1927 and 1973 data on fecundity and age were transformed to logarithms and compared by analysis of covariance.² The slopes of the regression lines for transformed data were not significantly different, but the intercepts were different at the 1% level. The equations, assuming common slope, are presented in Figure 2. Fecundity-at-age has more than doubled since the 1920's. For example, an average 12-year-old in 1927 produced about 330,000 eggs; whereas a 12-year-old in 1973 produced 740,000 eggs, an increase of 124%.

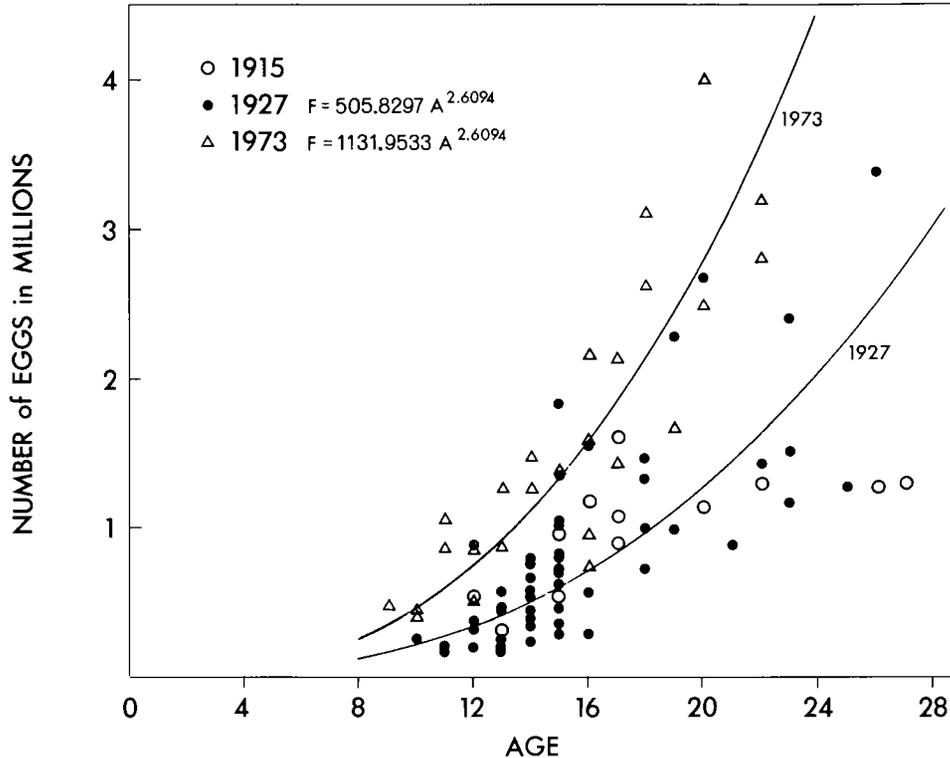


Figure 2. Fecundity-age relationship in 1927 and 1973, Area 3. The data from 1915 are presented for comparison.

Fecundity-At-Size

In Area 3, the mean length and weight of halibut increased markedly for all ages from the early 1920's until 1964, and in Area 2, the increase occurred after 1950 (Southward 1967). Recent data from commercial landings show that mean weight-at-age of halibut declined somewhat during the late 1960's but continued to increase thereafter. The increase is shown by the mean length-at-age of females from "W" Grounds in December, 1927 and 1973 (Figure 3). The mean lengths for ages 12 through 16 were converted to gross weights from a length-weight table and the percentage increase in weight since 1927 was calculated for each age. The increase ranged from 114% to 136% and averaged 124%, comparable to the increase in fecundity-at-age.

² We used BMD3R4V, combined regression and covariance analysis, which tests for both common slopes and intercepts. Dixon (1970).

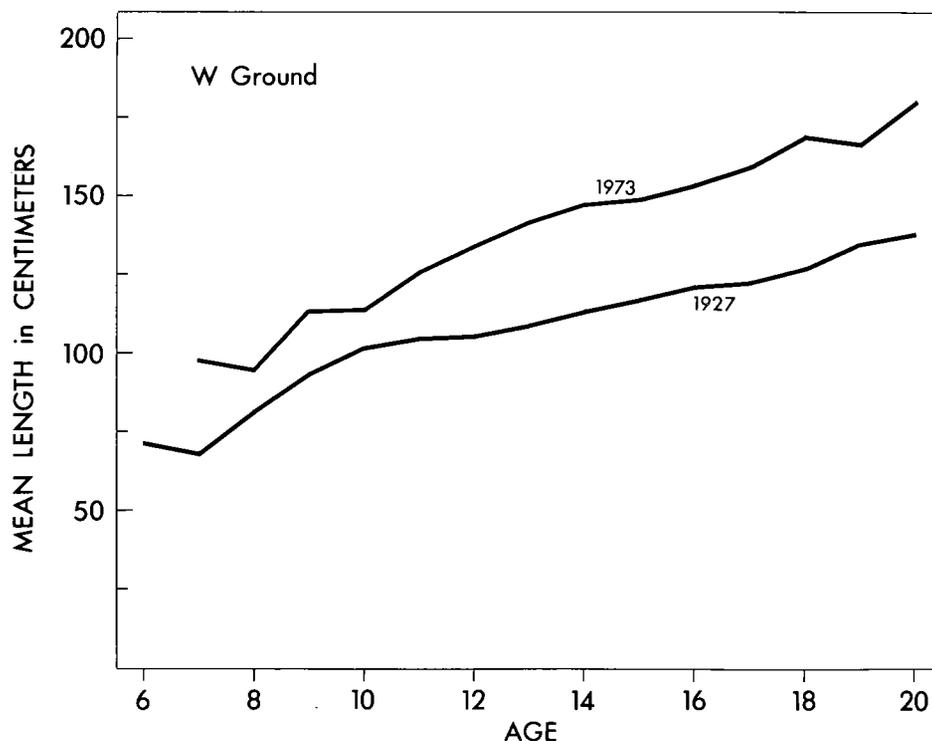


Figure 3. Mean length-at-age of females in 1927 and 1973, "W" Ground.

During the past fifty years, the relationships between fecundity and length and weight have changed only slightly compared to the marked increases in fecundity-at-age and size-at-age. Analyses of covariance of fecundity-size relationships showed that the slopes of the regression lines for 1927 and 1973 data were not significantly different, but the intercepts were different (Figures 4 and 5). Fecundity in 1973 was somewhat lower than in 1927 for fish of equal length or weight. For example, a 120 cm female produced about 646,000 eggs in 1927 or 573,000 eggs in 1973, approximately 13% fewer. An 88 pound (40 kg, gross weight) female would have produced approximately 1,575,000 eggs in 1927 or 1,227,000 eggs in 1973, about 28% fewer.

These differences in the fecundity-length and fecundity-weight relationships may be due to an increase in fecundity with age, independent of length. May (1967) and Ludwig and Lange (1975) reported such an interaction for Atlantic cod (*Gadus morhua*) and northern mottled sculpin (*Cottus b. bairdi*), respectively. However, Simpson (1951) and Bagenal (1966) reported that the effect of age on fecundity of plaice was insignificant. Kolloen (op. cit.) considered his material inadequate to determine whether at a given length, older females produced more eggs. In the 1973 data, fecundity did not consistently increase with age in any length class (10 cm). Results of stepwise regression analysis indicated that fecundity was best estimated by size, and that the addition of age data did not significantly increase the precision. Therefore, any age-length interaction on fecundity probably was not a significant factor, i.e., females in 1927 did not produce more eggs simply because they were older at length than those in 1973.

