J.L.Bengtson & R.M.Laws
(U.S.A. & U.K.)

SC-CAMLR-II/INF.3
30 August, 1983

TRENDS IN CRABEATER SEAL AGE AT MATURITY: AN INSIGHT INTO ANTARCTIC MARINE INTERACTIONS

Abstract

The crabeater seal, Lobodon carcinophagus, is a species which appears to be useful as an indicator of marine community interactions. Crabeater seals eat krill almost exclusively, live up to 40 years of age, have a circumpolar distribution and a large standing stock. The age at which crabeater seals reach sexual maturity is a parameter which might reflect changes in krill availability. Abundant food and relatively faster growth rates may lead to attaining sexual maturity earlier, decreased food availability would presumably have an opposite effect. The data on age at maturity previously published are reviewed in the light of recent material from the Antarctic Peninsula and an expanded sample from Marguerite Bay. A correlation is demonstrated between Baleen whale catch data and seal maturity data from the study area. The age of sexual maturity in crabeater seals apparently decreased as a result of whaling and subsequently increased when whaling ceased. The causes of observed changes are likely to be related to complex interactions within the marine ecosystem. This study demonstrated the value of one aspect of crabeater seals as an indicator species. It is important that sampling of crabeater seals continue for monitoring studies of the Antarctic marine ecosystem.

TENDANCES DANS L'AGE A LA MATURITE SEXUELLE DU PHOQUE CRABIER: POUR MIEUX COMPRENDRE LES INTERACTIONS MARINES EN ANTARCTIQUE

Résumé

Le phoque crabier, Lobodon carcinophagus, est une espèce qui paraît utile en tant qu'indice des interactions de la communauté marine. Les phoques crabiers se nourrissent presque exclusivement de krill, vivent jusqu'à près de 40 ans, ont une répartition circumpolaire et un stock permanent important. L'âge auquel les phoques crabiers atteignent la maturité sexuelle est un paramètre qui pourrait refléter les changements dans l'abondance du krill. Une nourriture abondante et des taux de croissance relativement plus rapides pourraient conduire à une maturité sexuelle plus précoce, et une diminution de la disponibilité de nourriture devrait avoir l'effet contraire. Les données qui ont déjà été publiées sont examinées à la lumière du matériel récent sur la Péninsule Antarctique et un échantillon élargi de la Baie Marguerite. Une corrélation est démontrée entre les données de prises de baleines mysticètes et les données de maturité des phoques dans la zone étudiée. L'âge à la maturité sexuelle du phoque crabier semble diminuer en raison de la chasse à la baleine puis augmenter lorsque la chasse est abandonnée. Les causes des changements observés sont probablement liées aux interactions complexes qui se produisent au sein de l'écosystème marin. Cette étude a démontré la valeur de l'un des aspects du phoque crabier en tant qu'espèce indicatrice. Il est important pour les études sur le contrôle de l'écosystème marin de l'Antarctique que l'échantillonnage des phoques crabiers soit poursuivi.

ТЕНДЕНЦИИ ИЗМЕНЕНИЯ ВОЗРАСТА ПОЛОВОЗРЕЛОСТИ ТЮЛЕНЕЙ-КРАБОЕДОВ: ОБЩЕЕ ПРЕДСТАВЛЕНИЕ О ВЗАИМООТНОШЕНИЯХ В МОРСКОЙ СРЕДЕ АНТАРКТИКИ

Резюме

Тюлень-крабоед, Lobodon carcinophagus, - вид, который представляется возможным использовать в качестве индикатора взаимоотношений между морскими сообществами. Тюлени-крабоеды питаются практически только крилем и имеют продолжительность жизни до 40 лет; их распределение циркумполярно и промысловый запас этого вида значителен. Возраст, при котором тюлени-крабоеды достигают половозрелости, является параметром, который может отразить изменения в наличии криля. Достаточное количество пищи и сравнительно высокие темпы роста могут привести к достижению половозрелости на более ранней стадии, в то время как сокращение количества пищи, возможно, имело бы противоположные последствия. Опубликованные ранее данные по возрасту половозрелости рассматриваются в свете недавно полученных данных исследования Антарктического полуострова и расширенной пробы из залива Маргерит. Доказывается существование взаимосвязи между данными улова гладких китов и данными по половозрелости тюленей в районе изучения. Возраст половозрелости тюленей-крабоедов, по-видимому, упал в результате китобойного промысла и поднялся, когда промысел прекратился. Причины наблюдаемых изменений, вероятно, связаны со сложными взаимоотношениями в морской экосистеме. Настоящее исследование доказало значение одного аспекта использования тюленя-крабоеда в качестве вида-индикатора. Для изучения морской экосистемы Антарктики с помощью мониторинга необходимо продолжение программ отлова особей тюленей-крабоедов.

TENDENCIAS EN LA EDAD DE LA FOCA CANGREJERA AL ALCANZAR LA MADUREZ: UN ESTUDIO DE LAS INTERACCIONES MARINAS ANTARTICAS

Resumen

La foca cangrejera, Lobodon carcinophagus, es una especie que parece ser útil como indicadora de las interacciones de la comunidad marina. Las focas cangrejeras se alimentan de krill casi exclusivamente, viven hasta los 40 años de edad, tienen una distribución circumpolar y grandes existencias permanentes. La edad en que las focas cangrejeras alcanzan la madurez sexual constituye un parámetro que podría reflejar los cambios en la disponibilidad de krill. La abundancia de alimento y las tasas de crecimiento relativamente rápido pueden dar como resultado el alcance de la madurez más temprano, una disminución en la disponibilidad de alimento probablemente tendría un efecto opuesto. Se revisan los datos previamente publicados con relación a la edad al alcanzar la madurez a la luz de material reciente de la Península Antártica y de una muestra tomada a lo largo de la Bahía Margarita. Se demuestra una correlación entre los datos de captura de las ballenas mysticetas y los datos de madurez de las focas en el área de estudio. La edad al alcanzar la madurez sexual de las focas cangrejeras aparentemente disminuyó como resultado de la caza de ballenas y posteriormente aumentó cuando cesó la caza de ballenas. Es posible que las causas de los cambios observados se relacionen con interacciones complejas en el ecosistema marino. Este estudio demostró el valor de una faceta de las focas cangrejeras como especie indicadora. Es importante que continue el muestreo de las focas cangrejeras para los estudios de control del ecosistema marino antártico.

