FECUNDITY OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*) FOR THREE STOCKS OFF THE WEST COAST OF NORTH AMERICA

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ABSTRACT

We compare fecundity for the three major stocks of Pacific hake off the west coast of North America: the large, migratory offshore stock that ranges from California to British Columbia, and smaller, discrete stocks in Puget Sound and the Strait of Georgia. Estimates of total fecundity for these stocks are similar, but estimates of "effective" fecundity (number of yolked oocytes that are released to be fertilized) differ between stocks. All three stocks resorbed a proportion of their yolked oocytes, ranging from 10%–12% for the offshore stock to 38%–58% for the Strait of Georgia stock. Investigators using fecundity for stock assessment or other purposes must consider the effect that resorption of a large proportion of viable eggs will have on their studies.

INTRODUCTION

Foucher and Beamish (1980) examined oocyte development of Pacific hake (*Merluccius productus*) from the Strait of Georgia and reported that "relatively large numbers of large and small yolked oocytes remained in some ovaries after spawning and were completely resorbed so that a second spawning did not occur." Foucher and Beamish suggested that this could be related to the general condition of the stock (stock dynamics) and to environmental conditions such as temperature, and that this phenomenon should be considered in fecundity estimates for this and other stocks. Mason (1986) also reported resorbing oocytes in the same stock but considered it of minimal importance.

Fecundity relationships are often used in stock assessment to estimate stock abundance (Mason 1986), to estimate potential recruitment to the stock (Hunter and Macewicz 1985), and as an indicator of change in the dynamics of a stock (McFarlane and Franzin 1978; Leaman 1991).

The production of yolked oocytes destined to resorb indicates that the assumption used in fecundity estimates for Strait of Georgia hake and perhaps other stocks and species must be clearly defined. We therefore define fecundity as the number of yolked oocytes that are actually released to be fertilized, i.e., "effective" fecundity.

As part of our studies on Pacific hake in Canadian waters, we wanted to determine if the oocyte resorption reported by Foucher and Beamish (1980) could be quantified for use in stock assessment, and if other stocks of Pacific hake showed the same phenomenon. In this paper we compare fecundity between three major stocks of Pacific hake off the west coast of North America and present estimates of "effective" fecundity for these stocks. The total potential fecundity of hake reported in this paper (all yolked oocytes) is considered to be the maximum number of oocytes that could be spawned in a season. We assume that during the spawning season no additional oocytes are recruited into the stock of eggs we have counted.

MATERIAL AND METHODS

Study Area

Three major stocks of Pacific hake were examined during 1983–85: Strait of Georgia (British Columbia), Puget Sound (Washington), and offshore (California to west coast of Vancouver Island). These stocks are considered discrete on the basis of growth; otolith morphology and the pattern of annuli formation; stock dynamics (year-class strength and spawning biology; McFarlane and Beamish 1985); size and age at maturity (Goni 1988); and the presence (or absence) of the myxosporean parasite *Kudoa paniformis* (Kabata and Whitaker 1981; Nelson 1985).

Fish Sampling

Pacific hake were collected with midwater trawls during February, March, and April 1983 and April 1985 in the Strait of Georgia; March 1983 and March, April 1985 in Puget Sound; and March 1983 and January, February 1984 off California (offshore stock).

Peak spawning in the Strait of Georgia and Puget Sound occurs in late March–early April (McFarlane and Beamish 1985; Goni 1988), and off California in late January–February (Woodbury et al. 1995). Therefore, ovaries were collected from ripe fish just prior to or during peak spawning, and from spent fish 2 to 3 weeks after peak spawning in all areas. All fish were sampled for length, sex, maturity, and paired otoliths for age estimation.

