

BREEDING BIOLOGY AND DEMOGRAPHY OF THE DOUBLE-CRESTED CORMORANT

phalacrocorax auritus



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SOME ASPECTS OF THE BREEDING BIOLOGY AND DEMOGRAPHY OF
THE DOUBLE CRESTED CORMORANTS (*Phalacrocorax auritus*)
OF MANDARTE ISLAND".

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1. INTRODUCTION.

1.a. Lack's hypothesis and how to test it.

Lack has postulated that "clutch-size is adapted to the greatest number of young that the parents can normally raise" (Lack-1966). In seabirds food is considered to be the principal factor determining the number of young that can be raised. In cold water areas there is a seasonal flush of food which usually results in a high breeding-success of the seabirds geared to it, whereas in tropical seas food is aseasonal but scarce, which results in a reduction of clutch-size or difficulties in raising young.

Richdale (in Lack-1966) found in the Yellow eyed penguin (*Megadyptes antipodes*) a deferred maturity and a low adult annual mortality (13%). It also appeared that older adult birds were able to raise more young than younger ones by having a greater clutch-size and being more successful breeders.

Coulson and White (in Lack-1966) showed that in the Kittiwake (*Rissa tridactyla*) also older parents were more successful in raising young than younger ones. Also in this species maturity was deferred and adult mortality was low (12%).

In the Procellariiformes maturity is most deferred (up to about 10 years in albatrosses) and clutch-size is always one (Lack-1966, and Harris-1966, 1970). Adult Procellariiformes have a very low mortality of less than 10%.

Lack considers the deferred maturity of many seabirds to be an adaptation to (temporarily) difficult feeding situations as years of experience seem to be necessary for maximal annual survival and optimal breeding results. Experience would favour older birds in two ways: in more efficient exploitation of food resources prior to the breeding season (which limits the possibility of the female to produce eggs), and during the breeding season (after hatching food can limit the number of young that will successfully fledge). If all successfully fledged young have an equal chance to survive until the age of breeding, natural selection would be in favour of the most productive parents.

The availability of food seems to control annual recruitment by at least three different mechanisms: by a reduction of clutch-size due to a scanty food supply before the breeding season (Lack-1966), by a reduction

of the number of fledged young when food during the breeding season is just too scarce to raise all of the young. (This would be specially applicable to tropical oceanic birds (Ahsmole-1963^a)), and by a high post-fledging mortality when feeding conditions are temporarily difficult. A high first year mortality is reported to be a common phenomenon in seabirds breeding in higher latitudes (e.g. in Coulson and White-1963^a, in Nelson-1964, 1970, in Robertson-1971, in Ward-in prep. and in Wynne-Edwards-1962).

Thus adaptation of population-size in seabirds to long-term feeding conditions would operate along the lines of less or more available food and less or more successfully fledged young, favouring genes of less or more productive individual parents, according to the neo-Darwinistic theory.

A controversial view is presented by Wynne-Edwards. In his 1962 book he interprets the facts of deferred maturity and reduced clutch-size as adaptations to avoid intraspecific competition and overexploitation of the food resources of a (sea)bird population. The mechanism by which this result would be achieved is called "group selection" as intraspecific individual competition (for food) is supposedly prevented. The theoretical weakness of this view, as Lack points out, is that it seems to compromise the validity of the orthodox neo-Darwinian view, of natural selection inevitably favouring increased reproductive success by any breeding unit up to the maximum such a unit can achieve. On Wynne-Edwards view, a single-egg clutch, for example, is a device for lowering recruitment rate, whereas the evolutionary view would be that it must necessarily have evolved because it is on the average the clutch that leads to the highest breeding success or otherwise it would not have been evolved.

Lack's view is based on the assumption that in a stable population normal clutch-size will be the most productive one because it is difficult for the parents to produce more eggs or to raise more young. This hypothesis can be tested by experiments on re-laying of eggs and by enlarging clutch- or brood-size.

Harris summarizes the research on twin-raising experiments done in Procellariiformes, where normal clutch-size is one (Harris-1970). It appeared that in the stable populations of the Laysan albatross (*Diodema immutabilis*, Rice and Kenyon-1962), the Leach petrel (*Oceanodroma leucorhoa*, Huntingdon in Lack-1966), the Madeirian storm petrel (*O. castra*, Harris-1969)

and in the Manx shearwater (*Puffinus puffinus*, Harris-1966, 1970) twinning experiments gave a production of young that was lower than normal. In the Manx shearwater results of twinning were different in different years: in at least one year they were able to raise twins, whose first year survival was not lower than singletons. However, it is questionable if Manx shearwaters are able to lay more than one egg in a short time as relaying seems to be a seldom reported phenomenon in shearwaters (Lack-1966).

The situation of the Manx shearwater seems to be comparable with that of the Galapagos swallow-tailed gull (*Creagus furcatus*). In this tropical bird twins gave a 86% higher fledging success than singles, but the female most likely cannot obtain sufficient food to produce more than a single egg at a time (Harris-1970).

These data seem to support Lack's hypothesis, but in growing populations the results of experiments are different.

Coulson and White (1963^a) showed that in the Kittiwake of the Farne Islands the young from all "supernormal" broods (4 in stead of 3) fledged. Of one of these broods of which the young were weighed just before fledging, all young appeared to be underweight. This might indicate a lower post-fledging survival compared with young from normal broods. As post-fledging survival in relation to brood-size was not studied, these findings do not necessarily conflict with Lack's view. Apart from supernormal nests, the most productive clutch-size was three.

Vermeer (1963) found that in the Glaucous winged gulls (*Larus glaucescens*) of the Mandarte Island colony up to six young could be successfully raised, whereas normal clutch-size is three. Data from research of Ward (in prep.) confirm these results.

Nelson (1964, 1970) proved that the Gannets (*Sula bassana*) of the Bass Rock colony were perfectly able to raise twins (normal clutch-size is one), provided that the young were equally old at twinning. Fledging success of twins was 76% higher than of singles. If difference in age was more than one day, the younger chick always died within a few days after twinning, in a period when food requirements of the chicks were still small. So death of the younger chicks in unequally-aged twins was not due to absolute shortage of food, but was caused by early sibling competition.

Robertson (1971) studied the influence of brood-size on reproductive success in two species of cormorants, the Double crested cormorant

(Phalacrocorax auritus) and the Pelagic cormorant (P. pelagicus), at Mandarte Island. Extra chicks were added to normal sized broods (1 to 4) so that the range of brood-sizes studied was 1 to 8 in Double-crests and 1 to 7 in Pelagics. Fledging success in Double-crests was generally 90% or higher in broods up to 6 chicks. In Pelagics fledging dropped sharply below 90% in broods greater than 4. In no Pelagic nest did more than 4 chicks fledge, whereas up to 7 chicks fledged in Double-crests nests. Post-fledging mortality in the first year of life (up to beginning of the second year of life) in normal broods of Double-crests was about 50% and slightly lower in supernormal broods, although the results in successive years were not quite consistent and sample-size of the largest broods (6 and 7) was rather small. The differing brood-rearing capabilities of the two species were correlated with their population status, i.e., growing versus stable, with the double-crests being the growing population. In the same way Lack explained the higher than normal brood rearing capabilities of Glaucous winged gulls and Gannets. The fact that in these cases the production from normal broods is less than from supernormal ones can be understood as a kind of "anachronism", i.e., these populations are still adapted to previous worse conditions of feeding. This explanation seems to fit in the dynamics of the populations observed, but it does not account for the fact that in the species mentioned above (Kittiwake, Glaucous winged gulls, Gannet, Double crested- and Pelagic cormorant) by far the greater part of the pre-fledging mortality happens within two weeks after hatching, when the siblings need for food is still limited. This strongly suggests that in these species factors other than absolute amount of food may be involved in determining the number of chicks that will be raised.

