

# POPULATION BIOLOGY OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, STOCKS IN THE WASHINGTON-QUEEN CHARLOTTE SOUND REGION, AND THEIR RESPONSE TO FISHING<sup>1</sup>

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## ABSTRACT

Production and catch per unit effort of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region have declined drastically in recent years, largely as a result of Soviet and Japanese exploitation during 1966-69. In the region off Washington and southern Vancouver Island, production declined from 39,000 metric tons in 1967 to 6,000 metric tons in 1969, and catch per hour declined 45% during the same period. Pacific ocean perch are ovoviviparous, and so their populations lack the resilience of highly fecund, oviparous groups such as the gadoids. Their ability to maintain even current levels of abundance is uncertain.

Age composition, growth rates, and mortality rates were estimated for two separate stocks occupying this region: one in Queen Charlotte Sound, B.C., and one occupying the area off northern Washington and southern Vancouver Island. Instantaneous rate of natural mortality was estimated to lie between 0.1 and 0.2. Recruitment to the fishing grounds is not complete until age 16 and the proportion of each age group vulnerable to fishing was estimated by stock for age groups 10 (0.31-0.35) through 15 (0.87-0.94).

Age at sexual maturity ( $t_{0.50}$ ) differed between stocks, ranging from 9 to 11 yr for females and 6 to 7 yr for males. Fecundity was determined for several females, and the fecundity-length and fecundity-age relationships discussed. For a variety of reasons, all fecundity estimates were regarded as tentative, bearing a rather uncertain relationship to the number of larvae released.

The effects of fishing on stocks of Pacific ocean perch were examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment, although the computer program developed for this study enabled estimation of exploitable biomass and population fecundity as well as yield per recruit.

Compensatory mechanisms that would tend to restore population fecundity and recruitment to preexploitation levels were discussed, and the limits of some of these mechanisms (density dependent growth and earlier sexual maturation) were explored with the computer program mentioned previously. The results of this analysis suggested that past levels of exploitation went far beyond those levels that could be sustained by Pacific ocean perch stocks on a long-term basis. It was concluded that future rates of exploitation should be regulated so that the annual catch never exceeds 10% of the mean stock biomass on hand during the year.

Pacific ocean perch, *Sebastes alutus* (Gilbert), are found throughout the northern Pacific, from California to the Bering Sea, and as far southwest as the Kurile Islands. Murphy (1968) has shown that species with several reproductive age-groups are well adapted to unpredictable levels of larval mortality, and Pacific ocean perch seem to be a prime example of this line of evolution. Twenty-year-olds are common in this species, and there are 10 or more reproductive age-groups of significance. In the unexploited state, large standing

stocks of *S. alutus* accumulated, furnishing a substantial hedge against uncertain larval survival. Quast (1972) estimated the original catchable biomass of *S. alutus* off western North America to be roughly 1,750,000 metric tons.

Commercial fishing for *S. alutus* was initiated in 1946 by U.S. trawlers operating off central Oregon (Alverson and Westheim 1961). Development proceeded slowly, but by 1955, United States and Canadian vessels were harvesting *S. alutus* from as far north as Queen Charlotte Sound, B.C. Westheim et al. (1972) have characterized the North American trawl fishery for Pacific ocean perch as undergoing a short development period (1946-51) with low production, a longer period (1953-60) of moderate production, and a short period (1961-66) of increasing production. Since

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1966, Pacific ocean perch production has fallen drastically in several areas fished by these North American trawlers, largely because of excessive catches by Japanese and Soviet fleets.

Japanese and Soviet trawl fisheries for Pacific ocean perch began in the Bering Sea about 1960 and expanded southward into the eastern Gulf of Alaska in 1963. The Soviet fleet operated throughout the Queen Charlotte Sound-Oregon region by 1965, and they were joined by Japanese trawlers in 1966. Catches from the Oregon-Queen Charlotte Sound region were quite high initially (Figures 1 through 3), but the stocks were far too limited to sustain these harvests. By 1969, *S. alutus* stocks were severely depleted throughout the Oregon-Vancouver Island region (Figures 1, 2). Production in the International North Pacific Fisheries Commission (INPFC) Vancouver and Columbia areas plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period (Westrheim et al. 1972). Data on catch per unit effort (CPUE) suggest that the exploitable biomass of Pacific ocean perch in the Vancouver-

Columbia region has changed little since 1969, despite the fact that a series of relatively strong year classes have recruited to the fishery.

Pacific ocean perch stocks in Queen Charlotte Sound were affected less drastically by fishing than those in the Oregon-Vancouver Island region. Biomass estimates and CPUE data (Westrheim et al. 1972) indicated that *S. alutus* were initially more abundant in the former area and that they did not undergo such intensive exploitation. During 1966-68, production declined 50% while CPUE of Washington trawlers declined 36%. Fishing effort was reduced substantially after March 1971, when most of Queen Charlotte Sound was declared to be an exclusive Canadian fishing zone. Bilateral agreements between Canada and the United States allowed the traditional United States fishery for *S. alutus* to continue, but Japanese and Soviet fishing was prohibited. Recent information, however, indicates that in 1974, large catches of Queen Charlotte Sound Pacific ocean perch were made by Japanese vessels

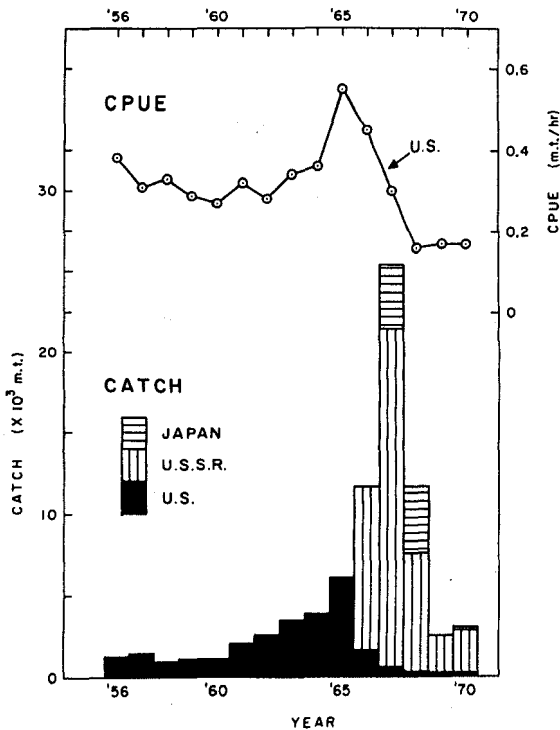


FIGURE 1.—Catch and CPUE data for Pacific ocean perch in the INPFC Columbia area (from Westrheim et al. 1972).

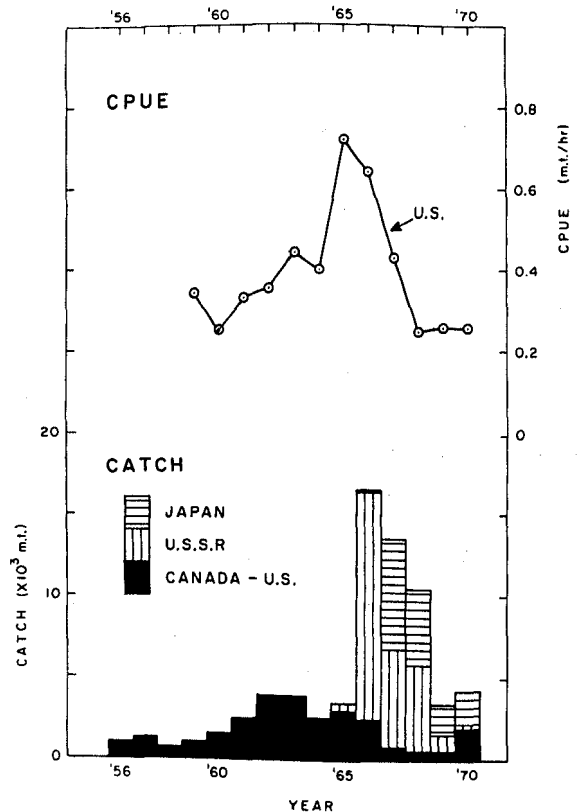


FIGURE 2.—Catch and CPUE data for Pacific ocean perch in the INPFC Vancouver Area (from Westrheim et al. 1972).

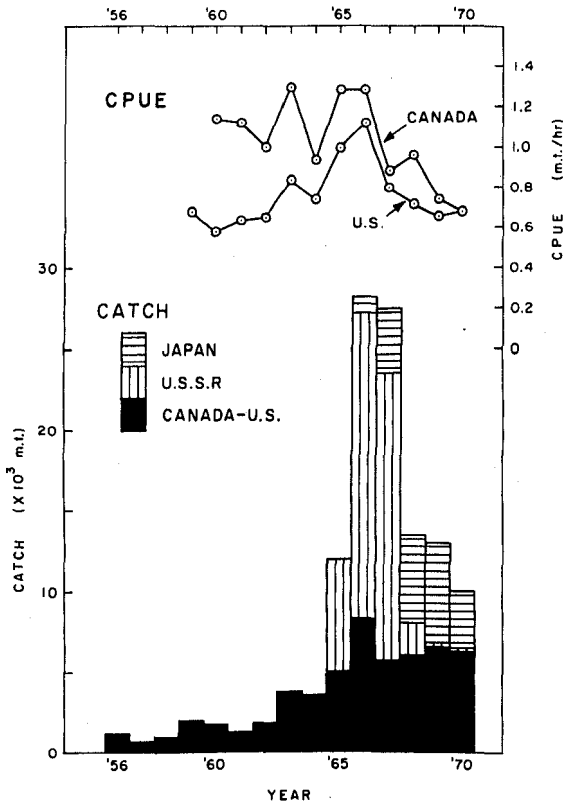


FIGURE 3.—Catch and CPUE data for Pacific ocean perch in Queen Charlotte Sound (from Westrheim et al. 1972).

operating outside the Canadian fishing zone (Gunderson et al. 1977).

Both biomass and longevity have been drastically reduced for Pacific ocean perch throughout the Washington-Queen Charlotte Sound region, and it seems unlikely that the current situation will be stable over the long term. The purpose of this study is to outline the population biology of *S. alutus* stocks in the Washington-Queen Charlotte Sound area and to examine their immediate and long-term response to different harvesting strategies.

## METHODS AND MATERIALS

### Delineation of Stocks

Two stocks of *S. alutus* will be examined and contrasted: one in Queen Charlotte Sound (QCS) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI).

The QCS stock is contained wholly within Queen Charlotte Sound. North of lat. 52°N, the continental shelf off western Graham Island is quite narrow and there is little available habitat for *S. alutus*. Recent work by Westrheim<sup>3</sup> has shown that previously unexploited stocks exist in Moresby Gully, an undersea canyon extending into Hecate Strait, north of lat. 52°N. The Triangle Islands form a definite southern limit for this stock, since Pacific ocean perch catches immediately south of these islands are almost negligible. Pacific Marine Fisheries Commission (PMFC) statistical areas 5A and 5B offer a convenient unit for studying this stock.

The northern limit of the WVI stock lies somewhere near the middle of Vancouver Island and, for practical reasons, this was represented by the northern boundary of PMFC area 3C (lat. 49°N). Pacific ocean perch catches in PMFC area 3D have been quite limited historically (Figure 4), and during 1966-72, only 13% of the Washington landings in the INPFC Vancouver area came from there (Table 1).

The southern limit of the WVI stock is more difficult to establish. Since Pacific ocean perch catches by Washington trawlers fall off sharply south of PMFC area 3B-3C (lat. 47°20'N), this was the boundary used throughout this study. This boundary, as well as the others used in this report, is in basic agreement with Snytko (1971), whose

<sup>3</sup>Westrheim, S. J. 1974 Echo-sounder and trawl survey of Queen Charlotte Sound and southern Hecate Strait, 1971-73. Fish. Res. Board Can. Manusc. Rep. 1307, 43 p.

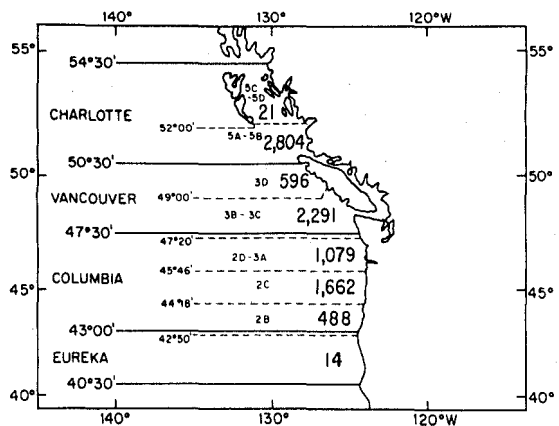


FIGURE 4.—Chart of the northeastern Pacific Ocean showing INPFC and PMFC statistical areas used in this study. Mean annual Pacific ocean perch catch (metric tons) during 1960-65 (heavy lettering) is shown for each PMFC Area.

TABLE 1.—Catches (in metric tons) of Pacific ocean perch by different components of the international trawl fleet, 1966-72.

Year	Washington			United States and Canada		All nations	
	3B-3C	3B-3D	5A-5B	3B-3D	5A-5B	3B-3D	5A-5B
1966	2,104	2,283	5,616	2,358	8,252	16,358	27,054
1967	701	783	5,341	805	5,745	17,746	26,741
1968	459	526	4,787	552	6,051	9,905	13,492
1969	462	573	4,992	583	6,628	4,513	12,951
1970	980	1,208	4,308	1,955	6,077	4,955	9,854
1971	638	718	2,925	1,155	4,165	4,138	4,867
1972	419	504	3,364	624	5,561	3,082	7,842
Total	5,763	6,595	31,333	8,032	42,479	60,697	102,801

research cruise data suggested that the two most significant aggregations of *S. alutus* in the Vancouver-Oregon region were found at lat. 48°-50°N and lat. 46°-47°N. For all practical purposes then, PMFC Statistical areas 3B and 3C offer a convenient unit for studying the WVI stock.

### Data Employed

Production records used in this study came from the Washington State Department of Fisheries, PMFC, INPFC, and from data furnished during U.S.-U.S.S.R. scientific meetings.

Landings by Washington trawlers made up a relatively small proportion of the total international landings during the 1966-72 study period, but the quality of their production records is such that the CPUE data from this fleet offer the best available index of stock abundance. During 1966-72, the Washington landings made up 30% of the total international catch from Queen Charlotte Sound, and 11% of the catch from the INPFC Vancouver area (Table 1). Washington trawlers accounted for the bulk of the North American landings in these areas, however, landing 74% of the Pacific ocean perch caught in Queen Charlotte Sound and 82% of those from the INPFC Vancouver area during 1966-72.

Most of the data on age composition (as determined from otoliths), length composition, and maturity were obtained by sampling the catches landed by Washington trawlers and were collected during 1967-72. Data from research vessel cruises off Washington and Oregon were used to estimate growth rates and fecundity-length relationships for the WVI stock.

## MIGRATIONS AND AVAILABILITY

### General Features of the Life History

Extensive investigations into the life history of

*S. alutus* have been carried out in the Bering Sea (Paraketsov 1963; Pautov 1972; Chikuni 1975), Gulf of Alaska (Lyubimova 1963, 1964, 1965; Fadeev 1968; Chikuni 1975), and in the Queen Charlotte Sound-Oregon region (Alverson and Westrheim 1961; Westrheim 1970, 1973, 1975; Gunderson 1971, 1974; Snytko 1971). These studies have shown that there are several basic similarities in the life history and biology of Pacific ocean perch throughout its range.

Age and growth analyses have shown that *S. alutus* attain sexual maturity relatively late in life (6-10 yr), grow slowly, and are long-lived. In lightly fished stocks, *S. alutus* may reach an age of 30 yr (Alverson and Westrheim 1961; Paraketsov 1963).

*Sebastes alutus* is an ovoviviparous species, with three distinct phases in its reproductive cycle. These are: mating (when spermatozoa are transferred from males to females), fertilization (when the ova are actually fertilized), and spawning (when the larvae are released).

Well-defined bathymetric migrations occur in all areas. Pacific ocean perch occupy relatively shallow water during the summer feeding period, then move to deep water during winter. The depths inhabited seem to vary little throughout the geographic range, despite significant differences in thermal conditions (Table 2). Mating occurs shortly before or during migration from shallow water, but fertilization and embryo release do not occur until the fish are in deep water.

The larvae of *S. alutus* are pelagic and do not settle into a demersal existence until 2-3 yr old. Juveniles and young adults are confined to the shallowest portions of the adult bathymetric range, so that size and age composition vary widely at different depths.

Despite these common characteristics, there are substantial geographic differences in life history and migration patterns, even within the relatively restricted region dealt with in this study. For this reason, migration patterns, seasonal availability, age composition, growth, age at maturity, and

TABLE 2.—Depth and temperature characteristics of Pacific ocean perch habitat.

Area	Depths of maximum abundance (m)		Temperature (°C)	
	Summer	Winter	Range	Optimum
Vancouver-Oregon (Snytko 1971)	200-300	350-450	4.0-9.5	6-8
Gulf of Alaska (Lyubimova 1965)	180-250	250-420	2.5-6.5	3-5
Bering Sea (Pautov 1972)	150-350	350-450	1.0-6.0	3-4

fecundity must be discussed separately for the QCS and WVI stocks.