Introduction *

The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) provides that the Antarctic marine ecosystem should be managed and conserved as a unit. Consideration must be given for the conservation of targeted species such as Antarctic krill (Euphausia superba) as well as species dependent on krill. However, obtaining data on the past and current status of all component groups within the ecosystem would be an exceedingly expensive, if not impossible, task. The use of ecosystem indices has therefore been suggested as a method whereby general ecological trends could be monitored.

In selecting suitable ecosystem indicators, it is necessary to find parameters which respond to perturbations of the ecosystem, particularly those reflecting changes in krill populations. Investigating the

---

*Preliminary draft of paper to be presented at the Fourth SCAR Symposium on Antarctic Biology. Wilderness, South Africa, 12-16 Sep 1983.

interactions between krill and its consumers represents one approach to this topic. Moreover, understanding the extent to which past commercial whaling and its presumed impact on krill availability affected various parameters of krill consumers would help identify useful indicators to evaluate future impacts of commercial fisheries.

The crabeater seal (Lobodon carcinophagus) is a species which appears to be useful as an indicator of community interactions. Crabeater seals eat krill almost exclusively (Øritsland, 1977; Bengtson, 1982), live up to 40 years of age (Laws, unpublished), have a circumpolar distribution (Erickson et al., 1971), and have a large standing stock estimated at between 15 and 30 million individuals (Gilbert and Erickson, 1977). Pending current re-evaluation of census correction factors, revised population estimates incorporating new data may well exceed 30 million individuals (A.W. Erickson, pers. comm.). Laws (1977a) estimated that crabeater seals (assuming a population of 15 million) consume approximately 63 million metric tons of krill annually, or about 1.5 times the quantity eaten by current baleen whale stocks. Therefore, changes in krill availability, whether increased by reduced competition from baleen whale stocks or decreased by direct krill harvests, might be reflected in growth, reproductive, and population parameters of crabeater seals.

The age at which crabeater seals reach sexual maturity is a parameter which might reflect changes in krill availability. Attainment of sexual maturity in mammals is often related to attainment of a certain body size (Leslie et al., 1946; Sadleir, 1969). Laws (1956) demonstrated that seals with high growth rates reached puberty at a younger age than slower-growing seals. Abundant food and relatively faster growth rates may therefore lead to attaining sexual maturity earlier. Decreased food availability would presumably have an opposite effect, "delaying" age at sexual maturity (Eberhardt, 1977).

Laws, (1977b) used tooth backcalculation (backcalculating age at maturity evidenced by the transition in rates of cementum deposition) from crabeater seals in the Marguerite Bay area to demonstrate a decline in age at maturity from approximately 4.5 years in 1945 to 2.5 years in the late 1960's. If that observed trend occurred in response to numerical and trophic changes within the marine food chain caused by decreasing whale stocks, one might have expected a subsequent increase in age of maturity through the 1970's with the slowdown of whaling and enhanced competition between increasing stocks of krill consumers. A small sample of crabeater seals was taken in 1977 near the South Shetland Islands to look for evidence of such an increase in age at maturity (Bengtson and Siniff, 1981). Although a mean age of 3.8 years was found from ovarian examination, tooth backcalculation did not show a clear fall and rise in age of maturity. The current paper reviews the data from these and other studies (Øritsland, 1970) in light of recent material from the Antarctic Peninsula and an expanded sample from Marguerite Bay.

Methods

Crabeater seals of both sexes and of all age classes were sacrificed in 13 seasons for specimen material and dogfood over an area extending from the southwestern coast of the Antarctic Peninsula northeast along the Scotia Arc to the South Orkney Islands. Øritsland (1970) collected

132 females and 86 males in 1964 from the area between Elephant Island and the South Orkney Islands. From 1966 through 1976, 753 females, 527 males, and 113 individuals of undetermined sex were collected from the Marguerite Bay area; 94 females were collected in Bransfield Strait and Admiralty Bay, King George Island, in 1977; and 261 females and 279 males were collected from the vicinity of the Argentine Islands, Bransfield Strait, Seymour Island, and James Ross Island in the 1981-82 season. Standard measurements, teeth, and reproductive tracts were collected from most seals sacrified.

Mandibles from freshly collected seals were boiled from 30 to 60 minutes prior to pulling all teeth, which were then stored in a 10% formalin solution. A longitudinal thin section (0.1 to 0.5 mm thick) was taken from the 3rd post canine tooth (or alternative if this tooth was damaged) in each individual using a high speed diamond circular saw. Tooth wafers were cleared through serial solutions of ethanol and xylene and mounted on glass slides with an artificial mounting medium (D.P.X. or Permount). These mounted thin sections were examined under transmitted polarized light at 150 - 300 power magnifiction. Teeth from the 1977 collection were decalcified, thin-sectioned, and stained prior to microscopic examination (Bengtson and Siniff, 1981).

The total age of each seal was estimated by counting the total number of cementum layers. Each main layer was assumed to represent one year. Replicate counts were made for all samples. For the 1966 to 1976 samples, two readers counted cementum layers, discussed discrepancies, and agreed on an appropriate score. For the 1977 and 1981-82 samples, the mean value of five blind replicate counts was used as the total age estimate.