1.b. On demography of Mandarte's DCC-population.

The situation on Mandarte Island is unique as juvenile mortality in Double crested cormorants can be directly measured, because the surviving one and two year old birds all can be assumed to return to the colony in the breeding season, as there is no evidence that they stay somewhere else during that period.

In order to collect more data on differences in survival of young from nests with different brood-sizes, Robertson made some additional series of supernormal DCC-broods in 1971.

Mandarte Island

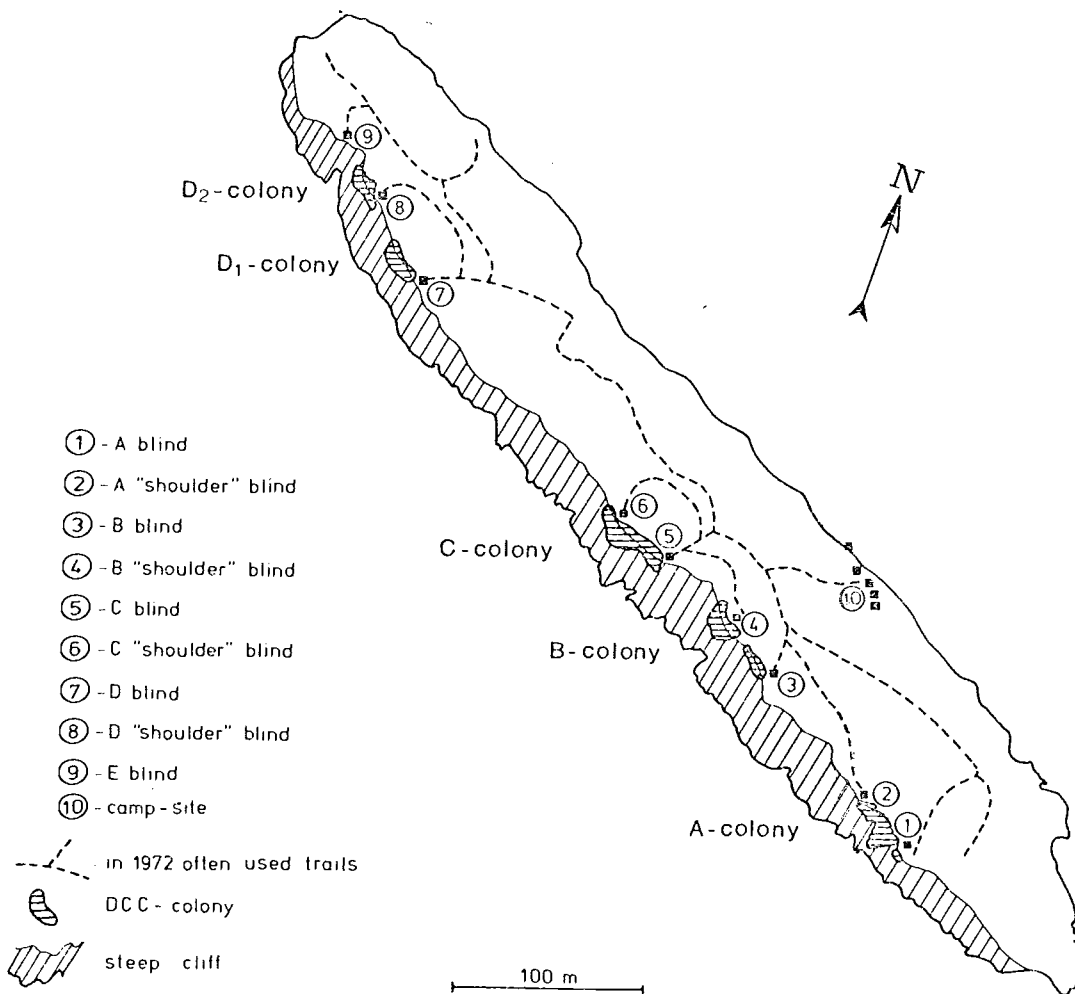


Fig. 1 Sketch map of Mandarte Island, showing location of the Double-crested Cormorant colonies and the blinds from which the observations were made (see key).

So in 1972 observations were done to check the results of the 1971 experiments. In addition data were collected concerning two and three year survival in Robertson's birds from nests with a known brood-size. Collecting these data was combined with making a survey of the older banded resident birds. Combining 1972 information on band reading and breeding success with what is known from these subjects about previous seasons offered the possibility to calculate some trends of the dynamics of Mandarte's DCC-population.

2. MATERIALS AND METHODS.

2.a. Brief description of Mandarte Island.

Mandarte lies among the Gulf Islands in Haro Strait, off the south end of Vancouver Island ($48^{\circ} 38' N$, $123^{\circ} 17' W$). The island is 100 m broad and 700 m long. The island consists of calcareous sandstone. A low broken cliff some 3-4 m high forms the N.E. facing shore. From this low side the land rises unevenly to the precipitous S.W. facing shore, composed of steep cliffs ranging from 10 to 29 m in height (fig. 1). Midway a groove scores the long axis of the island. Here soil accumulation supports shrubbery and a few gnarled trees; elsewhere bare rock and grass patches prevail. On the island are no mammalian predators, but there are more than 2000 breeding pairs of Glaucous winged gulls (*Larus glaucescens*) and some 20 pairs of Northwestern crows (*Corvus caurinus*) which are important predators of eggs and small chicks of both species of cormorants.

The Double-crested cormorant subcolonies are situated along the S.W. shore of the island on the rounded shoulders of the steep cliffs (fig. 1). The Pelagic cormorant breeds on the more precipitous cliffs along the whole of the island's steep S.W. side.

2.b. Observations.

Observations were done from permanent blinds, which could be approached without disturbing the birds. During the season 4 new blinds were erected (numbers 2, 4, 6 and 8, see fig. 1).

Observations were done daily except in the period from 5/7 - 10/7, when the roof of a cabin was reconstructed and two new blinds were built. Time spent in the blinds depended upon the number and activity of the banded birds that were visible; seldom were more than two hours spent at

