RESTRICTED

INTERNATIONAL COMMISSION FOR THE NORTHWEST ATLANTIC FISHERIES

Serial No. 2171
(D.c.11)

Seal Contribution No. 1
(also ICNAF Res.Doc.69/31)

ANNUAL MEETING - JUNE 1969

ON THE POPULATION DYNAMICS AND SIZE OF STOCKS OF HARP SEALS IN THE NORTHWEST ATLANTIC

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CONTENTS

31

Abstract

Two populations of harp seals Pagophilus groenlandicus Erxleben inhabit respectively the Gulf of St. Lawrence and the "Front" east of Newfoundland in winter and spring. One- and two-year immatures of the Gulf herd show considerable mixing with the Front herd but this has not yet been shown for older groups. The main fishery is for the young of the year, "whitecoats" within a few days of birth on the ice.

1. Photographic aerial survey

Photographic aerial survey of whelping seals showed a decline of about 50% in numbers of the Front herd between 1950 and 1960. A similar change was measured in the southern Gulf of St. Lawrence between 1950 and 1964. The method gives variable underestimates because (a) some adults remain in the water at all times; (b) variable numbers have not whelped by the time the fishery for young seals begins, which necessarily ends the survey; (c) low flying aircraft disturb unwhelped seals into the water. Most successful results probably occur in the absence of aircraft, and when seals whelp close to shore on fast ice. Photographic aerial survey of moulting seals was unsuccessful and would probably very rarely be successful.

2. Capture-recapture tagging

Tagging of young seals and their recapture at the fishery are not affected by the factors above, so long as all groups of young are sampled by the fishery. This method seems to have given the best estimates on the Front, when the catch was a very high proportion of total production.

3. Catch and survival

(a) Life history parameters including a density-dependent age at female sexual maturity indicate that the maximal sustainable yield of young for a balanced population is about one-third of the annual production.

(b) (i) The Gulf stock. In the Gulf a higher age of female maturation than on the Front had indicated exploitation in the Gulf in 1965 to be below maximal sustainable yield level, assuming a density-dependent age of maturation. Under these conditions, the population must be constant, and equal age samples represent equal fractions of it. For 16 years, samples of southward migrants have been collected and aged and one sample of moulting animals was available from the Gulf. By age four, the year classes are fully represented in these samples. Numbers of age 4 animals were expressed as a percentage of the total sample, and plotted against the previous catch, as young animals, of the same age class. Survival to age 4 was found to fall sharply at catches above 85,000 to 90,000 young seals, which is therefore considered to be the maximal sustained yield of young of the Gulf herd. Present reproductive and mortality rates of the Gulf stock are such that the yield is maximal at 0.33 of production, and production may be therefore about 270,000 young per annum. The total population of seals other than young of the Gulf herd should on this basis be about 1¼ million. The estimate of production is double that observed or calculated from capture-recapture tagging in the southern Gulf. This discrepancy has not been fully resolved by addition of estimates of seals whelping in other parts of the Gulf. However a sight record of about 1,000,000 animals was made in the northern Gulf in April, 1966.

(ii) The Front stock. For the Front herd, change in reproductive rates indicates heavy exploitation before 1961-62. In this case the survival of a year class is measured against samples of a population which has itself declined. The samples, unlike those from the Gulf are all of moulting seals. These usually show an excess of immatures aged 1-2 years. Within these limitations variations in year-class survival lead to estimates of the current sustainable yield of young of the Front herd of 90,000 or less. (Earlier estimates are given by Sergeant (MS 1967, ICNAF No. 1952.)) Capture-recapture tagging in 1966 gave an estimate of about 200,000 young produced, and the highest annual catch of young in an intensive fishery between 1960 and 1966 has been 197,000. Thus present sustainable yield on the Front likely is not higher than 200,000/0.33 or 70,000. For a recovered Front population, with adequate protection of older animals, it is probably about 180,000 (Sergeant, MS 1967), or double the maximum sustainable yield for the Gulf herd.

4. Age at first maturation

An independent confirmation of results from catch and survival was obtained from a further study of reproductive rates. It was found that the mean age at which female harp seals mature sexually varies sharply from year to year within the Gulf population. The annual figure has a high inverse correlation with the catch as young animals of the maturing year class, a catch which, being variable, has thinned the year class to a greater or lesser degree. Thus, intra-specific competition for food or space, which determines rate of growth and maturation, occurs within a single age class of young harp seals and not between age classes. For the Gulf, the mean age at sexual maturation is found to approach the biological maximum after catches of young near 90,000, which is therefore confirmed as the maximal sustainable yield of young.

5. Mixing

Mixing of immatures of age 1 and 2 years from the Gulf to the Front is estimated at about 25%, from tagging in 1966. Similar results are beginning to be shown from tagging in the Gulf in 1968. There is as yet no evidence whether this movement is permanent for the animals involved. The varying survival and density-dependent age at first maturity in different year classes of Gulf-born animals suggest that mixing between the two populations is small.

Text

Introduction

The western herds of harp seals inhabit the waters between eastern Canada and northwest Greenland, that is the ICNAF area, and carry out long seasonal migrations on the edge of the drift ice. As they move south along the Labrador coast in early winter just ahead of formation of the first ice, the herds divide into two, one entering the Gulf of St. Lawrence and the other remaining east of Newfoundland. Seals of the two herds remain separate till late April or May, whelping in March and moulting their haircoat in April. Evidence that the two herds retain their separate identity from year to year is as follows: (1) a constancy of return of the same number of seals to the same whelping areas even in years of unfavourable ice conditions in the Gulf[1]; (2) a mean difference of 5 days in mean birth date (Sergeant, 1965). Until very recently, one would have added (3) a mean difference in age at female maturity (Sergeant, 1966) and (4) a lack of mixing as shown by tag returns (Sergeant, 1965). There is now strong evidence from tag recoveries that a proportion of Gulf-born immatures mix into the Front herd at one and two years of age when they move south from the arctic in January to March, one to three months later than older groups (Sergeant, 1965). A reverse movement has not been demonstrated. The question of the degree of mixing between the two herds is examined in detail later, as is the significance of the figure for mean age at first maturity.

The results of photographic aerial surveys, and of capture and recapture experiments hitherto carried out on these seal populations, allow various interpretations. This document therefore includes the results of a third method of assessment of the western stock of harp seals: an analysis from age samples of the survival of successive year classes following catches of young of known magnitude. Such a method is empirical in that it measures survival instead of estimating production. Survival is supposed to be determined largely by fishing mortality, an assumption based on the necessary stability of population of a long-lived species, and the rarity of direct evidence for catastrophic natural mortalities of young animals.

A fourth, very recently discovered method is to measure accurately the age at first maturation of females, which has been found to vary directly with the density of the year class born 5 years previously. Since a biological limit to maturation age is reached, this method can be applied only to a population which has not already been over-hunted.

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[1] Ice conditions in the Gulf were unfavourable in 1969 and whelping areas will be scrutinized closely to further test this statement.

Two additional methods have proved useful at very high levels of the fishery. Where almost the total production is believed to have been taken, the catch of young seals may be used as a minimal estimate of production. Also, since the catch is then usually composed of whitecoats, the survival and hence the catch of newly moulted young (the "beaters", aged about 3-5 weeks), will vary inversely with the completeness with which the whitecoats are removed. Norwegian biologist T. Øritsland has introduced the second of these two methods (Øritsland, MS 1960, ICNAF Serial No. 1967). It is not discussed here since the relevant data are lacking from Canadian catch statistics.

Would catch per unit of effort provide a useful method for the estimation of stocks? The whelping animals are gregarious but maintain a minimal individual distance. Hence, allowing for differences in ice structure, the density of young is uniform whatever the absolute number of seals. Thus mean catch per unit effort will be constant until such time as the catching effort (number of ships) is high enough, or the number of animals low enough, for all to be taken, when total catch can better be used as a minimal estimate. In fact, annual variations due to weather and ice conditions are great, obscuring short-term trends in catch per unit effort.

1. Photographic aerial survey

Surveys of whelping animals were carried out by Dr. H.D. Fisher in 1950 and 1951, and by the writer a decade later in 1959-60 (Sergeant and Fisher, 1960). A survey on the Front in 1964 was incomplete and its results are not included here.

As a check, surveys of moulting immatures and adults were attempted in 1962-63 following the relatively successful Soviet attempts using this method in the White Sea (Dorofeev, 1928; Surkov, 1957; but also see Nazarenko and Yablokov, 1962).

A return to surveys of whelping adults was made in the southern Gulf in 1964, together with a capture-recapture experiment. Finally, most of the Gulf (including the previously unsurveyed northernmost part) was surveyed in 1967 but owing to the incompetence of the survey company only the northern estimate is of value. At the same time a study was carried out by low-flying helicopter at the Magdalen Islands, centre of the Gulf fishery that year, in order to determine the percentage of adult females with young under different conditions.