Backcalculation of the age at sexual maturity (first ovulation or first sperm production) was accomplished by locating the transition zone in cementum layers. Early layers are broader and irregular whereas layers laid down later in life are narrower and more regular (Hewer, 1964; Laws, 1977b; Bengtson and Siniff, 1981). For the current analysis only seals 7 years of age or older were considered for tooth backcalculation. This value was obtained by assuming that all seals were mature and had a visible transition zone by 7 years of age. Previous work (Bengtson and Siniff, 1981) indicated that all seals 7 years old or older had ovulated at least once. Inclusion of younger individuals who may not yet have matured would have biased the maturity estimates downward. Scoring of the transition zone was done with replicate counts as described for estimating total age. No tooth backcalculation was done on the the 1964 sample. The variance between the readers of the two main data sets, 1966-76 (RML) and 1977-82 (JLB) was evaluated by having both authors read an identical subset of 100 teeth from the 1972-73 sample.

In the current presentation, only reproductive material from females has been considered. Analysis of male reproductive material will be presented at a later time (Laws, in prep.). Ovaries were preserved, prepared and evaluated in a similar fashion as those used by Øritsland (1970) and Bengtson and Siniff (1981). Ovaries were preserved in a 10% formalin solution, sectioned serially by hand to approximately 2 mm thickness, and macroscopically examined. Copora and follicles were counted and measured. For this analysis only female seals 2-7 years old were considered. Assuming that 2 years is the youngest maturing age class and that corpora are macroscopically visible up to 5 years after formation, a corpus formed at 2 years should be visible 5 years later when that individual is 7 years old. An individual's age at maturity was calculated by subtracting the total number of corpora present in its ovaries from its total age estimated from cementum layers. Mean age at maturity was calculated separately for each collection year by calculating an arithmetic mean of all seals 2-7 years old in that sample.

Results

There was no difference between sexes for estimates of age at maturity calculated from transition zones in teeth (Laws, 1977b). Therefore, males and females were lumped in all subsequent analyses of tooth backcalculation. When age at maturity was plotted against cohort year, the expected rise in maturity through the 1970's was not evident. Instead, curves from recent collections (e.g., 1981-82) had slopes parallel to past collections (e.g., 1972-73/73-74) (Figure 1a). Two potential explanations for the differences in these curves include variation in the tooth scoring technique between readers and differential survival rates related to the age of maturity. Analysis of variance between the scores of RML and JLB indicated no difference in scores of age at maturity ($p < .001$). A more likely explanation for the observed trends in age at maturity is an effect on the survivorship of cohorts related to the age at which any particular individual matures. Plotting the age at maturity versus the age at collection (Figure 1b) illustrates that the age of maturity curves for animals between 7 and 30 years old, regardless of specific cohort year, are essentially the same. If seals that mature early tend to die relatively early, then these individuals would be under-represented in older cohorts. Conversely, seals from older cohorts which matured later would be the ones still present in the population at the time of sampling, producing elevated estimates for that cohort's mean age at maturity. If the age at maturity had no effect on the age at death, then there should be no change in the relative representation of the different ages at maturity between samples for any given cohort. This is not the case, as shown by an analysis of variance of the two samples considered. The majority of variation in age at maturity is accounted for by year of collection ($p < .001$).

An analysis of the relative strength of cohorts shows that in the 1950's and early 1960's seals apparently prospered if born in the seasons immediately after major whaling activity (Figure 2a). Conversely, as whaling slowed down, relative cohort strength declined. However, the occurence of two groups of strong cohorts starting in 1966 and 1970 does not appear directly related to whaling activities. The possibility of population cycles initiated by discrete blocks of heavy whaling is discussed later.

The estimates of mean age at maturity for each collection year as calculated by ovarian material show a drop in the age of maturity after the 1964 sample and a steady increase in the age of maturity through the 1960's and 1970's (Figure 2b). Because each of the points shown in that figure was calculated identically, even if the true mean age at maturity is not reflected exactly by each estimate, the estimates should indicate a true population trend. Unfortunately, no estimate could be made from the 1966-67 sample because reproductive tracts were not collected.

Discussion

The cause of the transition zone in the cementum of teeth is not immediately apparent. It has been suggested that the changing rates in cementum deposition may be related to the additional energetic costs experienced by sexually mature individuals (Laws, 1977b). Mature females (through pregnancy and lactation) and males (by fasting and defending females during pup-rearing) may utilize energy formerly directed to body (and tooth) growth and maintenance. However, even though both females and males fast during pup-rearing, the energetic drain on females is expected to be larger due to pregnancy. Given the similarity of the transition zone between sexes, perhaps it is related not to energetic demands, but to an overall physiological change at puberty. Variation in the rate of tooth formation near the time of puberty has been described in humans (Cherktov, 1980).

Mean age at maturity estimated by tooth backcalculation is related to the age at which seals were collected, not their year of birth. Possible causes for this trend include some aspect of tooth interpretation (e.g., systematic reader error) or a real interaction between age at maturity and longevity. In the first case, incorrect identification of ambiguous transition zones might bias estimates enough to artificially produce the observed trends. For example, in younger seals, with fewer layers laid down after maturity, the transition zone might be estimated at an earlier age. Conversely, older seals with more cementum layers might bias the reader to estimate the transition zone at a higher age. Reader error of this type has been proposed in cetacean studies where transition zones in earplugs are evaluated (Cooke and de la Mare, 1982). Because the layers are much clearer and more regular in crabeater seal cementum than in whale earplugs, we do not believe that such a bias is present in our analysis of crabeater seal teeth. However, the possibility of reader error remains.