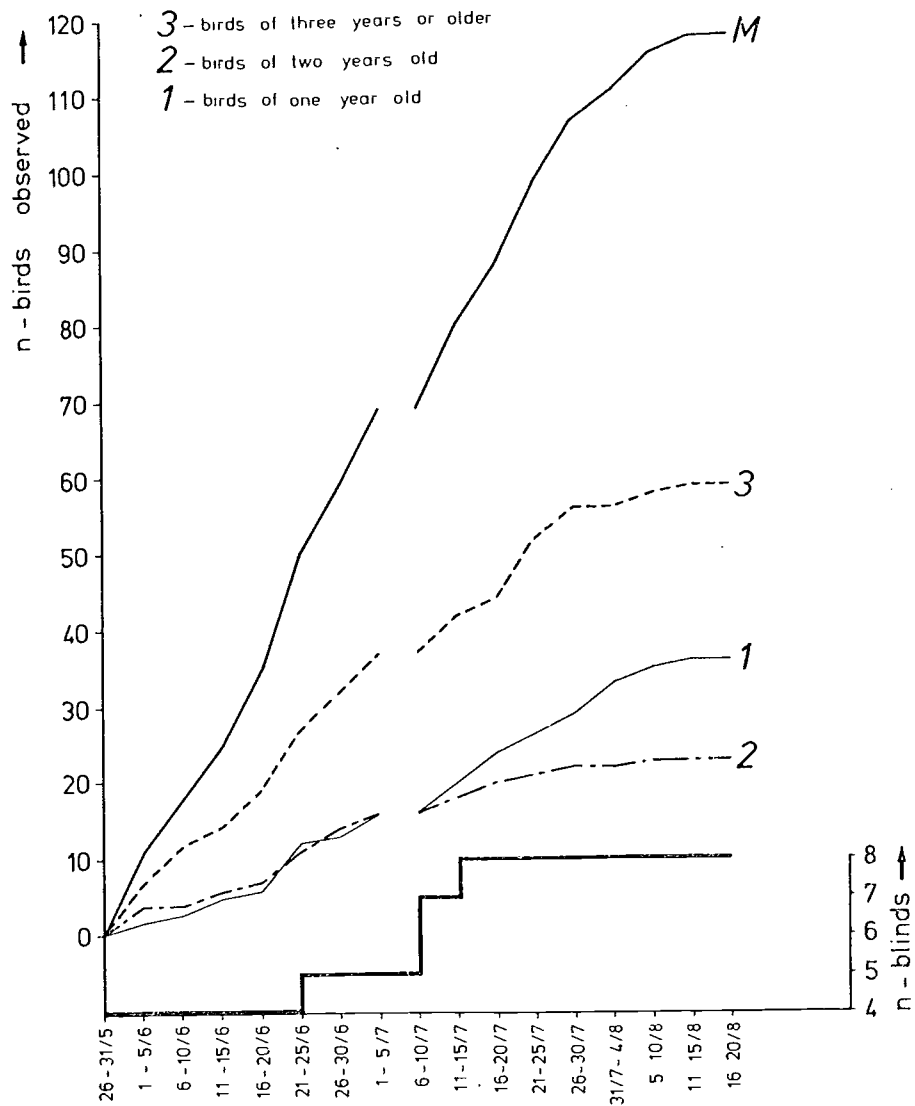


Fig. 2 Cumulative graph of first sightings of all individual Double-crested Cormorants identified at Mandarte Island in 1972 (period of observation 26 May to 20 August; the number of blinds in use is shown at the bottom of the graph).

a stretch in one blind, whereas mean daily observation time was 8-9 hours (from 2/6 - 18/8). Band reading was done with aid of binoculars and telescopes. As observations were often done by two persons from different blinds it soon appeared that the same banded birds were frequently seen in different colonies. All newly identified birds (complete and incomplete numbers) were registered. Thus it was possible to make at the end of the season a cumulative graph of the dates of first sightings (fig. 2) of all identified birds. From this graph it can be concluded that it is highly probable that all resident banded birds with readable bands have been recovered before the end of the season.

From the four original DCC-blinds (numbers 1, 3, 5 and 7) parts of the colonies could be easily observed and from these points data on hatching and fledging were collected. As criterion for fledging was used survival over the first three weeks after hatching as it was observed that all natural mortality happened within three weeks after hatching, which is in accordance with Robertson-1971.

In 1972 4 supernormal broods of⁹ equally aged chicks were made. Of one brood 4 chicks fledged, of two broods 5 chicks fledged and of one brood the results are not known (due to "banding operations"), but maybe five chicks survived.

2.c. Some remarks on annual mortality and recruitment.

Every banded bird recovered previously, which was not seen in the year thereafter was assumed to be dead, unless from observations in a subsequent year it was evident that the bird must have been overlooked. To avoid wrongly classifying some birds as dead, all data on recovered birds (alive and dead ones) were checked for survival in all years of which data are available (including 1972) after the first sighting.

To avoid complicated mathematics the age of each cohort of birds fledged in the same year was synchronized by assuming that all of them were hatched on the first of June.

From data on band recoveries it is obvious that mortality in Double-crests is largely confined to the period after fledging and before the breeding season. Thus it was assumed that during the breeding season mortality was zero, and birds observed in this period were thought to survive at least beyond the breeding season. No evidence was found that would compromise this assumption.

Natural brood-size in relation to fledging
 Data from four seasons combined
 (1969, 1970, 1971 and 1972)

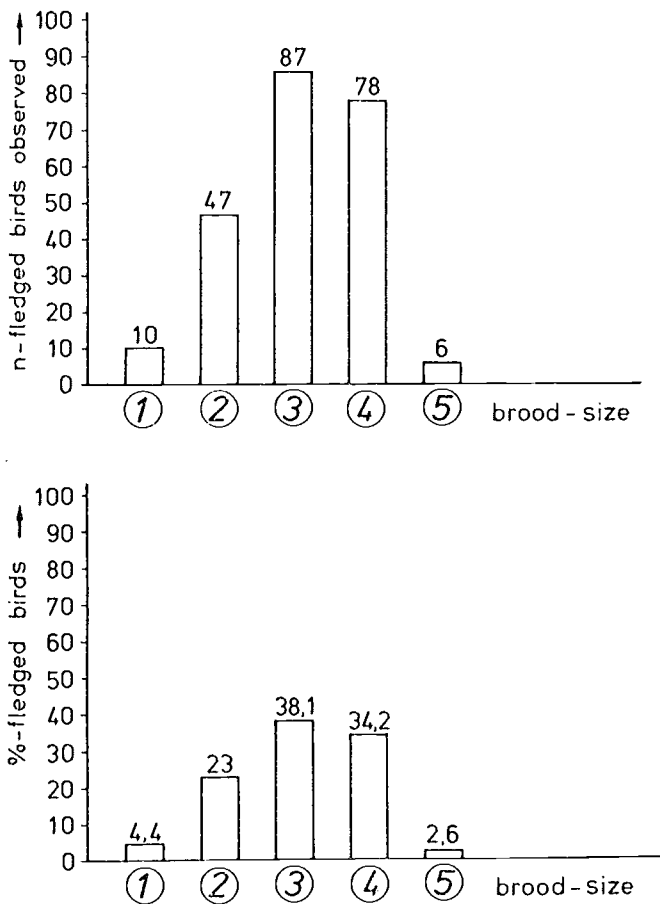


Fig. 3 Contribution made by each of the naturally occurring brood-sizes to the population of birds fledged, combined data from all years. Top: absolute numbers, Bottom: same data on percentage basis. It will be seen that upwards of 90% of all fledglings stem from broods of two, three, or four (size as determined at hatching).

Within the premises mentioned above annual recruitment in the year of observation can be defined as the number of fledged banded birds of the previous year minus that number of banded first year birds that proves to be absent. As only a part of the population is banded, extrapolation must be applied to make an estimate of recruitment in the whole colony.

3. SURVIVAL IN RELATION TO BROOD-SIZE.

3.a. Fledging success.