Ovaries were selected from ripe and spent fish according to the description of Foucher and Beamish (1977). Only fish that met the criteria for ripe or spent

TABLE 1
Macroscopic Characteristics of Different Stages in the Development of the Ovaries of the Pacific Hake (*Merluccius productus*)

Stage	Macroscopic characteristics
Immature 1 (I1)	Virgin; ovary small, light pink, and semi-transparent; no oocytes
Immature 2 (I2)	Same as above, but some yolkless oocytes visible
Ripening 1 (R1)	Ovary starting to enlarge up to 1/4 of volume of body cavity and light yellow; oocytes with yolk and opaque; blood vessels on ovary pronounced
Ripening 2 (R2)	Ovary filling more than 1/3 of body cavity and yellow; oocytes with yolk and opaque; blood vessels pronounced
Ripe (R)	Ovary fills 1/2 to 1/3 body cavity; yellow
1 Ripe (1R)	Ovary fills 1/2 to 1/3 body cavity; translucent yellow; less than half of the oocytes are translucent
2 Ripe (2R)	Ovary fills 2/3 body cavity, translucent yellow; more than half of the oocytes are translucent
Running ripe (RR)	Translucent oocytes flow from vent with slight pressure; ovaries almost fill body cavity; oocytes loose in translucent ovary
Spent (S)	Ovary bloodshot, purple, and flaccid; fills about 1/3 body cavity; some translucent oocytes may remain
Resorbing (Resb)	Fish has not spawned; ovaries large, about 1/2 of body cavity, soft and flaccid; oocytes large and watery
Recovering (Rec)	Ovaries not flaccid or bloodshot, moderately firm, filling less than 1/2 body cavity and returning to preripening size; oocytes small
Resting (Rest)	Ovaries less than 1/4 body cavity, moderately firm with white sheen on surface, not bloodshot

as outlined in table 1 were selected. Ovaries were preserved in 10% formaldehyde solution and transferred to the laboratory. In the laboratory, the ovaries were transferred to modified Gilson's solution (Simpson 1951) for several months to allow breakdown of connective tissue.

We made the assumption that no fish categorized as ripe had spawned previously during the season, and that the estimates of total fecundity are unbiased. Although it is possible that some fish could have released eggs prior to sampling, we believe the timing of the collections and our adherence to the criteria (table 1) for selecting ripe fish would ensure that any bias would be small.

Ovary Processing and Fecundity Estimates

Ovaries were washed thoroughly in cold water over an 850-µm stainless steel screen onto a 40-µm nylon fabric screen. When necessary, eggs were gently separated by hand from ovarian tissue.

Eggs from each ovary pair were transferred to a preweighed shallow cup, vacuum dried for 4 minutes, and weighed to obtain total egg weight per fish. Five random subsamples (.05 or .1 gm) were removed. One subsample (.05 gm) was sized and counted in 50-µm intervals of oocyte diameter. Four subsamples (.01 gm) were counted.

TABLE 2
Date and Maturity State of Samples Collected during 1983–85

Area	Year	Month	No. ripe	No. spent
Strait of Georgia	1983	Feb/Mar	23	—
	1983	Apr	—	22
	1985	Apr	—	16
Puget Sound	1983	Mar	12	—
	1985	Mar/Apr	13	30
Offshore	1983	Mar	4	43
	1984	Jan/Feb	15	—

The total number of eggs in the ovary was calculated as the product of the mean subsample count per unit weight and the total egg weight per fish. The number of eggs in various size categories was obtained by applying the appropriate proportional value to the estimated total eggs in the ovary.

RESULTS

A total of 250 fish were collected during 1983 and 1985 in the Strait of Georgia; 225 fish during 1983 and 1985 in Puget Sound; and 95 fish during 1983 and 1984 offshore of California (offshore stock). Of these, 319 were female. Under the criteria of Foucher and Beamish (1977; table 1), 23 ripe and 38 spent ovaries were preserved from the Strait of Georgia, 25 ripe and 30 spent ovaries from Puget Sound, and 19 ripe and 43 spent ovaries from the offshore stock. In order to examine as representative a range of size and age as possible for each stock, we selected fish by size and pooled them for each stock by year and maturity for the analysis (table 2). The age composition of the female Pacific hake examined (figure 1) is representative of fish captured during commercial fishing in these areas (Francis and Hollowed 1985; McFarlane and Beamish 1985; Pedersen 1985).