As discussed in Appendix I, the methods of treating the samples probably did not bias the fecundity estimates. Compared to other sources of variability, the

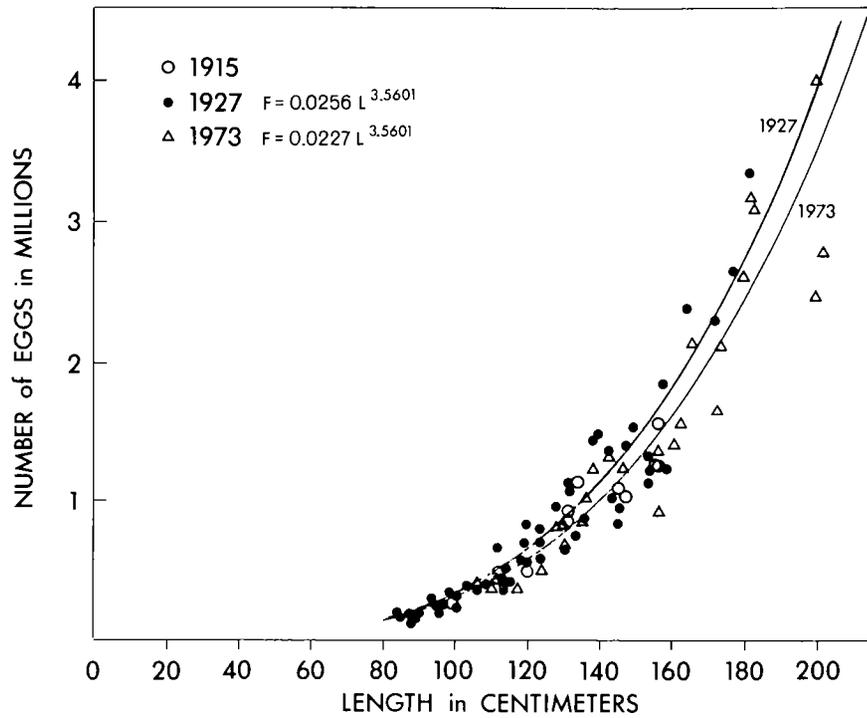


Figure 4. Fecundity-length relationship in 1927 and 1973, Area 3. The data from 1915 are presented for comparison. Standard lengths measured in 1915 were converted to fork lengths.

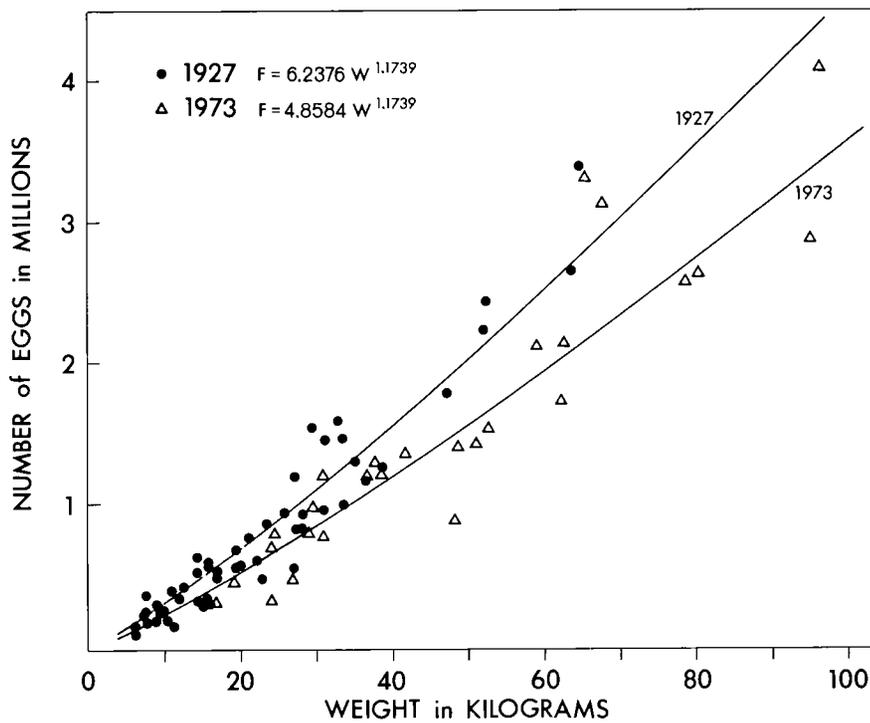


Figure 5. Fecundity-weight relationship in 1927 and 1973, Area 3. The equations were calculated with weight in grams.

observed differences were minor and are similar to fecundity variations in other flatfish. Annual variations in fecundity resulting from environmental fluctuations were reported by Bagenal (1957, 1963, and 1966) for plaice, witch (*Glyptocephalus cynoglossus*), and long rough dab (*Hippoglossoides platessoides*) and by de Veen (1976) for sole.

MATURITY

Maturity was recorded for females in 1914, 1927, and 1973, but we considered the data inadequate to determine the relation of maturity to age, length, and growth rate. First, Thompson's age readings in 1914 were not comparable to other age readings. Second, the 1927 and 1973 data were collected during the winter when immature females were not fully represented in the samples, and as explained below, these data were not considered appropriate for determining the age at which 50% of the females were mature. Therefore, we examined other unpublished data on maturity of females.

During the summer of 1954, maturity was recorded for 2,656 females caught in the Kodiak region, and we used these data to illustrate the relationship between maturity and age or length. Within each age class, the percentage of mature females consistently increased with length, and within each length class (5 cm) the percentage of mature females increased with age. Results of regression with logits³ confirmed the relation of maturity to length and age. Similar results were reported by Le Cren (1958) for perch and by Martin (1966 and 1970) for lake trout.

In our examination of other data, we found that the age of 50% maturity from winter samples was generally lower than it was from summer samples. Data from winter and summer research cruises in the Yakutat Region during the 1950's are presented in Table 1. Yakutat is a major spawning site and data from other regions showed similar results. We calculated the age of 50% maturity by regression with logits. During the summer, the age of 50% maturity was about 12 years, but in winter samples, it ranged from 8.8 to 10.7 years. The age of 50% maturity in summer samples from Kodiak, where many Yakutat spawners migrate in the summer, also was about 12 years. Skud (1977) discussed the movement of mature females to spawning sites during the fall and winter and suggested that many immature females may not participate in this migration. This suggestion could explain why the percentage of mature females was higher during the winter and why the age of 50% maturity was lower. Summer samples may not be entirely representative either, e.g., no females 8 to 10 years old were mature in the June sample (Table 1). Further, Thompson (unpublished) expressed uncertainty in distinguishing between immature and spent females collected in the summer. However, the critical point is that comparisons of maturity must be made with data from the same season and most of the available data were collected during the summer.

To show the relation of maturity to growth rate, we examined data collected on summer tagging charters. Maturity was determined for those females considered unsuitable for tagging, but we assume that the data, when grouped by regulatory areas, were representative of all ages that included mature fish. Except for Thompson's 1914 data, maturity was not recorded during the summer until 1949. The data were divided into two time periods for each regulatory area, 1949-1959 and

³ Berkson (1944). For our use, $\text{logit} = \ln[(1-q_{ij}) + q_{ij}]$ where q_{ij} = observed fraction of mature females at age i , and length class j . A weighted regression of logits on the natural logarithm of age and a power function of length was estimated by the nonlinear, least squares method.

Table 1. Percentage of mature females by age and age of 50% maturity from research cruises in the Yakutat Region.

Date	No. of Females	Age						Age of 50% Maturity*
		8	9	10	11	12	13	
Winter		% Mature						
November 1955	536	20	28	44	52	72	61	10.7
December 1955	85	40	29	55	84	78	90	9.4
December 1956	269	22	50	54	90	91	89	8.8
January 1957	357	0	39	50	81	87	89	9.3
Summer								
June 1954	324	0	0	0	28	54	64	11.8
August 1954	440	0	35	16	40	49	58	12.4

*Calculated with logits.

1960-1977. The changes in the age and length of maturity were greater in Area 3 than in Area 2. In Area 3, the estimated age of 50% maturity was 11.8 years during the first period and 10.9 years for data collected since 1960. In Area 2, the age of 50% maturity declined slightly, from 12.4 years in the 1950's to 12.1 years thereafter. The data also were grouped by 5 cm length intervals, and in Area 3, the length interval in which 50% of the females were mature has increased. During the 1950's, about 44% of the females in the 115-119 cm interval were mature, but during the 1960's and 1970's, only 20% of the females in that interval were mature. In Area 2, the length of maturity has not changed appreciably; 50% of the 120-124 cm females were mature during the 1950's and 53% were mature in that length interval during the 1960's and 1970's. Although it is not possible to adequately test the significance of these differences, we conclude that the changes in age and size of maturity were greater in Area 3 than in Area 2. The difference in maturity between areas presumably reflects the increase in growth rate, which was greater in Area 3 than in Area 2.

POPULATION FECUNDITY

The continuing decline in pre-recruits since the 1940's that was described by Hoag and McNaughton (1978) indicates that the increased growth rate and fecundity have not maintained the strength of incoming year-classes. Le Cren (1958) reported similar results for spawning stocks of perch. The decline in recruitment may result from either a reduction in spawning stock, so that population fecundity declined even though individual fecundity increased, or from a decrease in survival of eggs, larvae, or juveniles. To examine these possibilities, we estimated population fecundity, which is defined as the sum of the fecundities of all females in the population and represents the *potential* number of eggs spawned during one spawning season. We assumed that the fecundity-weight relationship was constant so that biomass was used to represent population fecundity.