In the second case, longevity may be related to the age at which a seal matures. If early maturing seals die sooner than those maturing later, representation of different ages at maturity would vary within any one cohort when sampled 10, 20, or 30 years later. Individuals that had matured early would have lower representation in older cohorts, resulting in an upwards bias in mean age at maturity estimates. [This is the case in penguins, where individuals that breed at an early age may be subject to higher predation (Ainley and DeMaster, 1980); however, predation does not seem to be the main factor in crabeater seals.] Seals with a relatively high metabolism may grow faster, mature earlier, and exhaust their physiological/energetic resources sooner. Experimental studies on mice have shown that longevity can be increased if metabolism and growth rates are experimentally lowered (McCay et al., 1935). Laws (1959) found that female seals of species with fast growth rates reached sexual maturity earlier and had shorter longevity than those species with slower growth rates.

The timing of changes in the age at maturity (estimated by ovarian material) and whaling activities strongly suggests that perturbations of one component of the marine ecosystem are reflected in other components. The seals considered here were taken from an area that had two discrete peaks of whaling. No whaling was allowed in Antarctic Area I (as defined for whaling statistics) from 1939 to 1955. In 1955 Area I was opened, and an estimated 70% of the fin whale (Balaenoptera physalus) stock was removed over the next 3 years (Breiwick, 1977). From 1958 to 1960 there was a lull in Area I whaling, but in 1961 large catches resumed for two more years (Committee for Whaling Statistics). Some additional fin and sei whales (Balaenoptera borealis) were taken through the 1960's; the minke whale (Balaenoptera acutorostrata) fishery began in 1971 (Figure 2c). The seals collected and analyzed for this paper were taken from Area I and the western portion of Area II. Although Area II begins along the eastern coast of the Antarctic Peninsula, the principal whaling undertaken in Area II occurred further east, nearer to South Georgia. Hence, from an ecological perspective, we consider the seals evaluated in this study to have been influenced by whaling in Area I alone.

There was an apparent drop in the female (ovarian) age at maturity from the 1959 to the 1963 cohort (Figure 2b). Unfortunately no samples were taken between the years these cohorts reached maturity or earlier, so our ability to estimate mean age of maturity in the interim years or earlier is limited. After 1963, there was a steady increase in female age at maturity through the 1976 cohort. This rise corresponds closely with the 1963 cessation of major whaling in Area I. We suggest that the decline and subsequent rise in age at maturity reflects an increasing krill availability as whales were being harvested; that abundant available food prompted faster growth and earlier maturity; and that with the conclusion of heavy whaling in 1963, subsequent seal cohorts grew slower and matured later as additional supplies of krill were no longer being made available by further reductions in whale consumption.

Prior to whaling in 1955, the mean age at maturity in the population may have been stable, perhaps approximately 4 to 4.5 years of age. This seems a reasonable assumption in light of the fact that the mean age at maturity for the 1976 cohort was nearly 4.2 years, and the trend was still increasing. If one assumes that the age at maturity prior to 1955 was approximately 4.5, then once whaling began, mean age at maturity may have fallen rapidly through the 1950's and 1960's as indicated by the one available estimate for the 1959 cohort (Figure 2b).

It is presently not known whether age at maturity is flexible enough to reflect short term fluctuations in food availability. If so, then one would not have expected a linear function as age of maturity declined during the two periods of heavy whaling in Area I. A possible pattern of declining age at maturity is proposed by the dashed line in Figure 2b and explained by the following scenario: With the onset of whaling, krill availability increases rapidly, allowing earlier attainment of maturity. As whaling slows, competition increases, and age at maturity begins to rise until whaling once again causes age of maturity to fall. Future studies will need to test the degree to which this variable can change in response to short term phenomena.

The strength of cohorts born in the whaling periods begun in 1955 and 1961 may be due to high pupping rates, high survival, abundant food, faster growth rates, or a combination of these factors. Abundant krill, for example, could have stimulated faster growth rates, which in turn may have led to lower levels of predation. Predation by leopard seals has a significant impact on young crabeater seals (Siniff and Bengtson, 1977), but this falls dramatically with increasing age and body size (Siniff et al., 1979). The occurence of weaker cohorts following the slowdown in whaling might result if environmental conditions became less favorable and survival rate declined.

The causes of the two peaks of strong cohorts starting in 1966 and 1970 is unclear. Why these cohorts showed relative strength in years when whaling was not undertaken in Area I remains to be determined. It is possible that the two groups of strong cohorts caused by whaling in the 1950's and 1960's may have had a shadow effect on the population in subsequent years. For example, seals from boom cohorts would have entered the breeding population at approximately 3 to 4 years of age. At that time, the recruitment of their pups into the population would further accentuate an unusual age distribution. The behavior of such reproductive pulses or cycles requires further study and modelling to determine their effect both on age distribution as well as the analysis of population parameters themselves. It is presently unknown what effect periodically strong age classes would have on a variable such as age at sexual maturity.

If the observed decrease and subsequent increase in age at maturity in crabeater seals is indeed related to changes in krill availability resulting from whaling activity, one would expect to see similar changes in parameters of some baleen whale stocks. Much attention has been given to the evaluation of growth and reproductive parameters in southern baleen whales (Gambell, 1973, 1975; Laws, 1962; Lockyer, 1972, 1977, 1979; Masaki, 1977, 1979). These studies have indicated declines in age at maturity and increases in pregnancy rates for various whale species. Unfortunately, few have evaluated trends since whaling declined in the mid-1970's. This is due both to the time lag required to allow all individuals in recent cohorts to mature before calculating mean age of maturity and also due to the lack of specimen material once provided by whaling. Masaki (1979) evaluated age at maturity in the minke whale by four different methods including examination of ovarian material and transition zone in earplugs. Using transition zones, he observed a decreasing age at maturity in all 6 statistical whaling areas. In Area I, he observed a decline in maturity from approximately 13 years in 1945 to 5 years in 1970. From 1963 to 1970, a period when age at maturity in crabeater seals apparently increased (estimates from ovarian material), he found a decline in minke whale maturity from 8 to 5 years. His sample was insufficient to allow calculation of age at maturity from ovaries in Area I, but areas III and IV showed no change in age at maturity. Backcalculating age at maturity using transition zones of crabeater seal teeth during that period falsely indicated a decreasing age at maturity whereas ovarian material has demonstrated an actual increase. Perhaps similar problems are present in backcalculating age at maturity using whale earplugs. If so, it may be that the true age at maturity in minke whales (estimated from ovarian material) was fairly constant during that time.