Frequency Distribution of Oocyte Diameter

Ovaries of prespawning (ripe) fish from all three areas contained a bimodal distribution of oocyte diameters with peaks at about 100 µm and between 500 and 700 µm, similar to that described by MacGregor (1966), Foucher and Beamish (1980), and Mason (1986). Oocytes smaller than 150 µm contained no yolk and may constitute a reserve fund for future years (Foucher and Beamish 1980). All analyses were conducted on yolked oocytes only. In all three areas yolked oocytes were present in all size classes of oocytes from 150 to 840 µm, in approximately the same proportions between areas (figure 2).

Post-spawning (spent) fish from the three areas exhibited very different distributions of oocyte diameters

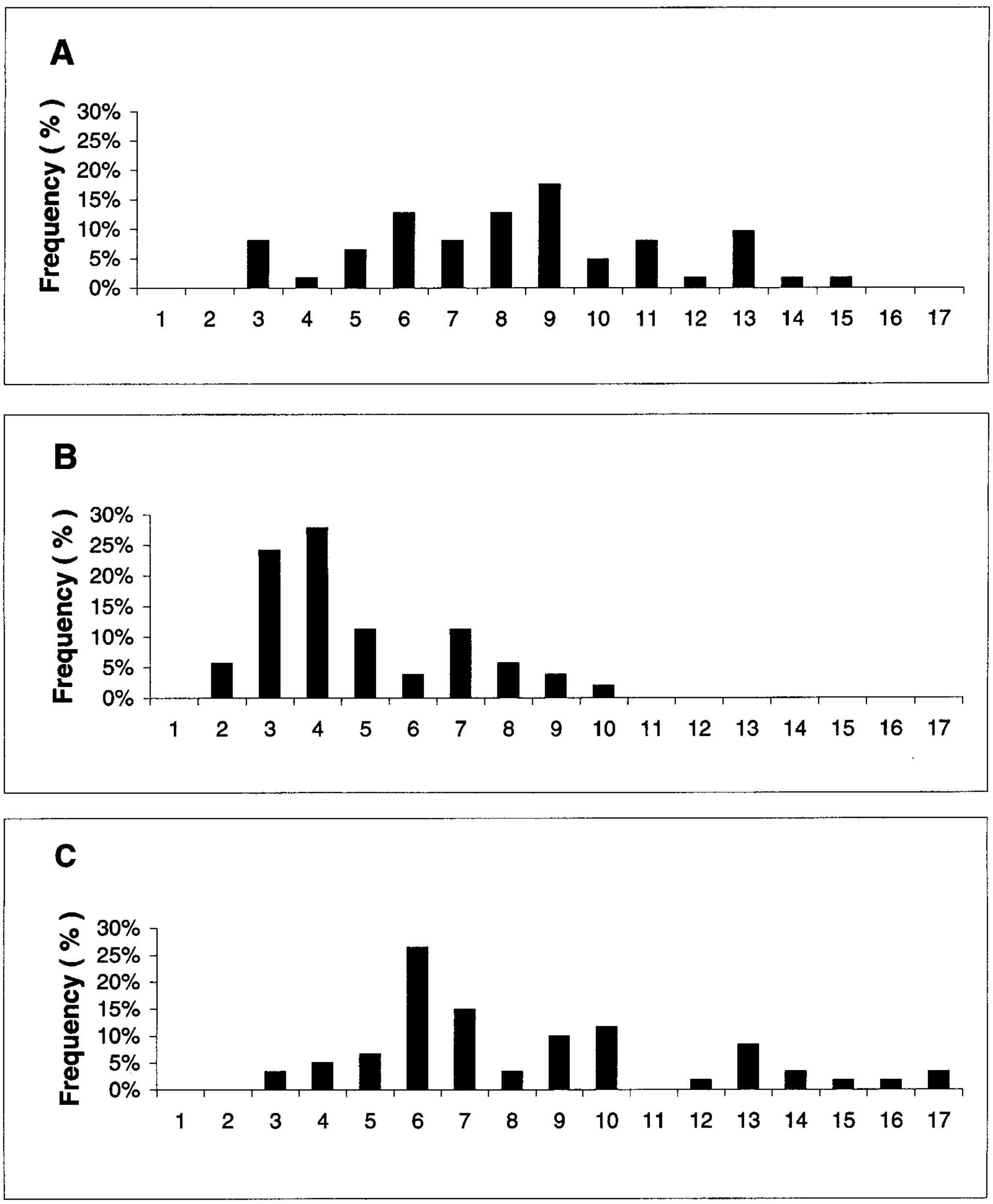

Figure 1. Age composition of fish collected from *A*, Strait of Georgia (1983, 1985); *B*, Puget Sound (1983, 1985); and *C*, offshore (California; 1983, 1984).

(figure 2). Of the oocytes remaining in the ovaries of spent offshore fish, approximately 70% were in the smallest size class of yolked oocytes (150–280 μm). Few oocytes larger than 360 μm were present. Puget Sound fish exhibited a similar trend: 40% of resorbing eggs in the smallest size class remained, but higher percentages in the larger size classes remained. Strait of Georgia fish exhibited a more even distribution of resorbing eggs across all size categories, with a peak at the smallest size (30%) at 150–280 μm and a smaller, secondary peak at 520–680 μm.

Size-Specific Resorption

Spent ovaries examined for all three stocks contained yolked oocytes (figure 2). In the offshore stock the percentage of retained oocytes was constant across the size range of fish examined: approximately 10%–12% of ripe ovaries. But ovaries examined from both the Strait of Georgia and the Puget Sound stocks showed an increasing percentage of eggs retained with decreasing fish length (figure 3). For Puget Sound, fish between 32 and 36 cm long retained from 44% to 32% of their eggs. But fish approaching the size of mature offshore