### Migrations and Availability Within the Study Area

Availability of *S. alutus* fluctuates widely over short periods of time. Short-term fluctuations in availability were quite evident during a series of 2- to 3-wk research cruises off the Washington coast (Gunderson 1974), and masked any long-term changes in biomass that occurred during 1968-72.

For this reason, catch and CPUE data can be used to study migration patterns and seasonal availability only if they are based on a large quantity of trawling effort, carried out more or less continuously. The data from the Washington trawl fleet seem well suited to this purpose, since these trawlers spend a great deal of time searching out and catching Pacific ocean perch. *Sebastes alutus* is frequently the target species for this fleet, and made up 29% of its total coastal landings during 1967-71.

In this section, catch and effort data from the Washington trawl fleet will be used to describe migration patterns and seasonal trends in the availability of *S. alutus*. Data on sex and length composition of the catch will also be brought into the analysis, since it is difficult to interpret trends in availability without them.

### Queen Charlotte Sound

#### Seasonal Patterns for the Region

The continental shelf is steep and untrawlable seaward of 150 fm (274 m) in Queen Charlotte Sound, so the fish in this area are inaccessible to trawlers when they move into deep water (January-April). Examination of gonads indicates that spawning occurs in March (Gunderson 1971), but there is no certainty as to where this occurs. Few fish are caught during January-April, and virtually all of these are males (Figure 5) that do not participate in the spawning migration.

Males precede females in their return from wintering areas, and when the fishery first begins in earnest (May), males constitute 68% of the catch. The availability of females increases sharply after May, and by July they dominate the catches.

During June-August, Pacific ocean perch are at the shallowest point in their bathymetric cycle. Catches are low during this period, and large quantities of fish 35 cm or smaller are landed (Figure 6).

Both catch and CPUE rise in September, and although the mean depth of catch is about the same as in July and August, there is a sharp increase in the proportion of fish larger than 35 cm in the catch. Aggregations of large adults must suddenly become available during September, probably because mating activities are beginning.

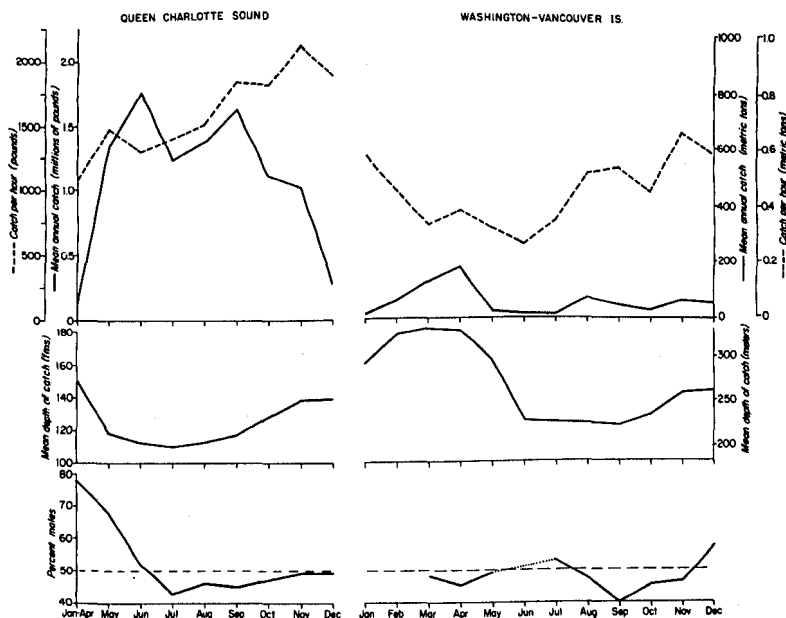


FIGURE 5.—Mean monthly catch, catch per hour, mean depth of catch, and sex ratio for the Washington trawl fleet during 1967-71. Data for the QCS and WVI stocks of Pacific ocean perch are represented separately.

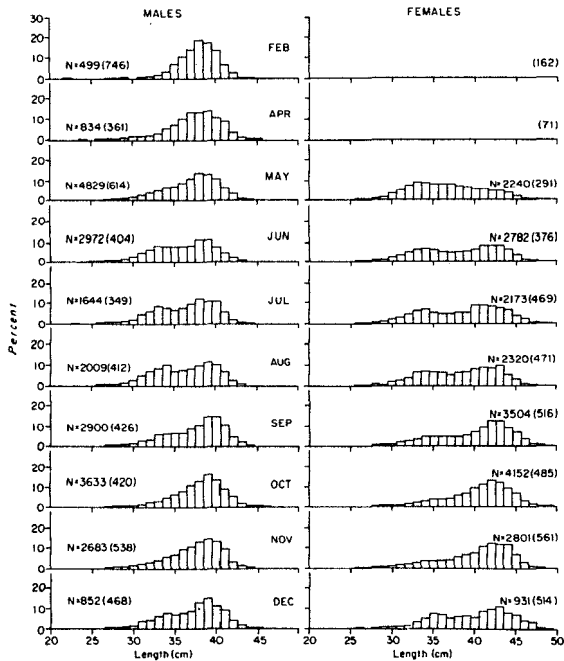


FIGURE 6.—Size composition of 1967-71 Pacific ocean perch catches from Queen Charlotte Sound, by month. Mean numbers caught per hour during 1967-71 are shown in parentheses.

Previous work (Gunderson 1972) has shown that these aggregations are faster growing, but only slightly older, than the rest of the stock.

Pacific ocean perch move into progressively deeper water during October-December, as they return to deepwater spawning areas. Catch per hour remains high during this period, but deteriorating weather conditions force a decline in trawling effort and landings.

Because catch, CPUE, sex ratio, length composition, and age composition all varied with season, the data from different time periods were treated independently in much of the later analysis. The

time periods utilized were January-April, May, June-August, and September-December.

#### Seasonal Patterns for Specific Grounds

The geographic distribution of the catch varied from month to month (Figure 7) and there is a possibility that between-ground variations in size composition could contribute to the results shown in Figure 6. Length and age composition data were analyzed by fishing ground (Figure 8) to examine this point further. To insure that the data used were as typical as possible of the grounds in question, only samples from characteristic fishing depths were chosen for this analysis. The 1967-71 mean depth of catch was computed for each month and ground in question, and only those samples whose range was within 15 fm (27 m) of this mean were analyzed.

The results (Figure 9) show that within a given time period, length composition differed somewhat between grounds, but the differences showed no consistent, predictable pattern. There was no ground that could always be characterized as having larger or smaller fish than the other grounds. Size composition data for SE Corner, SW Corner, and Triangle grounds, the three major fishing grounds, showed only slight between-ground heterogeneity within any given time period.

#### Washington-Vancouver Island

Unlike Queen Charlotte Sound where the continental shelf drops off abruptly past 150 fm (274 m), a wide range of depths can be fished off Washington and Vancouver Island (Figure 5). Trawlers can follow fish in this area into deepwater spawning areas, and exploit them year around. The year can be divided into a

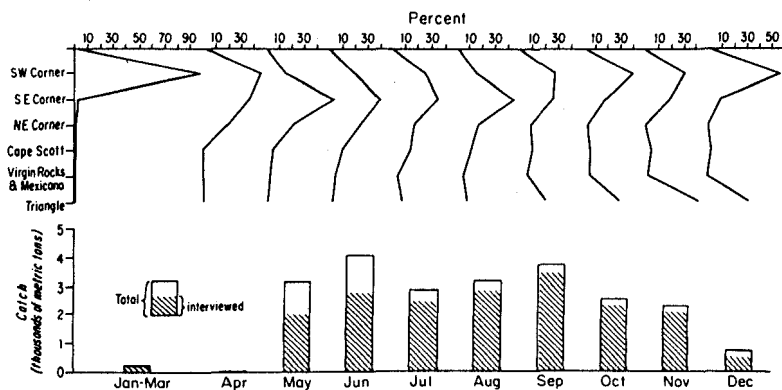


FIGURE 7.—Distribution of 1967-71 Pacific ocean perch catch from Queen Charlotte Sound by month and fishing ground. Data on distribution by ground were derived from the portion of the catch for which fishermen interviews were available. The Virgin Rocks-Mexicana ground includes Virgin Rocks and all grounds east of the Cape Scott ground.

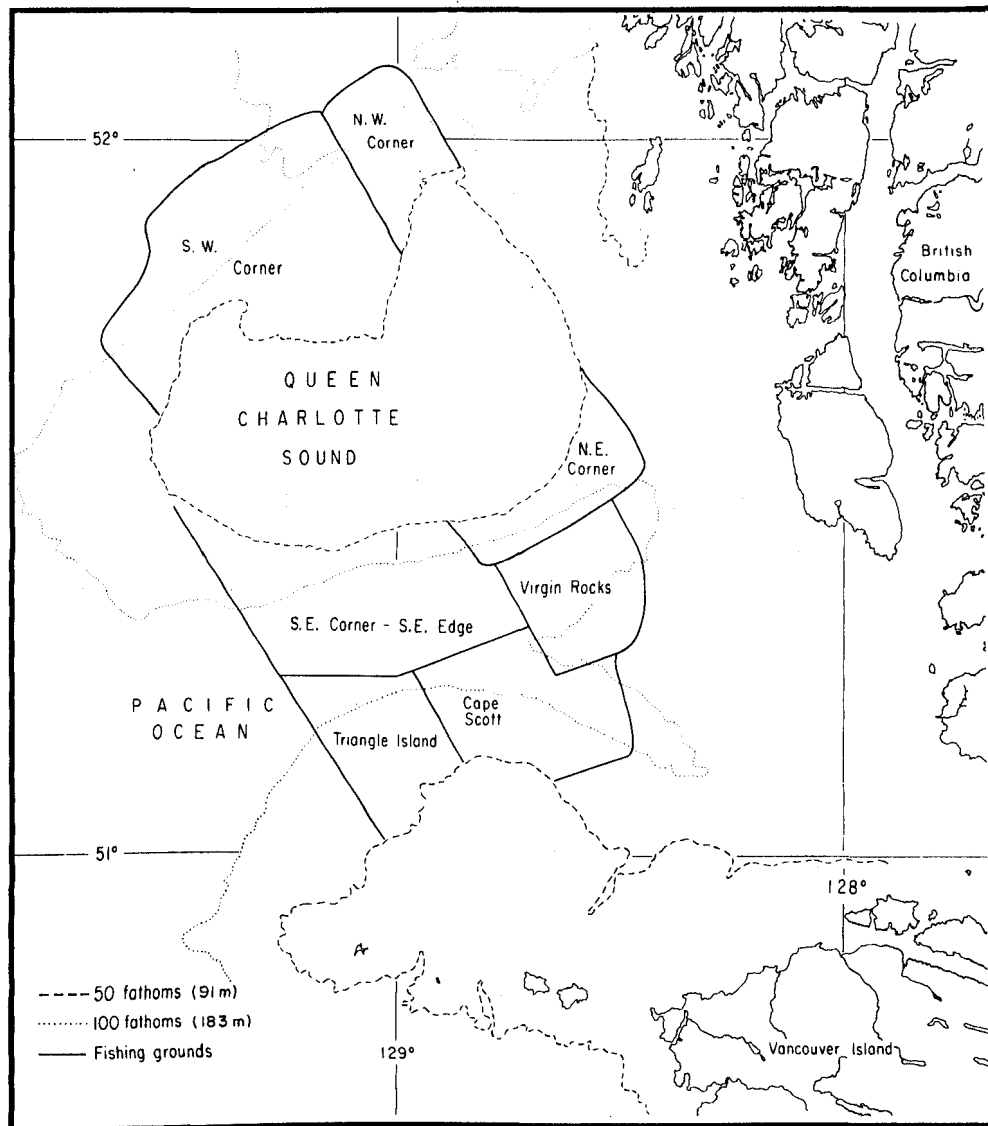


FIGURE 8.—Major Pacific ocean perch fishing grounds in Queen Charlotte Sound, B.C.

November-May period when most of the fish are in deepwater spawning areas, and a June-October period when they are in shallow water. Mean depth of catch is 140-180 fm (256-329 m) during the November-May period, and 120-130 fm (219-238 m) during June-October.

Seasonal variability in the biological composition of the catch is less significant than in Queen Charlotte Sound, since the sex ratio is close to 50% males all year. Data on the size composition of the catch was quite limited during certain months, but size composition generally seemed to depend

on the depths at which the fishery was operating. The proportion of small fish (35 cm or smaller) in the landings was highest during the shallow-water fishery, and decreased during November-May (Figure 10).

Considering the wide differences in the magnitude of the landings between Washington-Vancouver Island and Queen Charlotte Sound, CPUE levels are surprisingly similar (Figure 5). Results of research cruises have shown that the availability of Pacific ocean perch varies widely in the Washington-Vancouver Island region (Gun-

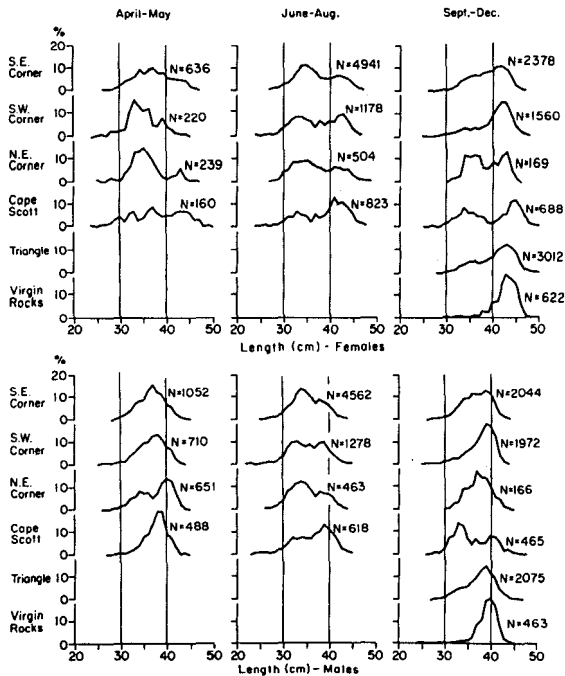


FIGURE 9.—Size composition of 1966-72 Pacific ocean perch catches in Queen Charlotte Sound, by fishing ground and season.

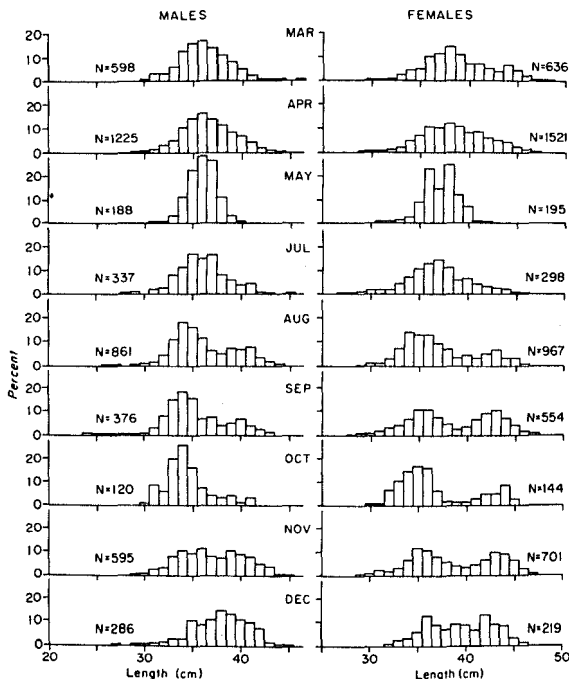


FIGURE 10.—Size composition in 1967-71 Pacific ocean perch catches from Washington-Vancouver Island, by month.

person 1974), and fishermen probably restrict their efforts to periods of high availability. If this is the case, the relative levels of monthly catch give the best index of stock availability. Peak availability occurs during March-April (near the time of embryo release) and in August-December (near the mating period). This pattern of seasonal availability agrees well with results from previous studies of the WVI stock (Gunderson 1971; Snytko 1971).

## AGE-LENGTH RELATIONSHIPS

### Queen Charlotte Sound

The age-length relationship in any sample of Pacific ocean perch from Queen Charlotte Sound is influenced by the availability of large, fast-growing fish, the depth at which the fish were captured, and the proportion of the annual growth completed. In order to examine the relative importance of these factors, analysis similar to that outlined by Gunderson (1974) was employed.

This involved fitting observed mean length at age data to the von Bertalanffy growth model,

$$l_t = L_\infty(1 - \exp(-K(t - t_0)))$$

where  $l_t$  = length of fish in centimeters at  $t$  years  
 $L_\infty$  = theoretical asymptotic length  
 $K$  = constant expressing the rate of approach to  $L_\infty$   
 $t_0$  = theoretical age at which  $l_t = 0$ .

The least squares technique of Tomlinson and Abramson (1961) was employed to do this, and a separate age-length relationship was computed for each combination of fishing ground and season (April-May, June-August, and September-December) where adequate data were available. All comparisons of the age-length relationship at different grounds and seasons could then be made by comparing fitted length at some common age (age 15 in this case).