The causes of the observed changes in age at maturity in crabeater seals are likely to be related to complex interactions within the marine ecosystem. Various functional and numerical responses probably occurred throughout the marine community in response to the massive removal of whale biomass from the Southern Ocean. Smaller whale stocks probably resulted in less competition for food, contributing not only to higher individual growth rates, but probably a higher growth rate for the crabeater seal population as a whole. With the decline of whaling in Area I, exploited whale populations may have begun increasing although this is unproven. It has been suggested that other groups such as penguins (Conroy and White, 1973; Conroy, 1975) have increased rapidly in numbers due to reduced whale competition and increased krill availability. Moreover, Antarctic fur seal (*Arctocephalus gazella*) numbers have recovered faster than expected (Laws, 1973, 1977b; Payne, 1977). The true extent to which other krill consumers, including fish and cephalopods, might have been increasing during this period is unknown. Numerical increases in any of these groups presumably would have led to increased inter- and intra-specific competition for food and a subsequent slowing in seal growth rates and age of maturity. Furthermore, we have no direct knowledge of the actual fluctuations in abundance of krill populations during this time. It is difficult, therefore, to identify which suites of factors are likely to be most important in leading to changes in age at maturity in crabeater seals. Nevertheless, changes in crabeater seal age at maturity do give insight into general ecological trends in the Antarctic marine ecosystem by providing an index of whether conditions are relatively good or bad for growth, survival, and reproduction.

Conclusion

Data are presented suggesting that the age of sexual maturity in crabeater seals decreased as a result of whaling in Area I and subsequently increased when whaling ceased. This trend may have been due to changing food availability and functional and numerical changes in krill-consumers. It would be instructive if we were able to compare the results presented here with other parameters such as growth rates, pregnancy rates, juvenile and adult survival rates, and food habits.

Modeling can serve a useful role in future evaluation of the interactions between different population parameters. Further attention should be directed to the significance of changes in relative cohort representation in various samples. How do periodically strong cohorts affect the population dynamics of crabeater seals in subsequent years? Do very strong cohorts affect survival, mean age of maturity, or competition for food? Does pulsed reproduction contribute to the formation of population cycles in crabeater seals? There is evidence for similar fluctuations in cohort strength in leopard seals (Rounsevell and Eberhard, 1980). Future work should also examine the hypothesis that early maturation leads to a relatively earlier death and the implications of this for life history strategies.

This study has demonstrated the value of one aspect of crabeater seals as an indicator species. It is important that sampling of crabeater seals continue for monitoring studies of the Antarctic marine ecosystem. Samples should be taken regularly to obtain growth, reproductive, and demographic data. Such a sampling program would provide insight into how crabeater seal population dynamics and variations in reproductive success with time reflect ecological interactions within the Antarctic marine ecosystem.

Acknowledgments

We are grateful for the field assistance provided by L. Airey, M.J. Baker, B. Bostlemann, D. Burke, D.P. DeMaster, I. Everson, A. Morgan, D. Ragland, R.A. Reichle, P. Salino, D.B. Siniff, I. Stirling, T. Øritsland, B. Weaver, personnel at Rothera Station, and the assistance and support of the officers and crew of R.R.S. *John Biscoe*, R.V. *Hero* and U.S.G.C. *Glacier*. Assistance in the laboratory by A. Baird, M. Fallows, and D. Regis is gratefully acknowledged. J. Beddington, I.L. Boyd, J.G. Cook, J.P. Croxall, W.K. de la Mare, R.C. Handley, D. Lavigne, and D.B. Siniff participated in helpful discussions. C. Ricketts is thanked for help with statistical analysis.

Financial and logistical support was provided by the British Antarctic Survey and the Division of Polar Programs, National Science Foundation (Grants # OPP 75-17719 and DPP 80-20087).

Literature Cited

Ainley, D.G., and D.P. DeMaster. 1980. Survival and mortality in a population of adelie penguins. Ecol., 61:522-530.

Bengtson, J.L., and D.B. Siniff. 1981. Reproductive aspects of female crabeater seals (Lobodon carcinophagus) along the Antarctic Peninsula. Can. J. Zool., 59:92-102.

Bengtson, J.L. 1982. Reproductive ecology of crabeater and leopard seals. Antarct. J. U.S. (in press).

Breiwick, J.M. 1977. Analysis of Antarctic fin whale stock in Area I. Rep. Int. Whal. Commn., 27:124-127.

Chertkov, S. 1980. Tooth mineralization as an indicator of the pubertal growth spurt. American J. Orthod., 77: 79-91.

Conroy, J.W.H. 1975. Recent increases in penguin populations in Antarctica and the subantarctic. Pp. 321-336 in Stonehouse, B. (ed.), The Biology of Penguins. Univ. Park Press: Baltimore. 555 p.

Conroy, J.W.H., and M.G. White. 1973. The breeding status of the king penguin (Aptenodytes patagonica). Brit. Ant. Surv. Bull., 32:31-40.

Cooke, J.G., and W.K. de la Mare. 1982. The effects of variability in age data on the estimation of biological parameters of minke whales (Balaenoptera acutorostrata). Rep. Int. Whal. Commn., 32.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environ. Conserv., 4:205-212.