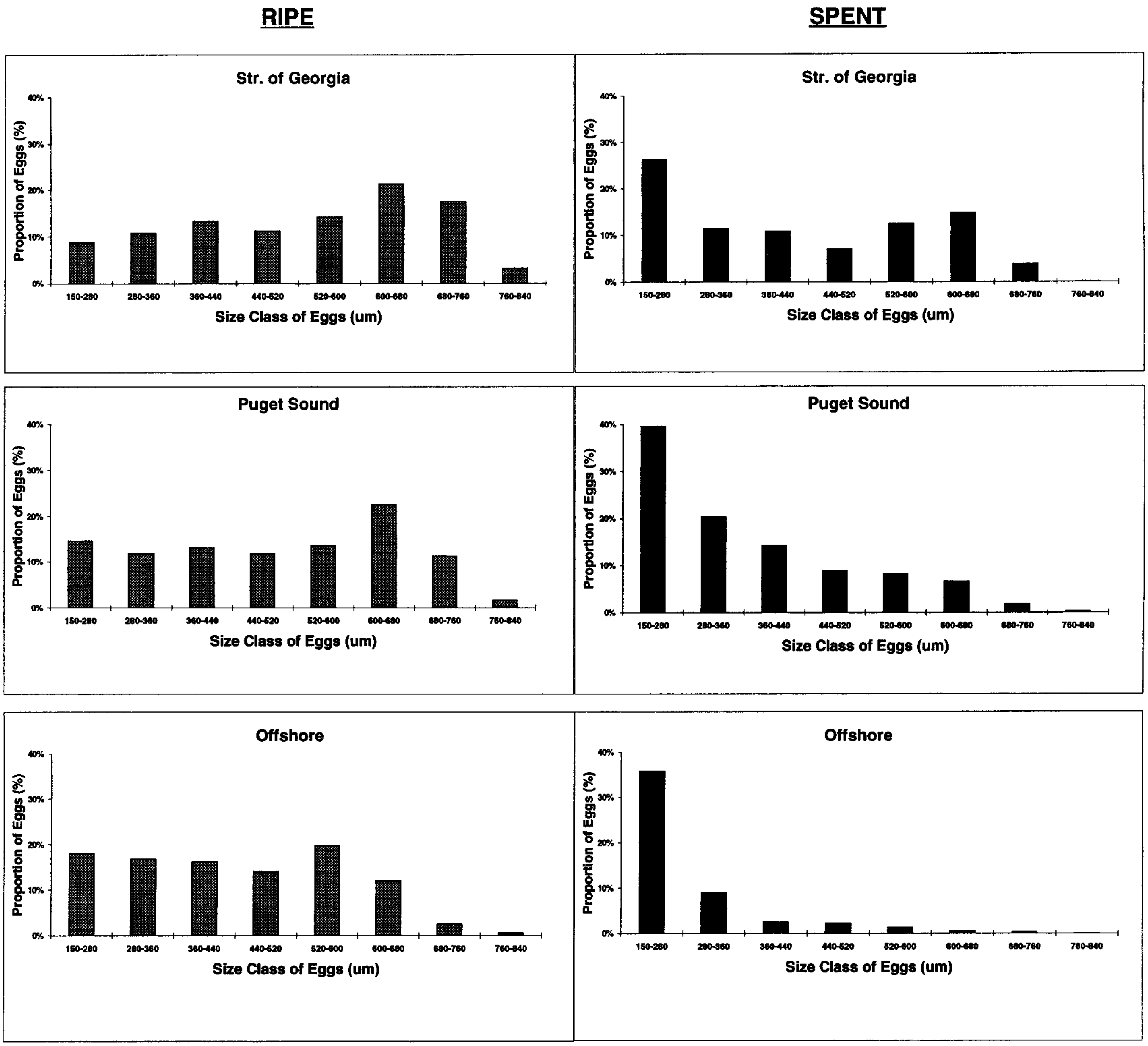

Figure 2. Representative frequency distribution of oocyte diameter from ovaries of Pacific hake collected in the Strait of Georgia, Puget Sound, and offshore (California).

fish retained a percentage of eggs similar to that of offshore fish (figure 3). The Strait of Georgia stock retained a percentage of eggs considerably higher at all fish lengths than either the Puget Sound or the offshore stocks, averaging between 38% (largest fish) and 58% (smallest fish).

Estimates of Total and Effective Fecundity

The relation of total fecundity to fish size was similar for all three areas (figure 4). Total fecundity (all yolked oocytes >150 µm) increased with length as follows: Strait of Georgia ($y = 0.0001x^{3.9576}$); Puget Sound ($y = 0.0003x^{3.6233}$); offshore (California; $y = 0.047x^{2.4311}$), where y = fork length in centimeters (figure 5).