The results (Figure 11) show that the age-length relation is more dependent on the availability of fast-growing fish to bottom trawls than on any other factor examined. The main line of evidence supporting this is the close correspondence between changes in fitted length at age 15 (Figure 11) and seasonal changes in size composition (Figure 9), a situation that would be expected if both depend on the availability of large, fast-growing



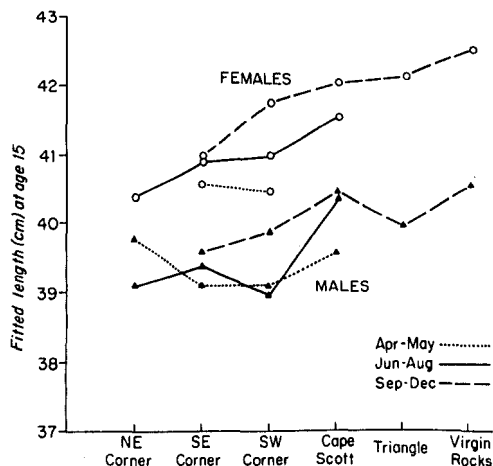


FIGURE 11.—Fitted length at age 15 for Pacific ocean perch in Queen Charlotte Sound (1966-72), by fishing ground, season, and sex.

fish. Both age-length and size composition data indicate that aggregations of these fish are least available during April and May, and that it is only during September-December that they are fully available on all fishing grounds. This general pattern seemed to hold throughout Queen Charlotte Sound, at least on the major fishing grounds. In some instances, however, availability of large, fast-growing fish was unusually high on a relatively minor fishing ground. This seemed to be the case at NE Corner during May and Cape Scott during June-August (Figures 9, 11).

Sampling problems caused by disproportionate fishing intensity in extremes of the bathymetric range are usually insignificant compared with the problems caused by differential availability. Research cruises have shown that mean length at age decreases as depth increases (S. J. Westheim, pers. commun.), so that fitted length at age 15 should either remain constant (if fishery shifts in response to stock location) or decrease (if fishery shift is independent of stock location) as the fishery shifts to deeper water during September-December (Figure 5). Instead, mean length at age actually increases during September-December (Figure 11) because this is the season when large, fast-growing fish are most available.

Considering all sources of data on catch, CPUE, and biological composition of the landings, it is apparent that there is a significant increase in the size of the exploitable population inhabiting Queen Charlotte Sound during September-December. Age-length data collected during

January-August consequently apply to only a fraction of the known population in Queen Charlotte Sound. If it is assumed that all Pacific ocean perch are fully vulnerable to fishing by fall, however, the September-December market sampling data can be taken as representative of the exploitable segment of the QCS stock.

Consequently, 1967-71 age-length data from September-December market samples were used to estimate growth parameters for the QCS stock. Queen Charlotte Sound was treated as a unit, mean length at each age was determined by sex, and the resulting data were fitted to the von Bertalanffy growth model. Both the original data and fitted mean length at age are shown in Table 3.

### Washington-Vancouver Island

Availability of Pacific ocean perch in this region influences the age-length relationship, but in a different manner than in Queen Charlotte Sound. Results from research surveys off northern Washington (Gunderson 1974) suggest that mean length at age actually decreases with increasing availability, rather than increasing. The highest rates of catch in this region were obtained when aggregations of large, old, slow-growing fish were most available.

The WVI and QCS stocks also differ substantially in the degree to which mean length at age varies with depth. In contrast to Queen Charlotte Sound, mean length at age has been shown to decrease sharply as depth increases off Washington and Vancouver Island (Westheim 1973; Gunderson 1974). The decline is so sharp, in fact, that Westheim (1973) has suggested that there are separate shallow and deepwater stocks in this region.

It is clear, then, that both depth of fishing and availability must be taken into consideration in order to arrive at an age-length relationship that characterizes the WVI stock. Research cruise data obtained off the coast of northern Washington (Gunderson 1974) are particularly well suited to do this, since age-length relationships and availability were systematically observed throughout the bathymetric range. Availability varied widely during these cruises, and, as previously mentioned, this phenomenon masked any long-term changes that occurred during 1968-72. Availability was maximal during the July 1972 cruise, however, and the results from that cruise were used to represent growth in the WVI stock.

TABLE 3.—Number of age-length observations, mean length (centimeters), and fitted length at each age for QCS and WVI stocks of Pacific Ocean perch.

Age	QCS stock						WVI stock					
	Males			Females			Males			Females		
	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length	Number of observations	Mean length	Fitted length
2							3	18.0	18.1	2	18.5	19.1
3							1	22.0	21.2	1	22.0	21.6
4							10	23.7	23.9	11	24.5	24.0
5	8	27.0	26.6	4	26.2	26.0	18	25.8	26.3	6	26.5	26.1
6	19	29.1	28.6	26	29.4	28.4	9	28.3	28.4	10	28.1	28.0
7	70	30.0	30.5	73	30.6	30.6	8	29.6	30.2	5	28.5	29.8
8	164	31.6	32.2	124	32.1	32.6	34	32.3	31.8	21	31.4	31.4
9	186	33.1	33.6	173	33.5	34.3	58	33.2	33.2	22	33.2	32.9
10	219	34.4	35.0	213	34.8	35.9	123	34.2	34.4	71	34.6	34.3
11	233	36.1	36.1	179	36.3	37.2	172	35.5	35.5	123	35.7	35.5
12	411	37.4	37.1	253	38.3	38.5	78	36.3	36.5	89	36.5	36.6
13	463	38.5	38.0	374	40.0	39.6	42	37.0	37.3	72	37.6	37.6
14	417	39.4	38.9	459	41.2	40.6	59	38.0	38.0	57	38.0	38.6
15	308	40.1	39.6	468	42.2	41.4	56	38.9	38.6	58	39.0	39.4
16	203	40.5	40.2	377	43.2	42.2	50	39.7	39.2	61	40.8	40.2
17	116	41.1	40.8	308	43.6	42.9	37	40.2	39.7	75	41.3	41.0
18	80	41.1	41.3	186	44.0	43.6	24	40.8	40.1	52	41.7	41.6
19	30	41.6	41.7	115	44.4	44.1	29	41.1	40.5	36	42.2	42.2
20	14	41.9	42.1	92	44.2	44.6	16	41.3	40.8	30	42.4	42.7
21	13	41.9	42.5	36	45.1	45.0	7	41.4	41.1	14	43.7	43.2
22				10	45.0	45.4	2	39.0	41.4	16	43.6	43.7
23				3	45.3	45.8				7	43.9	44.1
24				7	45.6	46.1				4	44.5	44.5

von Bertalanffy growth function parameters			
$L_{\infty}$	45.25	48.75	43.15
$K$	0.1192	0.1135	0.1320
$t_0$	-2.4157	-1.7159	-2.1186
SE of estimate	0.44	0.64	0.68
			0.45

Data from the 120-, 160-, and 200-fm (219-, 293-, and 366-m) sampling stations were combined by weighting the mean length at each age by the catch rate of Pacific ocean perch in that depth stratum and arriving at an overall weighted mean length for each age group (Table 3). The calculations were carried out separately for males and females, and the resulting age-length data were then fitted to the von Bertalanffy growth model using the technique described previously.

The results (Table 3) suggest that fish off Washington grow somewhat slower than those in Queen Charlotte Sound. In order for the results from the two stocks to be strictly comparable, however, several research cruises should have been made in Queen Charlotte Sound during September-December. The age-length data from those cruises where availability was maximal could then have been weighted in proportion to the catch rate for each depth stratum, as was done for the WVI stock. If fishermen effectively "sample" in proportion to abundance, however, the results from commercial fisheries data should agree well with those from research cruises.

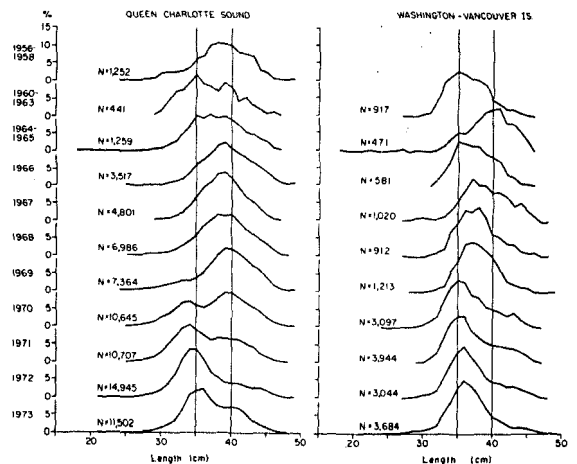
FIGURE 12.—Changes in the size composition (sexes combined) of Pacific ocean perch in commercial catches, 1956-73. N = number of fish sampled.

## ANNUAL CHANGES IN SIZE AND AGE COMPOSITION

### Size Composition

#### Queen Charlotte Sound

The Washington State Department of Fisheries has obtained size composition data on landings from Queen Charlotte Sound since 1956. Collection of such data was limited and sporadic prior to



1967, but a good series of data, taken over the entire year, is available for each year during 1967-73.

Because a limited number of samples was available during 1956-66, it was frequently necessary to pool data from adjacent years when examining temporal trends in size composition. The results (Figure 12) furnish the only available estimates of the size composition of Pacific ocean perch in 1956-66 Washington trawl landings.

Collection of biological data was quite intensive during 1967-73, and it was possible to make allowances for the extensive seasonal changes in length and sex composition that occur in Queen Charlotte Sound. The Sound was treated as a single geographic unit, but size composition was determined separately for each of the four time strata previously discussed (January-April, May, June-August, and September-December). If few landings were made in one of these strata, it was combined with an adjacent stratum, and biological data from the latter were used to represent it. Table 4 shows the time strata used for each year's catch data, the landings in each stratum, and the amount of biological data collected.

Males and females differ in relative abundance and size composition, so they were treated separately. Mean weights of males and females in each time stratum were obtained by employing the

length-weight relation (sexes combined) reported by Westrheim and Thomson (1971), together with the appropriate length frequencies in that stratum. The number of males and females landed in each stratum could then be estimated by dividing total pounds landed by the mean weight of fish in that stratum. These values were combined with size composition data to obtain the number of fish landed by time period, sex, and size group. Pooling these data by year and expressing the results in terms of percent frequency yielded the results shown in Figure 12.

Substantial quantities of large Pacific ocean perch were present in Queen Charlotte Sound during 1956-58. Subsequent changes in size composition reflect changes caused by the commercial fishery and by recruitment of two strong series of year classes. The first series of year classes was centered around the 1952 year class and included the 1951-53 brood years (Westrheim et al. 1972). The presence of this series first became apparent in the 1960-63 landings, when the modal size was 35 cm—corresponding to an age of about 10 yr. The 1952 year class series caused the modal size to move progressively toward the right during 1960-70 (as its members grew in length), but seemed to have little influence on size composition in subsequent years. This is probably the cumulative result of large fishery removals during 1965-69, when the 1952 year class would have been 13-17 yr old.

A second series of strong year classes, centered around the 1961 and 1962 brood years (Westrheim et al. 1972) first showed up in the 1970 landings, when there was a secondary mode at 34 cm. This series of year classes came to dominate the landings during 1971-73, since the abundance of older fish had been drastically reduced by commercial fishing.

#### Washington-Vancouver Island

Size composition data from this region were more limited than data from Queen Charlotte Sound and it was never possible to analyze different time strata separately. All size composition data were summarized by year to produce the data in Figure 12. Data from 1956 to 1965 were especially limited and size composition data from adjacent years frequently had to be combined. This was done in such a manner that direct comparisons with Queen Charlotte Sound could be made.

Research surveys during 1965 (Westrheim

TABLE 4.—Time strata used for analysis of 1966-73 size and age composition data from Queen Charlotte Sound. Pacific ocean perch catch by Washington trawlers (metric tons) and amount of biological data collected in each stratum are also shown.

Year	Time stratum	Washington trawl catch	Origin of biological data	Number of fish sampled for	
				Length-sex	Age
1966	Sept.-Dec.	2,723	Oct.-Dec.	3,517	1,419
1967	Mar.-May	868	May	1,104	433
	June-Aug.	2,817	June-Aug.	1,049	848
1968	Sept.-Dec.	1,656	Sept.-Dec.	2,648	1,183
	Jan.-Apr.	220	Jan.-Apr.	1,470	680
	May	842	May	1,310	505
	June-Aug.	1,870	June-Aug.	1,165	608
1969	Sept.-Dec.	1,855	Sept.-Nov.	3,041	1,011
	Jan.-May	687	May	648	298
	June-Aug.	2,205	June-Aug.	2,461	698
	Sept.-Dec.	2,099	Sept.-Dec.	4,255	714
1970	Jan.-May	546	Apr.-May	2,435	498
	June-Aug.	1,749	June-Aug.	4,214	649
	Sept.-Dec.	2,014	Oct.-Dec.	3,996	497
1971	Apr.-Aug.	1,446	May-Aug.	6,974	1,004
	Sept.-Dec.	1,480	Sept.-Dec.	3,733	1,232
1972	Apr.-May	379	May	3,174	887
	June-Aug.	1,568	June-Aug.	7,337	2,587
	Sept.-Dec.	1,417	Sept.-Nov.	4,434	1,321
1973	Mar.-Apr.	530	Apr.	2,940	942
	May	244	May	1,201	398
	June-Aug.	1,019	June-Aug.	5,058	1,658
	Sept.-Dec.	472	Sept.-Nov.	2,303	803

1970) suggested that the 1952 year class dominated here, as well as in Queen Charlotte Sound, and the results (Figure 12) tend to support this conclusion. The modal size was 35 cm for the 1960-63 period, and this corresponds to an age of about 10 yr. The 1966-67 size composition data also reflect the presence of a strong 1952 year class series, but is not possible to follow the series past 1967. Extensive fisheries removals during 1966-68 resulted in sharply attenuated right-hand limbs for 1968-73 size composition curves, and the 1952 year class series was presumably swallowed up in these removals.

As in Queen Charlotte Sound, the strong 1961-62 year class series first showed up on the 1970 landings, when there was a mode at 35 cm. Because the biomass of older fish had been drastically reduced by the extensive fisheries removals of 1966-68, these year classes dominated the catches in the first year they appeared and in each subsequent year.

## Age Composition

### Queen Charlotte Sound

Age composition data for the Washington trawl landings from Queen Charlotte Sound have been collected since 1966. A series of data taken over the entire year is available for each year during 1967-73.

The procedure used to estimate the age composition of the 1967-73 landings was identical to that employed in the section on size composition. The number of fish landed in each time stratum was combined with the age-frequency data for that stratum to estimate the number of fish landed by age-group, sex, and time stratum. Pooling these data by year and dividing by the total Washington trawl effort expended in Queen Charlotte Sound yielded annual estimates of the number caught per hour, by age-group, and of percent age composition (Figure 13).

The 1952 year class series was centered around age 13 in 1965 and was almost fully vulnerable to fishing when the Queen Charlotte Sound fishery began its dramatic expansion. The cumulative effects of the extensive removals of 1966-67 were such that the 1951-53 year classes no longer dominated the catches after 1967-68. The 1952 year class series was exploited far more intensively than preceding year classes, and by the time the 1951-53 year classes were 17-19 yr old, they were

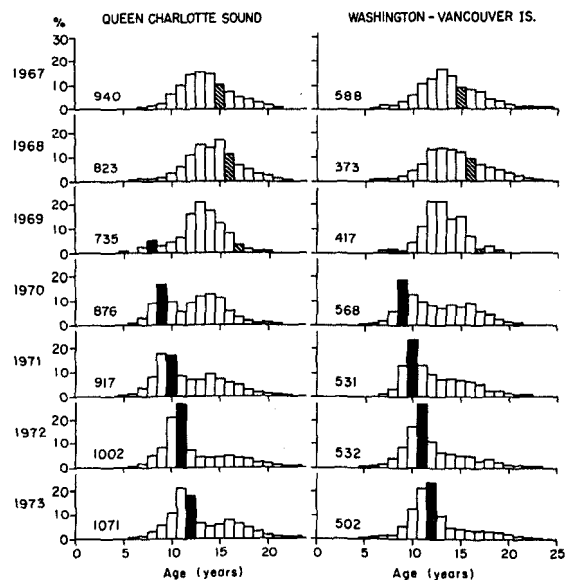


FIGURE 13.—Changes in the age composition (sexes combined) of Pacific ocean perch in commercial catches, 1967-73. The number of fish caught per hour is shown for each year, and the 1952 and 1961 year classes have been indicated by shading.

less abundant than the relatively weak 1948-50 year classes had been at corresponding ages. This can be seen by comparing the abundance of 17-19 yr olds in 1970 (45 fish caught per hour) with their abundance in 1967 (118 fish caught per hour).

During 1970 and 1971, recruitment of the strong 1961 and 1962 year classes to the fishery restored the abundance of Pacific ocean perch to 1967 levels (Figure 13) and the number of fish caught per hour continued to increase through 1973. The condition of the QCS stock in 1973 was far from satisfactory, however, since it was made up of much younger fish than those characterizing even the 1967 stock.

### Washington-Vancouver Island

No age composition data were available for Pacific ocean perch catches from the WVI stock until 1966, and it was not until 1967 that an adequate series of age composition samples was collected (Table 5). Age composition data on the WVI catches were quite limited, so no attempt was made to treat different time strata separately.

Age composition data for 1967-73 are remarkably similar to corresponding data from Queen Charlotte Sound (Figure 13). The harvests of 1966-68 sharply reduced the biomass of the 1952

TABLE 5.—Number of Pacific ocean perch from the WVI stock sampled for biological data.

Year	Length-sex	Age	Year	Length-sex	Age
1966	581	216	1970	3,089	1,124
1967	1,020	707	1971	3,944	1,460
1968	912	502	1972	3,044	1,036
1969	1,213	296	1973	3,684	1,335

year class series, which would have ranged from about 13 to 15 yr of age in 1966 and would have been almost fully vulnerable to trawling. Recruitment of the 1961 and 1962 year classes to the fishery began to restore abundance (as indicated by the number caught per fishing hour) to former levels and, as of 1970, the WVI stock was on the road to recovery. After 1970, however, the condition of the WVI stock followed an entirely different course than the QCS stock.