The technique of aerial survey is simple and has been gradually refined as follows. Over ice of suitable thickness for harp seals to occur, the aircraft runs search patterns 5 to 10 miles (7 to 16 km) apart. When a seal patch is discovered, its shape is delimited, and then vertical photographic lines are run across it from known altitude in at least two intersecting planes. A small overlap is necessary between photographs in order to join them but stereophotography is not used. From the resulting 9 X 9 in (23 X 23 cm) prints, the adult seals are easily counted and their mean density in the photographic lines is computed. By mounting strips of miniature (2 X 2 in; 5 X 5 cm) prints in their correct orientation and intersection, the borders of the patch can be extrapolated onto squared paper. Hence the total area is calculated, and the total number of adult seals determined by multiplying area and density.

(a) Aerial survey of whelping patches

Using counts of adults it is important to know the percentage of adult females attending their pups, to allow for those in the water. Preliminary data of this kind are available from the reports of a Soviet expedition which drifted among an undisturbed patch of harp seals in the White Sea (Popov, 1967). In 1967, assisted by Dr. D.H. Pimlott, I made counts at the Magdalen Islands using low-flying helicopter over herds in which all pups were believed born; the ice was not rough and the young seals were believed easily seen. Percentages of adults were as shown in Table 1.

These results confirm those of Popov that the percent of adult females on the ice is higher in bright than in dull weather. We have no observations that may confirm his finding that the percentage rises to a maximum in the evening. Our findings tend to suggest a highest percentage in the early afternoon of bright days when the light density is highest. This would be explained as a tendency of the adult females to bask in the sun, a habit also characteristic both of young and of older animals at the times of hair-moult.

There is also a suggestion from our data that the highest percentage of adult females is found with newborn young, which would be expected since suckling is most frequent soon after birth.

Aerial surveys are generally carried out in bright sun or light overcast, which give best flying and searching conditions for the aircraft; and near midday or in early afternoon, since a patch will not generally be found till this time of day after long searching. These conditions therefore suggest that a large percentage of adult females will be found with the young when the patch is photographed.

The few control data we have show that patches of whelping seals have frequently been under-estimated. Thus, in 1967, a compact patch of seals in the northern Gulf was photographed on March 10. Photographic lines covered some 0.25 of its estimated area and the resulting estimate was 20,000 adult seals. Sealing began on this patch on March 13-14 by several ships and it was soon "cleaned up" with a catch of about 35,000 young seals. Our survey therefore accounted for only 57% or less of the numbers. Clearly, many adult females must have been in the water. Since at the date of photography pupping had not been completed, unpupped females had probably not climbed out, or were very readily disturbed into the water by the aircraft.

The chief limitation on our surveys has been the early onset of the fishery: formerly beginning on March 5 and more recently on March 7 in the Gulf; formerly March 7 and recently March 12 on the Front. Thus, in many cases surveys had to be made before pupping was complete since once ships entered the patch, further photography became impossible. In the Gulf in 1967, many new pups were found on an old, sealed-over patch, and also newly formed patches were found as late as March 11 and 13 when the quota fishery had ended. Probably in the Gulf the increasing disturbance by low-flying aircraft in recent years has increasingly delayed pupping, and led to increasing incompleteness of aerial photographic surveys.

Should there be no fishery, or a very late-starting one, would aerial photographic survey be successful? Two factors work against success of late surveys: first, the adult females of early born pups will start to leave them, so that a correction factor, of the kind shown in Table 1, will have to be applied for these animals; secondly, ice-movement will become more likely, breaking up the patches from their original round or oval shape, and making area estimates very difficult. This occurred at the Front in 1964 as early as March 12.

In most surveys the whitecoated young, owing to their invisibility and tendency to hide in crevices, cannot be fully counted. On one occasion, in the Gulf in 1960, a patch had not been hunted up to late March when the young had moulted their white coats and become relatively conspicuous again. In these circumstances the young may perhaps be counted, but it is not an opportunity that can commonly be expected to occur.

Successful survey may be expected in years when there is little ice and the seals are forced to whelp on fast ice formed of frozen-together ice pans. The adult females cannot then enter the water. Such a condition existed at the Front, close to the Gannet Islands, Labrador, in March 1960 and the survey that year may have been rather complete (see Sergeant and Fisher, 1960).

Adult males occur in whelping patches from the time of their formation, as is evident from visual and olfactory observation at ice level. Many adults occur at the fringes of whelping patches undergoing formation; it cannot be determined from aerial observation photographs whether these are unpupped females or males. Adults are now totally protected at the whelping patches but were formerly shot. However, since males were not shot in proportion to their numbers, their frequency cannot be determined in this way.

The limitations on aerial survey of whelping patches discussed above make it likely that such surveys, unless carried out annually, will serve to indicate trends in population rather than absolute figures. In later sections results of aerial survey will be compared with results from other methods. For the time being the bare results of complete surveys are shown.

Largest estimate of adults at whelping patches

Years	Gulf	Front
1950 and 1951	215,000	430,000
1959 and 1960	150,000	215,000
1964	100,000	

(b) Aerial survey of patches of moulting adults and immatures

The techniques used were exactly the same as used for whelping surveys. However, the discontinuous nature of the ice made the use of two aircraft necessary: in 1962, one was used in the Gulf and one on the Front; in 1963, two at the Front and one in the Gulf.

Moulting patches are much denser than whelping patches and can frequently be seen from greater distance (under a thin overcast, sometimes at 1500 m altitude). However, moulting animals are not tied to one site and may move large distances in a few days. If possible, the whole area of ice should be surveyed in one day. Disturbance by sealing ships often affects survey results, if made during the sealing season. However, it appears that the most important source of error is again the number of seals in the water. This error is probably increased in the northwest Atlantic by the frequently discontinuous nature of the ice at both Gulf and Front. In the Gulf, estimates have been particularly low. Animals are found concentrated on the northern edge of the ice fringing the southern Gulf. They pass the Magdalen Islands where they are known to feed in open water and will not again find ice until reaching the northern Gulf.

The rule is proved by an exceptional year, 1966. Then, ice in the southern Gulf completely disappeared by April 20. Thus, Gulf moulters seeking ice were forced to find it in the northern Gulf. On one day, April 6, from M.V. Theron I observed moulting seals covering an area estimated from the ship to cover 20 X 5 miles and at a density which I have estimated, from the least density obtained from previous aerial surveys of moulters, at 900/sq mile. This gives a rough estimate of about 900,000 animals present, or the greater part of the calculated Gulf herd. On only one day out of 24 days spent hunting in the area was such a concentration of seals observed; thus, the chances for effective aerial survey that year would have depended entirely on that one day.

On the Front, the same distribution of ice is commonly found. In most years a belt of ice remains in White Bay throughout April, separated by open water from ice along the southern coast of Labrador. Moulting groups are seen gradually to diminish in the southern ice belt, and to increase in the northern belt. Probably seals are in the intervening water under such conditions.

Greatest counts of moulting seals are as follows:

Year	Southern Gulf	Front
1962	30,000	216,000
1963	20,000	215,000

The Gulf results are clearly below expectations. For the Front, an estimate of 215,000 whelping females made in 1960 would necessitate the existence of approximately four times as many, or 860,000 adult and immature seals in moult (see Section 3). Thus, to date, the results of surveys of moulting animals have been inadequate. For whelping animals, surveys would have to be carried out annually for any chance of complete results.

2. Capture-recapture tagging

Three experiments of this kind have been carried out, in each case just before the beginning of the fishery for young seals, twice in the Gulf and once on the Front.

In the Gulf in 1964, 2550 young seals were tagged from a helicopter based on the Magdalen Islands, between March 1 and 7, with the fishery beginning on March 8.

At the Front in 1966, 3581 young seals were tagged from a helicopter based on an icebreaker, between March 9 and 15, with the fishery beginning on March 12.

At the Gulf in 1968, 2217 young seals were tagged from a helicopter, between March 8 and 15, with the quota fishery beginning on March 18.

In the 1964 Gulf experiment, recoveries could be analyzed separately between sealers who worked from aircraft together with some landsmen from Magdalen Islands, and sealers who worked from ships. The analysis (Table 2) gives a larger estimate from ships. Variability of returns was large as between individual ships (Table 3) indicating that mixing of returns was incomplete. For landsmen, mixing of returns was assumed to be better since the sampling units were smaller, more numerous and more frequently changed position than with ships. A photographic aerial survey of the same two patches of seals, corrected for local disturbance of the seals by ships' crews, gave an estimate of 100,000 attending adults. Landsmen's returns from a capture-recapture experiment therefore gave an estimate of 20% higher, ship returns 50% higher, than photographic survey.