The number of yolked oocytes (>150 µm) remaining in the ovaries of spent fish varied between areas (figure 5) and had the following relationships: Strait of Georgia ($y = 0.0013x^{3.1055}$); Puget Sound ($y = 3.6878x^{0.7117}$); offshore (California; $y = 4E\text{-}07x^{4.7875}$).

Our definition of effective fecundity—the number of yolked oocytes that are actually released for fertilization—suggests that the real, or effective, fecundity will be lower for all three stocks than previous estimates of fecundity or the estimates presented here as total fe-

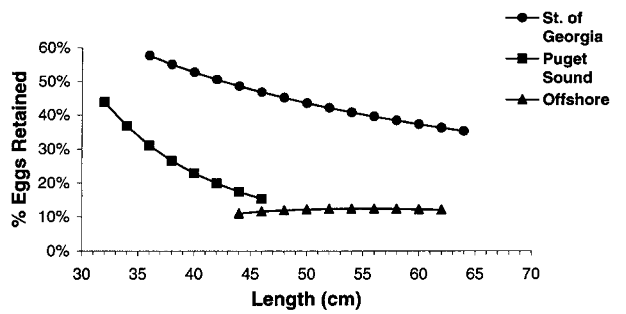

Figure 3. Percentage of oocytes retained in the ovaries of Pacific hake from the Strait of Georgia, Puget Sound, and offshore (California).