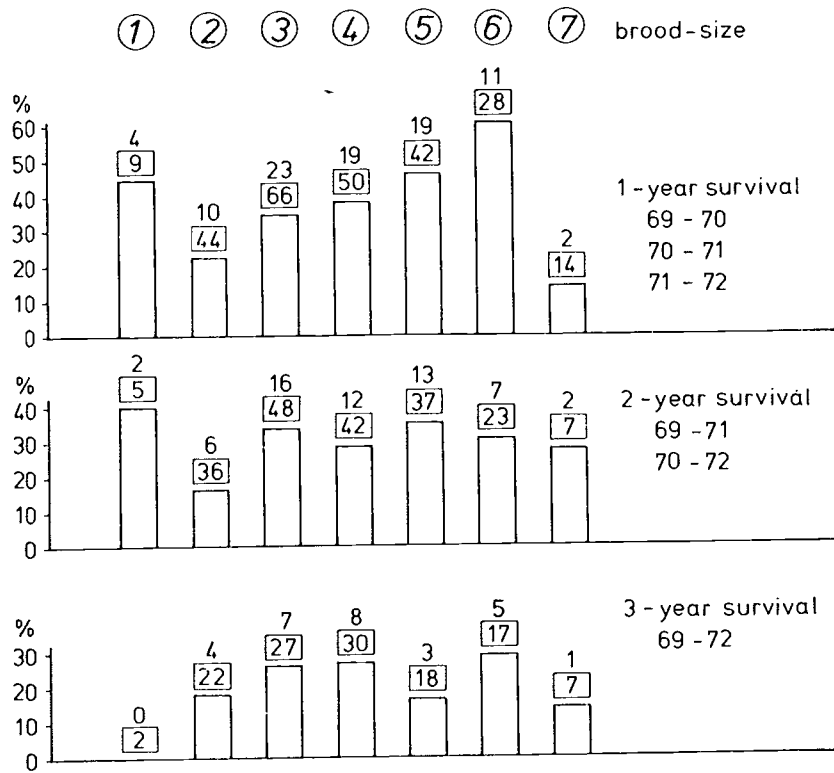
In figure 3) data on natural brood-size and fledging success are compiled from data covering four seasons. ("brood-size" will mean here "the maximum number of chicks that have been observed in a nest after hatching"). It is evident that the greater part of the fledged young is raised in nests with 3 or 4 chicks, whereas in very small and very large broods only a few percent of the total number of fledged chicks were raised. Thus the most productive brood-sizes are 3 and 4.

3.b. Post-fledging survival.

In table 1) data on survival from normal and supernormal broods are listed. Mortality appears to be highest in the first year after fledging. In the second and third year mortality tends to be lower. There is however an apparent discrepancy in first year mortality in the 1969-cohort on the one hand and the 1970- and 1971-cohorts on the other hand; first year mortality in the last ones is much higher. In the 1969-cohort first year survival from supernormal broods of 5 and 6 young is even slightly better than from normal ones. In the 1970- and 1971-cohorts sample size from supernormal broods is rather small, but it seems that survival from broods of 5 and 6 young is about the same as from normal broods. Young from supernormal broods of 7 and 8 suffered a very high mortality. After the first year, annual mortality for all brood-sizes is lower and seems to be independent of brood-size.

In figure 4) data on survival in relation to different brood-size are presented in histograms. Although there are some differences in survival in different cohorts the data on survival are combined to make greater samples. Also from this figure it can be concluded that young from supernormal broods of 5 and 6 survive equally well as do young from normal broods and here too it can be shown that young from a brood of more than 6 will suffer a very high first year mortality.

survival in relation to brood-size in D.C.C.



A - number of birds still alive
B - total number of fledged birds

Fig. 4 Post-fledging survival in the Double-crested Cormorant in relation to the brood-size at fledging, data from all years combined: three year classes for the year following fledging (top), two year classes for the second year (centre) and one year class for survival in the third year following fledging (bottom). The number of birds on which the computations are based is shown (see legend).

Table 1.

SURVIVAL FROM NORMAL- AND SUPERNORMAL BROODS.

Brood-size:	"normal"	5	6	7	8
<u>1969-cohort</u>					
N-fledged chicks	81	18	17	7	
N-alive in 1970 (1-year old)	38	10	9	2	
%- - - -	46,9	55,5	52,9	28,6	
N- - - - (2-years old)	26	6	7	2	
%- - - -	31,2	33,3	41,1	28,6	
%-survival 1970-1971	68,4	60	47	100	
N-alive in 1972 (3-years old)	19	3	5	1	
%- - - -	22,4	16,7	29,4	14,3	
%-survival 1971-1972	73	50	71,4	50	
<u>1970-cohort</u>					
N-fledged chicks	81	19	6		
N-alive in 1971 (1-year old)	18	8	1		
%- - - -	22,2	42	16,7		
N- - - - (2-years old)	15	7	0		
%- - - -	18,5	36,8	0		
%-survival 1971-1972	83,3	88,5	0		
<u>1971-cohort</u>					
N-fledged chicks	120	5	5	7	11
N-alive in 1972 (1-year old)	35	1	1	0	0
%- - - -	29,2	20	20	0	0

Comparison of differences in survival in the larger samples of fig. 4) strongly suggests that increasing brood-size and first year survival are positively correlated, whereas survival beyond the first year is not correlated with brood-size.

A comparison in this figure of the data concerning survival of young of broods of 1 and 7 clearly shows the hazards of small samples.

4. DEMOGRAPHY OF THE MANDARTE COLONY.

4.a. Production in 1972.

From the original blinds (no. 1, 3, 5 and 7) 85 DCC-nests could be easily observed. From 48 of these nests accurate data on clutch-size, hatching and fledging were collected. These data are presented in table 2). From another 35 nests minimum numbers of eggs and chicks are available, which are added to the more accurate data to make larger samples. The combined data are given in table 3).

From table 2) it can be concluded that, although sample size is rather small, the trends observed in the colonies A, B and C are remarkable consistent. Only chick mortality in the B-colony is a little higher than in the other two colonies.

The data from D₁-colony are however much more at variance with the general trends in the A, B and C-colony; here hatching- and fledging success are only just over 50%. Production in D₁-colony is very low too.

The low hatching success in D₁-colony can be explained because breeding in this colony was out of synchrony with the other colonies; in fact the whole colony was about two weeks later than the other ones, which would inevitably result in this colony being for some time the only one with eggs and small chicks. In this way this colony would suffer a higher toll by the crows than the other colonies where predation pressure was not concentrated on one colony.

The relatively high chick mortality in the B- and D₁-colony might be experimentally induced, as chicks for metabolism trials have been taken almost exclusively from these colonies.

Combination of the data from the least disturbed colonies A, B and C would offer the opportunity to make an estimate of general trends of the 1972 breeding season. In this way average clutch-size would be 3, 12, hatching success 79,3% (2,5 chicks/nest) and fledging success 69,5% (1,74 chicks/nest).

Table 2.

ACCURATE COUNTS.

colony	clutch-size	N-nests	N-eggs	N-hatched eggs	N-fledged chicks	produc- tion per nest
A	1	1	1	1	1	
	2	3	6	4	3	
	3	6	18	12	9	
	4	1	4	4	4	
mean clutch-size 2,67		<hr/> 111	<hr/> 29(72,5%)	<hr/> 21(72,5%)	<hr/> 17(81%)	1,55
B	1	1	1	0	0	
	2	0	0	0	0	
	3	4	12	11	5	
	4	9	36	29	19	
	5	1	5	5	4	
mean clutch-size 3,60		<hr/> 15	<hr/> 54	<hr/> 45(83,3%)	<hr/> 28(51,8%)	1,86
C	1	2	2	0	0	
	2	0	0	0	0	
	3	3	9	9	7	
	4	2	8	6	5	
	5	1	5	4	2	
mean clutch-size 3,00		<hr/> 8	<hr/> 24	<hr/> 19(79,2%)	<hr/> 14(73,6%)	1,75
A,B,C.	1	4(11,8%)	4	1 (25%)	1(100%)	
	2	3(9,8%)	6	4 (66,6%)	3 (75%)	
	3	13(38,2%)	39	32(82%)	21(63,7%)	
	4	12(35,3%)	48	39(81,1%)	28(71,8%)	
	5	2 (5,9%)	10	9 (90%)	6 (66,6%)	
mean clutch-size 3,12		<hr/> 34	<hr/> 107	<hr/> 85(79,3%)	<hr/> 59(69,5%)	1,74
D ₁	1	0	0	0	0	
	2	1	2	2	2	
	3	4	12	10	6	
	4	9	36	15	6	
mean clutch-size 3,56		<hr/> 14	<hr/> 50	<hr/> 27(54%)	<hr/> 14(51,8%)	1,00

Table 3.