Relation to Spawning Stock

Directional changes in the sex composition of the adult population can bias the estimates of relative population fecundity. Southward (1967) examined

sex ratio data collected during May and June, 1960 through 1965, and concluded that "there is little indication of a trend in the proportion of females on any of the grounds, although the data are highly variable." To determine whether the sex composition of the adult population had changed over a longer term, we examined data collected on research cruises from 1925 to date. Because the proportion of females-by-age was consistently greater in Area 3 than in Area 2, the data were grouped by season and regulatory area and were divided into three time periods: 1925-1939, 1940-1959, and 1960-1977. The proportion of females-by-age differed between winter and summer, apparently because of spawning migrations, and therefore, only summer data were used to estimate the sex composition. In Area 2, the percentage of females at a given age (10- to 20-year-olds) usually was lower during the period from 1925 to 1939 than in the periods after 1939 (Table 2). In Area 3, data on sex composition during the summer were not collected before 1949, but the percentage of females at each age in 1960-1977 data was about 8% greater than in 1949-1959. Whether these changes represent actual changes in the population that are fishery-induced, rather than spurious changes due to availability or selectivity is uncertain, but the subject merits further study. We used the biomass of the total adult population (ages 12-20) rather than the biomass of mature females to calculate population fecundity because differences in sex composition were not large, relative to the long-term trends in biomass.

Table 2. Percentage of females by age, time period, and regulatory area in summer samples.

Time Period	Age										
	10	11	12	13	14	15	16	17	18	19	20
Area 2											
	Percentage of Females										
1925-1939	26	29	36	34	70	46	54	—	—	—	—
1940-1959	37	38	42	42	48	51	54	67	70	71	88
1960-1977	34	39	42	46	48	53	43	57	49	57	59
Area 3											
1949-1959	63	61	69	72	74	78	81	86	86	88	88
1960-1977	70	74	77	81	84	84	89	94	92	94	96

Relative population fecundity since 1935 was estimated for halibut in Areas 2 and 3. Estimates of numbers of halibut by age in each regulatory area (Hoag and McNaughton 1978) were multiplied by the corresponding mean gross weights from commercial samples (IPHC, unpublished data). We assumed that the age of maturity was 12 years in Area 2 from 1935 to 1974; whereas in Area 3, the age of maturity was 12 years from 1935 to 1959 and 11 years from 1960 to 1974. Relative population fecundity was estimated with 1935 as the base year.

The contribution to population fecundity decreased with increasing age. For example, 12-year-olds generally produced 20 - 30% of the total; 13-year-olds produced about 20%; and 14-year-olds contributed about 16%. This trend occurred in most years and was evidence of the decline in numbers with age.

Although egg production in Area 3 usually was twice as large as that in Area 2, relative population fecundity in the two areas showed the same trend with time, and therefore, the data were combined. Population fecundity (moving average of threes) increased substantially from the mid-1930's until about 1955, but declined to

its former level by the early 1970's (Figure 6). The abundance of spawners showed a similar trend; i.e., it increased slightly from 1935 to about 1950, but declined sharply until the early 1970's when abundance was less than 40% of the 1935 level. The greater increase in population fecundity compared to abundance of spawners during the 1930's and 1940's and slower decline since then reflects the effect of the increased growth rate. If we had assumed the age of maturity was 12 years in both areas since 1935, the trends in relative population fecundity would not have changed, although the decline since 1960 would have been slightly greater. Thus, the decline in population fecundity since 1955 indicates that the increased growth rate and fecundity did not compensate for the reduction in numbers of spawners.

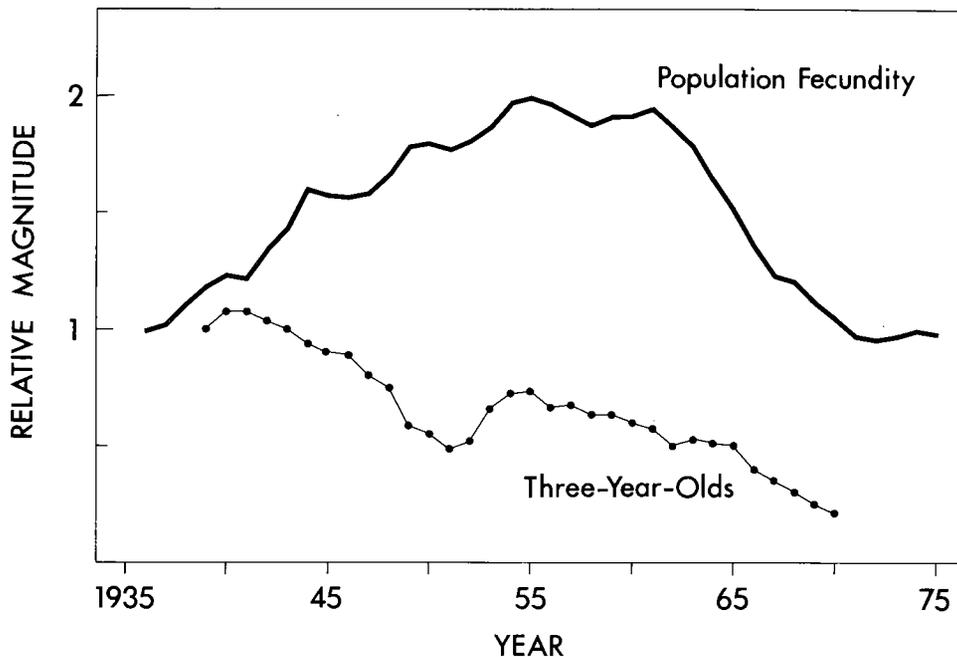


Figure 6. Relative population fecundity and relative abundance in numbers of 3-year-olds.

Relation to Recruitment

To determine the relation of population fecundity to juvenile survival, we compared the abundance of 3-year-olds (Hoag and McNaughton 1978) with the biomass of spawners. The number of 3-year-olds represents the abundance of juvenile halibut before they enter the trawl and setline fisheries. The results indicated that the abundance of young halibut was inversely related to population fecundity from 1940 to 1955, but paralleled it thereafter (Figure 6). The abundance of 3-year-olds began decreasing in the early 1940's, before the decline in population fecundity, and although the population fecundity was nearly the same in the early 1970's as in the mid-1930's, the abundance of juveniles in 1970 was less than one-third that in the mid-1930's.

Other authors have considered the relation of parent stock size to recruitment. Thompson and Bell (1934) proposed that a reduction in the number of mature halibut must affect the annual recruitment of young into the commercial fishery, but for their population models, they assumed that recruitment was constant. Thompson and Van Cleve (1936) also suggested that an increase in number of

mature adults would be followed by an increase in the number of young. Van Cleve and Seymour (1953) compared estimates of annual egg production at Cape St. James from 1935 to 1943 with recruitment on Goose Islands grounds. No correlation was evident, but they were concerned about the representativeness of their sampling. Ketchen and Ricker (unpublished, circa 1960) compared year-class strength at age 5 and ages 8 through 10 with stock size (catch per skate) in Areas 2 and 3 and concluded that the parent-progeny relationship was density-dependent and could be represented by a dome-shaped curve (Ricker 1954). Fukuda (1962) also analyzed Areas 2 and 3 separately and compared the abundance of the parent stock with progeny, 10 years later. He concluded that "year to year fluctuations in recruitment are great enough to obscure relationships, if any, between parent and progeny stocks." His analysis included catch and effort data before 1930, which are not considered reliable (Skud 1975). Southward (1968) compared the number of halibut between ages 10 and 20 with the number of 4-year-olds from Goose Islands (Area 2). Although his results suggested a dome-shaped, spawner-recruit curve, he concluded that the results did not provide realistic estimates of recruitment and used an adjusted, asymptotic relationship for analyses of data from Areas 2 and 3. Cushing (1971) reported that recruitment of flatfish, including halibut, was practically independent of parent stock size.