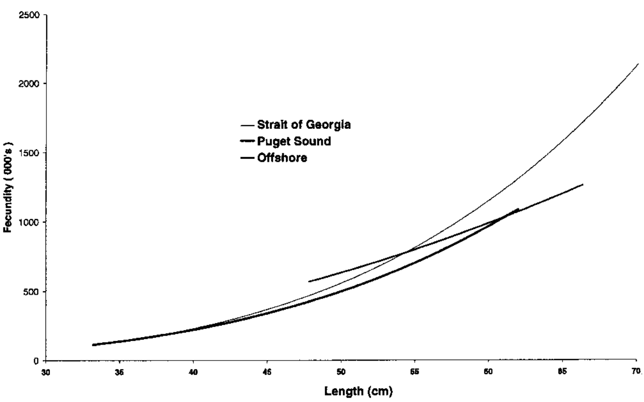

Figure 4. Estimates of number of yolked oocytes (>150 µm) in hake ovaries from the Strait of Georgia, Puget Sound, and offshore (California) plotted against fork length of female hake.

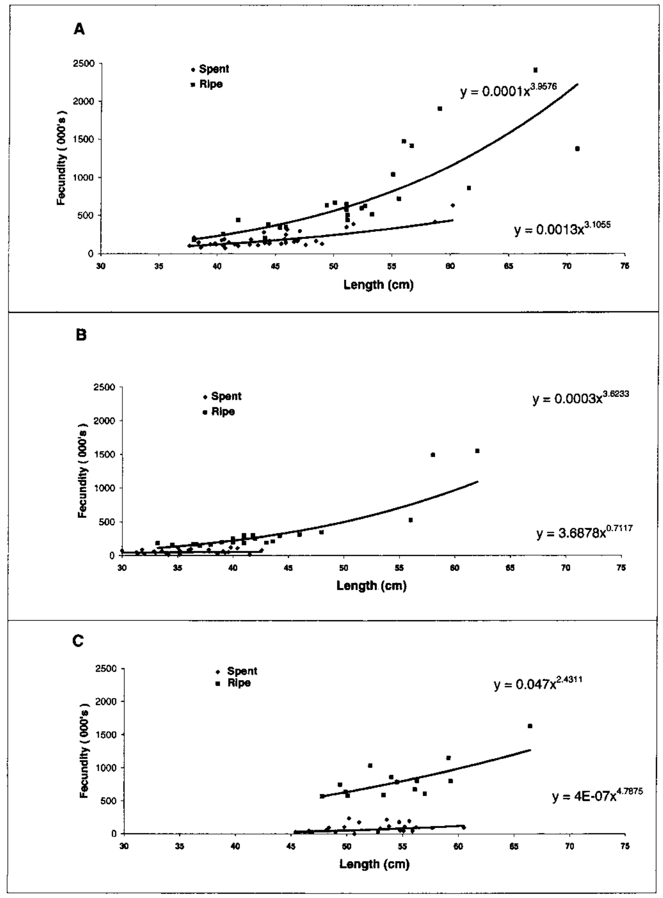

Figure 5. Estimates of number of yolked oocytes (>150 µm) in ripe and spent ovaries from *A*, Strait of Georgia; *B*, Puget Sound; and *C*, offshore (California) plotted against fork length of female hake.

cundity (figure 6). Effective fecundity increased with length as follows: Strait of Georgia ($y = 0.0035x^{4.6746}$); Puget Sound ($y = 0.0021x^{4.9268}$); offshore (California; $y = 46.713x^{2.4004}$).