On the Front in 1966, variability of returns from Canadian ships was high (Table 3) as expected after the 1964 experiment, but the number of ships was large (9) so that grouping the returns may be permissible.

For this experiment I (Sergeant, ICNAF 1967) analyzed recaptures from Canadian ships at the Front, citing evidence that Norwegian returns were incomplete. Figure 1 gives further evidence for this statement. Canadian returns are nearly twice as great as Norwegian returns, although Norwegian catches were nearly twice as great as Canadian catches (107,000 vs. 65,000). Since the Norwegian and Canadian ships were all together at the fishery, the lower rate of Norwegian returns can only have been due to the fact that they were incomplete. If Norwegian returns were incomplete, an estimate of production based on them will be too high.

In the Gulf in 1968, a later fishery beginning on March 18 made it necessary to tag before the fishery in order to study migrations and mixing of immature seals between Gulf and Front. The catches and tag returns from ships and from aircraft (which made only subsidiary catches) were combined to give an estimate (Table 2) of 119,000, much the same as the estimate for aircraft in 1964. However the existence of a quota in 1968 restricted the Gulf catch of young, and it is not certain that the results are therefore valid.

Best estimates of production of young harp seals from capture-recapture survey (2) are compared with best estimates from photographic aerial survey (1) for the same, or nearest, years, as follows:

Year	Southern Gulf		Front	
	(1)	(2)	(1)	(2)
1964 direct	100,000	127,000		
corrected		154,000		
1966			(215,000)*	193,314
1968		119,000		

* The latest complete aerial survey, made in 1960.

For the Front in 1968 the estimate based on Canadian tag returns was 193,314. This estimate is in line with a maximum catch at the Front (in 1963) of 197,000 young seals (Table 8), a catch which has not subsequently been exceeded.

While other evidence suggests that the capture-recapture estimate for the Front is realistic, perhaps because of an intense fishery, the incomplete results in the Gulf (as compared with later described methods) cannot yet be explained, but may be due, as believed for photographic survey carried out in recent years, to lower whelping induced by disturbance from aircraft. This cause, however, could not have operated in 1968 when tagging and sealing both began late.

3. Catch and survival

The key to this method was obtained from the discovery in 1965 that the Front females in the early 1960's showed a mean age at sexual maturity one year lower than the Gulf females (Sergeant, 1966). The Front population, assumed from aerial survey to be rapidly declining, was believed to be reproducing at full efficiency. This suggestion is supported by Yakovenko and Nazarenko's (1967) data on the heavily overhunted White Sea harp seals which show that the reproductive efficiency of females is the same as was the Front herd in the early 1960's. The Gulf herd, on the other hand has been hunted at a level lower than that which gives maximal reproduction, and therefore maximal yield.

This method uses inspection of individual age classes in age samples to estimate, empirically, balanced survival and hence yield. Before this is possible, however, the proportion of young giving maximal sustainable yield must be calculated from estimates of life history parameters, especially those of mortality and reproduction.

(a) Life-history parameters and maximal sustainable yield

Sex ratio was close to 53% males for whitecoats and for moulted young or "beaters" (Table 4). Moulting adults and immatures (see Table 4, also Nazarenko and Yablokov, 1962 for the White Sea herd) show a sex ratio of 53%-56% males late in the moulting season. However there is here some suspicion that not all adult females have arrived at the moulting grounds. Samples shot at random in the water off the Saguenay River, Quebec in January-February 1969 show, for data analyzed to date, a sex ratio of 38 males and 35 females, or close to parity. Owing to variations in year-class survival as well as selection in capture it is hard to obtain a true ratio of immatures to adults, but a ratio of parity again seems reasonable (see age frequencies in Sergeant and Fisher, 1960, and the lowest age frequency in Figure 2 of this paper, for examples).

Annual mortality rates were calculated from age frequencies, a large number of which have been obtained (Table 5). Examples are shown in Figures 2 to 4. The results are summarized in Table 6, most of the data being taken from Sergeant and Fisher, 1960.

Deficiencies of these samples are believed to be as follows: (1) all netted samples are deficient in immatures (Fig. 2) which have not arrived from the north; (2) moulted animals, at least from Front samples, are not randomly distributed till late in April (Sergeant, 1965), and frequently have too many immatures (Fig. 3, 4); (3) netted samples from the regularly sampled site in the northern Gulf are apparently deficient in older adults (Table 6).

Results of estimates of mortality rates are shown in Table 6. Mean values are about 0.20 for immatures aged 1 to 5 years and 0.10 for adults aged 6 to 12 years. Mortality rates of young animals after the fishery are not known but are assumed to be equal to those at older ages. (The data from the West Greenland sample gave an estimate of 0.20 for mortality from 6 to 18 months, which does not invalidate this assumption.) Mortality estimates from samples of adults netted in the Gulf do not agree with estimates from other sources and are suspect. Almost invariable absence of adults over 25 years in these samples supports the view that older adults avoid the nets at La Tabatière.

Reproductive rates. I have calculated the mean age at first maturation of females to be between 4 years for a heavily exploited population (Front, 1961-62 4.0 years--Sergeant, 1966; White Sea 1958-64 4.3 years--data from Yakovenko and Nazarenko, 1967), to 5 years in a lightly exploited population (Front in 1950-54; Gulf, 1963-67), to 6 years in an almost unexploited population (Gulf, 1951-52). First whelping occurs one year later than first maturation.

Reproductive success of adult females was almost complete in the heavily exploited Front population, and about 0.9 in the more lightly exploited Gulf population (Sergeant, 1966, Table 2).

Let R = reproduction, C = catch, P = female reproductive rate, S_1 and S_2 survival rates of immatures and adults respectively. S_1 is the survival rate from age 1 to n years.

The female population at n years $= \frac{1}{2}(R-C)\, S_1^{\,n}$

The total adult female population $= \frac{1}{2}(R-C)\, S_1^{\,n}\,(1+S_2+S_2^{\,2}+\ldots)$

$$= \frac{(R-C)\, S_1^{\,n}}{2\,(1-S_2)}$$

Production $R = \dfrac{P(R-C)\, S_1^{\,n}}{2(1-S_2)}$

Whence $\dfrac{C}{R} = 1 - \dfrac{2(1-S_2)}{P.S_1^{\,n}}$

(1) For the heavily exploited population, letting $S_1 = 0.8$, $S_2 = 0.9$, $P = 1$ and $n = 5$, $\frac{C}{R} = 0.38$. This gives the maximal sustainable yield, with the population stable.

(2) For the lighter exploited population, $P = 0.9$ and $n = 6$, so that $\frac{C}{R} = 0.24$.

(3) For an almost unexploited population, $P = 0.9$, $n = 7$, and $\frac{C}{R} = 0.15$.

(b) Estimates of yield for the two areas

Age samples had been collected from both populations over a number of years, with the need to estimate mortality rates. It was early noted that after a very heavy catch of young in both areas in 1951, survival of that year class was permanently depressed.

(i) The Gulf stock. The most constant set of age samples has come from a net fishery in the northern Gulf with only one year's failure of catch and therefore of sample since 1951. This net fishery samples Gulf entrants but immature age classes are not fully represented, owing to their late southward migration (Sergeant, 1965). There may also be a bias to younger adults, presumably due to some factor of selection of a shore-based net, since older animals show higher mortality rates than by other methods. It appears however, that the four-year-old seals are fully represented, and their survival may therefore be compared with their catch as young, four years previously.

For each year class, the catch of young has been plotted against survival of that year class at 4 years of age, expressed as percentage of total sample. If the Gulf population has not declined, percent of sample is an estimate of percent of population. The survival of each year class depends on natural mortality plus fishing mortality, the latter largely the mortality of young seals since catches of older seals are low in the Gulf.

To calculate the balanced representation of four-year-old seals, as percent of total netted sample, the survival of young animals after the end of the spring catch is assumed to be equal to that of older immatures, i.e. $S_0 = S_1$.

Then the population at four years of age = $(R-C)\ S_1^{\ 4}$.

The immature population up to four years

$= (R-C)\ (S_1^{\ 2}-S_1^{\ 3}-S_1^{\ 4})$.

The adult population, five years and up $= \dfrac{(R-C)\ S_1^{\ 4}}{1-S_2}$

If R = 1, C = 0.38 (for balance), $S_1 = 0.9$, $S_2 = 0.8$, then the four year olds = 0.25, the immatures = 1.9, the adults = 2.0, i.e. the whole population = 3.9, the four year olds = 0.25/3.9 = 0.064 of total population.

In the netted samples part of the population, including many younger immatures plus, apparently, many older adults, is missing. The proportion of missing seals can be estimated by comparison of the netted sample with the moulted sample (see Fig. 5). It happens that numbers of animals aged 3 to 6 years are almost identical in the two samples, so that no adjustment for scale is needed.