ACCURATE COUNTS AND MINIMUM COUNTS COMBINED.

colony	clutch-size	N-nests	N-eggs	N-hatched eggs	N-fledged chicks	produc- tion per nest
A	1	2	2	2	2	
	2	9	18	16	13	
	3	18	54	45	39	
	4	3	12	8	7	
mean clutch-size 2,68		<u>32</u>	<u>86</u>	<u>71(82,5%)</u>	<u>61(85,9%)</u>	1,90
B	1	1	1	0	0	
	2	0	0	0	0	
	3	5	15	13	7	
	4	10	40	32	23	
	5	1	5	5	4	
mean clutch-size 3,58		<u>17</u>	<u>61</u>	<u>50(82%)</u>	<u>34(68%)</u>	2,0
C	1	2	2	0	0	
	2	2	4	4	4	
	3	10	30	30	25	
	4	3	12	8	7	
	5	1	5	4	2	
mean clutch-size 2,94		<u>18</u>	<u>53</u>	<u>46(86,8%)</u>	<u>38(82,5%)</u>	2,10
A,B,C	1	5(7,5%)	5	2 (40%)	2(100%)	
	2	11(16,4%)	22	20(90,8%)	17(85%)	
	3	33(49,3%)	99	88(88,9%)	71(80,7%)	
	4	16(23,9%)	64	48(75%)	37(77,1%)	
	5	2(3%)	10	9(90%)	6(66,7%)	
mean clutch-size 2,98		<u>67</u>	<u>200</u>	<u>167(83,5%)</u>	<u>133(79,6%)</u>	2,00
D ₁	1	0	0	0	0	
	2	2	4	3	3	
	3	5	15	13	8	
	4	9	36	15	6	
mean clutch-size 3,37		<u>16</u>	<u>55</u>	<u>31(56,4%)</u>	<u>17(54,9%)</u>	1,06
From D ₂ only data on nest success as these colony was not observed before 1/7		in D ₂	24 nest produced 17 chicks			0,71
		in D ₁ ,D ₂	40 nests produced 34 chicks.....			0,85

Data on breeding from the enlarged samples (table 3) confirm the general trends observed on the net counts. However, from these data production in the colonies A, B and C is somewhat higher and production in the D-colony appears to be even lower. As only minimum counts have been added to the accurate numbers, the more diverging trends from the combined samples are due to larger sample size. Thus the data from table 3) provide a better basis considering trends on breeding than the most accurate data. So average clutch-size should be 2,98, hatching success 83,5% (2,49 chicks/nest) and fledging success 79,6% (2,0 chicks/nest). So hatching success is still the same as in 1958 and 1959 (Drent et al-1964), but nest success is 20% lower. This might be related to external causes (e.g. disturbance, experiments). However, in the least disturbed colony (A) production per nest is lowest.

Arguments for external factors being responsible for 1972 low nest success would be more acceptable if internal factors could be proven to be responsible for the low nest success in the A-colony. From the data in table 2) and 3) it can be concluded that not only mean clutch-size is smallest in the A-colony, but also that the smallest clutches are proportionally much more common in this colony than in the other ones.

Considering the most common clutch-sizes in the other colonies, it is evident that small clutches (1 and 2) are scanty or absent here. In the C-colony the most common clutch-size is 3, whereas in the B- and D-colony a clutch of 4 is the most common one.

It is interesting to realize that the A-colony is the most recent subcolony, whereas the other colonies were already established before 1960 (Drent et al-1964).

The parts of the B- and D-colony from where data on breeding were collected include the central areas of these colonies. Data on breeding from the C-colony were mainly from peripheral nests.

As 6 out of 7 known three year old banded birds were observed breeding in the A-colony, it is likely that the A-colony is not only the youngest subcolony, but also the colony with the youngest adult birds.

These facts would nicely fit in Nelson's hypothesis (1970) that in expanding seabird populations the younger adults tend to settle in the peripheral parts of the colony, whereas the older adult birds tend to breed on the traditional breeding grounds. The low nest success would also be in accordance with the low breeding success of young parents,

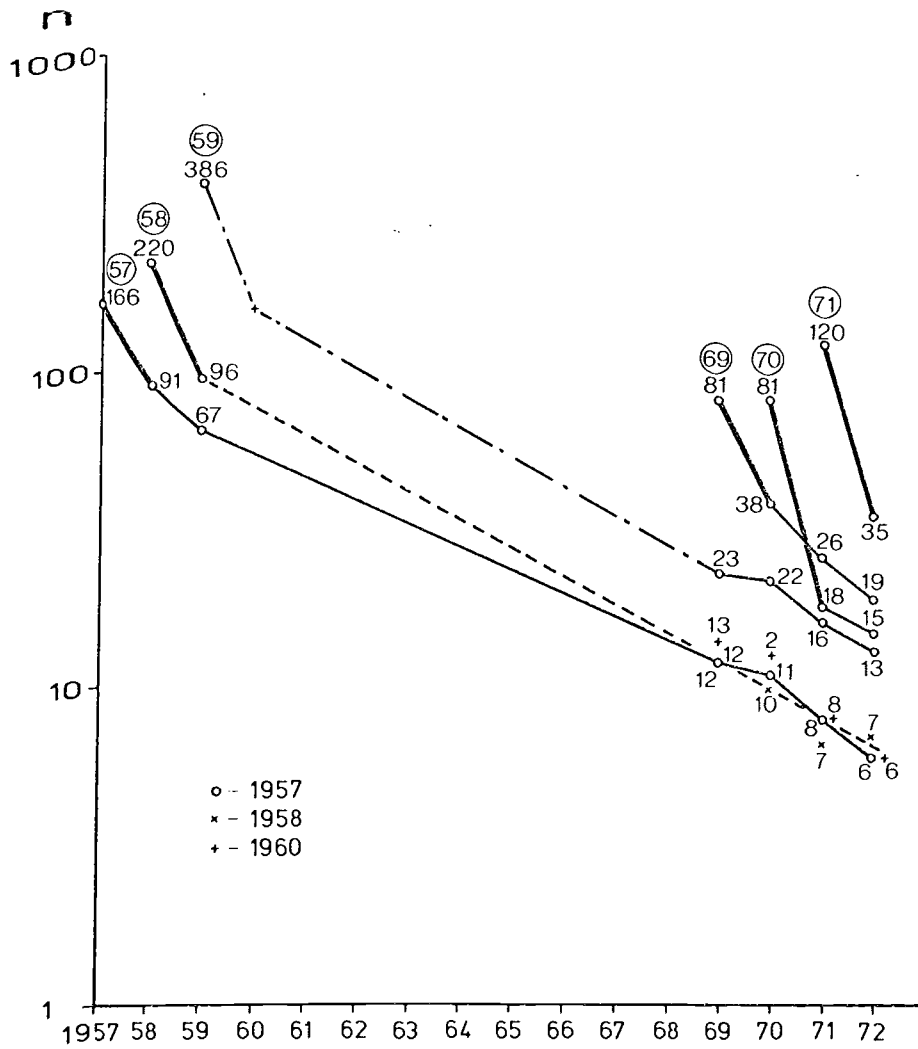


Fig. 4a Survival of the 1957, 58, 59 and 1969, 70 and 71 cohorts of the Double-crested Cormorant, according to sightings made at Mandarte Island. The data are presented in full in Table 4.