We also examined the relation of only the larger size classes of yolked eggs to length, as other authors have suggested might be appropriate (MacGregor 1966; Mason 1986). We chose eggs larger than 360 µm because our observations indicated that most fish in two of the stocks (Puget Sound and offshore) retained only a small percentage of eggs larger than 360 µm in the ovary after spawning. The relation of eggs larger than 360 µm to length is: Strait of Georgia ($y = 0.0099x^{4.4254}$); Puget Sound ($y = 0.067x^{3.9623}$); offshore (California; $y = 133.8x^{2.0894}$).

DISCUSSION

Our estimates of total fecundity (all yolked oocytes >150 µm) are similar among stocks and comparable to the estimates presented by MacGregor (1966). For the Strait of Georgia our estimates of total fecundity are substantially higher (~30%) than those presented by Mason (1986), but the methods Mason used to estimate fecundity have been shown to consistently underestimate fecundity in other species (Leaman 1988).

Our study indicates that all three stocks of Pacific hake resorb a proportion of their yolked oocytes after spawning; the proportion ranges from 10%–12% for the offshore stock to 38%–58% for the Strait of Georgia stock.

The size-specific trend in resorption (retained eggs) in the Puget Sound and Strait of Georgia stocks may indicate a physiological response to maturation at a smaller size. The mechanisms for this are unknown; however, we do note that for the small fish in which this is most pronounced (Puget Sound: 32–35 cm) the impact on total or effective fecundity for the range of mature fish is small.

For some stocks of fish the effective fecundity, or number of viable eggs released to be fertilized, may be substantially less than the number of yolked oocytes produced in the ovary. It is important that investigators using fecundity to monitor the health of a stock, or to estimate abundance or potential recruitment for stock assessment be aware of how the resorption of a large percentage of seemingly viable eggs will affect their studies.

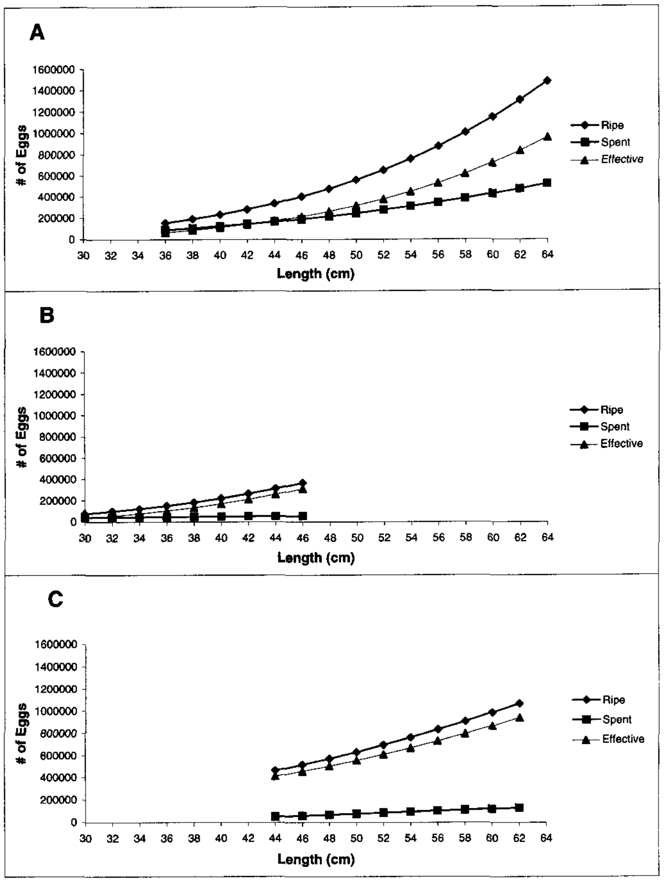

Figure 6. Relationship between total fecundity (ripe) and effective fecundity (ripe–spent) for Pacific hake in *A*, Strait of Georgia; *B*, Puget Sound; and *C*, offshore (California).

Other researchers have reported on this phenomenon for Pacific hake (Foucher and Beamish 1980; Mason 1986), other forms of *Merluccius* (Hickling 1930; Christiansen 1971), and other species (Hoar 1955). This study, to the best of our knowledge, is the first to attempt to quantify this resorption.

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