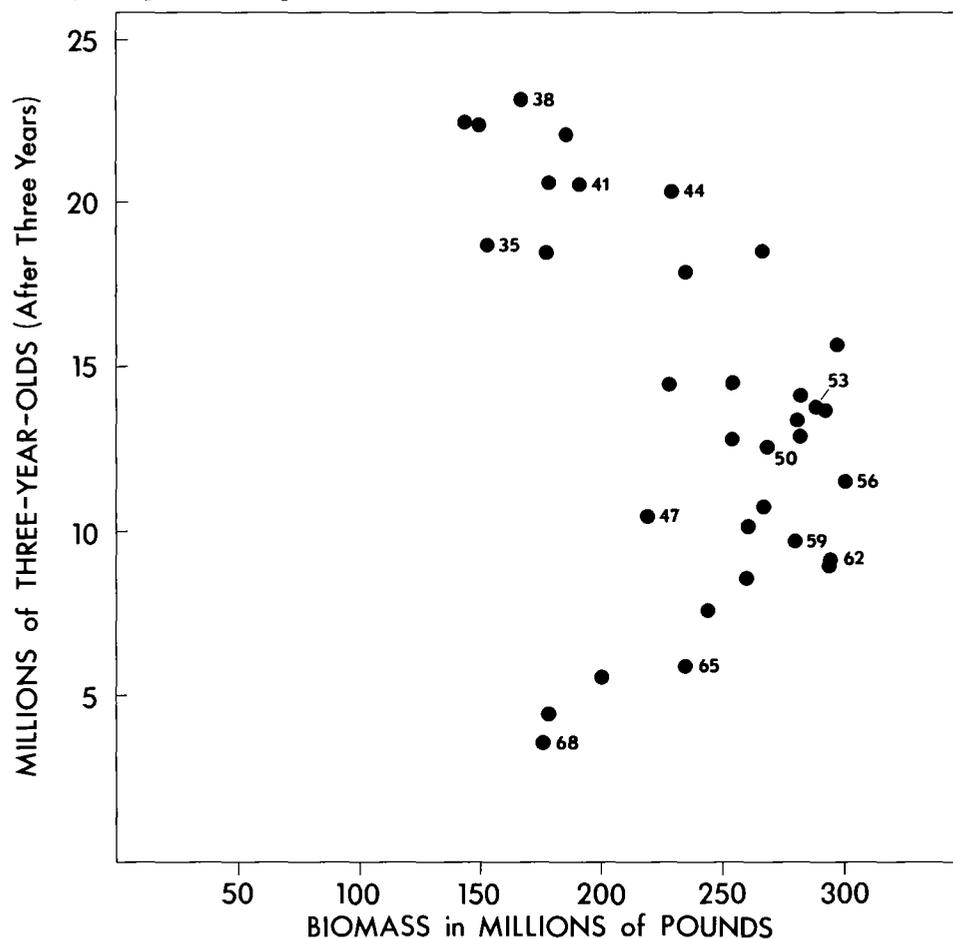


Figure 7. Relation of biomass of spawners (1935-1968) to numbers of 3-year-olds (1938-1971), Areas 2 and 3. Every third year of parent stock is identified.

Our comparison (Figure 6) showed that the abundance of 3-year-olds was declining when population fecundity (biomass of 12- to 20-year-olds) was high and suggested that recruitment was density-dependent. We calculated Ricker and asymptotic curves for data on population fecundity and numbers of 3-year-olds, but neither curve adequately described the relationship (Figure 7). Recruitment was lowest during the most recent years (1968-1971) which suggests that the abundance of spawners will continue to decline in succeeding years. However, these estimates from cohort analysis are calculated with constant rates of natural and fishing mortality, and deviations can cause large errors in the estimates of abundance, particularly for the younger age groups (Hoag and McNaughton 1978).

We also compared population fecundity in a given year with that twelve years later (Figure 8). The best fit was a Ricker curve for Areas 2 and 3 combined.⁴ The fact that we obtained a better fit with a Ricker curve by combining data from both areas rather than by analyzing them separately lends support to the thesis that the stocks in the two areas may be more closely interrelated than formerly appreciated (Skud 1975 and 1977). We suggest that the different conclusions reached in previous studies of stock and recruitment and the failure of the results to show a density-

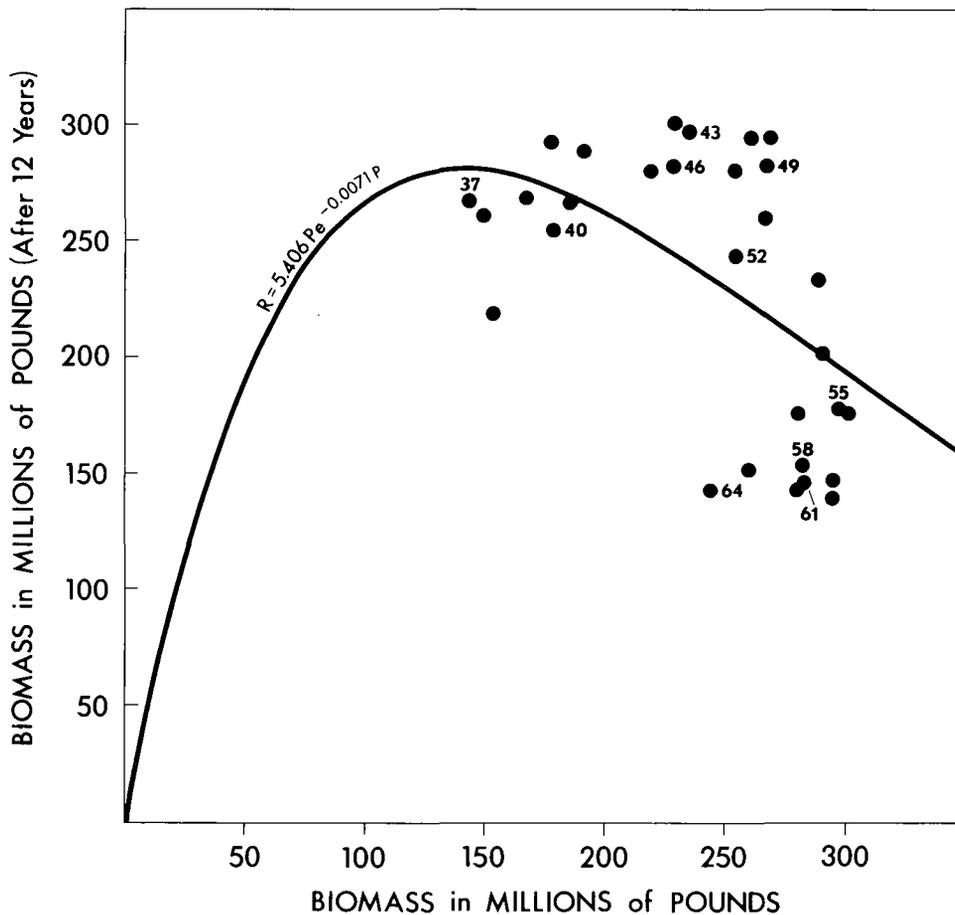


Figure 8. Relation of biomass of spawners (1935-1964) to biomass of spawners (1947-1976), Areas 2 and 3. Every third year of parent stock is identified.

⁴ The residual sum of squares from nonlinear regression was smaller for the Ricker curve ($R = \alpha Pe^{-\beta P}$) than for the asymptotic (Beverton and Holt 1957) curve, $R = P/(\alpha + \beta P)$.

dependent relation may be due to the limitations of the data and perhaps to the fact that the stocks were studied separately. A definitive examination of the stock-recruitment relation is needed and should be undertaken now that the data base (maturity, fecundity, growth, CPUE and abundance) has been improved.

Although our results show that population fecundity has now been reduced to the level of 1935, recruitment (to 1971) has not increased. The long-term decline in recruitment appears ominous and whether long-term environmental changes, such as those discussed by Ricker et al. (Ms)⁵ and Wickett (1973), are affecting recruitment or whether it is controlled by density-related factors has yet to be determined. The marked increase in growth raises questions about associated physiological changes that may have affected the viability of the eggs and larvae. However, IPHC (1978) reported that the abundance of juvenile halibut has been increasing in certain areas since the mid-1970's; whether this increase represents an actual change in abundance or a reduction in the incidental catch by trawlers is uncertain.

DISCUSSION

Density-dependent recruitment implies that compensatory mortality controls population size and Ricker (1954) and Beverton (1962) discussed several kinds of compensatory mechanisms. These controls included predation, cannibalism, competition, food supply, etc. We think the indirect effect of growth may be another factor to consider, particularly in its relation to fecundity and competition. To paraphrase Lack (1954), the interactions of factors limiting population size in fishes are more complex than in other animals because these factors affect not only survival and reproduction but also growth.

When the increase in the growth rate in Area 3 was first reported, IPHC (1954) concluded that the "Observed differences are in keeping with the differences in the density of the stocks as measured by the catch per unit effort." Halibut caught during 1950 "had lived under the relatively low stock densities of the 1930's" and the weight-at-age of older fish was nearly double that of halibut caught during the late 1920's which "had lived under the crowded conditions that exist in little-fished stocks." Southward (1962) reiterated these conclusions and later (1967) concluded that changes in growth rate "... are no doubt the result of a combination of changes in the environment as well as a density-dependent response." His conclusion was based on the increase in growth rate from 1950 to 1964, as determined from back-calculations with otolith measurements. Although biomass, as indicated by catch per unit effort, CPUE in pounds, was increasing during this period (Myhre et al. 1977), Southward stated that the high level of catch had reduced the overall abundance and the numbers of older fish, but he did not provide supporting evidence. Beyond that, Southward's (1967) data showed that the growth rate in Area 3 (Portlock Bank) had been increasing since 1920; whereas biomass (CPUE) had fluctuated widely since that time (Figure 9). He did not explain the lack of correlation between growth and apparent abundance (biomass) before 1950. The trends of growth and abundance in Area 2 were quite different from those in Area 3 and the relationship of these factors is obscure. Although abundance was declining in Area 2 before 1950, growth was relatively stable.