annual survival versus age

*compilation based on annual survival in
different cohorts at different age*

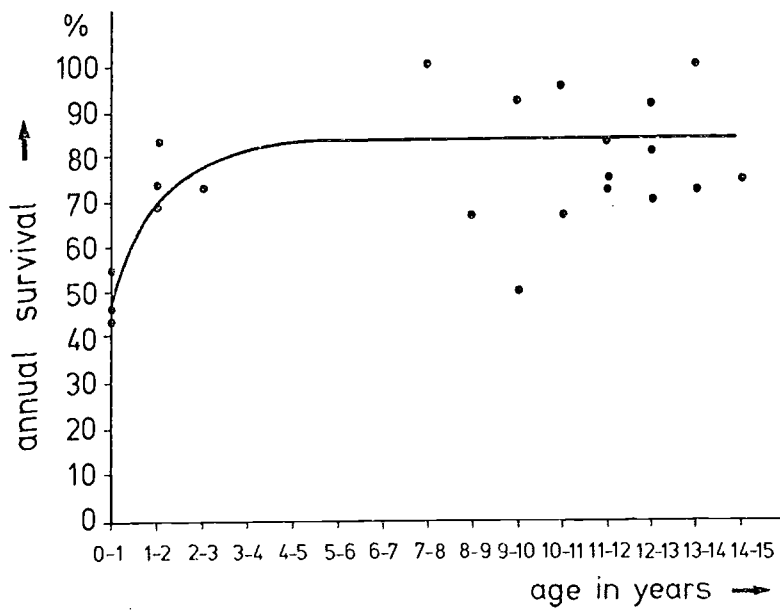


Fig. 5 Annual survival in relation to age in the Double-crested Cormorant population of Mandarte Island, summarized from Fig. 4a.

observed in the Gannet (Nelson-1970). From 6 pairs with at least one two year old parent nest success is known. The mean nest success is 1,50, which is low indeed.

Thus, summing up, it can be concluded that there is strong evidence that internal factors are responsible for the observed lowest nest-success in the A-colony; so for the whole of Mandarte very probably external factors can be considered to be responsible for the observed low production per nest in 1972.

4.b. Post-fledging survival.

1. First year survival.

Data on first year survival are available from 6 cohorts (table 4). The 1957-, 1958- and 1969-cohort show a survival of about 50%, 1959-cohort scores 21,1% and the 1970- and 1971-cohort survive only slightly better. In 1960 time spent on band reading was sharply reduced. From table 4) it can be concluded that all the data obtained from that year are extremely low, so data from 1960 should not be used as a measure for survival.

In 1971 time spent on band reading was low in comparison with 1970 and 1972. Apart from that, the colonies were in 1970 and 1971 often visited for experimental purposes, which might have influenced post-fledging survival. So the low values for the 1970-cohort might be the combined result of experiments and a reduction of observation time, whereas the relatively low survival of the 1971-cohort is probably due to experiments, as time spent on observations in 1972 was about the same as in 1958 and 1959.

An estimate of the difference in accuracy from observations in 1970 and 1971 can be made by compiling the percentage of "apparently overlooked" birds from normal broods, which appeared to be alive after the season of observation. From the 1969-cohort 8 out of 64 birds were overlooked, which is 12,5%. From the 1970-cohort 11 out of 29 were overlooked, which is 38%. The data from 1958 and 1959 give percentages on overlooking of respectively 3,3% (3/90, 1957-cohort) and 5,2% (5/96, 1958-cohort) with an average of about 4%. Thus the data from 1972 on first year survival have to be enlarged minimally with about 4% too, which makes a survival of the 1971-cohort of 30,3%.

Combination of the results from least disturbed cohorts (1957, 1958 and 1969) and of good observation years gives an estimate of first year survival of 225 out of 467, which is 48,1%,

age composition Mandarte D.C.C.-population

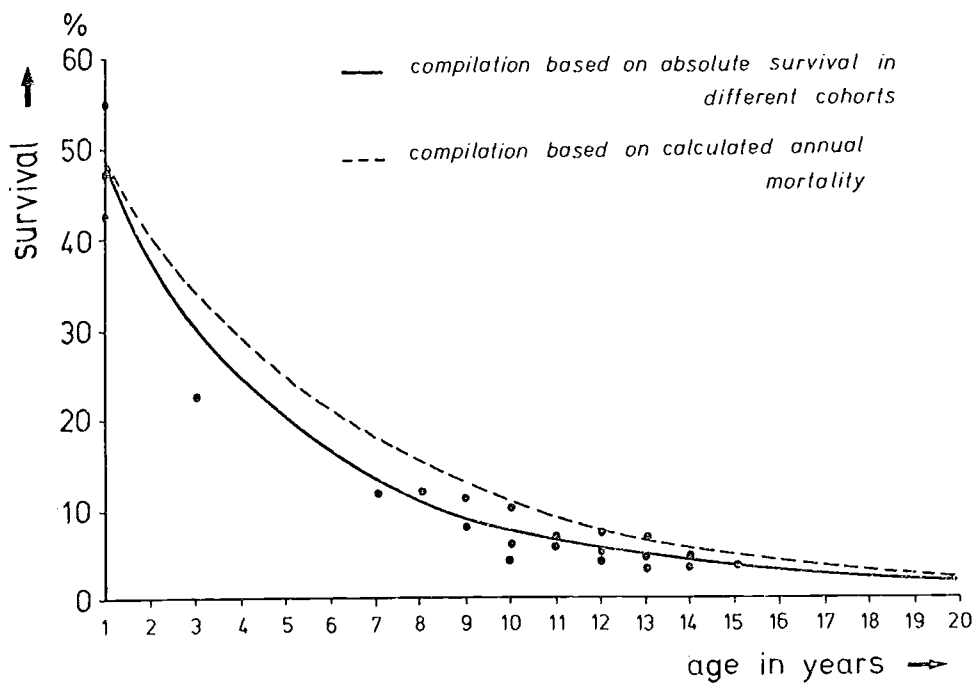


Fig. 6 Attenuation with age in the Double-crested Cormorant, based on setting the number of birds fledged at 100%. For the alternative methods of computation consult the text.

2. Survival from first to second year.

Here also the data from 1960 are very low and should not be used as a measure for survival (table 4),

From the 1957-cohort Van Tets had overlooked 2 birds out of 67, which is 2,9%. Thus the surviving part of the 1970-cohort must be enlarged with about 3%, which makes a survival of 86%.

Combined results from 1957-, 1969- and 1970-cohort make a survival of 108,5 out of 147, which is 73,8%.

3. Annual survival after the second year.

In table 4) all available data on annual survival after the second year are presented. With the exception of observations from 1960 and a very small sample from the 1962-cohort, all calculated values are between 66,7 and 100%.

In figure 5) is set out annual survival versus age of the cohorts. From this figure it might be concluded (with a little wishful thinking) that mortality after the second year is independent of age. This would imply that the data on annual survival may be combined, which makes an annual adult survival of 151 out 178, which is 84,9%.

4.c. Age composition of the population.

From the available data on survival of different cohorts in relation to age, the age composition of the population can be reconstructed in two ways, provided that the conditions responsible for the observed trends in the population are still unchanged.

First, by plotting absolute survival of different cohorts against age. For the same reason as in 4.b. counts from 1960 and incomparable recent counts from 1970 and 1971 are excluded. In figure 6) a line has been drawn through these plotted points.

Second, by assuming that annual survival in subsequent years is independent of survival in any previous year. So the age composition of the population can be calculated using the values of 48,1% for first year survival, of 73,8% for survival from first to second year and of 84,9% for annual survival thereafter. The broken line in figure 6) is drawn according to this method.

The apparent discrepancy between the two graphs is probably due to lack of information about absolute survival in early adult years, so the one based on calculated annual mortality is the more accurate one.