Exploitation rates for the QCS stock were low enough to allow an increase in abundance (number caught per hour) during 1970-73 (Figure 13), as the 1960-61 year classes became fully available to the fishery. Off Washington and Southwest Vancouver Island, however, exploitation rates remained at high levels during 1970-73, and the 1961-62 year classes were cropped off as soon as they recruited to the fishing grounds. Abundance consequently declined during 1970-73, opposite to the trend in Queen Charlotte Sound. The abundance of fish 15 yr and older was reduced below even 1970 levels, and 10 to 13 yr-old fish dominated the WVI stock as of 1973.

## RECRUITMENT TO THE FISHERY

Consideration of the length-maximum girth data presented by Westrheim and Nash (1971) indicates that gear selection should begin at a relatively small size. The internal (between-knot) measure of the cod end mesh size commonly used by Washington trawlers is about 3.25 inches (8.26 cm) and the smallest fish retained should have a girth of  $2 \times 3.25 = 6.5$  inches. This assumes that escape is not facilitated by compressibility on the one hand and that the rigidity of the trawl meshes does not hinder escape on the other. If these assumptions are valid, and the girth at 50% retention is 6.5 inches, Westrheim and Nash's results show that the 50% selection length should be 24.5 cm.

A 25.4-cm fish would be too small for market acceptance, but previous comparisons of Pacific ocean perch size composition in research catches and commercial landings (Gunderson 1972) have

indicated that 50% of all 32- to 34-cm fish on the grounds are retained by Washington trawlers. Virtually all fish 36 cm and larger are retained by the fishermen. Reference to the age-length information in Table 3 shows that the length at 50% retention corresponds to an age of about 8 or 9 yr, and that all fish older than 11 yr would be retained. Slight between-stock differences in retention would be expected, owing to differences in growth rate.

Despite the fact that all fish older than age 10 are vulnerable to the fishing gear in use, and large enough that almost all are retained for market sales, age composition data from commercial catches (Figure 13) and research surveys (Gunderson 1974) show that recruitment to the fishing grounds is not complete until much later than age 10. On the assumption that the modal age of the catch lies near the first year in which recruitment is complete, these data would imply that full recruitment could occur anywhere from age 11 to 14.

The high variability in modal size is caused by year to year variation in availability, year class strength, and fishing mortality, and one way to reduce its significance is to deal with long-term averages of relative abundance. In order to do this, a relative abundance index ( $U_i$ ) was calculated for each age group using the 1967-73 age composition data for the QCS and WVI stocks. This index was calculated as:

$$U_i = \frac{1}{7} \sum_{n=1967}^{1973} \left( \frac{C}{f} \right)_n$$

where  $U_i$  = the relative abundance of the  $i$ th age-group and  $\left( \frac{C}{f} \right)_n$  = the number of fish in the  $i$ th age-group caught per hour. Percentage age composition during 1967-73 has been calculated from these  $U_i$  data and is shown by stock in Figure 14.

The results show that although the modal age in both stocks is 11 yr, recruitment to the fishing grounds is quite gradual. In fact, it is not until age 15 that the full force of fishing mortality seems to be exerted on any given year class. Estimates of the exact proportion of the fish in each age-group that have recruited to the fishing grounds, and are vulnerable to fishing, can be derived from  $U_i$  values, starting with the relation:

$$C_i = uV_iN_i$$

where  $C_i$  = catch of fish in the  $i$ th age-group

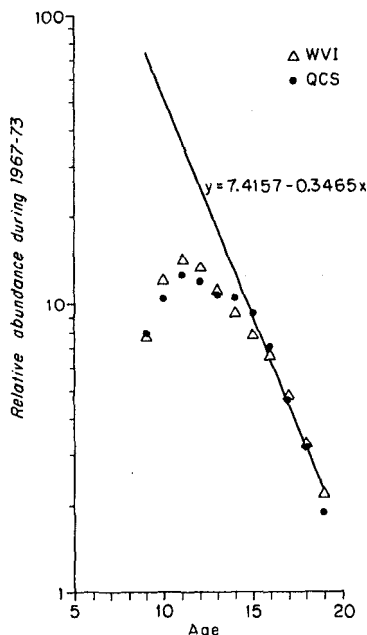


FIGURE 14.—Relative abundance of age groups 5-19 during 1967-73, for the QCS and WVI stocks of Pacific ocean perch.

- $u$  = exploitation rate
- $V_i$  = proportion of population vulnerable at age  $i$
- $N_i$  = total number of fish in the  $i$ th age-group.

Similarly,  $C_{i+1} = uV_{i+1}N_{i+1} = uV_{i+1}N_i \exp -(V_i F + M)$  if we assume that  $V_i$  remains constant throughout the year, and:

$$\frac{U_i}{U_{i+1}} \approx \frac{C_i}{C_{i+1}} = \frac{V_i}{V_{i+1} \exp -(V_i F + M)}$$

This equation can be solved iteratively for  $V_i$  if we have estimates of  $F$  (fishing mortality),  $M$  (natural mortality),  $V_{i+1}$ , and the ratio  $U_i/U_{i+1}$ .

The estimates of  $Z$  (total instantaneous mortality) and  $F$  were derived directly from the data in Figure 14. Trends in the relative abundance of 15-19 yr olds were quite similar in the QCS and WVI stocks, and  $Z$  was estimated by fitting a common regression line to the data for both stocks. The resulting regression equation for 15-19 yr olds was:

$$\log Y = 7.4157 - 0.3456X,$$

where  $Y$  = relative abundance during 1967-73,

expressed as percent frequency  
 $X$  = age in years.

The slope of this line (0.35) was used to represent  $Z$  for fully recruited age-groups. This was then separated into  $F$  and  $M$  by assuming a known value for  $M$ .

Estimation of  $V_i$  schedules began by assuming that the vulnerability coefficient for 16 yr olds ( $V_{16}$ ) was 1.0. Using the QCS data, and  $M = 0.12$  for example:

$$\frac{U_{15}}{U_{16}} = 1.31 = \frac{V_{15}}{1.0 \exp -(0.23 V_{15} + 0.12)}$$

By iteration, it was determined that  $V_{15} = 0.94$  and this value was used to determine  $V_{14}$  from:

$$\frac{U_{14}}{U_{15}} = 1.14 = \frac{V_{14}}{0.94 \exp -(0.23 V_{14} + 0.12)}$$

Again this was solved iteratively, giving  $V_{14} = 0.79$ . Proceeding backwards, the vulnerability coefficients for Queen Charlotte Sound were estimated for all age-groups 10 and older. The calculations could not be carried past age 10, since younger age-groups may be subject to substantial rates of discard by fishermen.

Estimates of the  $V_i$  schedules for both the QCS and WVI stocks are shown in Table 6. Calculations

TABLE 6.—Proportion of Pacific ocean perch population vulnerable to fishing, by age-group and stock.

Stock	$M$	10	11	12	13	14	15	16
QCS	0.12	0.32	0.45	0.53	0.62	0.79	0.94	1.00
	0.15	0.30	0.43	0.52	0.61	0.78	0.94	1.00
	Mean	0.31	0.44	0.53	0.62	0.79	0.94	1.00
WVI	0.12	0.36	0.53	0.64	0.69	0.75	0.87	1.00
	0.15	0.34	0.51	0.63	0.68	0.75	0.87	1.00
	Mean	0.35	0.52	0.64	0.69	0.75	0.87	1.00

were carried out for  $M = 0.15$ ,  $F = 0.20$  as well as for  $M = 0.12$ , but this had little effect on the estimates of vulnerability. The geometric means of the vulnerability coefficients obtained by assuming different values of  $M$  have been plotted graphically in Figure 15 and suggests that the proportion recruited to the fishery is a linear function of age. There is no obvious reason why this should be so, however, and no attempt was made to fit a straight line (or lines) to these data, or to extend the relationship to fish less than 10 yr old. The geometric means of the  $V_i$  estimates were used directly in all later work.

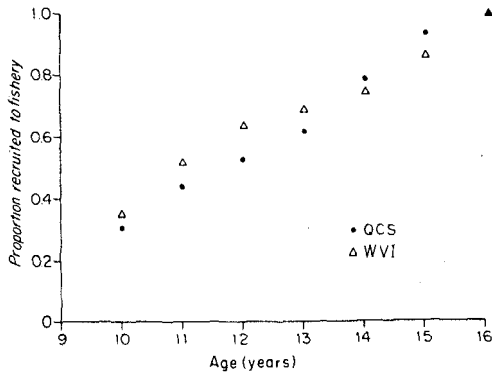


FIGURE 15.—Estimated proportion of each age group recruited to the fishing grounds, for the QCS and WVI stocks of Pacific ocean perch.

MORTALITY

All estimates of Pacific ocean perch mortality rates depend on a knowledge of the age structure of the population. Virtually all fish caught die from the effects of decompression, so that no successful tagging studies have ever been carried out.

In this section, data on number caught per hour by age-group were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year *n* to ages 15-19 in year *n* + 1, or to ages 16-20 in year *n* + 2. These age-groups were chosen so as to strike a balance between problems with incomplete recruitment on the one hand and age determination problems on the other. Previous analysis has suggested that recruitment is not complete until age 16, about the same time that age determination becomes difficult (Table 7) and the ages of some individuals are presumably underestimated. No age-groups older than 20 should be included in survival estimates, and restricting mortality estimates to fully recruited age-groups (16-19 yr olds) could result in underestimation of survival rates. Inclusion of the incompletely re-

cruited 14 and 15 yr olds offset this to some degree and had the additional benefit of basing the survival estimates on five age-groups rather than three.

All survival estimates were expressed on an annual basis (*S*), and then used to estimate *Z*. On the assumption that *M* is density independent and that *F* is a linear function of total hours trawled, the model  $Z = q\bar{f} + M$ , where *q* = proportion of population caught by trawling 1 h and  $\bar{f}$  = mean annual number of hours trawled, was employed. Linear regression of *Z* on  $\bar{f}$  yields estimates of *q* and *M* where the model is appropriate.

Total international fishing effort (*f*) was estimated by dividing the total international catch in a given year by the corresponding CPUE for the Washington trawl fleet (after Gulland 1969). The value of  $\bar{f}$  was obtained by averaging *f* over the years that each estimate of *Z* pertained to.

Queen Charlotte Sound

Calculation of total international fishing effort is outlined in Table 8. The 1967-72 Soviet catch data for the INPFC Charlotte area was taken from unpublished analyses by T. A. Dark and N. B. Parks. These data were derived from analysis of fleet location and catch by quarter and give the most detailed breakdown of the Soviet catch that is currently available. Soviet catch estimates for 1965, 1966, 1972, and 1973, as well as all Japanese and North American data for the years 1963-73, were derived from Westheim et al. (1972) and a recent update of that report.

Estimates of *Z* are plotted against mean international fishing effort (Table 8) in Figure 16 and the results indicate that the information collected so far can provide only tentative estimates of *M*. Pacific ocean perch vary widely in their availability to on-bottom trawls and the CPUE indices used in mortality estimation are consequently suscep-

TABLE 7.—Deviations of Canada's final otolith readings from those of United States, by age-group, for a collection of Pacific ocean perch from Queen Charlotte Sound, June 1972.<sup>1</sup>

Deviations from Washington	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	22	25	Total	Per-cent	
+5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	—	3	3.6	
+4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4.8
+3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2.4
+2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	6.0
+1	—	—	—	—	—	—	—	—	—	—	3	1	1	2	—	1	—	—	—	—	—	—	8	9.5
0	6	11	10	4	4	3	1	3	2	9	4	—	—	—	2	—	—	—	—	—	—	—	59	70.2
-1	—	—	—	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	3	3.6
Total	6	11	10	4	5	3	1	3	3	11	7	2	1	2	2	4	1	1	2	4	1	84	100.1	

<sup>1</sup>S. J. Westheim and W. R. Harling. 1973. Report on the 1972 comparison of Pacific ocean perch otolith and scale interpretations. Unpubl. manusc., 24 p.

TABLE 8.—Calculation of total international fishing effort for Pacific ocean perch in Queen Charlotte Sound and the INPFC Vancouver area.

Year	Catch (metric tons)			Total	Washington CPUE (metric tons/hour)	Total international effort (Wash. hours)
	U.S.-Can.	Jap.	U.S.S.R.			
Queen Charlotte Sound						
1963	3,712			3,712	0.841	4,414
1964	3,507			3,507	0.731	4,798
1965	4,889		7,000	11,889	1.040	11,432
1966	8,254	few	18,800	27,054	1.132	23,899
1967	5,745	3,196	17,800	26,741	0.800	33,426
1968	6,051	5,614	1,827	13,492	0.722	18,687
1969	6,628	6,268	55	12,951	0.656	19,742
1970	6,077	3,775	2	9,854	0.714	13,801
1971	4,165	702	few	4,867	0.670	7,264
1972	5,561	2,281	0	7,842	0.710	11,045
1973	3,626	958	0	4,584	0.812	5,644
Vancouver area						
1966	2,358	few	14,000	16,358	0.640	25,559
1967	805	6,678	10,263	17,746	0.434	40,889
1968	552	4,751	4,602	9,905	0.247	40,101
1969	583	1,787	2,143	4,513	0.242	18,649
1970	1,955	2,186	814	4,955	0.298	16,628
1971	1,155	1,838	1,145	4,138	0.317	13,054
1972	624	1,580	878	3,082	0.312	9,878
1973	344	2,989	490	3,823	0.228	16,768

tible to fluctuations that have no relation to abundance. Fluctuations of this nature were responsible for much of the variability in Figure 16 and resulted in negative mortality estimates for 1972-73. The low quality of the data on international catch (especially U.S.S.R. data) also contributed to this variability, however.

Linear regression was carried out for the data in Figure 16, and the resulting estimates of  $M$  and  $q$  were 0.065 and 0.00002, respectively. As expected, correlation between  $Z$  and  $f$  was quite low ( $r = 0.30$ ).

### Washington-Vancouver Island

Calculation of international effort in the INPFC Vancouver Area is outlined in Table 8. The data sources used to estimate total international effort are the same as for Queen Charlotte Sound.

Annual estimates of  $Z$  are plotted against mean international effort in Figure 17. Research cruises off Washington (Gunderson 1974) have shown that extreme fluctuations in the availability of Pacific ocean perch occur here and that changes in the age composition of the catch seem to be associated with them. As in Queen Charlotte Sound, these changes in availability, together with the low quality of the international effort data, generate a high degree of variability in the relation between  $Z$  and  $f$ . Correlation between these variables was higher than in Queen Charlotte Sound ( $r = 0.49$ ), however, and the data seemed to con-

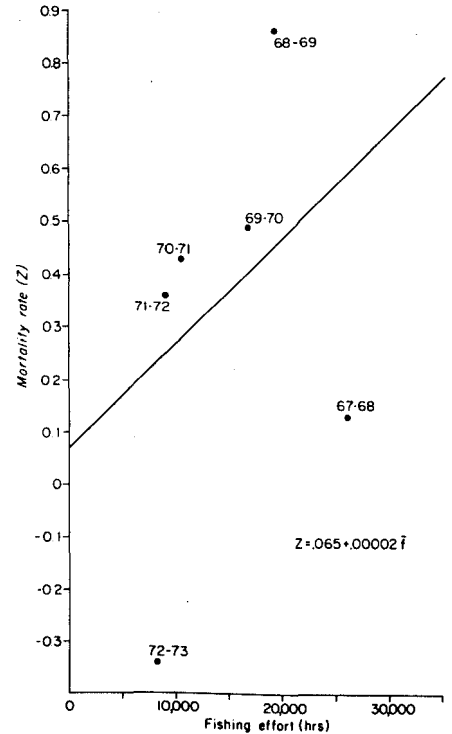


FIGURE 16.—Relation between total instantaneous mortality rate ( $Z$ ) and fishing effort for the QCS stock of Pacific ocean perch, based on data from the Washington trawl fleet.

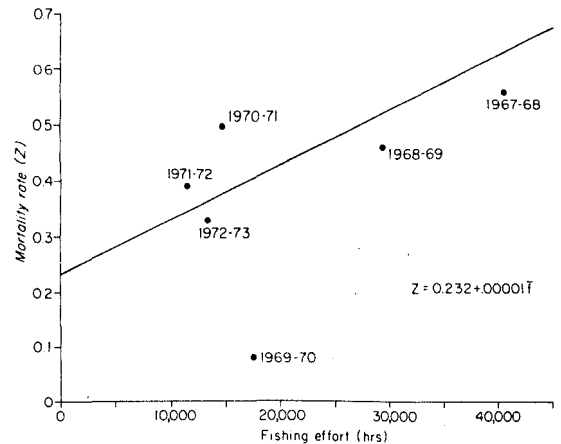


FIGURE 17.—Relation between total instantaneous mortality rate ( $Z$ ) and fishing effort for the WVI stock of Pacific ocean perch, based on data from the Washington trawl fleet.

form more closely to the model proposed. Linear regression analysis resulted in estimates of  $M = 0.232$  and  $q = 0.00001$  for the WVI stock.



The estimate of  $M$  obtained for the WVI stock agrees well with an estimate obtained by Chikuni (1975). Chikuni used CPUE and age composition data from the Japanese trawl fleet, and estimated  $M$  to be 0.227 for Pacific ocean perch in the Oregon-British Columbia region.