Skud (1975) suggested that numerical abundance may have begun to decline before the 1950's: "... the CPUE (by weight) of older fish can register an increase

⁵ "Causes of the decrease in size of pink salmon (*Oncorhynchus gorbuscha*)" by W.E. Ricker, H.T. Bilton, and K.V. Aro, Pacific Biological Station, Nanaimo, 115 p.

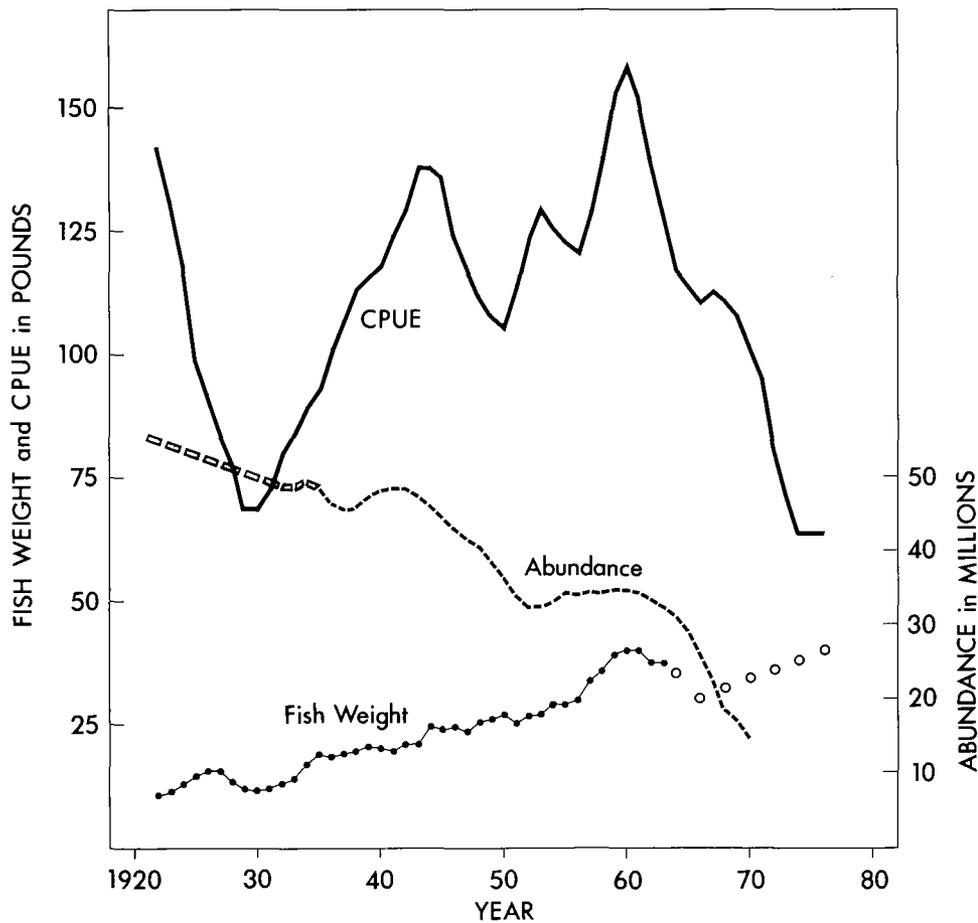


Figure 9. Long-term trends of growth, biomass (CPUE) and numerical abundance in Area 3 (moving average of threes). Growth data (mean gross weight of 12-year-olds from Portlock) from 1920 to 1964 is after Southward (1967) and has been extrapolated for more recent years based on samples of commercial landings. CPUE data (pounds per skate) from 1930 to 1976 are from Myhre et al. (1977); data before 1930 are from Chapman, Myhre and Southward (1962). Estimates of abundance are from cohort analysis (Hoag and McNaughton 1978) and have been extrapolated to earlier years based on CPUE and growth.

when the growth rate increases, whereas the number of fish may not change or may decrease. *Indeed, this phenomenon may explain much of the apparent improvement of stock conditions from 1930 to 1940 and beyond.* In fact, estimates of numerical abundance in Area 3 (ages 3-20) from cohort analysis (Hoag and McNaughton 1978) indicated that abundance has declined almost continuously since 1941. These results may explain the lack of correlation mentioned above and although estimates of abundance before 1935 are not available from cohort analysis, the increase in growth rate prior to 1935 suggests that the abundance had declined before that time as well. To examine this relationship between growth and abundance in earlier years, we extrapolated the cohort data based on changes of fish size and biomass and extrapolated Southward's data using estimated weights from recent commercial samples. Although the relationship of growth to abundance needs further study, the results indicate that abundance has been declining since 1920 and that growth has been increasing continuously (Figure 9).

The long-term change in growth suggests that food was a limiting factor, controlling the growth rate of halibut when abundance was high. To be effective, this limitation presumes that halibut generally frequent the same grounds at all levels of abundance and that the density on these favored grounds changes accordingly. Hence, at lower densities, competition for food would decrease and growth would increase. However, as Hamley and Skud (1978) suggested, the "feeding territory" may be governed by the size of halibut and this relation could be an important mechanism, along with density, that determines the effects of competition. As growth increased, demand for food would increase and territories would expand; each individual would have greater access to food; and the larger fish would be more successful in capturing the available food. This is consistent with Skud's (1978) findings regarding competition for bait on longline gear. As territories expanded, competition could become as severe as when densities were high, except that fewer, but faster-growing, fish would be involved. This suggests that the competition between older, larger fish and younger, smaller fish, whose diets are similar, would be accentuated and could affect recruitment, as proposed by Herrington (1948) for adult haddock and scrod.

Assuming that changes in growth are the result of competition for food, the comparisons suggest that numerical abundance is more important than biomass in regulating growth. This conclusion is consistent with Dawes' (1931) results from feeding experiments with plaice. He showed that a seven-fold increase in weight required only a three-fold increase in the food necessary to maintain the larger size. Because the growth rate of halibut continued to increase even as biomass of the population increased, it seems evident to us that the increase in biomass did not cause a proportional decrease in the food supply. Rather, the availability of food to each halibut increased because the effect of reduced abundance of halibut was greater than the demand for food due to increased biomass; and we hypothesize that, with the continued decline in abundance, these circumstances caused the perpetual increase in growth.

Beyond these speculative thoughts, it is readily apparent that reliance on biomass as an indication of "well-being" can be misleading in the halibut fishery. Although growth changes of the magnitude observed with halibut probably are unusual, the same general effect can be expected for other species, raising questions about the reliance on total biomass for stock assessment. Using biomass to assess stock condition in a multi-species fishery, as suggested by Edwards (1975), would presumably compound the problem. Hence, we fully support Murphy's (1960) thesis that evaluation of stock size should include estimates of numerical abundance as well as biomass. Because cohort analysis does not provide estimates of abundance by age for the most recent years, one should measure changes in the growth rate to aid in the interpretation of changes in biomass (CPUE). Further, as our results show, biomass also is a useful statistic in the examination of the relation between population fecundity and recruitment.

SUMMARY AND CONCLUSIONS

The long-term increase in growth rate in Area 3 has been accompanied by an increase in fecundity. Comparison of data over a 50-year period indicates that fecundity-at-age in the 1970's has more than doubled since the 1920's. In Area 3, the age of 50% maturity has decreased by one year since the 1950's, and the length at 50% maturity has increased by about 5 cm. The age of 50% maturity in Area 2 has also decreased but the change was small.

The increases in fecundity and growth rate since the 1920's, as well as the decline in the age of maturity in Area 3, apparently are related to the decline in abundance. The number of juveniles has declined substantially since 1940 and the number of spawners has declined since the 1950's, indicating that the increase in the fecundity of individuals has not compensated for the reduction in numbers of halibut. Population fecundity increased during the 1930's and 1940's but declined to its former level by the 1970's. Recruitment was inversely related to population fecundity before 1955 but paralleled it thereafter, indicating that factors other than population fecundity are affecting abundance. The fact that the increases in growth and fecundity of individuals have not maintained the population fecundity and that the abundance of both adults and juveniles are decreasing suggests that the reproductive capacity has been impaired. Viability of the eggs and larvae may have been affected by the rapid growth or by long-term, environmental changes.