Table 4.

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Data on survival in relation to age.

1. First year survival.

cohort	N-fledged chicks	N-alive after one year	%-alive after one year	Remarks
1957	166	91	54,8	
1958	220	96	43,6	
1959	386	82	21,2	time spent on band-reading was sharply reduced in 1960!
1969	81 ¹⁾	38	46,9	1)-chicks from "normal" broods only
1970	81 ¹⁾	18	22,2	
1971	120 ¹⁾	35	39,3	

2. Survival from first to second year.

cohort	N-one year old birds	N-birds alive after two years	%-birds alive after two years	Remarks
1957	91	67	73,6	
1958	96	41	42,6	observations from 1960!
1969	38 ¹⁾	26	68,4	
1970	18 ¹⁾	15	83,8(86)	+ 3% correction (Van Tets index)=86%

3. Annual survival after the second year.

cohort	age at year A	age at year A + 1	N-birds alive at A	N-birds alive at A + 1	%-annual survival	remarks
1957	2	3	67	33	49,3	observations from 1960!
1957	12	13	12	11	91,7	
1957	13	14	11	8	72,6	
1957	14	15	8	6	75	
1958	11	12	12	10	83,3	
1958	12	13	10	7	70	
1958	13	14	7	7	100	
1959	10	11	23	22	95,7	
1959	11	12	22	16	72,7	
1959	12	13	16	13	81,1	
1960	9	10	13	12	92,4	
1960	10	11	12	8	66,7	
1960	11	12	8	6	75	
1962	7	8	3	3	100	
1962	8	9	3	2	66,7	
1962	9	10	2	1	50	
1969	2	3	<u>26</u>	<u>19</u>	<u>73</u>	
<u>all cohorts together:</u>			178	151	84,9	(data from 1960 excluded)

4.d. Age at first breeding and mean span of adult life.

In 1972 one female bird in first year plumage was seen breeding in the C-colony. This was the only first year bird noted breeding in the regularly observed parts of the island, which contained 85 nests. At the end of the breeding season a total of 320 used nest sites was counted. From the 85 regularly observed nests 9 nests disappeared before the end of the breeding season. Thus the ratio: number of breeding pairs in the whole colony to the number of breeding pairs in the regularly observed parts was $320/76$, which is 4,2. As first year plumage is very conspicuous it is most unlikely that any other breeding first year bird would have been overlooked. So $1 \times 4,2$ which is 4,2 female first year birds may be expected to have bred in the 1972 season. If male birds would breed at the same age as female ones, 8,4 first year birds might have been involved with breeding in 1972. This figure can be related to the total first year cohort by the following calculations.

In 1971 428 nest sites were counted in the beginning of the breeding season. After subtracting 10% representing nest failures and then using the calculated 1971 first year survival of 29,2% with a nest success of 2,0 the size of the 1971-cohort after one year is estimated to be $(428-43) \times 0,292 \times 2,0$ which is 225 birds. We can now state that $3,7\%(8,4/225)$ probably bred.

In 1972 one bird of the 1970-cohort was also observed to be breeding. As the sex of this bird was not known males and females will be treated together. Apart from this breeding bird 23 other banded second year birds were observed; some of these may have been breeding in the not regularly controlled parts of the colonies. The breeding fraction of the second year birds may be estimated to be $1 \times 4,2/24$, which is 17,5%. From the 1969-cohort 30 birds were observed in 1972. 7 of these birds were observed to be breeding in the regularly controlled parts of the colonies, so the breeding fraction of the third year birds may be estimated to be $7 \times 4,2/30$, which is 98,4%.

From the data mentioned above it is evident that the greater part of the three year old birds is involved with breeding. The data on first and second year breeding indicate that breeding might start even in the beginning of the second year, but sample size is minimal, so generalisations from these observations should be considered with care.

From the 32 old birds (from 1957-, 1958-, 1959- and 1960-cohort) observed in 1972 16 were observed to be breeding in the regularly observed parts of the colonies.

Applying straight-forward extrapolation, this number would indicate a well over 200% (210!) breeding proportion of the old birds. As only a maximum of 100% can breed, the assumption on which the extrapolation was based is false. For one thing, the nests of the old birds are not distributed at random over the colonies.

However, these old birds comprise only 2,5% of the living population (fig. 6, compilation based on calculated annual mortality), whereas the one-, two- and three year old birds comprise about 13%, so the data from the younger birds are related to a much larger fraction of the population than the data from the old birds. As the results of straight-forward extrapolation of data on breeding from the young cohorts are real and thus do not necessarily detract from the applicability of this method, the data from the young cohorts must be considered separately.

As there is evidence (ch.4.a., Nelson-1970) that young birds of colonial seabirds tend to breed among equally aged conspecifics, whose nests are mostly situated at the peripheral parts of the colony, and because the blinds were placed at the edge of the colony, it is very likely that the percentage given of first breeders are maximum figures (e.g.: no more and probably less than 98,4% of the third year birds are breeders).

By using the data on the age of first breeding from the young cohorts mean age of first breeding and the beginning of reproductive age can be calculated according to the following scheme:

age in years	%-first breeders	estimated production/pair
1	3	0 (?)
2	17,5	1,5
3	98,4	2,0

Assuming a first year cohort of 100 pairs, 75 and 60 pairs will respectively survive over the second and third year of life. From the first and second year breeders maximally 5 and 18 birds may survive into the next year:

age in years	N-pairs	N-breeding birds	N-new breeding birds
1	100	6	0
2	75	26	21 (26-6 x 0,74)
3	60	118	100 (118-21 x 0,85)

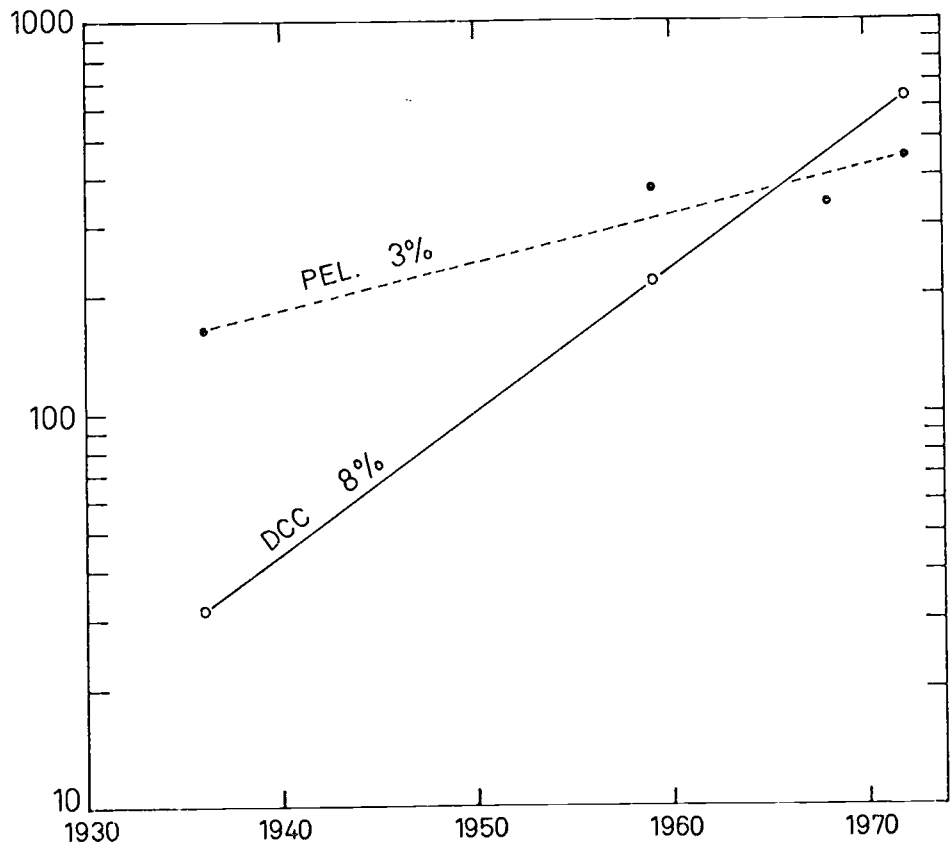


Fig. 7 Total population counts of the breeding stock (number of occupied nests) of Double-crested (DCC) and Pelagic Cormorant (Pel) at Madarte Island 1936-1972. The mean annual increment estimated from these counts is shown as a percentage figure on each line.