The estimate gives 0.25 of the population missing as immatures, 0.20 as adults, or 0.45 in all. The four year olds then appear as 0.064/0.55 or 0.12, that is 12% of the netted sample, in a balanced population. Figure 5 shows that the four year olds survive at a rate above 0.12 for the majority of catches. A simple analysis is as follows:

Catch of young seals in the Gulf of St. Lawrence	Number and percent of years in which Age Class 4 among Gulf entrants: exceeded 12% of sample		was less than 12% of sample	
	Number	Percent	Number	Percent
20,000 - 39,000	1	50	1	50
40,000 - 59,000	2	67	1	33
60,000 - 79,000	2	100	0	0
80,000 - 99,000	5	63	3	37
100,000 - 119,000	0	0	1	100

For catches of 80,000 to 99,000, survival was less than 12% in nearly half the years. This suggests that the mean catch for maximal sustainable yield lies close to 90,000. A more elaborate analysis has not been helpful. A regression line using all points assumes survival inversely proportional to catch at all catch levels, while a regression line using only catches over 70,000 young assumes density-dependent natural mortality to increase at low catch levels. The two lines give widely differing intercepts on the x axis where zero survival would indicate total production.

(ii) The Front stock. Figures 3 and 4 show age samples of moulting seals from the Front giving information on survival of year classes since 1959. Survival was calculated semi-quantitatively as "very good", "good", "poor" and "very poor." The results are expressed in Table 7. It can be seen that in recent years survival has been "good" (and never "very good") only after catches of around 95,000 seals. This would agree with evidence from capture-recapture tagging in 1966, and highest catches in 1959-68, which measure recent production at no more than 200,000 young seals on the Front (see above, and Sergeant, MS, 1967). Indeed, these survival rates are only "good" by comparison with other years, and may still have taken as much as 50% of production. Thus, present sustainable yield on the Front is probably lower than 95,000 and possibly close to 70,000. The latter figure is suggested from the most recent direct estimates of production of no more than 200,000 young.

One recent arctic sample is available from eastern Baffin Island in the summer of 1967 (Fig. 3, lower). Its additional evidence is useful since this agrees with the separate results from the Gulf and the Front (Table 7) to show an overall "good" survival only in the years 1960, 1961 and 1965. In these years alone, the combined catches numbered less than 200,000 young seals, ranging from 174,000 to 184,000. Subtracting a sustainable yield of 90,000 for the Gulf the result is an approximate yield from the Front in 1960-65 for "good" survival of 84,000 to 94,000 young. The arctic data show that no important additional stocks of harp seals, not hunted by ships, occur northward of the Front.

4. Age at first maturation

Support for 90,000 as maximal sustainable Gulf yield is given by the effect of past catch levels on female reproductive potential, as measured by first maturation in 50% of females. This parameter has now been monitored annually for 6 years, and sharp fluctuations rather than smoothed changes show that the mean age of maturation, varying between 4 and 6 years, is the result of density-dependent competition within a single year class. Data are shown in Table 8 and Appendix Table 1. A sudden and unique drop to a mean age of 4.3 years occurred in 1968. This is close to the biological maximum as shown by comparable data from the heavily exploited White Sea and Front herds (see p.). It occurred five years after a uniquely heavy Gulf catch of 110,000 young, which resulted also in unusually low survival of the 1963 year class (Fig. 2). No other catch had such an effect, though catches of 85,000 and 89,000 young produced some lowering of mean age at maturity (Table 3).

Up to and including 1968, I developed the working hypothesis that the mean or smoothed level of exploitation of young would, after a lapse of about 5 years, determine the age at maturity, explaining the rather sudden lowering to 4.3 years in 1968 by a general increase in the level of catch 4-5 years previously, which had been maintained subsequently. But in 1969, the mean age rose abruptly again, which could not be explained by the above hypothesis.

The conclusion is inevitable that the rate of maturation is dependent on the density of each year class, i.e. when the density of such year class is increased, there occurs within a single year class either direct competition for food, or some behavioural disturbance leading to lowered food intake and hence to lowered growth and maturation. It has not yet proved possible, however, to measure variations in age-specific weight either between populations or between years in one population.

A key to the mechanism is given by observations in the estuary of the St. Lawrence River near Escoumains, Quebec (48°10'N, 69°20'W) in January, 1969 by W. Hoek and T. Smith who were collecting harp seal specimens for a study of food habits. In this area adult harp seals evidently occupied the better feeding area to the southeast of the confluence of the Saguenay River, where upwelling was apparent. Further downstream, below Escoumains, most seals encountered were less than 1 year old. The adults were schooling but the juveniles were scattered, each in its own feeding territory. I have noticed the solitary habits of juveniles soon after weaning (Sergeant, 1966), and P. F. Brodie and W. Hoek (verbally) confirm this observation for juveniles in the arctic in summer. It therefore seems to be typical of at least the first year of life, when an important fraction of growth occurs.

In Section 3 I have used as the best index for sustainable yield of harp seals the strength of each year class in comparison with its kill as young. It is assumed that survival is determined largely by hunting mortality, while production and natural mortality are both rather constant.

An additional index now presents itself: the mean age at maturity of the females 5 years after each kill. Use of the first method gave a figure of maximal sustainable yield for the Gulf herd of harp seals of about 90,000 young seals. As may be seen from Table 7, as the level of catch of young is increased past this figure, the mean age at maturity is falling rapidly at about 4.5 years. The figure of about 90,000 young seals for maximal sustainable yield for the Gulf herd is therefore confirmed.

5. <u>Mixing of Gulf and Front stocks</u>

After tagging in the 1950's no mixing could be demonstrated (Sergeant, 1965), although tagging and possibly also catching of age groups one year and up was only adequate on the Front for returns to be expected (Sergeant, MS, 1967. ICNAF No. 1952).

It has not been possible to tag subsequently on the Front and ensure survival of tagged animals to recheck the question because of the high proportion of young which have been killed at the Front. In 1966 tagging of 3500 young was carried out at the Front in a capture-recapture experiment, but apparently nearly all were killed in the subsequent fishery since the escapement to West Greenland that summer was only 4 tagged animals. By contrast, 1500 young tagged in the Gulf after the quota fishery in 1966 gave 31 recoveries the same summer in West Greenland (Sergeant, MS, 1967. ICNAF No. 1952).

Recaptures in 1967 from the Gulf tagging in 1966, when considered together with the distribution between Gulf and Front of catches of seals one year old and up in 1967, suggest that there is an emigration to the Front at one year of age of about 25% of young born in the southern Gulf (Sergeant, MS, 1967. ICNAF No. 1952 together with new data, see Table 9). At 2 years of age, the few recoveries suggest the same degree of cross movement. Very few recoveries can be expected by age 3 years but efforts are being made to improve the tag in order to reduce the rate of loss.

Very early results from an estimated escapement of 1100 young seals tagged in the Gulf in 1968 again show the cross movement, as described above, for at least a percentage of animals.

The relatively low kill of young in the Gulf in 1968 might suggest that the cross movement will increase for this year class, except that the kill of young on the Front was also low in 1968, as compared with 1966, for example. One may suppose that some cross movement has always occurred, but will tend to occur from a denser to a thinner population. In this connotation Rasmussen and Øritsland (1964) note at least one cross movement of a tagged harp seal from the West Ice to the White Sea, which was probably also in the same direction, from greater to lesser density of population.

Study of the permanency of such movement would probably require branding, which is quite feasible on young seals, but the retrieval of information from recoveries of brands appears difficult in the harp seal fishery.

It seems to the writer that the density-dependent effects on maturation of females of the Gulf herd constitute evidence for the general separateness of Gulf and Front herds. The Front herd is now so depleted that it does not seem possible that such marked density-dependent effects could be produced in the arctic in summer among the mixed herds of juveniles, but only in the Gulf itself, either at first independent feeding in April-May of age 0, or during wintering in January-April of age 1, or both, and less importantly (since growth rate is then decreasing) at subsequent ages up to sexual maturation.

This hypothesis can only be tested by simultaneous collection of maturity samples from the Front. An attempt to do this was made in 1968 for the first time since 1962, but it was found that 4-, 5- and 6-year-old females were so reduced from heavy hunting that no adequate samples of them could be obtained (Table 10). Thus, of females aged 5 years, 1 out of 2 was mature. Consequently, the only conclusion that could be drawn from a sample of 144 females taken at the Front in 1968 was that the mean age of female maturity lay between 4 and 6 years.

Acknowledgements

The age sample from West Greenland (Tables 1 and 2) was collected by Dr. Paul Hansen and staff of Grønlands Fiskeriundersøgelser of the Danish Government. I am indebted to Mr. T. Øritsland for part of the 1967 age sample from the Front shown in Figure 2. I am also grateful to Dr. A.W. Mansfield and staff of the Arctic Biological Station for the age sample of

harp seals from Baffin Island shown in the same Figure. For mathematical aid I am indebted to Dr. J Paloheimo and Mr. K. R. Allen.