Our results indicate that food is a limiting factor and that abundance, more so than biomass, determines the availability of food. We hypothesize that the decline in the abundance of halibut and the associated changes in competition for food led to the perpetual increase in growth. It is evident that reliance on biomass alone as an indication of "well-being" of the halibut stock has been misleading and that estimates of numerical abundance are needed in addition to CPUE to assess stock condition.

In addition to these generalized results, we found that the fecundity relationships with size differed among spawning grounds, particularly between those in Area 3 and Area 2. Our data also showed that fecundity is more closely related to fish size than age and confirmed that fecundity increases with growth rate. In contrast, the onset of maturity is related to both size and age. Estimates of the age of 50% maturity from data collected in the winter (spawning season) were lower than those estimated from summer samples, presumably because immatures are not fully represented on the spawning grounds. Similarly, the sex composition in winter samples differed from that in summer samples. We also noted that the percentage of females, ages 10 to 20 years, increased with time in Areas 2 and 3.

DEDICATION AND ACKNOWLEDGMENTS

This paper is dedicated to Lawrence N. Kolloen who was killed in an airplane crash on Admiralty Island, Alaska on September 1, 1954, while on official business for the U.S. Fish and Wildlife Service. The thorough research he conducted on fecundity of halibut was submitted as partial fulfillment of requirements for his Master of Science Degree at the University of Washington in 1934. Without his data for comparison, our study would not have been possible.

Many past and present members of the Commission staff provided valuable assistance in collecting the samples, counting the eggs, and reviewing the manuscript. In particular, we thank Maureen S. Schmid for her help in processing the ovaries and William H. Hardman for his guidance in interpreting early data and reading the otoliths. We also acknowledge R. Ian Fletcher, Keith S. Ketchen, Loh-Lee Low, Jyri E. Paloheimo, William E. Ricker, Ralph P. Silliman, and G. Morris Southward for their reviews and comments.

LITERATURE CITED

- Alm, Gunnar
1959 Connection between maturity, size, and age in fishes. Institute of Fresh-water Research, Drottningholm, Report No. 40, pp. 5-145.
- Bagenal, T.B.
1957 Annual variations in fish fecundity. Journal of the Marine Biological Association of the United Kingdom, Volume 36, pp. 377-382.
1963 Variations in the plaice fecundity in the Clyde area. Journal of the Marine Biological Association of the United Kingdom, Volume 43, pp. 391-399.
1966 The ecological and geographical aspects of the fecundity of the plaice. Journal of the Marine Biological Association of the United Kingdom, Volume 46, pp. 161-186.
1973 Fish fecundity and its relations with stock and recruitment. Conseil Permanent International pour l'Exploration de la Mer, Rapports et Procès - Verbaux des Réunions, Volume 164, pp. 186-198.
- Bell, F. Heward and Gilbert St-Pierre
1970 The Pacific halibut. International Pacific Halibut Commission, Technical Report No. 6, 24 p.
- Berkson, Joseph
1944 Application of the logistic function to bio-assay. Journal of the American Statistical Association, Volume 39, pp. 357-365.
- Beverton, R.J.H.
1962 Long-term dynamics of certain North Sea fish populations. [IN] The exploitation of natural animal populations. Edited by E.D. Le Cren and M.W. Holdgate. John Wiley and Sons, Inc., New York, 399 p.
- Beverton, Raymond J.H. and Sidney J. Holt
1957 On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food (U.K.), Fishery Investigations, Series II, Volume XIX, 533 p.
- Boyar, H.C. and R.A. Clifford
1967 An automatic device for counting dry fish eggs. Transactions of the American Fisheries Society, Volume 96, No. 3, pp. 361-363.
- Chapman, Douglas G., Richard J. Myhre and G. Morris Southward
1962 Utilization of Pacific halibut stocks: Estimation of maximum sustainable yield, 1960. International Pacific Halibut Commission, Report No. 31, 35 p.
- Cushing, D.H.
1971 The dependence of recruitment on parent stock in different groups of fishes. Journal du Conseil Permanent International pour l'Exploration de la Mer, Volume 33, No. 3, pp. 340-362.
- Dawes, Ben
1931 Growth and maintenance in the plaice (*P. platessa*, L.). Part II. Journal of the Marine Biological Association of the United Kingdom, Volume 17, No. 3, pp. 877-947.

- de Veen, J.F.
 1970 On some aspects of maturation in the common sole *Solea solea* (L). Verichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung, Volume 21, pp. 78-91.
 1976 On changes in some biological parameters in the North Sea sole (*Solea solea* L.). Journal du Conseil Permanent International pour l'Exploration de la Mer, Volume 37, No. 1, pp. 60-90.
- Dixon, W.J. (Editor)
 1970 BMD Biomedical Computer Programs. Automatic Computation No. 2, University of California Press, Berkeley, 600 p.
- Edwards, R.L.
 1975 The total biomass approach to fisheries management. [IN] Advisory Committee on Marine Resources Research, FAO Fisheries Reports No. 171, Supplement 1, pp. 91-96.
- Fukuda, Yoshio
 1962 On the stocks of halibut and their fisheries in the northeastern Pacific. International North Pacific Fisheries Commission, Bulletin No. 7, pp. 39-50.
- Hagerman, Frederick B.
 1952 The biology of the Dover sole, *Microstomus pacificus* (Lockington). California Department of Fish and Game, Fish Bulletin No. 85, 48 p.
- Hamley, John M. and Bernard E. Skud
 1978 Factors affecting longline catch and effort: II. Hook-spacing. International Pacific Halibut Commission, Scientific Report No. 64, pp. 15-24.
- Herrington, William C.
 1948 A symposium on fish populations. 9. Limiting factors for fish populations. Bulletin of the Bingham Oceanographic Collection, Volume XI, pp. 229-283.
- Hoag, Stephen H. and Ronald J. McNaughton
 1978 Abundance and fishing mortality of Pacific halibut, cohort analysis, 1935-1976. International Pacific Halibut Commission, Scientific Report No. 65, 45 p.
- Hosie, Michael J. and Howard F. Horton
 1977 Biology of the rex sole, *Glyptocephalus zachirus*, in waters off Oregon. U.S. Department of Commerce, National Marine Fisheries Service, Fishery Bulletin, Volume 75, No. 1, pp. 51-60.
- International Pacific Halibut Commission
 1954 Regulation and investigation of the Pacific halibut fishery in 1953. International Pacific Halibut Commission, Report No. 21, 22 p.
 1978 Annual Report 1977. International Pacific Halibut Commission, 40 p.
- Kipling, C. and W.E. Frost
 1969 Variations in the fecundity of pike *Esox lucius* L. in Windermere. Journal of Fish Biology, Volume 1, pp. 221-237.

- Lack, David
 1954 The natural regulation of animal numbers. Clarendon Press, Oxford, 343 p.
- Le Cren, E.D.
 1958 Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. *Journal of Animal Ecology*, Volume 27, No. 2, pp. 287-334.
- Ludwig, Gerald M. and Eugene L. Lange
 1975 The relationship of length, age, and age-length interaction to the fecundity of the northern mottled sculpin *Cottus b. bairdi*. *Transactions of the American Fisheries Society*, Volume 104, No. 1, pp. 64-67.
- Martin, N.V.
 1966 The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. *Transactions of the American Fisheries Society*, Volume 95, pp. 415-422.
 1970 Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. *Journal of the Fisheries Research Board of Canada*, Volume 27, pp. 125-146.
- May, A.W.
 1967 Fecundity of Atlantic cod. *Journal of the Fisheries Research Board of Canada*, Volume 24, No. 7, pp. 1531-1551.
- Merriner, John V. and Joanne L. Laroche
 1977 Fecundity of the northern puffer, *Sphoeroides maculatus*, from Chesapeake Bay, *Chesapeake Science*, Volume 18, No. 1, pp. 81-83.
- Murphy, Garth I.
 1960 Estimating abundance from longline catches. *Journal of the Fisheries Research Board of Canada*, Volume 17, pp. 33-40.
- Myhre, Richard J., Gordon J. Peltonen, Gilbert St-Pierre, Bernard E. Skud and Raymond E. Walden
 1977 The Pacific halibut fishery: Catch, effort, and CPUE, 1929-1975. International Pacific Halibut Commission, Technical Report No. 14, 94 p.
- Nikolskii, George V.
 1969 Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh, 323 p.
- Ricker, W.E.
 1954 Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, Volume 11, No. 5, pp. 559-623.
- Simpson, A.C.
 1951 The fecundity of the plaice. Ministry of Agriculture, Fisheries, and Food (U.K.), Fishery Investigations, Series II, Volume XVII, 27 p.