Erickson, A.W., D.B. Siniff, D.R. Cline, and R.J. Hofman. 1971. Distributional ecology of Antarctic seals. Pp. 55-76 in Deacon, G. (ed.), Symposium on Antarctic Ice and Water Masses (Tokyo, 1970). Scientific Committee on Antarctic Research: Cambridge.

Gambell, R. 1973. Some effects of exploitation on reproduction in whales. J. Reprod. Fert. Suppl., 19:533-553.

Gambell, R. 1975. Variations in reproduction parameters associated with whale stock sizes. Rep. Int. Whal. Commn., 25:182-189.

Gilbert, J.R., and A.W. Erickson. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. Pp. 703-740 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Hewer, H.R. 1964. The determination of age, sexual maturity, longevity and a life-table in the grey seal, (Halichoerus grypus). Proc. Zool. Soc. London, 142:593-624.

The Committee for Whaling Statistics. 1955-1979. International whaling statistics. Compiled for the International Whaling Commission. Grøndahl and Sons: Oslo.

Laws, R.M. 1956. Growth and sexual maturity in aquatic mammals. Nature, 178:193-194.

Laws, R.M. 1959. Accelerated growth in seals, with special reference to the Phocidae. Norsk Hvalfangst-T., 9:425-452.

Laws, R.M. 1962. Some effects of whaling on the southern stocks of baleen whales. Pp. 137-158 in LeCren, E.D. and M.W. Holdgate (eds.), The Exploitation of Natural Animal Populations. Oxford Press: Oxford.

Laws, R.M. 1973. Population increase of fur seals at South Georgia. Pol. Rec., 16:856-858.

Laws, R.M. 1977a. Seals and whales in the Southern Ocean. Phil. Trans. Roy. Soc. Lond. B., 279:81-96.

Laws, R.M. 1977b. The significance of vertebrates in the Antarctic marine ecosystem. Pp. 411-438 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Leslie, P.H., J.S. Perry, and J.S. Watson. 1946. The determination of the median body weight at which female rats reach maturity. Proc Zool. Soc. Lond. B., 115:473-488.

Lockyer, C. 1972. The age at sexual maturity of the southern fin whale (Balaenoptera physalus) using annual layer counts in the earplug. J. Cons. perm. int. Explor. Mer., 34:276-294.

Lockyer, C. 1977. A preliminary study of variations in age at sexual maturity of the fin whale with year class in six areas of the Southern Hemisphere. Rep. Int. Whal. Commn., 27:141-147.

Lockyer, C. 1979. Changes in a growth parameter associated with exploitation of southern fin and sei whales. Rep. Int. Whal. Commn., 29:375-395.

Masaki, Y. 1977. Yearly change in the biological parameters of the Antarctic sei whale. Rep. Int. Whal. Commn., 28:421-429.

Masaki, Y. 1979. Yearly change of the biological parameters for the Antarctic minke whale. Rep. Int. Whal. Commn., 29:375-395.

McCay, C.M., M.F. Cromwell, and L.A. Maynard. 1935. The effect of retarded growth upon the length of life span and upon ultimate body size. J. Nutrit., 10:63.

Øritsland, T. 1970. Sealing and seal research in the southwest Atlantic pack ice, Sep - Oct, 1964. Pp. 367-376 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. Pp. 749-768 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Payne, M.R. 1977. Growth of a fur seal population. Phil. Trans. Roy. Soc. Lond. B., 279:67-79.

Rounsevell, D., and I. Eberhard. 1980. Leopard seals, Hydrurga leptonyx, (Pinnipedia), at Macquarie Island from 1949 to 1979. Aust. Wildl. Res., 7:403-415.

Sadleir, R..M.F.S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen: London.

Siniff, D.B., and J.L. Bengtson. 1977. Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. J. Mammal., 58:414-416.

Siniff, D.B., I. Stirling, J.L. Bengtson, and R.A. Reichle. 1979. Social and reproductive behavior of crabeater seals (Lobodon carcinophagus) during the austral spring. Can. J. Zool., 57:2243-2255.