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Recommendations

1. A closing date at the Front of not later than April 25 is needed fully to protect the adult females. For biological evidence on this point see Sergeant (1965).

2. A quota of no more than 70,000 young seals at the Front will allow the present herd to stabilize, and possibly to recover slowly to its optimal size. Recent high kills, however, make a decrease in production inevitable in the immediate future years.

3. The effect of immigration from the Gulf, if it continues into mature years, will be to slow down the present rate of decline, or with effective management, to hasten the recovery of the population, to a maximal sustainable yield estimated at about 180,000 young (Sergeant, 1967. ICNAF No. 1952).

Table 1. Proportion of attending females to young harp seals, vicinity of Magdalen Islands, 1967. All observations were made on the same herd, containing older pups, except the last, which comprised mostly newborn pups.

Date	Time	Weather	Number of adults	Number of pups	Proportion of adults	Observer
March 10	0845-0930	Overcast	73	221	0.26	D.H. Pimlott
	0845-0930	Overcast	38	143	0.25	D.E. Sergeant
March 13	0800-0810	Clear	72	116	0.62	D.E. Sergeant
	0945-0950	Clear	44	62	0.71	D.E. Sergeant
	1315-1320	Hazy	80	103	0.77	D.E. Sergeant
	1450-1500	Hazy	52	88	0.60	D.E. Sergeant
March 14	1415-1430	Overcast	102	114	0.89	D.E. Sergeant

Table 2. Results of capture-recapture tagging of young harp seals (a) in the Gulf of St. Lawrence 1964, (b) on the Front in 1966, (c) in the Gulf of St. Lawrence 1968. Recoveries are those from the area and season of tagging.

	Gulf 1964		Front 1966	Gulf 1968
Number of seals tagged	2,844		3,581	2,219
	Ships	Aircraft and landsmen	Canadian ships	Ships and aircraft
Number of tags recovered	782	876	1,018	1,055
Catch	42,256	39,252	54,955	56,600
Estimate of production	153,677	127,432	193,314	119,047

Table 3. Ranked variability of percentage returns between individual ships in three capture-recapture tagging experiments.

	Returns as percent tagged		
Ship no.	Gulf 1964	Front* 1966	Gulf 1968
1	5.71	9.45	4.36
2	3.75	1.56	3.53
3	1.87	1.11	3.21
4	0.72	1.07	2.13
5	0.48	0.99	1.70
6	0.39	0.93	1.66
7	0.28	0.08	0.18
8	0.22	0.08	0.18
9	0.07	0.07	
Mean	1.84	1.84	2.07

* Canadian ships only

Table 4. Sex ratios of harp seals.

a: of juveniles (all at Front except in 1966 when in Gulf).

Date		Stage	Observer	Males	Females	Ratio
1953	March 13	Whitecoat	D.E. Sergeant	93	85	
	15	Whitecoat	D.E. Sergeant	129	106	
1965	17	Whitecoat	G.A. Williamson	67	58	
			Subtotals	289	247	53.35
1965	April 7-17	Beater	G.A. Williamson	91	80	
1966	March 29-April 5	Beater	D.E. Sergeant	56	51	
			Subtotals	147	131	52.87

b: of Front moulters, April 28-30, 1968.

Age	Males	Number females	Total	Percent males
1-5 years	62	51	113	54.9
6+ years	93	72	165	56.4
Total	155	123	278	55.7

Table 5. Age frequency sampling up to late 1968.

Population	Locality	Type of catch	Number of samples exceeding 250 animals	Comments
Mixed herds	West Greenland	Shot	1	Excellent sample
	Baffin Island	Shot	1	Excellent sample
	Port Burwell, Labrador	Netted	2	Lacks immatures
	Nain to Hebron, Labrador	Netted	3	Lacks immatures
Gulf herd	La Tabatière and Harrington Hbr., Quebec	Netted	17	Lacks immatures
	Magdalen Islands, Quebec	Shot	3	Lacks immatures
	Moulting animals, northern Gulf icefields	Shot	1	Excellent sample
Front herd	Moulting animals, Front icefields	Shot	9*	Bias towards immatures
	St. Anthony area, Newfoundland	Netted	2	Bias towards adults

*Including two published Soviet age samples.

Table 6. Tabulated values of mean annual total mortality rates from the samples of Table 1. Data from Sergeant and Fisher (1960) with additional age frequency from Figure 1, lowest histogram of this paper.

Herd	Sampled	Immatures 1-5 years	Adults 6-12 years	Shown in
Mixed herds	Netted, Labrador	--	0.09	Fig. 1
	Greenland	0.21	0.11	
Gulf herd	Netted, North Shore	--	0.19*	Fig. 2
	Moulting, icefields	0.20	0.10	Fig. 2
Front herd	Moulting, icefields	0.21	0.08	Fig. 3, 4

*Sample suspect, believed to be deficient in older adults.

Table 7. Catch of young and survival of year classes for Gulf, Front and combined herds of harp seals for the last decade.

	Catch of young (thousands)			Survival		
Catch	Gulf	Front	Total	Gulf	Front	Arctic
1959	62	180	242	+	-	-
1960	85	93	178	++	+	++
1961	41	133	174	++	-	+
1962	89	163	252	+	--	-
1963	110	197	307	-	--	--
1964	84	178	262	+	--	-
1965	90	94	184	++	+	++
1966	84	180	264	Selection suspected		
1967	92	184	276	Selection suspected		
1968	57	98	155	No data		

++ = "very good"; + = "good"; - = "poor"; -- = "very poor"

Table 8. Harp seals entering the Gulf of St. Lawrence: Catch of young and mean age at female maturation five years later.

Year	Catch of young	Year	Sample size	Mean age at female maturation (years)
1948	ca. 25,000	1953	70*	5.5
1959	62,000	1964	75	5.0
1960	85,000	1965	281	4.7
1961	41,000	1966	238	5.2
1962	89,000	1967	241	4.7
1963	110,000	1968	173	4.3
1964	84,000	1969	298	5.0

*1951-1954

Table 9. Recoveries at 1 and 2 years of age of young harp seals tagged in the Gulf of St. Lawrence in 1966.

Year of recovery	Catch, in thousands of immature and adult seals *		Numbers of recoveries		Ratio of recoveries, corrected for catch	
	Gulf	Front	Gulf	Front	Gulf	Front
1967	9.9	44.75	12	17	3.2	1
1968	4.5	30.00	1	2	3.3	1

* The source of catch figures is ICNAF Serial No. 2106, being the Report of Scientific Advisers to Panel A, Annual Meeting, June 1968. Final catch figures for 1968 are not available at time of writing. It is assumed that catches of 1- and 2-year-old seals are proportional to catches of total (immature and adult) moulting seals.

Table 10. Data on attainment of sexual maturity of female harp seals of the Front herd from moulting sample, April, 1968. For earlier results see Sergeant (1968).

Age (years)	Number				Percent mature
	Immature	Ovulated	Mature, pregnant	Mature, non-pregnant	
1	13				0
2	25				0
3	13				0
4	4		1		20
5	1		1		(50)
6	1		6		86
7			7		100
8 and up	—	-	68	4	100
N	57	-	83	4	144

Appendix

Data on maturity status of female harp seals of maturing ages, in samples from different years. All were samples of migrant entrant seals except in 1966 when such a sample was combined with a sample from moulting seals in the northern Gulf. For earlier results see Sergeant, 1966.