The general applicability of the  $Z = q\bar{f} + M$  model for both the QCS and WVI stocks was encouraging and suggests that further collection of data on mortality rates should give increasingly more reliable estimates of  $M$ . At present, however, it probably is unwise to overemphasize the between-stock differences found in natural mortality. The results of the current study should be regarded as somewhat tentative and serve mainly to show that  $M$  in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

## SEXUAL MATURATION

### Maturity Criteria Used

Seasonal changes in the gross morphology of Pacific ocean perch gonads have previously been used to describe the reproductive cycle in the Washington-Queen Charlotte Sound region (Gunderson 1971; Snytko 1971). This technique was again employed in this study, and, during 1968-73, 9,548 mature fish were classified as to maturity state using the criteria in Table 9.

Mating and insemination activities cause a reduction in the proportion of males whose gonads are swollen with sperm (Stage 3), and seem to occur during August-September in both the QCS and WVI stocks (Table 10). About 3 mo pass before

TABLE 9.—Description of the stages used to describe Pacific ocean perch maturity.

Maturity		Description of gonads
Code	Stage	
Males		
1	Immature	Stringlike, translucent
9	Maturing	Stringlike, translucent brown or white
8	Resting	Ribbonlike, triangular in cross-section, brown or white
3	Large white	Large and swollen, somewhat rounded in cross-section, glistening white
Females		
1	Immature	Ovary small and translucent
2	Maturing	Ovary small and yellow
3	Large yellow	Ovary firm, oocytes yellowish and opaque
4	Yolk cleared (eggs fertilized)	Ovary not firm, eggs yellowish and translucent
5	Eyed embryos or larvae	Ovary not firm, eggs translucent with black dots or visible larvae
6	Spent	Ovary large and flaccid with a red, purple, or dark gray color
7	Resting	Ovary firm, gray or pink, some with black blotches.

ovulation and fertilization of eggs occur, and this is first detectable when females in maturity Stage 4 are encountered. Embryonic development begins after fertilization and continues for about 2 mo before embryos are released.

The peak of the embryo-release period occurs during March in the WVI stock (Table 10). Most of the females examined in February were in the "fertilized" stage (Stage 4), while most of those examined during April were in the "resting" stage (Stage 7). Few observations could be made for QCS females during February-April, but the results suggest that embryo release occurs near March. The relatively high proportion of recently spent fish (Stage 6) encountered during May suggests that spawning occurs somewhat later in Queen Charlotte Sound than it does off Washington and southwest Vancouver Island.

Age and size at first maturity should be determined during the period when mature gonads are most fully developed, near August-September for males and near March for females. The central problem in determining length or age at maturity is the status of "maturing" fish (Table 9), and further work was carried out to determine whether or not these fish are sexually mature. Two hundred sixteen fish covering a broad range of lengths were selected from the 1971-72 commercial landings for this purpose. The length (centimeters), sex, and weight (decigrams) of each fish were determined, and the gonads classified as to maturity state. The gonads were then removed from the fish and weighed to the nearest 0.01 g. The results (Figure 18) were expressed in terms of relative gonad weight ( $g$ ), where

$$g = \frac{\text{gonad weight (grams)}}{\text{body weight (grams)}} \times 10^2$$

i.e.; gonad weight expressed as a percentage of body weight.

### Males

Between-season comparisons show that the relative gonad weights of "maturing" males are virtually the same during the mating season (August-September) as they are during March, when all male gonads are in a quiescent state. These fish are obviously immature and seasonal changes in their relative gonad weight contrast sharply with those of adult fish. Fish classified as "maturing" should therefore be grouped with

TABLE 10.—Percentage of adult Pacific Ocean perch in each maturity stage, by stock, during 1968-73.

Item	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
<b>Males:</b>											
QCS Stock											
Total examined		231		339	659	486	279	328	407	430	340
Percent in each maturity stage:											
Stage 8		100		100	99	71	27	58	55	82	100
Stage 3					1	29	73	42	45	18	
Total		100		100	100	100	100	100	100	100	100
<b>Females:</b>											
Total examined		7		11	219	364	212	358	442	675	512
Percent in each maturity stage:											
Stage 3		71		18		18	63	75	99	100	99
Stage 4				9							1
Stage 5				18	1						
Stage 6		14		18	2	2	1				
Stage 7		14		55	80	80	35	25	1		
Total		99		100	99	100	100	101	100	100	100
<b>Males:</b>											
WVI Stock											
Total examined		234	223	448			1183	151	102		225
Percent in each maturity stage:											
Stage 8		100	100	100			26	32	65		100
Stage 3							74	68	35		
Total		100	100	100			100	100	100		100
<b>Females:</b>											
Total examined	1101	197	213	537			1129	178	118		210
Percent in each maturity stage:											
Stage 3	30	4	1	1			78	100	100		100
Stage 4	69	63	11								
Stage 5	2	30	43	4							
Stage 6		2	15	14							
Stage 7		1	30	81			22				
Total	101	100	100	100			100	100	100		100

<sup>1</sup>All fish examined during this month came from research vessel catches.

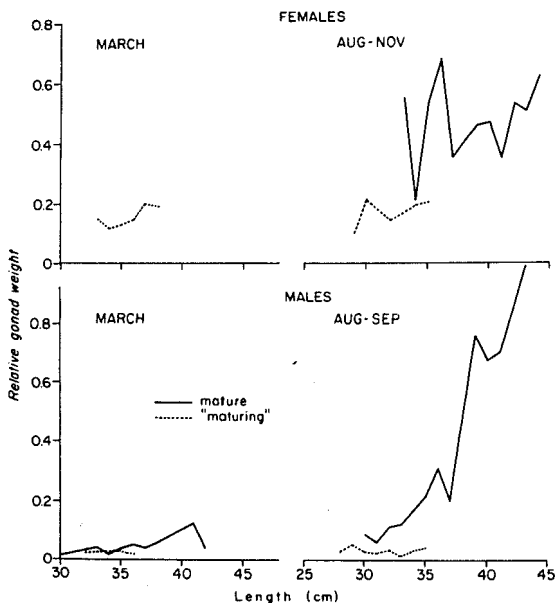


FIGURE 18.—Seasonal changes in the relative gonad weight of mature and "maturing" Pacific ocean perch by length group and sex.

"immature" males in all analysis of length or age at maturity.

There was considerable overlap in the relative gonad weight of mature and "maturing" males during March. Relative gonad weight of adult males examined during the mating season increased exponentially with size, however, so that mature and immature fish were readily differentiated for fish longer than about 32 cm. For smaller fish, however, the relative size of the gonad was not sufficient to determine whether or not a fish was mature, and color had to be relied on to a large degree. If the gonads were white rather than brown, this was taken to indicate the presence of developing sperm and the fish was classified as mature. Whether or not these small males actually participate in mating remains an unanswered question, however.

Because mature and "maturing" males were most readily differentiated when mature fish had white, swollen gonads, only data collected during June-October were used to determine size and age at maturity. The data in Table 10 show that significant quantities of males with Stage 3 gonads were found during this period.

## Females

Female gonads are difficult to weigh during the embryo release period, since they are easily ruptured then. Furthermore, eggs and embryos can be extruded with slight pressure on the body cavity during this period, and it is possible that significant quantities of these sex products are lost when fish are compacted in the cod end of a trawl. For these reasons, no data on gonad weight of mature females were taken during March.

Between-season comparisons for "maturing" females (Figure 18) show that their relative gonad weights were virtually the same during August-November as they were during the embryo release period in March. This is conclusive evidence that "maturing" fish are not sexually active, and they were grouped with immature fish in all later analysis.

Differentiation of "maturing" and mature fish was less difficult for females than for males. It was most difficult during July-November, when most adult fish were in maturity Class 3 (Table 10), and had gonads that were similar to "maturing" gonads in color. There was also some overlap in the relative gonad weights of mature and "maturing" individuals of the same length during this period (Figure 18).

During the embryo release period, or when females were in the resting state, adult gonads were readily differentiated from the small, yellowish gonads of "maturing" fish. Consequently, only maturity data collected during February-June were used to examine the size and age at first maturity for females.

## Length and Age at Maturity

Data on maturity of Pacific ocean perch have been gathered since 1968, during the course of routine biological sampling of commercial catches. In addition, some maturity data were available from research cruises off the northern Washington coast. The data for 1968-72 combined were examined by stock to determine size and age at maturity.

In most instances, age, length, and maturity data were available for individual fish, and the proportion of mature fish in each cell of an age-length matrix could be calculated. This type of analysis was carried out for both males and females from Queen Charlotte Sound (Tables 11,

12) and for females off Washington and southwest Vancouver Island (Table 13).

Only 213 age-length-maturity observations were available for WVI males, too few to allow direct analysis of maturation by age-groups. Examination of the relation between length and maturity was possible, however, as 551 length-maturity observations were available.

## Length-maturity relation

Tables 11 through 13 show the proportion of mature fish in each cell of an age-length matrix. The region in which 50-80% of the fish were mature is delineated by the isopleths drawn in these tables and can be interpreted as a maturity response surface. For all three sets of data, the 50-80% region occupied a narrow range of size groups (3-5 cm) and a relatively wide range of age-groups (5-6 yr). Hence it seems that maturation of both male and female Pacific ocean perch depends more on the size of a fish than its age.

Raw data on length versus proportion mature were plotted for each area and sex (Figure 19) and seemed to conform to a logistic equation (Finney 1971) of the form:

$$P_l = \frac{1}{1 + \exp - \left( \frac{l - l_{0.50}}{\sigma} \right)}$$

where  $l$  = length in centimeters

$P_l$  = proportion mature at length  $l$

$l_{0.50}$  = length where:  $P_l = 0.5$  = maturation length

$\sigma$  = constant.

The length-maturity curves are quite steep in the vicinity of  $P_l = 0.2-0.8$  and maturation can be regarded as knife-edged, taking place at  $l_{0.50}$ . Because the above equation is symmetrical about  $l_{0.50}$ , the area under the curve and to the left of  $l_{0.50}$  is equal to the area above the curve and to the right of it. Hence, the errors introduced by assuming knife-edged maturation at  $l_{0.50}$  tend to balance.

By algebraic manipulation, the above equation can be linearized to:

$$\ln \left( \frac{1}{P_l} - 1 \right) = \frac{l_{0.50}}{\sigma} - \frac{l}{\sigma}$$

The equation was then in the form  $y = \alpha + \beta l$  and

TABLE 11.—Proportion mature in each length and age-group, for female Pacific ocean perch from the QCS stock. Cells with only one observation were not considered.

Length (cm)	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
22														1
24													0.00	2
25			0.00										0.00	3
26			0.00										0.00	3
27			0.00										0.00	4
28			0.00	0.00									0.00	10
29		0.00	0.00	0.00	0.00								0.00	23
30			0.00	0.00	0.00								0.00	20
31			0.00	0.00	0.00	0.00	0.00						0.00	45
32				0.00	0.06	0.00	0.00	0.05					0.04	79
33			0.00	0.20	0.09	0.04	0.00	0.00					0.07	85
34				0.00	0.03	0.15	0.11	0.25	0.00				0.09	90
35				0.00	0.22	0.48	0.27	0.30	0.00				0.29	85
36				0.00	0.56	0.32	0.28	0.64	0.67	1.00	1.00		0.44	87
37					1.00	0.56	0.92	0.56	0.57	0.83	1.00		0.68	73
38						0.67	0.64	0.83	0.75	0.82	1.00		0.74	53
39							1.00	0.83	1.00	1.00	0.88		0.95	60
40							0.89	1.00	1.00	0.90	1.00	1.00	0.95	66
41								1.00	1.00	1.00	0.95	0.88	0.97	69
42								1.00	1.00	1.00	1.00	0.93	0.99	75
43									1.00	1.00	1.00	1.00	1.00	65
44									1.00	1.00	1.00	1.00	1.00	53
45									1.00	1.00	1.00	1.00	1.00	28
46										1.00	1.00	1.00	1.00	11
47											1.00	1.00	1.00	4
49												1.00	1.00	1
Proportion mature by age		0.00	0.00	0.03	0.13	0.25	0.37	0.64	0.81	0.96	0.97	0.95		
Number examined	1	4	35	75	152	143	139	77	116	135	108	110		

TABLE 12.—Proportion mature in each length and age-group, for Pacific ocean perch males from the QCS stock. Cells with only one observation were not considered.

Length (cm)	≤4	5	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
21															1
23															1
24															1
25														0.33	3
26		0.00		0.00	0.33									0.14	7
27			0.00	0.00										0.00	7
28				0.00										0.00	6
29			0.00	0.00	0.00	0.50								0.10	21
30				0.40	0.25	0.50								0.33	21
31				0.80	0.57	0.61	0.64	0.50						0.61	59
32				0.50	0.61	0.80	0.69	1.00						0.75	67
33					0.69	0.97	0.94	0.92						0.91	113
34				1.00	1.00	0.97	0.93	0.93	0.88	1.00				0.94	166
35					1.00	1.00	0.98	1.00	1.00	1.00	1.00			0.99	150
36						1.00	0.94	0.98	1.00	1.00	1.00	1.00		0.98	157
37						1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.99	167
38							1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	202
39							1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	207
40								1.00	1.00	1.00	1.00	1.00	1.00	1.00	224
41									1.00	1.00	1.00	1.00	1.00	1.00	149
42									1.00	1.00	1.00	1.00	1.00	1.00	77
43										1.00	1.00	1.00	1.00	1.00	29
44											1.00	1.00	1.00	1.00	5
45												1.00	1.00	1.00	2
Proportion mature by age		0.00	0.14	0.29	0.56	0.89	0.92	0.97	0.98	1.00	1.00	1.00	1.00		
Number examined	1	5	7	34	94	150	225	230	241	250	217	158	230		

the data in Tables 11-13 could be used in weighted linear regression of  $\ln [(1/P_l) - 1]$  on  $l$ . The weights used for  $y$  observations were  $1/\text{Var}(y) = nP_l(1 -$

$P_l)$ . Regression coefficients obtained were then used to estimate  $l_{0.50} (-\alpha/\beta)$  and  $\sigma (-1/\beta)$ .

These estimates were made by sex for Pacific

TABLE 13.—Proportion mature in each length and age-group, for female Pacific ocean perch from the WVI stock. Cells with only one observation were not considered.

Length (cm)	6	7	8	9	10	11	12	13	14	15	16+	Proportion mature by length	Number examined
28		0.00										0.00	3
29												0.00	2
30		0.00										0.00	3
31			0.00									0.00	5
32				0.00	0.00							0.00	7
33			0.67		0.00	0.00	1.00					0.33	15
34				0.40	0.38	0.25	0.57	1.00	0.50			0.44	32
35				0.33	0.59	0.70	0.67	1.00	1.00	1.00		0.65	46
36		1.00		0.67	0.77	0.50	0.92	0.88	0.85	1.00	0.80	0.79	100
37			1.00	1.00	0.75	0.70	0.95	1.00	0.83	0.80	1.00	0.87	105
38				0.75	0.89	1.00	0.86	1.00	1.00	1.00	1.00	0.97	123
39					1.00	1.00	0.88	1.00	0.93	1.00	1.00	0.97	111
40							1.00	1.00	1.00	1.00	1.00	1.00	65
41								1.00	1.00	1.00	1.00	1.00	69
42								1.00	1.00	1.00	1.00	1.00	34
43									1.00	1.00	1.00	1.00	46
44										1.00	1.00	1.00	26
45											1.00	1.00	13
46												1.00	11
47												1.00	2
48												1.00	2
49												1.00	1
Proportion mature by age	0.33	0.25	0.42	0.46	0.60	0.65	0.87	0.98	0.94	0.98	1.00		
Number examined	3	8	12	24	67	81	101	105	103	98	219		

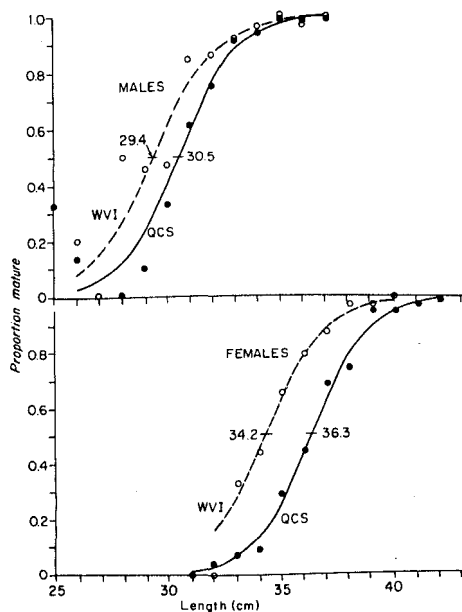


FIGURE 19.—Length-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

ocean perch in the QCS and WVI stocks (Table 14). Predicted curves for proportion mature at each length have been calculated and are represented by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 19. These curves, and the  $l_{0.50}$  estimates they are based on, indicate that both

TABLE 14.—Estimated values of parameters for the equations used to examine length and age at maturity for Pacific ocean perch.

Item	Males		Females	
	QCS stock	WVI stock	QCS stock	WVI stock
Length at Maturity				
$l_{0.50}$	30.4627	29.3782	36.2705	34.2335
$\sigma$	1.2791	1.4170	1.2405	1.3252
Var ( $l_{0.50}$ )	0.0492	0.0809	0.0105	0.0316
Z statistic <sup>1</sup>	3.0067		9.9277	
Age at Maturity				
$t_{0.50}$	7.5884	—	11.3775	9.2899
$\sigma$	0.9799	—	1.1819	1.6132
Var ( $t_{0.50}$ )	0.0543	—	0.0204	0.1068
Z statistic <sup>2</sup>	—		5.8533	
$t'_{0.50}$	7.0	6.5	10.3	10.0

<sup>1</sup>For test of between-stock differences in  $l_{0.50}$ .  
<sup>2</sup>For test of between-stock differences in  $t_{0.50}$ .

males and females mature at a much smaller size off Washington and Southwest Vancouver Island than they do in Queen Charlotte Sound.