FIGURE 1

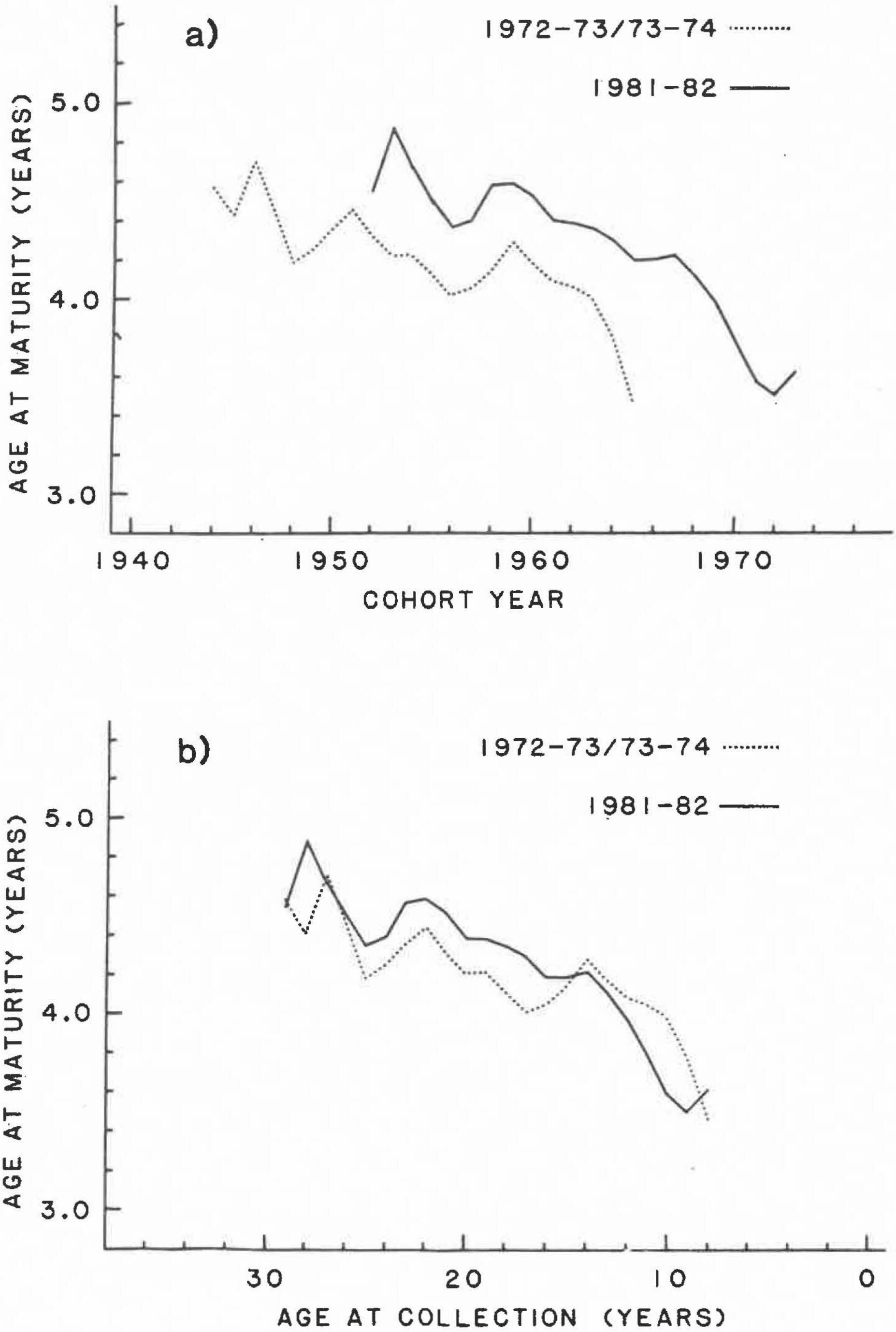
a)
1972-73/73-74
1981-82
AGE AT MATURITY (YEARS)
5.0
4.0
3.0
1940
1950
1960
1970
COHORT YEAR
b)
1972-73/73-74
1981-82
AGE AT MATURITY (YEARS)
5.0
4.0
3.0
30
20
10
0
AGE AT COLLECTION (YEARS)

FIGURE 2

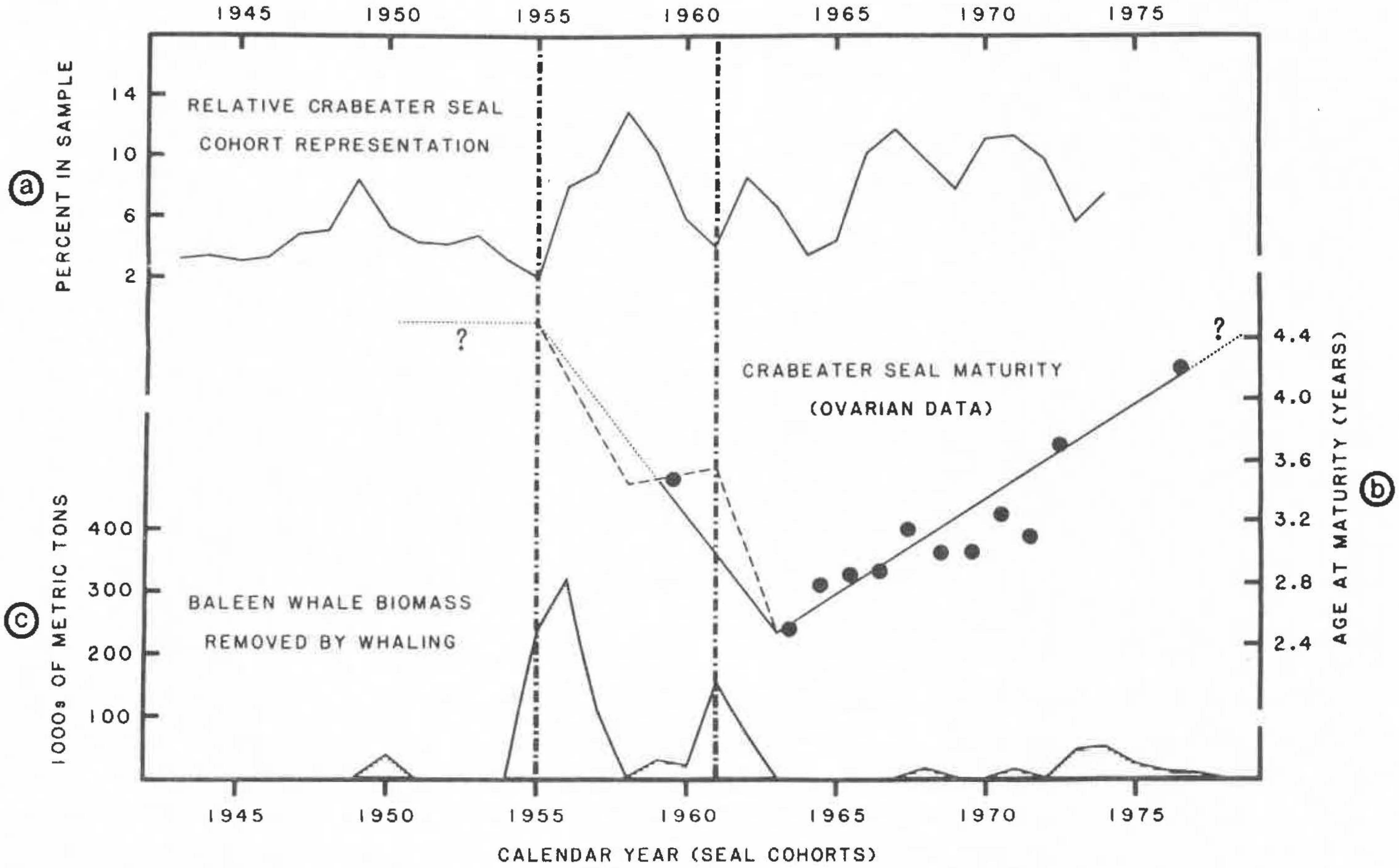
1945
1950
1955
1960
1965
1970
1975
ⓐ
PERCENT IN SAMPLE
14
10
6
2
RELATIVE CRABEATER SEAL
COHORT REPRESENTATION
?
CRABEATER SEAL MATURITY
(OVARIAN DATA)
?
ⓑ
AGE AT MATURITY (YEARS)
4.4
4.0
3.6
3.2
2.8
2.4
ⓒ
1000s OF METRIC TONS
400
300
200
100
BALEEN WHALE BIOMASS
REMOVED BY WHALING
CALENDAR YEAR (SEAL COHORTS)