Age in years	1965	1966 migrants	1966 moulters	1966 total	1967	1968	1969
	Number Immature						
3	29	7	10	17	10	27	24
4	39	10	10	20	19	19	25
5	39	17	10	27	33	20	16
6	38	10	14	24	29	12	29
7	35	10	11	21	23	11	26
8	14	3	4	7	18	4	17
	Number Mature						
3	2	-	-	-	-	-	-
4	4	1	1	2	4	7	5
5	25	6	6	12	20	15	8
6	29	7	11	18	28	11	24
7	33	9	11	20	20	10	24
8	14	2	4	6	16	4	17
	Percent Mature						
3	7	-	-	-	-	-	-
4	11	10	10	10	21	37	20
5	64	35	60	44	61	75	50
6	76	70	79	75	97	91	82
7	94	90	100	95	87	90	92
8	100	(67)	100	(86)	90	100	100
Mean age at maturity	4.7	5.4	4.7	5.2	4.7	4.3	5.0

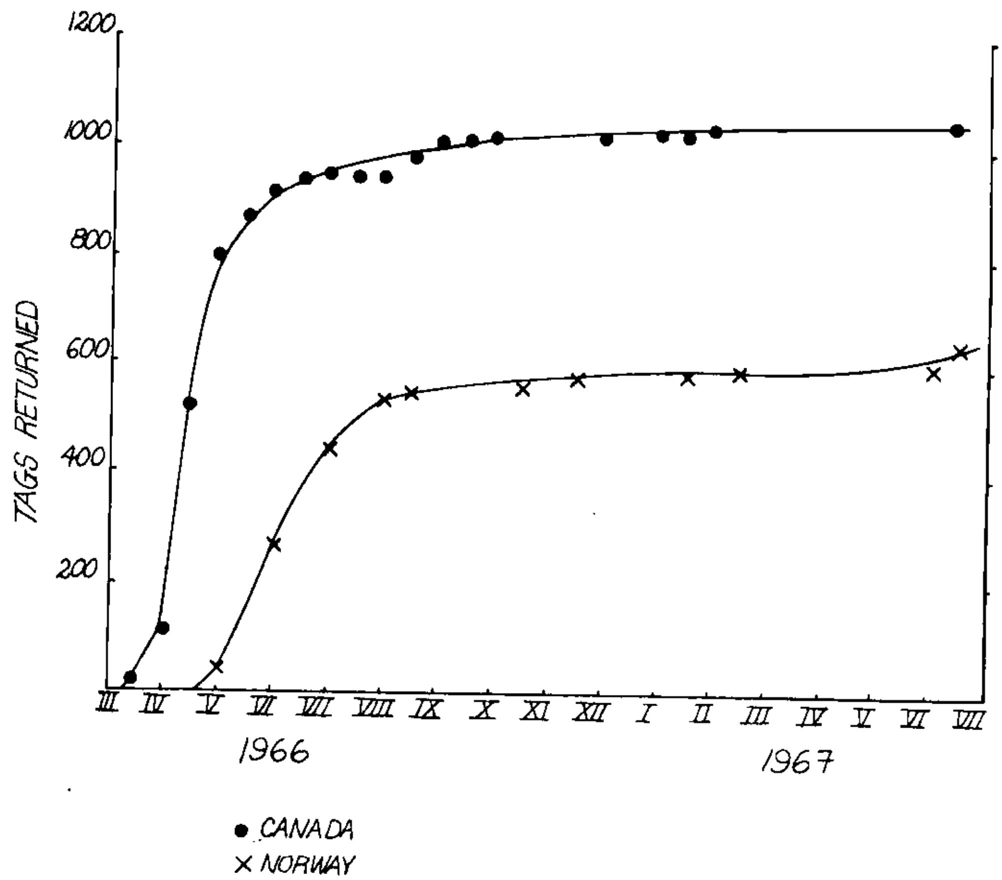

Figure 1. Cumulative returns by country of seals tagged on the Front in 1966 and recovered the same spring.

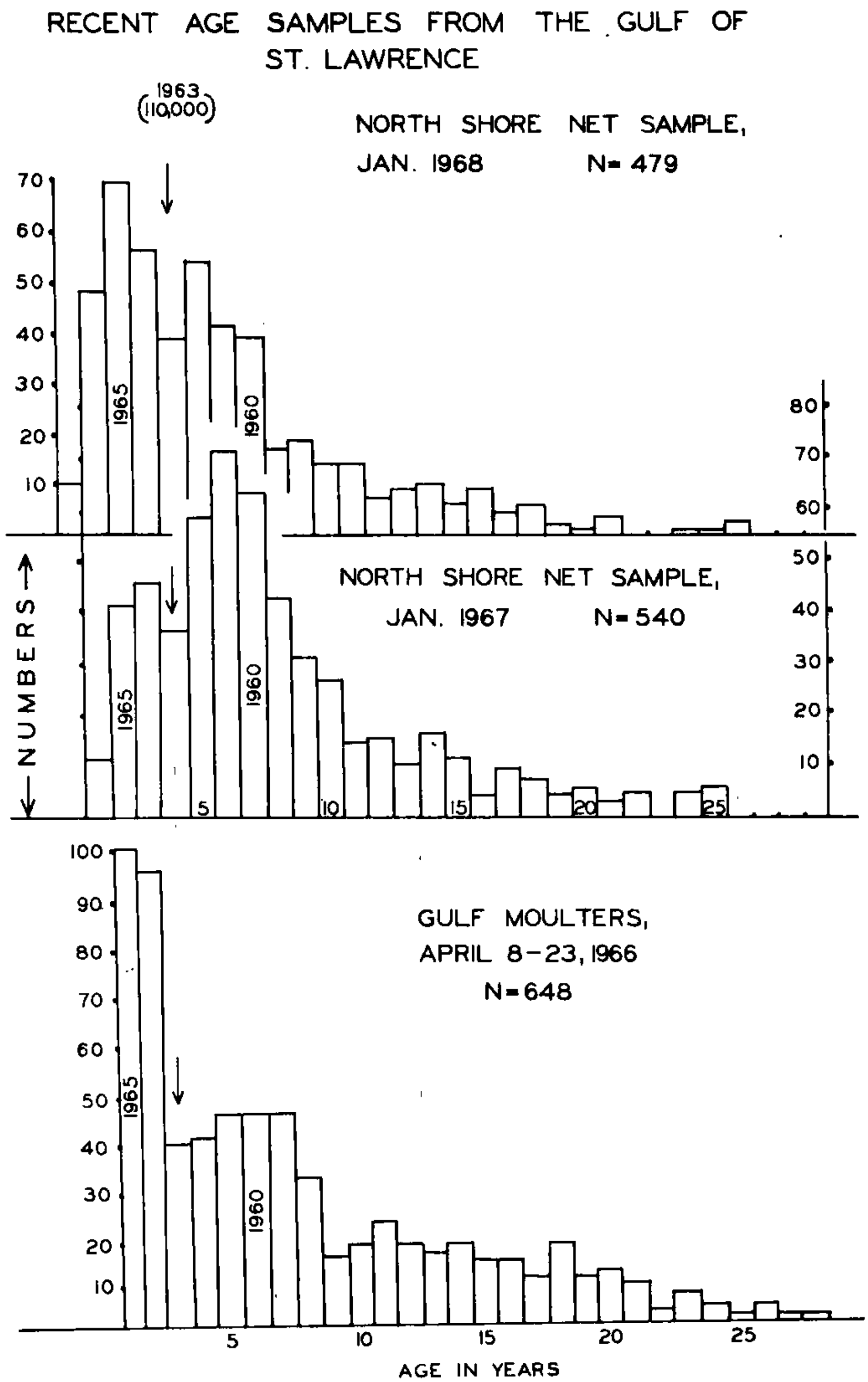

Figure 2. Recent age frequencies of southward migrants into the Gulf of St. Lawrence (upper two histograms) and moulting harp seals in the Gulf (lowest histogram).