In order to examine the significance of between-area differences further, the variance of  $l_{0.50}$  was approximated by using the delta method:

$$\text{Var} (l_{0.50}) = \text{Var} \left( \frac{-\alpha}{\beta} \right) = \frac{1}{\beta^2} (\text{Var} \alpha) + \frac{\alpha^2}{\beta^4} \text{Var} (\beta) - 2 \frac{\alpha}{\beta^3} \text{Cov} (\alpha, \beta).$$

This variance was estimated for each sex and area considered (Table 14) using information from

the linear regression program previously employed. If it is assumed that the estimates of  $l_{0.50}$  are normally distributed, then the quantity

$$\frac{\frac{\alpha_1}{\beta_1} - \frac{\alpha_2}{\beta_2}}{\sqrt{\text{Var}\left(\frac{\alpha_1}{\beta_1}\right) + \text{Var}\left(\frac{\alpha_2}{\beta_2}\right)}}$$

is distributed as  $Z$  and can be used to test the hypothesis that there is no difference in  $l_{0.50}$  between areas. The  $Z$  values obtained for both males and females (Table 14) indicate that the observed differences in length at maturity are highly significant, since  $P(Z > 3.0067) = 0.0013$  and  $P(Z > 9.9277) \approx 0$  under the hypothesis being tested.

#### Age-maturity relation

Age at maturity was estimated by two methods. The first series of estimates was developed by using the logistic equation:

$$P_t = \frac{1}{1 + \exp - \left( \frac{t - t_{0.50}}{\sigma} \right)}$$

where  $P_t$  = proportion mature at age  $t$   
 $t_{0.50}$  = age when  $P_t = 0.50$  = age at maturity  
 $\sigma$  = constant.

The parameters for this equation were estimated in the same manner described in the length-maturity section, through weighted linear regression analysis of the data in Tables 11-13. The resulting estimates of  $t_{0.50}$  and  $\sigma$  are shown in Table 14, and the predicted relationships between  $P_t$  and  $t$  are shown by the solid lines (QCS stock) and dashed lines (WVI stock) in Figure 20. The  $t_{0.50}$  estimates obtained in this way are estimates of the age when males mate for the first time and when females release their first brood of embryos. The  $Z$  statistic shows that between-stock differences in age at first brood release were statistically significant, since  $P(Z > 5.8533) \approx 0$ .

A second series of estimates for the age at maturity ( $t'_{0.50}$ ) was obtained by utilizing the  $l_{0.50}$  values obtained in the previous section, and von Bertalanffy growth parameters from Table 3. The equation used was:

$$t'_{0.50} = t_0 - \frac{1}{K} \ln \left( 1 - \frac{l_{0.50}}{L_\infty} \right)$$

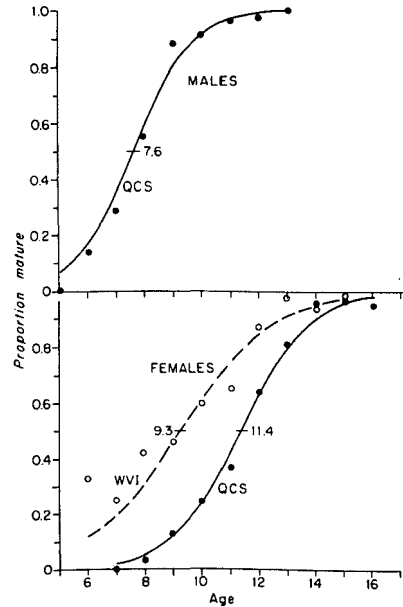


FIGURE 20.—Age-maturity relation for QCS and WVI stocks of Pacific ocean perch, by sex.

Resulting estimates for males (Table 14) are probably quite accurate, since both  $l_{0.50}$  and the age-length relations in Table 3 were based on data collected during June-December (near the mating season). The  $t'_{0.50}$  estimates for females are biased, however, since a significant amount of growth occurs between the period when  $l_{0.50}$  was estimated (February-June) and the period when the age-length data were collected (July for the WVI stock, September-December for the QCS). The bias is relatively small for the WVI stock, but in Queen Charlotte Sound most of the annual growth probably occurs during the intervening time period. The  $t'_{0.50}$  value obtained for QCS females consequently underestimates age at first brood release by almost a year.

The results from both methods used to estimate age at maturity (Table 14) indicate that both males and females mature at an earlier age off Washington and southwest Vancouver Island than they do in Queen Charlotte Sound. When biases in  $t'_{0.50}$  are considered, it appears that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. Estimates of age at first mating for males were not subject to the same bias as those for females and can be taken directly from Table 14. These results suggest that males first mate at age 6

in the WVI stock and age 7 in Queen Charlotte Sound.

## FECUNDITY

### Methods Used in Fecundity Determination

#### Collection of Ovaries

Previous fecundity work on *Sebastes* has indicated that the time of ovary collection must be carefully controlled. Lisovenko (1965) determined fecundity for two groups of Pacific ocean perch in the Gulf of Alaska, the first consisting of 61 fish collected prior to fertilization and the second of 29 fish with fertilized ova. He found that the estimated fecundity of the first group was 1.5-2.0 times higher than that of the second, considering females of comparable size. Lisovenko attributed this difference to eggs bursting when females were hauled to the surface, but accidental extrusion of the fertilized eggs could also have been implicated. Pacific ocean perch containing fertilized eggs can be made to extrude these eggs by slight pressure on the body cavity and make poor specimens for determination of fecundity.

If ovary samples are collected too far in advance of fertilization, however, maturing oocytes that will be fertilized in the fall are too small to be differentiated from immature oocytes. The optimal time to collect material for fecundity observations is therefore August-November, when immature and maturing oocytes can be differentiated, but fertilization of ova has not yet occurred.

Collection dates and times for fecundity samples used in this study are shown below:

Date (1973)	Location	Number collected
22 Aug.	Destruction Island, Wash.	14
26 Aug.	Tillamook Head, Oreg.	27
19 Sept.	S.E. Corner, Goose Island	40

All fish from Queen Charlotte Sound were taken from the landings of a commercial trawler, while those from the southern region were collected aboard the U.S.S.R. research trawler *Seskar*. The cruise objectives of the *Seskar* were such that only limited quantities of Pacific ocean perch were caught off Washington, and collections made off the Oregon coast were used to supplement those from the WVI stock.

Since between-area fecundity comparisons were to be made, the attempt was made to collect ovaries from Queen Charlotte Sound when the fish were in the same stage of the reproductive cycle as those off Washington and Oregon. Despite this, gross examination of male gonads and data on oocyte diameters (Gunderson 1976) indicated that fish in the Queen Charlotte Sound collection were not quite as advanced as those collected 1 mo earlier off Washington and Oregon.

All ovaries collected were placed in modified Gilson's solution (Bagenal and Braum 1968) to harden the eggs and separate them from surrounding ovarian tissue. After about 1 mo, ovarian tissue was removed from the eggs and the fluid was changed. After the samples had been in Gilson's solution for a total of 3 mo, they were removed and stored permanently in 10% ethyl alcohol.

#### Differentiation of Mature and Immature Oocytes

A series of ovaries was collected over the whole range of the reproductive cycle so that the growth progression of maturing oocytes could be followed. All specimens were collected in the Washington-Oregon region and their ovaries were placed in Gilson's solution until the oocytes separated from ovarian tissue. Subsampling of the eggs in an ovary was accomplished by the same technique used to estimate fecundity (described below).

The size frequency for the eggs in a specimen was obtained by systematically measuring (nearest 0.01 mm) those eggs lying on transect lines drawn on a Petri dish, until a desired sample size had been attained. Many of the eggs were elliptical or irregularly shaped and, in these cases, the longest axis parallel to the counting scale was selected for measurement. One specimen was in the "embryo or eyed larvae" stage of maturity and, in this particular instance, all eggs with embryos were measured along the longitudinal axis of the embryo.

The results (Figure 21) showed that there was a significant overlap in the size of immature and maturing oocytes during the period when fecundity samples were collected. By October, the size of maturing oocytes had increased substantially and differentiation of maturing oocytes was straightforward. Following fertilization of the first brood, however, it appears that other groups of oocytes begin to mature, so that several sizes of eggs and embryos are present in ovaries that have

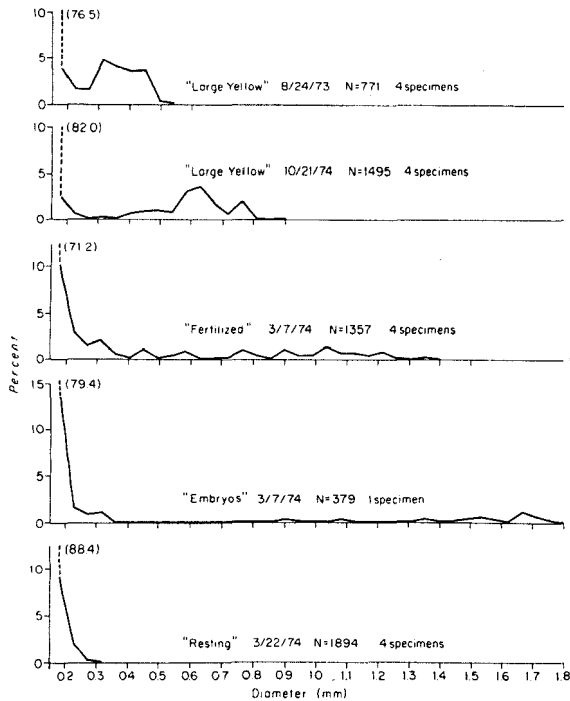


FIGURE 21.—Size composition of oocytes, ova, and larvae within Pacific ocean perch ovaries at different stages of the reproductive cycle. Maturity stage of the gonads these data were collected from is shown above each size frequency curve. Numbers in parentheses indicate the percentage of oocytes that are 0.15 mm or smaller.

passed the fertilization stage. There was no single dominant mode of mature eggs or larvae in any of the fertilized specimens that were examined (Table 15).

Despite the wide range of egg size and development within fertilized specimens, most of their progeny will probably hatch and be released at about the same time. Field observations (Gunder-

son 1974) indicate that most embryos are released during a single spawning peak that lasts only 2 or 3 wk.

In view of the oocyte measurement results and the fact that studies on the fecundity of *Sebastes marinus* have suggested a strong element of failure in oocyte fertilization (Raitt and Hall 1967), it seems that current estimates of fecundity must be regarded as somewhat tentative. Complex changes in fecundity probably occur after the first brood of oocytes has been fertilized and detailed morphological work will be required to determine their significance.

For purposes of this study, fecundity was estimated from the number of mature oocytes present prior to fertilization. All oocytes less than 0.30 mm in diameter were classified as immature on the basis of preliminary comparisons of oocyte size frequencies for juvenile and adult specimens. The data in Figure 21 suggest that this cutoff point was somewhat high, however, and that many of the oocytes in the 0.25- to 0.30-mm size class eventually mature. Even if all oocytes that were in the 0.249- to 0.293-mm size class during the collection period were actually maturing, the error generated by calling them immature would be less than about 10%.

#### Counting the Oocytes

Fecundity was estimated through subsampling by volume. The ovarian contents from each fish were removed from the storage solution, passed through a 1.17-mm screen to remove large particles of ovarian tissue that remained, and placed in a large beaker; water was then added until 2,000 ml of oocytes and water had been obtained. The mixture was stirred magnetically until all oocytes were distributed throughout the water column and a 5-ml subsample withdrawn with a pipette. Care was taken to sample all parts of the water column with the pipette. Four to six subsamples were taken in this manner, the exact number depending on the standard deviation of the first four subsamples.

The oocytes in each subsample were then counted, using a binocular microscope. Two or three replicate counts of each subsample were made by two different observers during the early phases of the study. The number of replicate counts was gradually reduced, however, as it became clear that there was little variation between them. Throughout the study, all counts for a given

TABLE 15.—Oocyte size frequencies for individual specimens of "fertilized" Pacific ocean perch females.

Oocyte size class (mm)	Number observed				Oocyte size class (mm)	Number observed			
<0.159	262	237	240	227	0.789-0.833	4	1	—	—
0.159-0.203	30	30	26	54	0.834-0.878	—	1	—	—
0.204-0.248	13	10	7	10	0.879-0.923	11	2	1	2
0.249-0.293	5	6	4	7	0.924-0.968	4	—	2	—
0.294-0.338	19	5	3	1	0.969-1.013	4	2	1	—
0.339-0.383	6	1	1	—	1.014-1.058	2	4	10	3
0.384-0.428	1	1	—	—	1.059-1.103	2	4	4	—
0.429-0.473	7	2	1	6	1.104-1.148	1	2	5	1
0.474-0.518	1	—	—	1	1.149-1.193	—	2	2	2
0.519-0.563	3	—	—	2	1.194-1.238	—	5	6	—
0.564-0.608	1	2	2	7	1.239-1.283	—	—	1	—
0.609-0.653	—	—	—	1	1.284-1.328	—	—	—	—
0.654-0.698	2	—	—	—	1.329-1.373	—	2	1	—
0.699-0.743	2	1	—	—	Total	395	321	317	324
0.744-0.788	15	1	—	—					



fish were partitioned between two different observers to balance out the effects of any bias.

The mean number of eggs per milliliter was calculated for each of the 4-6 subsample means from a given specimen and the coefficient of variation ( $CV = \text{standard deviation}/\text{mean of subsample counts}$ ) for these subsample means had the following distribution:

Range of CV (%)	Washington-Oregon	QCS	Total
0.0- 4.9	5	4	9
5.0- 9.9	10	16	26
10.0-14.9	17	12	29
15.0-19.9	4	7	11
20.0-24.9	3	1	4
Total	39	40	79

For most specimens (81%), the standard deviation of the subsample means was within 15% of the grand mean. The fecundity of each specimen was estimated by using the formula:  $F = 2,000n$ , where  $F = \text{fecundity}$  and  $n = \text{mean number of eggs per milliliter in the subsamples}$ .

### Results of Fecundity Study

May (1967) reviewed the results of fecundity work on several species (cod, *Gadus morhua*; herring, *Clupea harengus pallasii*; long rough dab, *Hippoglossoides platessoides*), which showed that, for most practical purposes, variation in fecundity is adequately explained in terms of length alone. Raitt and Hall (1967) came to the same conclusion in their work on the Atlantic redfish, *Sebastes marinus*, a species belonging to the same genus as Pacific ocean perch. They carried out multiple regression of  $\log F$  and  $\log L$  using weight or age as second independent variables, and it was found that inclusion of variates other than length did not significantly reduce residual variation. As a result, the fecundity work in the current study was directed primarily toward determining the relation between fecundity and length.

Fecundity data for *Sebastes alutus* seemed to fit the relation  $F = aL^b$ , where  $F = \text{number of oocytes in thousands}$ ,  $L = \text{fork length in centimeters}$ , and  $a$  and  $b = \text{constants}$ .

The values of  $a$  and  $b$  were determined by transforming this equation into:  $\log F = \log a + b \log L$  and using linear regression techniques to fit  $\log F - \log L$  data to a straight line. Data from Washington-Oregon and Queen Charlotte Sound

were treated separately, and the following results were obtained:

$$\begin{aligned} & \text{Washington-Oregon} \\ & F = (0.19295 \times 10^{-9}) L^{7.32506} \\ & \text{Queen Charlotte Sound} \\ & \bar{F} = (0.12240 \times 10^{-6}) L^{5.51258} \end{aligned}$$

Predicted fecundity at each length was calculated from these relationships, and is shown in Figure 22. The significance of between-area differences in the length-fecundity relation was examined statistically, using the BMD 3R4V<sup>4</sup> computer program for analysis of covariance. The results of this analysis showed that between-area differences in the fecundity-length relation are statistically significant at the 95% level and that they are due to differences in the intercepts of the  $\log F - \log L$  regression lines ( $F = 5.85$  with 1,76 df) rather than to differences in their slope ( $F = 3.43$  with 1,75 df).

Two workers (Westrheim 1958; Snytko 1971) have previously examined the length-fecundity relation for Pacific ocean perch off Washington-Oregon, although neither carried out corresponding studies for the Queen Charlotte Sound stock. Westrheim's results were the first available and were based on examination of 13 specimens. Westrheim collected his fecundity samples during September-November (1951 and 1952), estimated

<sup>4</sup>BMD 3RV. Regression with Analysis of Covariance. This is an addition to the University of California BMD program series, developed at the University of Washington Computer Center by W. Farr.