Figure 1. (a) Mean values of age at maturity in relation to cohort year (year of birth). Sample sizes for the two collections shown are 1972-73/73-74 = 358, 1981-82 = 341. (b) Mean values of age at maturity in relation to age of seals at time of collection (year of death). Sample sizes are the same as in (a).

Figure 2. (a) Relative representation of seal cohorts. The percent age distribution of 7 - 21 year olds was plotted for each collection year. Means of these values were calculated for each calendar year, yielding the curve shown. (b) Age at maturity as estimated from ovarian material. Mean values for 2 - 7 year olds from each collection year are plotted by mean cohort year (4.5 years prior to collection year). Dotted line shows presumed trend of maturity, and dashed line shows alternative trend of decline. (c) Baleen whale biomass removed from Area I annually. Assumes the following average body sizes (metric tons): blue, 88; fin, 50; humpback, 27; sei, 18.5; and minke, 7.

Figure 1. (a) Valeurs moyennes de l'âge à la maturité par rapport à l'année de la cohorte (année de la naissance). La taille des échantillons pour les deux relèvements présentés est la suivante: 1972-73/73-74 = 358, 1981-82 = 341. (b) Valeurs moyennes de l'âge à la maturité par rapport à l'âge des phoques au moment du relèvement (année de la mort). La taille des échantillons est la même que pour (a).

Figure 2. (a) Représentation relative des cohortes de phoques. Les pourcentages de la répartition par âges des individus de 7 à 21 ans ont été déterminés pour chaque année de relèvement. Les moyennes de ces valeurs ont été calculées pour chaque année civile, avec pour résultat le fléchissement de la courbe. (b) Age à la maturité estimé d'après les matières ovariennes. Les valeurs moyennes pour les individus de 2 à 7 ans pour chaque année de relèvement sont déterminées par année de cohorte moyenne (4,5 ans avant l'année de relèvement). La ligne pointillée indique les tendances présumées de la maturité, et la ligne brisée indique la tendance alternative de déclin. (c) Biomasse de baleines mysticètes soustraite de la Zone I chaque année. Assume les tailles moyennes suivantes (en tonnes métriques): bleue, 88; rorqual commun, 50; à bosse, 27; rorqual boréal, 18,5; et petit rorqual, 7.

Рисунок 1. (a) Средние величины возраста половозрелости, соотнесенные с поколением (год рождения). Даны размеры проб при взятии двух образцов: 1972-73/73-74 = 358, 1981-82 = 341. (b) Средние величины возраста половозрелости, соотнесенные с возрастом тюленей во время отлова (года смерти). Размеры проб подобны (a).

Рисунок 2. (a) Относительное количество (в процентах) тюленей одной возрастной группы. Количество (в процентах) особей возрастом от 7 до 21 года было отмечено на схеме по каждому году отлова. Средние значения этих величин были вычислены за каждый календарный год, что дало данную кривую. (b) Данные по возрасту половозрелости, полученные в результате исследования яичников. Средние значения для особей от 2 до 7 лет за каждый год отлова нанесены на график по поколениям (4,5 года до года отлова). Пунктирная линия указывает предполагаемое направление изменений половозрелости, а штриховой пунктир указывает альтернативное направление снижения. (c) Биомасса гладких китов, берущаяся ежегодно в Районе 1. Предполагаются следующие средние размеры особи (метрические тонны): синий кит - 88, финвал - 50, горбатый кит - 27, сейвал - 18,5, остромордый полосатик - 7.

Ilustración 1. (a) Valores medios correspondientes a la edad al alcanzar la madurez con relación al año de la manada (año de nacimiento). Los tamaños de las muestras con respecto a las dos recolecciones mostradas son: 1972-73/73-74 = 358, 1981-82 = 341. (b) Valores medios correspondientes a la edad al alzanzar la madurez con relación a la edad de las focas al momento de la recolección (año de muerte). Los tamaños de las muestras son iguales a (a).

Ilustración 2. (a) Representación relativa de las manadas de focas. Se hizo una gráfica de la distribución de porcentajes de edad de los de 7 a 21 años de edad por cada año de recolección. Los medios de estos valores se calcularon para cada año civil, produciendo la curva indicada. (b) Edad al alcanzar la madurez calculada partiendo de material ovárico. Los valores medios correspondientes a los de 2 a 7 años de edad cada año de recolección se trazan por año medio de manada (4.5 años antes del año de recolección). La línea de puntos muestra la supuesta tendencia en la madurez y la línea de guiones muestra la tendencia alternativa de declinación. (c) Biomasa de ballenas mysticetas eliminadas anualmente del Area I. Supone los siguientes tamaños promedio de cuerpo (toneladas métricas): ballenas azules, 88; rorcuales comunes, 50; jorobadas, 27; rorcuales negros, 18.5; y ballenas enanas, 7.