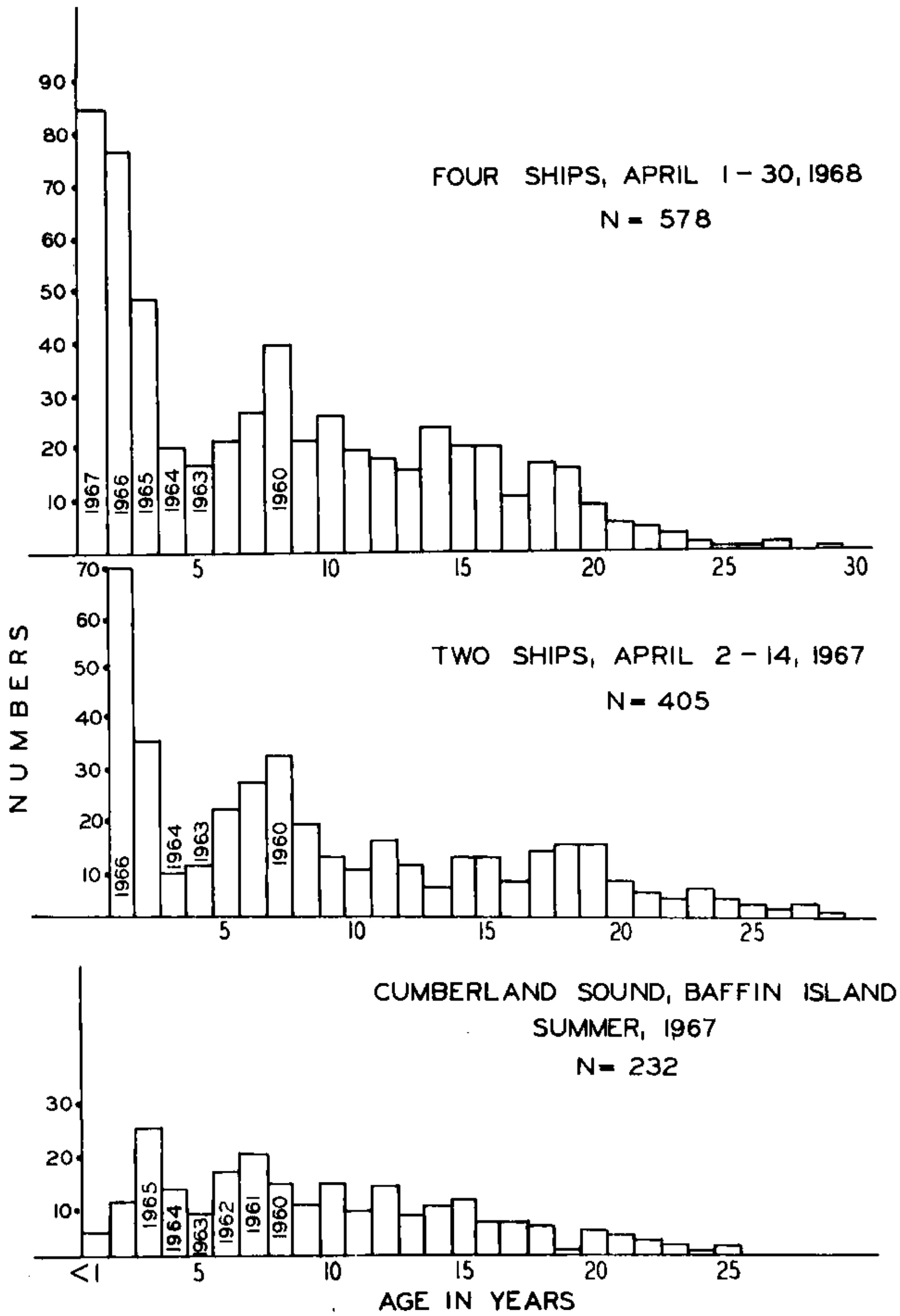

Figure 3. Recent age frequencies of Front moulters (upper two histograms) and from the mixed herds in the arctic (lowest histogram).

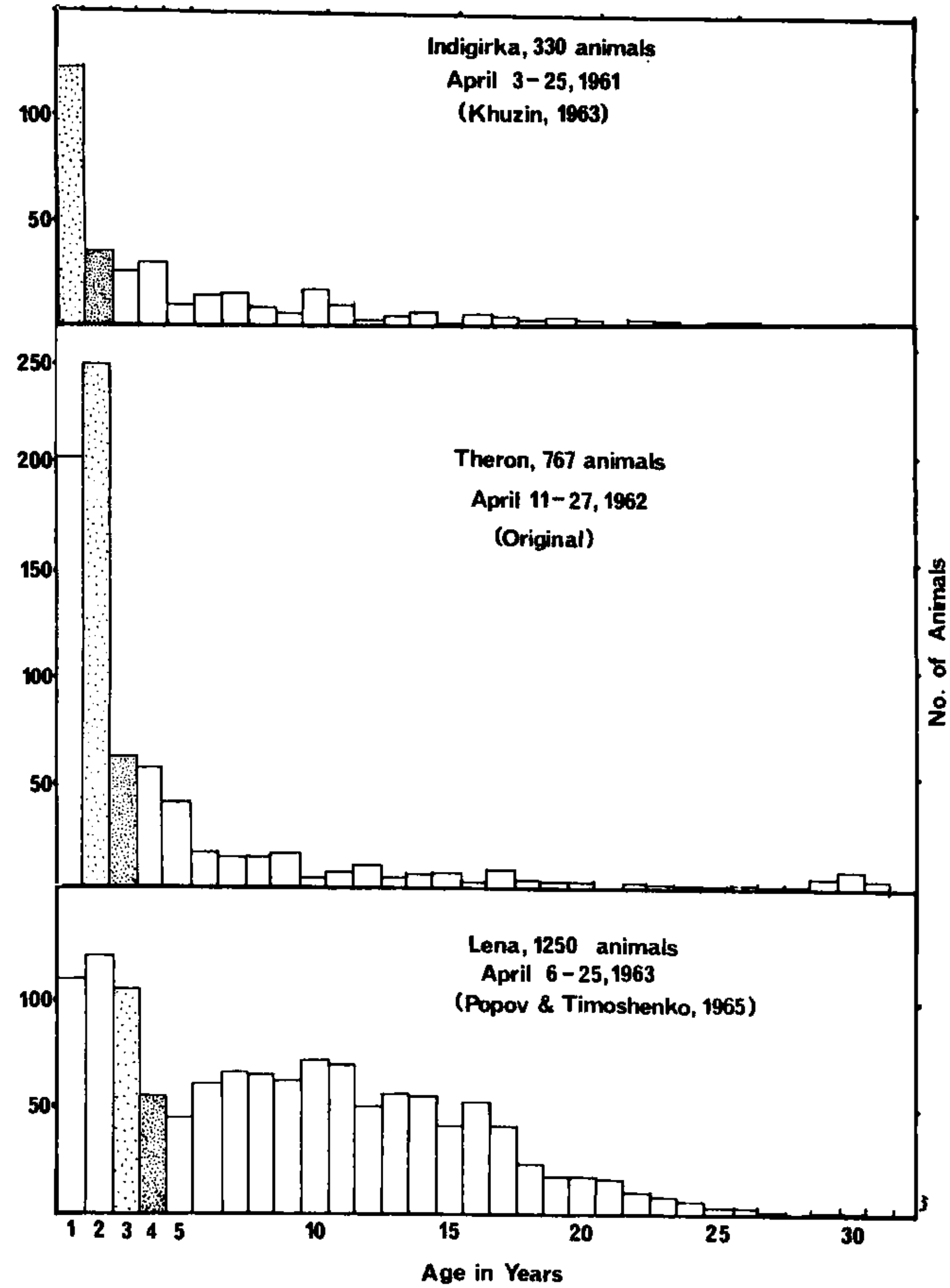

Figure 4. Age frequencies of Front moulters in 1961-1963.

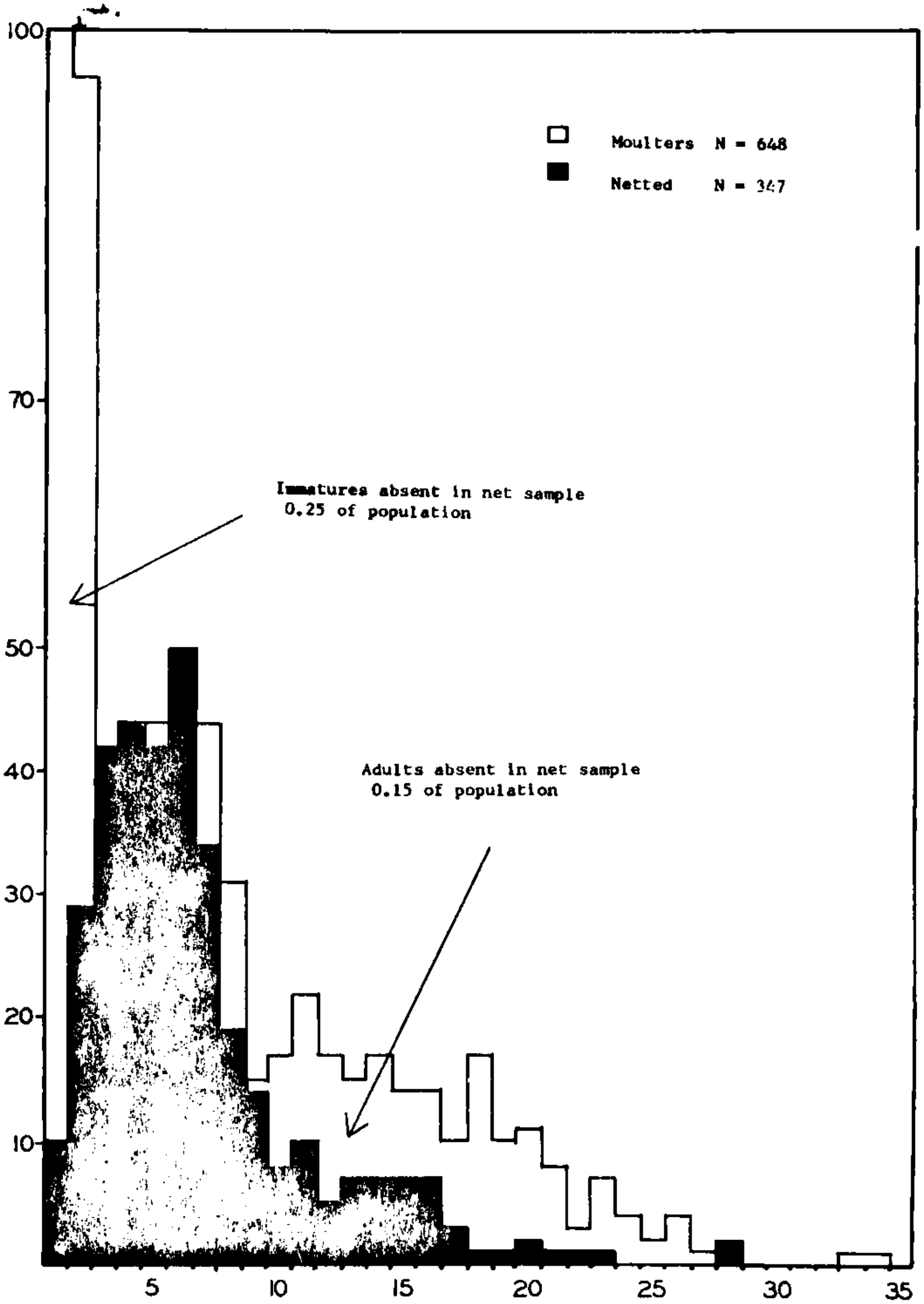

Figure 5. Raw Gulf age samples for 1966 from netted migrants (stippled histogram) and moulting animals (open histogram).