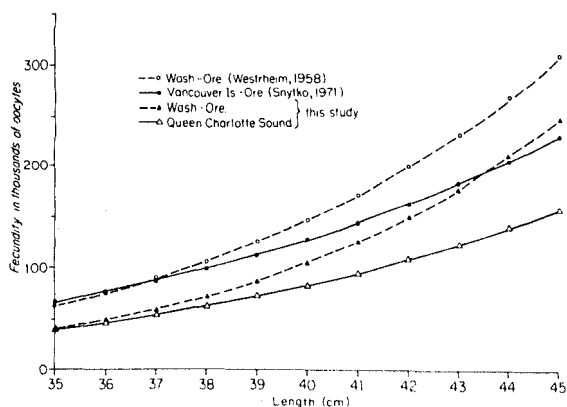


FIGURE 22.—Relation between fecundity and length for Pacific ocean perch off Washington-Oregon (as determined by three different workers) and in Queen Charlotte Sound.

fecundity by a gravimetric method, and found that his results could be represented by the relation:  $F = (4.8556 \times 10^{-15})L^{6.33454}$ , where  $L$  = fork length in millimeters.

Snytko's (1971) fecundity observations on 171 specimens were the most extensive made to date in the Washington-Oregon region. Snytko collected his fecundity samples during November-March 1967-68, in the "Vancouver-Oregon region" (lat. 40°-50°N). The ovaries were collected before fertilization of the oocytes had occurred and fecundity was determined gravimetrically by counting the oocytes present in 0.5- to 1.0-g subsamples of the ovaries (Snytko and Borets 1972). Snytko (1971) presented his data in terms of mean fecundity at a given length and regression of  $\log F$  on  $\log L$  indicates that they can be represented by the relation:  $F = (0.13103 \times 10^{-5})L^{4.98838}$ , where  $L$  = length in centimeters.

Length-fecundity relationships for Pacific ocean perch off Washington-Oregon, as predicted by Westrheim (1958), Snytko (1971), and myself are shown in Figure 22. There was substantial variation in the results obtained by different workers and this is to be expected in view of the differences in the timing of ovary collection, techniques used to subsample and count oocytes, and the wide expanse of time (1951-73) covered by the studies. There is also a strong possibility that length-fecundity differences exist between substocks within the Washington-Oregon region and could have contributed to these differences.

The variability in the results of different workers reflects only the difficulties in estimating the number of maturing oocytes a given fish will produce and leaves a larger question unanswered. What we would really like to estimate is the number of viable larvae that fish of a given length or age will give birth to during the embryo-release period, and yet we are totally ignorant of the relationship between the estimated number of maturing oocytes and the number of larvae that will result from them.

Preliminary estimates of the number of larvae that will be released at each age can be made, however, if it is assumed that all oocytes present immediately after fertilization will develop into viable larvae. It should be kept in mind that even though this assumption is patently false, the resulting estimates are still well-suited to between-area comparisons if oocyte-larval mortality does not differ between areas.

It will be recalled that fecundity observations

applied to fish collected during August-September, while estimates of mean length at each age applied to the September-December period for Queen Charlotte Sound and to July in the case of the WVI stock. The estimate of the number of larvae released during March of any given year of life (Table 17) was consequently obtained by combining the age-length and length-fecundity relationships pertaining to the previous July-December. For example, the estimated number of larvae released by 11-yr-olds in Queen Charlotte Sound was estimated from predicted mean length at age 10 (Table 3), and the length-fecundity relationship appropriate to that stock ( $F = 0.12240 \times 10^{-6}L^{5.51258}$ ).

## RESPONSE OF PACIFIC OCEAN PERCH STOCKS TO FISHING

### Methods Used to Examine the Effects of Fishing

In the past, management recommendations for Pacific ocean perch in the INPFC Vancouver area have been developed by arriving at some estimate of the fishing mortality ( $F$ ) that the stock can withstand, then applying this value to the best available estimate of stock biomass to arrive at a quota. Much discussion has consequently focused on what levels of  $F$  can be sustained.

In this section, the effects of different levels of fishing intensity on a hypothetical cohort of fish will be examined, with an approach similar to the yield per recruit analysis that is commonly used in stock assessment. In contrast to conventional yield per recruit analysis, however, I have attempted to look at the costs involved in exerting high levels of fishing intensity on a population, as well as the benefits of increased yield. In particular, the decline in exploitable biomass (CPUE/ $q$ , where  $q$  is the catchability coefficient) and population fecundity that go hand in hand with increases in yield have been evaluated quantitatively.

The basic computations used to accomplish this are shown in Table 16. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity (Table 17). The mean weight schedule represents average values for the entire year, while the fecundity schedule applies to the embryo release period at the beginning of the year. Vulnerability and mortality were assumed to be constant throughout the year.

TABLE 16.—Example of computations used to estimate exploitable biomass, yield, and population fecundity for a hypothetical Pacific ocean perch population based on  $N_0$  recruits. Input parameters needed are indicated by asterisks.

Age	$M_i^*$ Natural mortality coefficient	$V_i^*$ Vulnerability coefficient	$s_i$ Proportion alive at beginning of age $i$	$N_i$ Number alive at beginning of age $i$	$W_i^*$ Mean weight	$B_i$ Mean biomass	$B_i^*$ Mean exploitable biomass	$Y_i$ Yield	$m_i^*$ Fecundity	$E_i$ Population fecundity
$0 = t_p$	$M_0$	$V_0$	$s_0 = 1$	$N_0 s_0 (=N_0)$	$W_0$	$\frac{N_0 W_0}{V_0 F + M_0} [1 - \exp -(V_0 F + M_0)]$	$V_0 B_0$	$F V_0 B_0$	$m_0$	$N_0 m_0$
1	$M_1$	$V_1$	$s_1 = \exp -(V_0 F + M_0)$	$N_0 s_1$	$W_1$	$\frac{N_1 W_1}{V_1 F + M_1} [1 - \exp -(V_1 F + M_1)]$	$V_1 B_1$	$F V_1 B_1$	$m_1$	$N_1 m_1$
2	$M_2$	$V_2$	$s_2 = s_1 \exp -(V_1 F + M_1)$	$N_0 s_2$	$W_2$	$\frac{N_2 W_2}{V_2 F + M_2} [1 - \exp -(V_2 F + M_2)]$	$V_2 B_2$	$F V_2 B_2$	$m_2$	$N_2 m_2$
3	$M_3$	$V_3$	$s_3 = s_2 \exp -(V_2 F + M_2)$	$N_0 s_3$	$W_3$	$\frac{N_3 W_3}{V_3 F + M_3} [1 - \exp -(V_3 F + M_3)]$	$V_3 B_3$	$F V_3 B_3$	$m_3$	$N_3 m_3$
							$\sum V_i B_i = B'$	$\sum Y_i = Y$	$\sum E_i = E$	

TABLE 17.—Vital statistics for females from the QCS and WVI stocks of Pacific ocean perch.

Age	Mean length (cm)	Mean weight <sup>1</sup> (g)	Fecundity (thousands)	Proportion vulnerable to fishing <sup>2</sup>
WVI Stock				
8	31.4	433	12.1	0.10
9	32.9	502	17.8	0.20
10	34.3	573	25.1	0.35
11	35.5	639	34.0	0.52
12	36.6	704	43.7	0.64
13	37.6	766	54.7	0.69
14	38.6	833	66.6	0.75
15	39.4	889	80.8	0.87
16	40.2	947	93.9	1.00
17	41.0	1,008	108.8	1.00
18	41.6	1,056	125.7	1.00
19	42.2	1,105	139.8	1.00
20	42.7	1,147	155.2	1.00
21	43.2	1,190	169.2	1.00
22	43.7	1,234	184.3	1.00
23	44.1	1,270	200.5	1.00
24	44.5	1,307	214.3	1.00
QCS Stock				
9	34.3	573	—	0.20
10	35.9	662	—	0.31
11	37.2	741	45.7	0.44
12	38.5	826	55.7	0.53
13	39.6	903	67.3	0.62
14	40.6	977	78.6	0.79
15	41.4	1,040	90.1	0.94
16	42.2	1,105	100.4	1.00
17	42.9	1,164	111.5	1.00
18	43.6	1,225	122.1	1.00
19	44.1	1,270	133.5	1.00
20	44.6	1,316	142.2	1.00
21	45.0	1,354	151.3	1.00
22	45.4	1,392	158.9	1.00
23	45.8	1,431	166.9	1.00
24	46.1	1,461	175.2	1.00

<sup>1</sup>Estimated from the age-length data in Table 3 and Westrheim and Thomson's (1971) all-B.C. length-weight relation for females:  $W = 0.0078571 L^{3.16734}$ .

<sup>2</sup>Vulnerability coefficients for 8- and 9-yr-olds were assigned arbitrarily. The values used were more conservative than those predicted by extrapolation of the straight line obtained for 10- to 16-yr-olds (0.20 for 8-yr-olds and 0.29 for 9-yr-olds).

Yield, exploitable biomass, and total fecundity are calculated for each age group, then summed. The results give the annual yield to the fishery, annual production of larvae, and average exploit-

able biomass on hand during the year for an equilibrium population of Pacific ocean perch. This population is based on a constant number of recruits ( $N_0$ ), with individual growth and mortality being determined by the input values of the constants used to describe mortality, vulnerability to fishing, and mean weight at each age.

A computer program<sup>5</sup> was written to carry out the calculations in Table 16 and offers a variety of ways to evaluate the effects of different fishing strategies on a stock. The basic calculations can be carried out for any combination of instantaneous rates of fishing mortality ( $F$ ) and age of entry into the fishery ( $t'_p$ ) that the user specifies.

The mesh size used when fishing for Pacific ocean perch is dictated primarily by convenience, since the incidence of "gilling" and entanglement in the meshes is reduced sharply when using 3.0-inch mesh (internal measure) in the cod end. This was not found to be the case in mesh studies with Atlantic redfish (Templeman 1963), where use of smaller cod end mesh sizes simply "gilled" fish of a smaller size. In the Pacific ocean perch stocks examined in this paper, recruitment to the fishing grounds is quite gradual and the fish that would normally be "gilled" in a 3.0-inch cod end are poorly represented on the grounds.

Pacific ocean perch offer a special case then, where evaluation of the effects of different size or age restrictions is of no practical interest for fisheries management. Consequently, all analysis in this section was focused on determining the optimal intensity of fishing for the Pacific ocean

<sup>5</sup>D. Gunderson and J. Buss. 1976. Users guide to ASSESS: Assessment of the effects of different fishing strategies on fish populations (FORTRAN IV). Norfish Pap. NC09, 8 p.

perch stocks being examined and the effects of varying the age at entry into the fishery ( $t'_p$ ) were ignored.

In addition, the analysis was restricted to the female portion of the stock. Over the long term, the population will be far more sensitive to removals of females and reduced population fecundity than it will to removals of males, and the optimal harvest rate for females will determine the level of  $F$  that should be applied to the stock as a whole.

The input data used to describe the QCS and WVI stocks are shown in Table 17. The values used for mean weight at age, vulnerability coefficients, and fecundity at age were derived from the information in Tables 3 and 6 and Figure 22. Natural mortality was assumed to be the same for all age groups concerned and computations were carried out for both  $M = 0.1$  and  $M = 0.2$ .

### Assessment of Immediate Response to Fishing

Only a small fraction of fish less than 8 yr old are recruited to the fishing grounds and, for the purposes of this study, it was assumed that recruitment begins at age 9 ( $t_p = 9$ ). It is possible that significant quantities of 9-yr-olds are discarded by fishermen, however, making it difficult to estimate their vulnerability coefficient from market samples. For this reason,  $t_p = 10$  was also consid-

ered, so that the sensitivity of the results to changes in  $t_p$  could be evaluated.

The results (Figure 23) showed that different values of  $t_p$  had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing  $F$ . In fact, the relative levels of each followed almost identical trends for both stocks and both values of  $t_p$  considered. However, the value of  $M$  used in the calculations had a pronounced effect on the results.

In all cases examined, there was a sharp rise in yield as  $F$  increased from 0.0 to 0.2, and a more gradual increase for  $F$ -values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as  $F$  increased from 0.0 to 0.2, then declining more gradually for  $F$  greater than 0.2.

Relative changes in population fecundity were almost identical to changes in exploitable biomass, indicating that changes in CPUE can be used directly to estimate the magnitude of changes in population fecundity. During 1966-68, then, population fecundity for stocks in the Oregon-Queen Charlotte Sound region must have declined in the same manner as CPUE and is currently only about 50% of what it was prior to intensive fishing.

Preliminary examination of the data (Figure 23) shows that the most significant changes in yield, exploitable biomass, and population fecun-

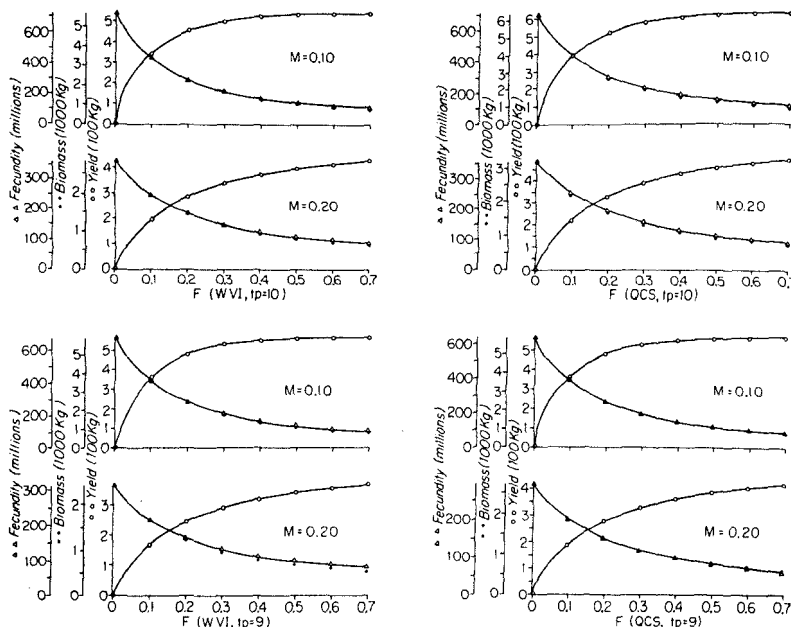


FIGURE 23.—Population fecundity (estimated number of larvae released annually), exploitable biomass, and annual yield for hypothetical populations based on 1,000 recruits per year. Results are presented by stock, for two different ages at recruitment ( $t_p$ ) and two different levels of instantaneous natural mortality ( $M$ ).

TABLE 18.—Relative yield ( $Y/Y_{\max}$ ), population fecundity ( $E/E_{\max}$ ), and exploitable biomass ( $B'/B'_{\max}$ ) at  $F = 0.1$  and  $0.2$ .<sup>1</sup> The range of values obtained by taking  $t_p = 9$  or  $10$ , for two different stocks of Pacific ocean perch is presented.

Item	$F = 0.1$		$F = 0.2$	
	$M = 0.1$	$M = 0.2$	$M = 0.1$	$M = 0.2$
$Y/Y_{\max}$	0.62-0.64	0.45	0.84-0.85	0.67
$E/E_{\max}$	0.59-0.62	0.68-0.70	0.40-0.43	0.51-0.53
$B'/B'_{\max}$	0.60-0.61	0.68	0.40-0.41	0.50-0.51

<sup>1</sup> $Y_{\max}$  = yield when  $F = 0.7$ ;  $E_{\max}$  and  $B'_{\max}$  = population fecundity and exploitable biomass when  $F = 0.0$ .

ity occurred when  $F = 0.1$  and  $F = 0.2$ , and the results for these two levels of fishing intensity have been summarized in Table 18. All data were presented in terms of the range of values obtained when considering different stocks and  $t_p$  values. The ranges were always quite narrow, attesting to the fact that consideration of different stocks and  $t_p$  values had little influence on the results.

The conclusions that can be drawn from Table 18 depend to a large degree on what is considered to be the best estimate of  $M$ . If  $M = 0.1$ , the costs of letting  $F$  reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. From this consideration alone, it would seem advisable to limit  $F$  to 0.1.

If  $M = 0.2$ , however, the costs of letting  $F$  reach 0.2 are somewhat lower with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock. Limiting  $F$  to 0.1 would reduce the yield to only 45% of the level attainable at  $F = 0.7$ , while population fecundity and exploitable biomass would undergo reductions of about 30% from virgin stock levels.

On the basis of this analysis, then, there is a reasonable possibility that if  $M = 0.2$ , the optimal level of  $F$  could be as high as 0.2. From a biological point of view, however, a central question still remains unanswered, since we have not yet evaluated the consequences of reducing population fecundity. It is one thing to point out the degree to which population fecundity will be reduced by various levels of fishing intensity and quite another to determine the impact this reduction will have on future recruitment.

### Effects of Fishing on Future Recruitment

Variability in egg and larval survival is extremely high for marine teleosts. Larvae grow rapidly during the planktonic phase and require

large quantities of food. For example, haddock larvae initially grow at rates of about 12% per day, increasing in weight by a factor of  $10^5$  during their first year of life (Jones 1973). When food is not plentiful, available supplies can be exhausted rapidly, resulting in starvation and high rates of density-dependent mortality. Even if larval mortality is not directly due to starvation, density-dependent mortality could easily result from slow growth and prolonged exposure to predators (Cushing 1974).

Density-independent mortality, such as that suffered when eggs or larvae are swept into unfavorable nursery areas, can also be quite variable. Ketchen (1956) and Ketchen and Forrester (1966) found that in the case of English sole and petrale sole, mortality of this nature seems to account for a high proportion of the variability in year class strength.

Marine fish have evolved three basic ways of adapting their life history to cope with the highly variable survival of their progeny: 1) iteroparity (repeat spawning), 2) high fecundity, and 3) complete elimination of the egg and/or larval stage through ovoviviparity or viviparity. Murphy (1968) has shown that iteroparity is favored under conditions of high variability in larval survival and relatively constant adult mortality. This line of evolution leads to the existence of a large number of adult age-groups—a common situation in marine fishes. With several adult age-groups in the population, the size of the adult stock is buffered somewhat against variations in the strength of individual year classes.