Skud, Bernard Einar

- 1975 Revised estimates of halibut abundance and the Thompson-Burkenroad debate. International Pacific Halibut Commission, Scientific Report No. 56, 36 p.
- 1977 Drift, migration, and intermingling of Pacific halibut stocks. International Pacific Halibut Commission, Scientific Report No. 63, 42 p.
- 1978 Factors affecting longline catch and effort: III. Bait loss and competition. International Pacific Halibut Commission, Scientific Report No. 64, pp. 25-50.

Southward, G. Morris

- 1962 A method of calculating body lengths from otolith measurements for Pacific halibut and its application to Portlock-Albatross grounds data between 1935 and 1957. Journal of the Fisheries Research Board of Canada, Volume 19, No. 2, pp. 339-362.
- 1967 Growth of Pacific halibut. International Pacific Halibut Commission, Report No. 43, 40 p.
- 1968 A simulation of management strategies in the Pacific halibut fishery. International Pacific Halibut Commission, Report No. 47, 70 p.

Thompson, William F.

- 1915 A preliminary report on the life-history of the halibut. British Columbia Report of the Commissioner of Fisheries, pp. 76-99.
- 1917 The egg production of the halibut of the Pacific. British Columbia Report of the Commissioner of Fisheries, pp. 35-38.

Thompson, William F. and F. Heward Bell

- 1934 Biological statistics of the Pacific halibut fishery (2) Effect of changes in intensity upon total yield and yield per unit of gear. International Fisheries Commission, Report No. 8, 49 p.

Thompson, William F. and Richard Van Cleve

- 1936 Life history of the Pacific halibut (2) Distribution and early life history. International Fisheries Commission, Report No. 9, 184 p.

Van Cleve, Richard and Allyn H. Seymour

- 1953 The production of halibut eggs on the Capt St. James spawning bank off the coast of British Columbia 1935-1946. International Fisheries Commission, Report No. 19, 44 p.

Wickett, W. Percy

- 1973 Our changing ocean environment. Fisheries Research Board of Canada, Circular No. 94, 29 p.

Woodhead, Avril D.

- 1960 Nutrition and reproductive capacity in fish. Proceedings of the Nutrition Society, Volume 19, pp. 23-28.

APPENDIX I. TREATMENT OF OVARIES

The treatment of halibut ovaries collected in 1915, 1927, and 1973 differed and the methods are described below. The ovaries were taken from females off Icy Bay in 1915, on Portlock and "W" Grounds in 1927, and "W" Grounds and Cape St. James in 1973.

1915

Thompson (1917) estimated fecundities of 12 females. He recorded standard lengths and collected otoliths for age determination. In a description of egg development within the ovary, Thompson (1915) concluded that the presence of large, translucent eggs in ovaries collected during the winter indicated that the female was spawning. Therefore, any ovaries containing translucent eggs were excluded from fecundity determinations and only those containing opaque, unripe eggs were used. He estimated the number of eggs in an ovary by a gravimetric analysis of wet material. Formaldehyde was injected into the lumen of each ovary, which was then sealed in a cask of formaldehyde. Several months later, the eggs of each ovary were separated manually. Tissue fragments were picked from the mass with forceps. The eggs were mixed until the mass appeared homogenous and weighed in an air-tight jar. Thompson counted the eggs in three 5-g samples, one each from the upper, middle, and lower layers of the mass. Knowing the weight of the eggs in the ovary and the average weight per egg, he calculated the number contained in the ovary. The number of eggs in the left and right ovaries were summed to obtain an estimate of fecundity. He estimated a 0.1% error due to evaporation.

1927

Kolloen (op. cit.) estimated the number of opaque eggs in an ovary by a gravimetric analysis of dried material. Immediately upon collection in 1927, the ovaries were placed in formalin. When removed from storage five years later, the ovaries had hardened satisfactorily for the egg separation process, and the outer ovarian membrane was peeled from the egg mass. This mass then was crumbled manually in water and worked through a wire screen to separate the eggs. The floating particles of connective tissue were decanted until only individual ova (ca. 2 mm) remained. Kolloen then dried and weighed the group of eggs to the nearest 0.1 g. He weighed two subsamples to 0.0001 g, and counted the dried eggs in each. The number of eggs in the ovary was calculated by averaging the estimates from the two subsamples. Kolloen estimated the number of eggs in 59 left ovaries and 7 right ovaries and compared the number of eggs in 6 pairs of ovaries. He found no consistent difference between the right and left ovaries and summed the counts from both ovaries to estimate fecundity. When the eggs in subsamples of only one ovary, either right or left, were counted, he doubled that number to estimate fecundity.

1973

The treatment of ovaries in the 1970's was based on Kolloen's method to maintain comparability. We encountered several difficulties that necessitated modifications, but doubt that the changes affected the comparability of the two studies. The ovaries were frozen at sea. When thawed a few weeks later, they were

separated into large chunks before being placed in Davidson's solution¹. Although the solution was changed once a month, the eggs in most ovaries had not entirely hardened a year later. To hasten the process, the outer membrane was removed; each ovary was broken into clumps less than 1 cm in diameter and boiled for approximately three hours. The boiling denatured and hardened the egg protein so that each egg could be teased, intact, from the connective tissue. After decanting most of the tissue, the eggs were dried and passed through a stream of air to remove the remaining tissue. Each group of eggs was weighed to 0.01 g; three subsamples were removed and weighed to 0.0001 g. Fecundity estimates for 29 left ovaries and 5 right ovaries were based on this gravimetric analysis of the dried eggs, similar to Kolloen's method.

Aside from hardening the eggs, teasing the eggs from the connective tissue was the slowest step in the process. Halibut ovaries often weigh more than 10 pounds (4.5 kg) and this procedure for separating eggs usually required more than a month per ovary. To speed the process, a gravimetric analysis of wet, rather than dried, material was introduced. The eggs in three subsamples, rather than the entire ovary, were separated and dried. This change shortened the procedure to about three days, regardless of ovary size. The comparability between the gravimetric analyses of wet and dried material was tested by treating five ovaries both ways. The results of a paired *t* test indicated that the fecundity estimates were not significantly different and confirmed Thompson's results.

The gravimetric analysis of wet material was used for the remaining 27 left ovaries and 3 right ovaries. After the outer membrane was removed, the ovary was broken into clumps and boiled as previously described. This mass was poured into a net bag that was suspended in air for three hours. Every half hour the mass was thoroughly stirred to insure a uniform moisture loss. After draining, the mass was weighed to the nearest quarter ounce. Three subsamples, approximately 30 g each, were removed from the center of the mass and weighed to 0.01 g. After weighing, the eggs in the wet subsamples were separated and dried for counting the same way as entire ovaries had been treated previously.

Boyar and Clifford (1967) reported that an automatic counter rapidly and accurately counted dried herring eggs. We tested the counter (Decca Mastercount) with dried halibut eggs but could not obtain accurate or reproducible counts, possibly because the counter was not sensitive enough to distinguish between small particles of tissue and the eggs. Consequently, the eggs in all subsamples were counted manually. Three estimates of the number of eggs per ovary were calculated by extrapolating the number of eggs in each subsample to the total ovary weight. The mean of these three estimates was used in fecundity calculations. Whenever the coefficient of variation among subsamples exceeded 1%, replicate counts were made.

All methods involved gravimetric analyses and, as previously shown for 1973 data, the analysis of dried material was not significantly different from the analysis of wet material. Because Kolloen's procedures initially were followed as closely as possible, his analysis of dried material in 1927 should be comparable to the same analysis in 1973.

¹ Davidson's solution contains 30% ethyl alcohol, 30% distilled water, 20% neutralized formalin, 10% glacial acetic acid, and 10% glycerin. Frank Perkins (NMFS, personal communication) recommended this solution as a substitute for Gilson's fluid, which contains highly toxic mercuric chloride.

APPENDIX II. FECUNDITY OF LEFT AND RIGHT OVARIES

Data collected in 1973 indicated that left ovaries usually contained more eggs than right ovaries. Estimates of the number of eggs contained in eight pairs of ovaries were compared and, in every pair, the left ovary contained more eggs than the corresponding right ovary. Forty-six of the 56 halibut examined had heavier left ovaries (wet weight), an indication that the left ovary usually contained more eggs because fecundity and wet ovary weight are linearly related (see Appendix III). Similar differences between ovaries also have been observed in other species (Hagerman 1952; Hosie and Horton 1977; Merriner and Laroche 1977). Because the majority of data in 1973 was from left ovaries, fecundity was calculated by doubling the number of eggs in the left ovary.