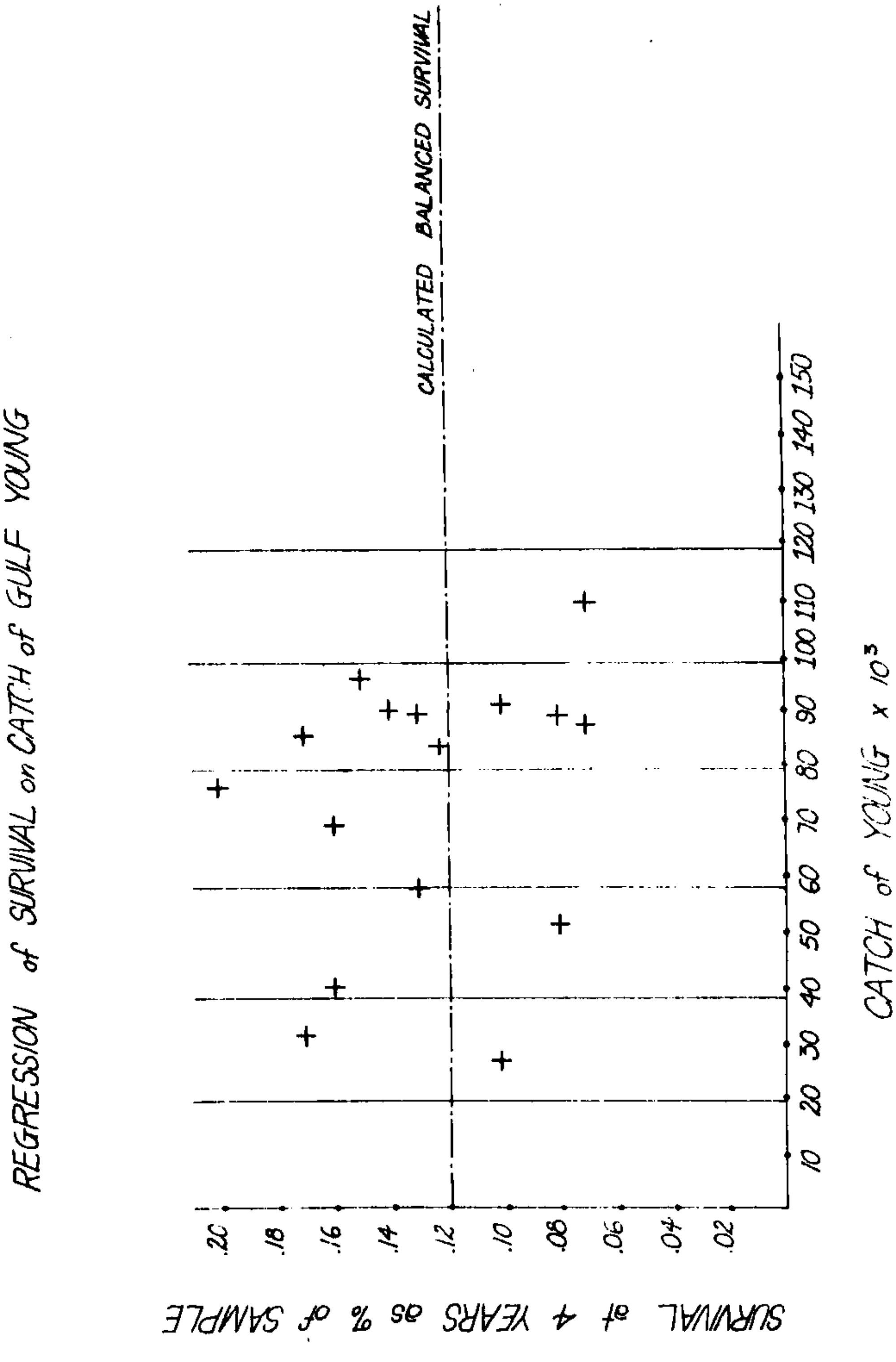

Figure 6. Regressions of survival on catch of Gulf young.

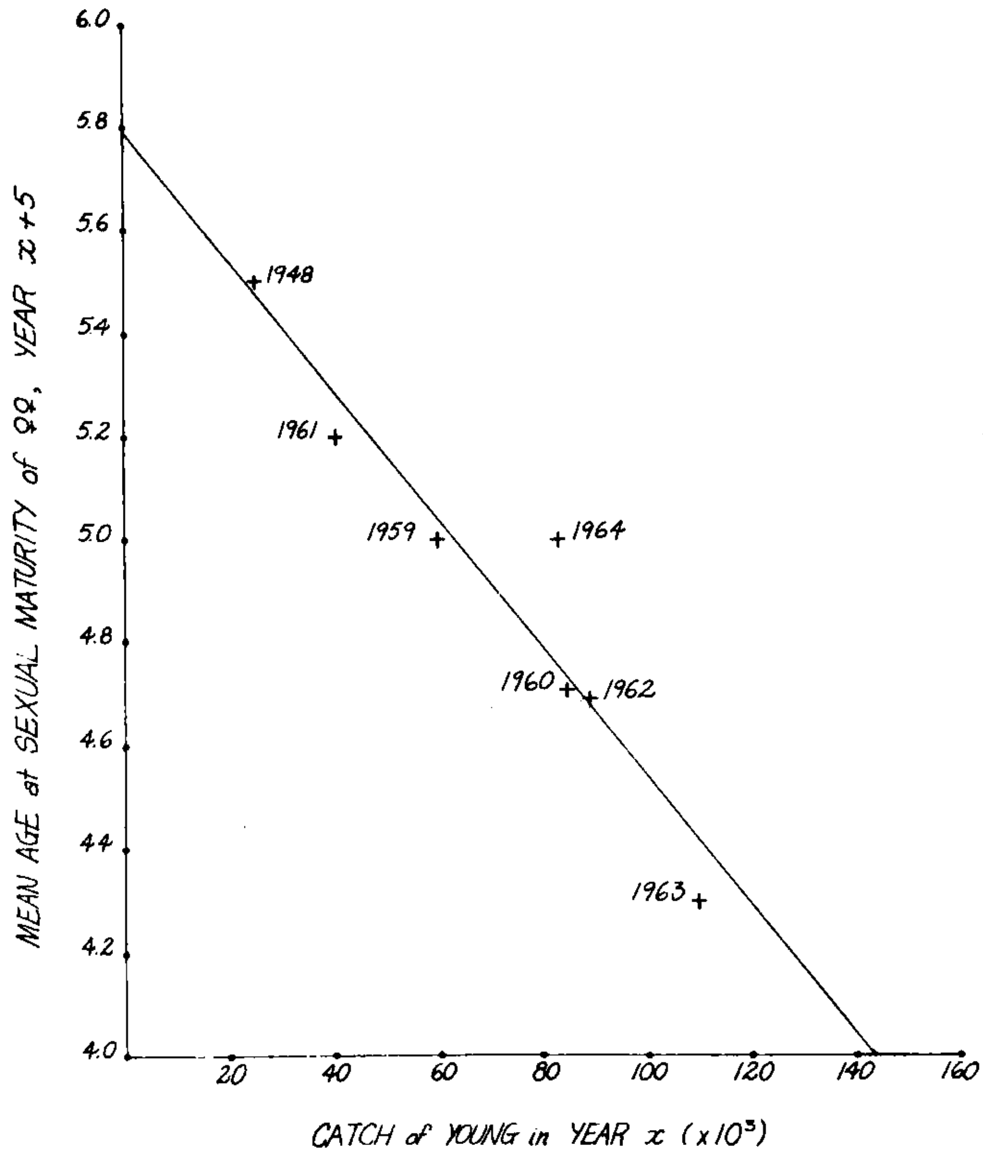

Figure 7. Regression on catch of young seals in the Gulf of St. Lawrence, of mean age at maturation of female harp seals entering the Gulf 5 years later. The year of catch is shown.