High fecundity and elimination of the planktonic phase offer two divergent means of coping with variable larval mortality and are typified best by the gadoids on one hand and by elasmobranchs on the other. Atlantic cod commonly produce several million eggs per adult, and Cushing and Harris (1973) have shown that the spawner-recruit relation for this species is distinctly convex or dome-shaped (curve a in Figure 24). This relationship implies that eggs are "overproduced" at high parental stock densities, with attendant declines in larval survival. At stock densities below the replacement point ( $P_r$ ), the high fecundity allows for great resilience and rapid return to  $P_r$ .

The development of most elasmobranchs is characterized by the elimination of the larval stage found in the majority of teleosts and the young are fully developed when born. Fecundity is extremely low, with 2-108 young being produced

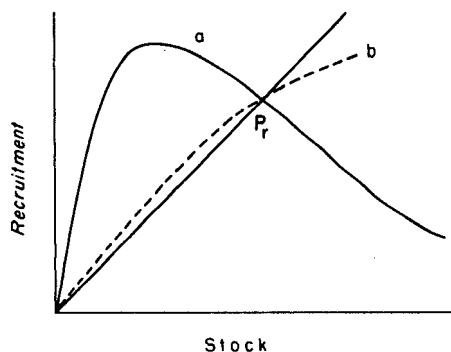


FIGURE 24.—Relationship between parent stock and recruitment for gadoids (a) and elasmobranchs (b).

per year (Holden 1973). Any compensatory responses to increase the number of recruits must act through changes in growth (with attendant changes in the age at maturity) or fecundity, and are relatively sluggish. Holden (1973) has suggested that the stock-recruitment relation for most elasmobranchs is probably of the form of curve b in Figure 24, departing little from the bisector on either side of the replacement point.

By eliminating the free-living larval stage, elasmobranchs have reduced the susceptibility of adult stock size to environmental perturbations. In the natural state, then, the compensatory mechanisms that return the stock to  $P_r$  do not need to provide the same degree of resilience they do in the gadoids. This lack of resilience makes the elasmobranchs poorly adapted to harvests by man, however, and they are quite susceptible to over-fishing.

Pacific ocean perch are ovoviviparous, and, like the elasmobranchs, they are probably much less resilient to perturbations from  $P_r$  than a highly fecund, oviparous species like cod. It is important, therefore, that population fecundity be kept quite near the levels found in the virgin stock when the adult stock was presumably near  $P_r$ . Any reduction in population fecundity from virgin stock levels could easily result in reduced recruitment.

Some increases in the number of larvae released could probably come through compensatory growth, since the age at sexual maturity and level of individual fecundity are both correlated strongly with size. There must be some limits to the degree of compensation this mechanism is capable of, however, and this was explored quantitatively by using the model (Table 16) and computer program described previously.

This analysis was begun by setting up four sets of hypothetical populations (one set for each stock) and calculating the population fecundity under different levels of fishing mortality. In the first population, the "standard" age-length data in Table 17 were used to describe individual growth in each stock. In the second and third populations, the mean lengths at each age were increased 3% and 5% (Figure 25) to simulate compensatory growth. In the fourth population, mean length at each age was again increased 5% above standard, and it was also assumed that sexual maturation occurred 1 yr earlier than in the other populations. The latter assumption was justified by the fact that a 5% increase in growth brought 8-yr-olds from the WVI stock and 10-yr-olds from the QCS stock up to the size at which sexual maturity occurred in the standard population (Figure 25). The last population was presumed to embody the maximum possible degree of compensation in population fecundity, since the projected increases in mean length at age would be quite remarkable in a species growing as slowly as *S. alutus*. The assumption that the age at sexual maturity would decline because of earlier attainment of a critical maturation size is also tenuous, and only time will tell if this actually occurs.

The age of recruitment was taken as age 8 for the WVI stocks and age 10 for the QCS stocks, in

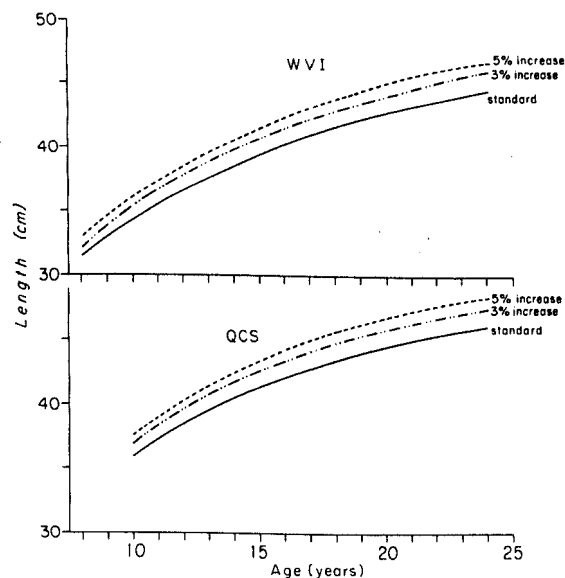


FIGURE 25.—Mean length at age for female Pacific ocean perch in the WVI and QCS stocks, assuming standard growth, and two different levels of compensatory increase in growth.

TABLE 19.—Estimated population fecundity (millions of larvae released) for hypothetical Pacific ocean perch populations based on 1,000 recruits per year, under different levels of fishing mortality and compensatory growth and maturity.

Item	WVI stock			Item	QCS stock		
	0.0	0.1	0.2		0.0	0.1	0.2
$M = 0.1$							
Standard growth, mature at age 9	607	356	237	Standard growth, mature at age 11	703	437	302
3% increase, mature at age 9	753	442	294	3% increase, mature at age 11	828	515	356
5% increase, mature at age 9	867	510	339	5% increase, mature at age 11	920	572	396
5% increase, mature at age 8	884	527	357	5% increase, mature at age 10	966	618	442
$M = 0.2$							
Standard growth, mature at age 9	256	174	130	Standard growth, mature at age 11	358	251	191
3% increase, mature at age 9	318	216	162	3% increase, mature at age 11	422	296	225
5% increase, mature at age 9	366	249	187	5% increase, mature at age 11	469	328	249
5% increase, mature at age 8	383	266	204	5% increase, mature at age 10	515	375	296

order to accommodate the changes in age at maturity. It was assumed that the length-weight relationships, length-fecundity relationships, and vulnerability coefficients characterizing the standard populations would apply to the other populations as well. All calculations have been carried out for  $M = 0.1$  and  $M = 0.2$ .

The results (Table 19) for standard growth when  $F = 0$  give the estimated population fecundity for the virgin stock. In actual fact, biomass was reduced below virgin stock levels several years prior to the time when the "standard" rates of growth were estimated and some compensatory changes could already have occurred. The population fecundity in the "standard" population when  $F = 0$  could consequently overestimate preexploitation fecundity to some degree.

For both stocks considered, fishing mortalities greater than  $F = 0.1$  doom Pacific ocean perch to lower levels of population fecundity than those existing prior to exploitation. None of the populations examined were able to recover preexploitation levels of population fecundity when  $F = 0.2$ , even when mean length at age increased by 5% and sexual maturation occurred a year earlier than normal.

Even if  $F$  is restricted to 0.1, the ability to regain virgin stock levels of fecundity varies sharply with  $M$ . If  $F = M = 0.1$ , the results for both stocks show that even if growth increases by 5% and sexual maturation occurs a year earlier than normal, population fecundity will be 12-13% less than in the virgin stock. If  $M = 0.2$ , the outlook is better, since the stocks were able to recover 92-97% of the preexploitation fecundity with a 5% increase in growth.

The main point to be considered, however, is that even when  $F = 0.1$ , Pacific ocean perch would have to undergo significant compensatory changes

in growth to regain virgin stock levels of population fecundity and would possibly have to mature a full year earlier than normal. In this light, the intensive fishing of the U.S.S.R. and Japanese trawl fleets in the past has been quite remote from the concept of long-term equilibrium yield.

In the case of the WVI stock, exploitation was most intensive during 1967, and, depending on the value of  $M$  used, 1967-68 estimates of  $F (= Z - M)$  would range from 0.36 to 0.46 (Figure 17). In almost every year since, the estimated value of  $F$  would exceed 0.1, regardless of whether  $M = 0.1$  or 0.2. The situation is less clear in the case of the QCS stock, but mortality estimates based on the age composition of the Washington trawl fleet (Figure 16) indicate that  $F$  was between 0.66 and 0.76 during 1968-69 and exceeded 0.1 during 1969-72.

Drastic action will probably be required to return Pacific ocean perch to their former levels of population fecundity, beginning perhaps with a total ban on commercial fishing, such as that proposed by Snytko (1971). Once this has been accomplished, harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed  $0.1 \beta$ , where  $\beta$  is the estimated stock biomass.

## SUMMARY

Pacific ocean perch are a dominant component of the fauna of the North Pacific, attaining a wide geographic distribution and high levels of population density prior to exploitation. Intensive exploitation by man created a sudden change in their population biology, and one that they were poorly adapted to cope with. Pacific ocean perch stocks lack the resilience of highly fecund, oviparous groups like the gadoids and their ability to main-

tain even current levels of abundance is uncertain.

The biology and population dynamics of Pacific ocean perch in the Washington-Queen Charlotte Sound region were examined in detail, to gain some insight into the effects of different fishing strategies on this species. Two stocks were delineated: one in Queen Charlotte Sound (QCS stock) and one inhabiting the waters off northern Washington and southern Vancouver Island (WVI stock).

Production in the region occupied by the WVI stock plummeted from 39,000 metric tons in 1967 to 6,000 metric tons in 1969 (an 85% decline), and catch per hour by North American trawlers declined 45% during the same period. The QCS stock was affected less drastically by fishing, since biomass estimates and CPUE data indicated that *S. alutus* were initially more abundant in the former area and did not undergo such intensive exploitation. During 1966-68, production declined 50%, while CPUE of Washington trawlers declined 36%.

Changes in size and age composition of Pacific ocean perch in the commercial landings were examined for the years 1967-73. Substantial quantities of large *S. alutus* were present in Queen Charlotte Sound during 1956-58 and subsequent changes in size and age composition reflected the changes caused by commercial fishing and recruitment of two strong series of year classes. The first series was centered around the 1952 year class and included the 1951-53 brood years, while the second series centered around the 1961 and 1962 brood years. Size composition data for the WVI stock were too limited to be useful prior to 1961, but data for subsequent years suggested that the same year classes that predominated in Queen Charlotte Sound were also predominant in landings from the WVI stock.

Fisheries exploitation has resulted in drastic reductions in the abundance of the 1951-53 year class series in both the QCS and WVI stocks and the 1973 Washington trawl catches from these stocks were dominated by 10- to 13-yr-old fish.

Growth rates were estimated from commercial fisheries and research cruise data, taking pertinent features of the life history such as seasonal and bathymetric variability in the age-length relation into consideration. Parameters of the von Bertalanffy growth model were estimated by sex for both the QCS and WVI stocks.

Although fish older than age 10 are large enough that almost all can be caught by conven-

tional trawling gear and retained for market sales, age composition data from commercial catches and research surveys showed that recruitment to the fishing grounds is not complete until much later than age 10. The proportion of each age group vulnerable to fishing ( $V_i$ ) was estimated by employing a model that assumed that natural mortality ( $M$ ) and  $V_i$  were constant throughout the year. The results suggested that recruitment to the fishing grounds differed somewhat between stocks, but that  $V_i$  ranged from 0.31-0.35 during age 10 to 0.87-0.94 during age 15. Estimation of  $V_i$  could not be made for fish less than 10 yr old, since these age groups may be subject to substantial rates of discard by fishermen.

Any yield per recruit analysis of Pacific ocean perch stocks must take these recruitment patterns into consideration to be meaningful. Recruitment to the fishing grounds is quite gradual, and many age groups that could potentially be retained by conventional mesh sizes are poorly represented on the fishing grounds. Evaluation of the effects of different size or age restrictions would be quite misleading if this were not considered.

Age composition data (number caught per hour by age-group) were used to estimate the survival of 14- to 18-yr-old Pacific ocean perch in year  $n$  to ages 15-19 in year  $n + 1$ , or to ages 16-20 in year  $n + 2$ . These survival estimates were then converted to total instantaneous mortality rates ( $Z$ ) and plotted against total international effort ( $\bar{f}$ ) on the assumption that they conform to the model:  $Z = q\bar{f} + M$ , where  $M$  = instantaneous natural mortality rate. The data seemed to fit this model in a general way but there was a relatively low correlation between  $Z$  and  $\bar{f}$  ( $r = 0.3-0.5$ ), due principally to wide variability in the availability of Pacific ocean perch to on-bottom trawls (totally unrelated to variations in actual abundance) and to the low quality of the data on international fishing effort. Despite this, there was good agreement between the estimates of  $M$  derived from this study (0.07 for the QCS stock and 0.23 for the WVI stock) and results obtained in previous studies. It was concluded that between-stock differences in natural mortality probably should not be overemphasized, and that the results of the mortality studies served mainly to show that  $M$  in the Washington-Queen Charlotte Sound region lies in the range between 0.1 and 0.2.

Data on the proportion of sexually mature individuals in each age-length group were sum-



marized by stock and suggested that maturation of both male and female Pacific ocean perch depends more on the size of a fish than on its age. The maturation length (where 50% of the fish in that length group are sexually mature) showed statistically significant differences between stocks, fish from the WVI stock maturing at a smaller size than those from the QCS stock. Males matured at 29.4 cm in the WVI stock and 30.5 cm in the QCS stock, while corresponding values for females were 34.2 and 36.3 cm.

Estimates of the age at sexual maturation indicated that WVI females release their first brood when 9-10 yr old, while those in Queen Charlotte Sound are 11 yr old. The results for males suggest that males from the WVI stock mate for the first time when 6 yr old, while this occurs at age 7 in the QCS stock.

Measurement of oocyte diameters from a series of ovaries collected over the complete extent of the reproductive cycle suggested that any estimates of fecundity must be regarded as tentative, owing to the uncertain significance of auxiliary modes of oocytes. Incomplete fertilization of oocytes also complicates the situation, and there is very little known about the relation between the number of developing oocytes and the number of viable larvae that will result from them.

Length ( $L$ )-fecundity ( $F$ ) data were summarized by stock and were described by the relation:  $F = aL^b$ . Analysis of covariance showed that there were significant between-area differences in the length-fecundity relationship, females from Washington-Oregon being more fecund than Queen Charlotte Sound females of comparable length.

The effect of fishing on stocks of Pacific ocean perch was examined through an approach similar to the yield per recruit analysis that is commonly used in stock assessment. However, the model and computer program developed for this study differ from conventional methods in that they allow for estimation of exploitable biomass and population fecundity as well as yield per recruit. Data required included age-specific schedules of instantaneous natural mortality, vulnerability to fishing, mean weight, and fecundity. Annual yield to the fishery, annual production of larvae, and average exploitable biomass on hand during the year were then calculated for a population based on a constant number of female recruits, assuming different combinations of instantaneous fishing mortality ( $F$ ) and age of recruitment to the fishery ( $t_p$ ).

The results showed that different levels of  $t_p$ , or between-stock differences in the input parameters had very little effect on the relative trends in yield, population fecundity, and exploitable biomass with increasing  $F$ . In all cases examined, there was a sharp rise in yield as  $F$  increased from 0.0 to 0.2 and a more gradual increase for  $F$ -values greater than 0.2. Relative levels of exploitable biomass and population fecundity showed a reciprocal trend, decreasing sharply as  $F$  increased from 0.0 to 0.2, and declining more gradually for  $F$  greater than 0.2.

The value of  $M$  used in the calculations had a pronounced effect on the results. If  $M = 0.1$ , the costs of letting  $F$  reach 0.2 are quite high, since exploitable biomass and population fecundity would be reduced to about 40% of their virgin stock levels. If  $M = 0.2$ , however, the costs of letting  $F$  reach 0.2 are somewhat lower, with exploitable biomass and population fecundity declining to about 50% of their level in the virgin stock.

This preliminary analysis provided some estimates of the reductions in population fecundity that could be expected under different levels of fishing intensity, but gave no insight into the effects of this reduced fecundity on future recruitment. As a result, the analysis was carried one step further and it was assumed that, at reduced levels of population density, all compensatory changes in recruitment are mediated through increases in growth. Attendant changes in fecundity at age and age at sexual maturation would then tend to increase the level of population fecundity and recruitment, since both fecundity and maturation are related to size.

Three hypothetical levels of compensatory growth and sexual maturation were considered, and none of these were effective in restoring preexploitation levels of population fecundity when  $F = 0.2$ . This was true even when mean length at each age increased 5% and sexual maturation occurred a year earlier than normal. Even when  $F$  is restricted to 0.1, Pacific ocean perch would have to undergo significant compensatory changes in growth to restore population fecundity to virgin stock levels, when the stock was presumably near the replacement point ( $P_r$ ) on the spawner-recruit curve.

Since Pacific ocean perch stocks are poorly adapted to extensive displacements from  $P_r$ , it was suggested that drastic action will probably be required to return them to their former levels of population fecundity, beginning perhaps with a

ban on fishing. Once the stocks approach their former levels of abundance, the harvest from both the QCS and WVI stocks should be regulated so that the catch does not exceed  $0.1\beta$ , where  $\beta$  is the estimated stock biomass.

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