Differences between ovaries in six pairs collected in 1927 were inconsistent as to which ovary contained more eggs, and paired ovary weights were usually unavailable. Several fecundity estimates in 1927 data were based on the number of eggs in both ovaries. To make them comparable with 1973 fecundity estimates, they were recalculated by doubling the number in the left ovary. The number of eggs in each ovary was not published for females collected in 1915. Because Thompson estimated fecundities of only 12 females and did not report the number of eggs in the left ovaries, his 1915 data were not included in calculations of fecundity relationships.

APPENDIX III. FECUNDITY AND OVARY WEIGHT

Kolloen did not develop a relationship between fecundity and ovary weight because of the variation in weight with the stage of egg development. However, he determined the relationship between ovary weight and length for fish from each spawning ground, and the power relationship was approximately the same as that between fecundity and length, an indication that fecundity was nearly proportional to ovary weight. We reexamined his data, and fecundity estimates and wet weights of left ovaries collected in 1927 were linearly related as shown in Figure 10. The lower slope of the regression line for "W" Grounds probably reflects a difference in average ovary development. Ovary weight, but not fecundity, increases as the spawning season approaches, and females from "W" Grounds were collected nearly a month later than those from Portlock Bank. Thus, ovaries from "W" Ground females weighed more than those from equally fecund females collected at Portlock Bank.

Fecundity and ovary weight for each set of samples collected in 1973 apparently are linearly related, an indication that mean egg weight does not vary significantly with ovary weight. The relationships among wet weights of left ovaries and fecundity estimates for females from each ground are presented in Figure 10. The slope of the line was lower for data collected in December than in November, just as for 1927 data. The linear relationship between fecundity and ovary weight may substantially reduce the amount of work required in future fecundity studies because ovaries need only be weighed to determine their egg numbers, once this relationship is established.

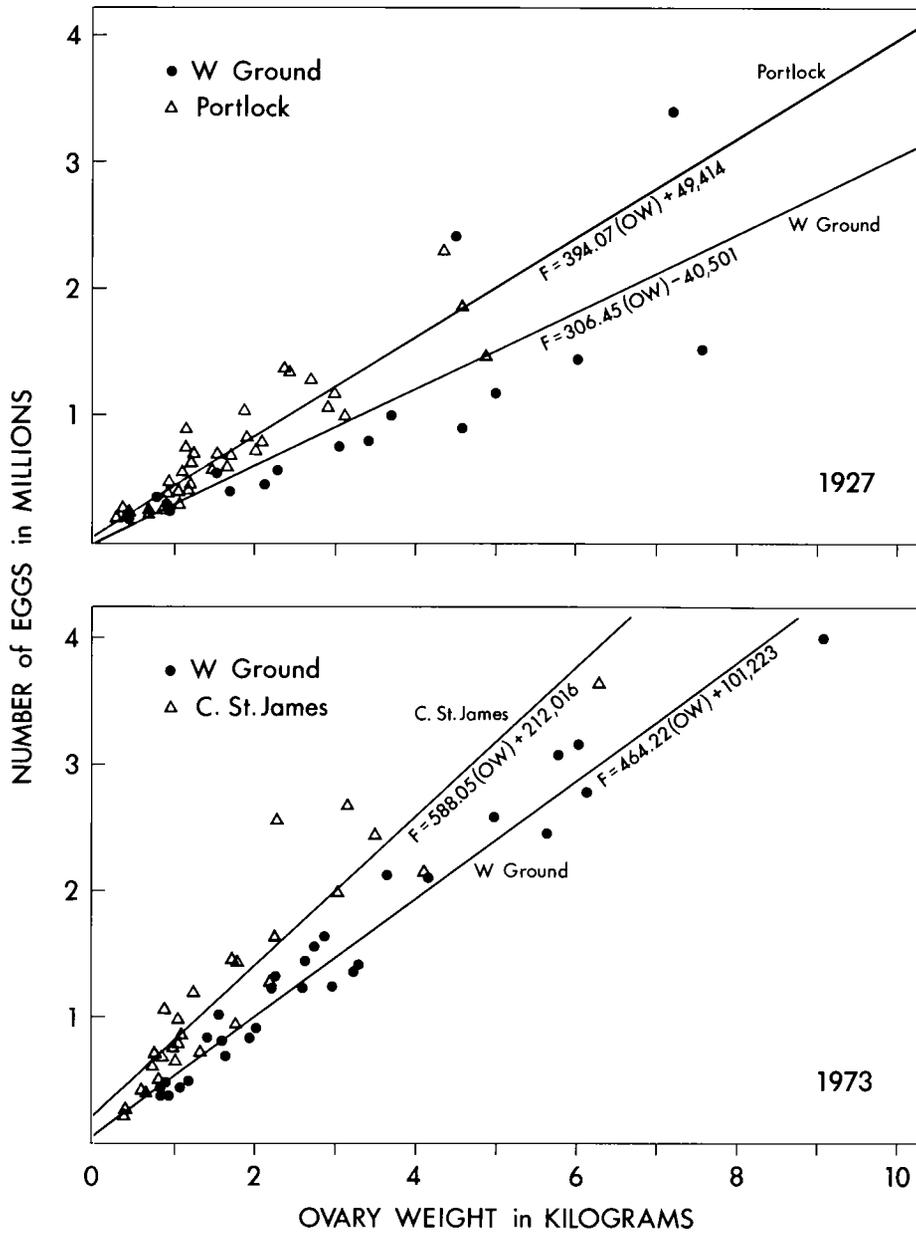


Figure 10. Fecundity-ovary weight relationship by spawning ground, 1927 and 1973. The equations were calculated with weight in grams.

APPENDIX IV. COMPARISONS AMONG SPAWNING GROUNDS

Fecundity relationships among females from different spawning grounds were examined to determine appropriate combinations of data for comparisons. Although Kolloen acknowledged that small differences in productivity may have existed, he chose to combine data from Portlock Bank and "W" Grounds to maximize their usefulness for statistical treatment. Analyses of covariance were performed on the revised 1927 data and the results showed that the relationships among fecundity, length, weight, and age were not significantly different between the two grounds, corroborating Kolloen's conclusion.

The fecundity relationships for females from Cape St. James and "W" Grounds were compared. The relation of fecundity and length is a power function and all data were transformed to logarithms for analysis. Results from least squares, linear regression and covariance analyses indicated that the fecundity-length relationship was not significantly different between grounds. The equations for data from Cape St. James and "W" Grounds, separately and combined, are presented in Table 3. The fecundity-age relationship also is a power function, and the same statistical analyses were applied as with length data. The age relationship was not significantly different between grounds. Log-log plots of fecundity and fish weight data indicated that either a linear or a power function might apply. Both relationships were calculated for each ground and the correlation coefficients were slightly greater for the power function. Also, the exponents were significantly different from one. Thus, the data were transformed to logarithms for linear regression and covariance analysis. The regression lines from each ground had equivalent slopes, but the intercepts were significantly different at the 1% level. Based on covariance analysis for the common slope case, females from "W" Grounds produced, on the average, 19% fewer eggs per unit of gross weight. In addition, the power function between length and weight was calculated for both grounds. The results were similar to those for fecundity and weight, i.e., the regression lines had common slopes, but the intercepts were different at the 1% level. On the average, females from "W" Grounds were 8.5% heavier per unit length than females from Cape St. James. Cape St. James is located at a much lower latitude than "W" Grounds and differences in growth rate, time of spawning, and sampling may have contributed to the differences in the weight relationships. Because of these differences and because data were not collected at Cape St. James in 1927, only data from 29 females caught at "W" Grounds in 1973 were compared with 1927 data from Portlock Bank and "W" Grounds.

Table 3. Fecundity and length-weight relationships by spawning ground, 1973.

Relationship	Cape St. James	"W" Grounds
Fecundity x Length		
By ground	$F = 0.3149 L^{3.0506}$	$F = 0.0398 L^{3.4476}$
Common line	$F = 0.1732 L^{3.1626}$	
Fecundity x Age		
By ground	$F = 3348.6079 A^{2.1996}$	$F = 1983.2655 A^{2.3995}$
Common line	$F = 2628.5825 A^{2.2939}$	
Fecundity x Weight		
By ground	$F = 15.1758 W^{1.0847}$	$F = 4.5901 W^{1.1793}$
Common slope	$F = 9.8355 W^{1.1274}$	$F = 7.9502 W^{1.1274}$
Length x Weight		
By ground	$W = 0.0185 L^{2.8999}$	$W = 0.0271 L^{2.8399}$
Common slope	$W = 0.0212 L^{2.8724}$	$W = 0.0230 L^{2.8724}$