So mean age of first breeding can be calculated as follows:

age in years	N-breeding birds x age		
1	6 x 1	which is	6
2	21 x 2	- -	42
3	<u>100 x 3</u>	- -	<u>300</u>
	127		348

mean age of first breeding is 348/127 which is 2,74.

By introduction correction factors for nest success the beginning of reproductive age can be calculated as follows:

age in years	productivity/bird x N-new breeders	subtracting 10% nest failure
1	zero	zero
2	0,75 x 21 which is 15,8	14,2
3	<u>1,00 x 100 - - 100,0</u>	<u>90,0</u>
Thus	14,2 x 2 - - 28,4	
	<u>90,0 x 3 - - 270,0</u>	
	104,2	298,4

So beginning of reproductive age is 298,4/104,2 which is 2,86, indicating that by far most of the birds start effective breeding in the beginning of their fourth year.

According to Wood (1971) mean adult life expectancy can be calculated from data on adult mortality according to the formula:

$$\frac{2 - m}{2 \times m} = \frac{2 - 0,151}{2 \times 0,151} = 6,1 \text{ years in the case of the Mandarte doublecrest.}$$

If the populations were to be stable, 2 parents must in 6,1 years produce 2 new breeding adults. From data on nest counts it can be concluded that Mandarte's DCC-population has grown from 1936 with an annual increase of 8,4%. Thus the production/bird required to balance the observed rate of increase is $1,084^{6,1}$ which is 1,64. So production/pair over 6,1 years must be 2 x 1,64 which is 3,28. From these data expected age of first breeding can be calculated. If young birds would start breeding in the beginning of the fourth year they must have survived over the preceding three years. Total survival over the first three years is 30,2% (0,481 x 0,738 x 0,849). With a production/pair of 2,4 or 2,0, production over three years would be 14,6 x 0,302 = 4,4 or 12,2 x 0,302 = 3,7 new adults. In this way production/pair over 6,1 years can be plotted

against age of first breeding, provided that breeding success from the first year of breeding onwards would be maximal:

		age of first breeding (years)			
		2	3	4	5
recruitment over 6,1 years	(annual production/nest= 2,4)	7	5,2	3,7	3,1
	(annual production/nest= 2,0)	5,9	4,3	3,1	2,6

As the observed recruitment is 3,28, the requirements for an annual growth of 8,4% are met with an annual production/pair of 2,4 when breeding would start in the beginning of the sixth year (5 years old) and with a production/pair of 2,0 breeding would be deferred till the beginning of the fourth year (3 years old). As breeding success is not maximal in the first year of breeding, breeding must start even earlier, which is in account with the calculated mean age of first breeding (2,74 years) and calculated beginning of effective reproductive age (2,86 years).

Thus the bias in the estimates of breeding fractions of the young cohorts, due to the non-random distribution of nest sites, must be very small.

Leslie (1966) presents a method relating annual production per nest to the age of first breeding on the one hand (assuming breeding success would be maximal from the first year of breeding onwards) and to the intrinsic rate of increase on the other. For our data we calculate:

annual prod/nest	age at first breeding	intrinsic rate of increase
	(2	11 %
2,0 fledged young	(3	8,6 %
	(4	5,6 %

As the observed rate of increase is 8,4%, this relationship indicates a mean age of first breeding slightly less than three years, which is in accordance with the other results. Capildeo and Haldane (1954) present a method suitable to calculate mean age of first breeding from data on annual production per nest, first year mortality, adult mortality and intrinsic rate of increase of the population. Here the relationship

$f = \frac{m}{s^a}$ can be applied, in which f is fecundity (defined as

$$f = \frac{\text{ann.prod./nest} \times \text{first year surv.})}{2 \times \text{adult survival}}$$

m is annual mortality (is $1 - s$),

s is adult survival and

a is mean age of first breeding, provided that breeding success would be maximal from the first year of breeding onwards.

Substituting data from Mandarte's DCC-population it can be concluded that:

if ann.prod/nest is	f	intrinsic rate of increase of the population	mean age of first breeding may be expected to be:
2,4	0,68	zero	9,21 years
2,4	0,68	8,4%	5,2 --
2,0	0,57	8,4%	3,89 -

As breeding success is not maximal from the first year of breeding onwards, mean age of first breeding must be slightly less than 5,2 or 3,89 years, indicating a mean first age of breeding of 5 or 3 years, according to a productivity of 2,4 or 2,0. These results nicely conform with the other data.

Summing up, it may be concluded that independent methods yield almost identical results, indicating a mean first age of breeding of 3 or 5 years, depending on nest success being 2,0 or 2,4 and assuming equal mortality and equal age of first breeding of males and females.

One of predicted values can be tested using the 1972 observations. The nest success figure of 2,0 is taken to be most realistic for this period (2,4 was valid in 1957/59) so the prediction becomes 3 years. The observed value for age of effective breeding worked out to be 2,9 years, so the models conform to reality.

5. DISCUSSION.

In the Double Crested Cormorant natural clutch-size is up to 5, but experimental broods up to 8 can be raised.

As replacement clutches are very common and new eggs can be laid within 8 days (Drent et al-1964) it is most unlikely that food-shortage prior to and during the breeding season would limit clutch-size. In 1972 average clutch in the least disturbed colonies was 2,98, whereas production was 2,0/nest. As average hatching success was 83,5%, more than 1 out of every 4 chicks died prior to fledging. Here clearly a brood-size reducing process can be observed, so the question arises which factors might induce this mortality?

The fact that all chick mortality happens within the first 3 weeks after hatching and by far most of it within the first 2 weeks, dismisses the possibility that the ultimate food gathering capabilities of the parents should be limiting.

Inkster (1971), who studied sibling competition in the DCC, observed that, when the chicks were very small, they cannot be fed unless the parent will rise from the nest. After rising of the parent the chick(s) will start begging immediately. Inkster concluded that, if the parents do not rise frequently at this stage, the chicks would never be fed. In this period, to which chick mortality is restricted, feeding frequency must be high and meals are small and it was observed that under these conditions competition is in favour of the older chicks.

Robertson (1971) found that DCC-parents adapted food gathering efforts to brood-size as the surviving chicks grew older. Nevertheless, young from very large supernormal broods (7 and 8) appeared to be underweight at fledging and may be assumed to have a smaller chance to survive than young from smaller broods (none of these birds was seen in the 1972-season). Birds from smaller supernormal broods (5 and 6) were at least as successful in fledging as birds from normal broods, whereas first year survival of the young from these broods was even better.

However, the high fledging success and subsequent survival of large broods is misleading, because the chicks from these artificial broods are all of the same age. As Inkster points out, the fourth and fifth chick in natural broods will often not survive over the first 2 weeks, which is due to differences in age, caused by asynchronous hatching.

So clutch-size would be adjusted before absolute food gathering capabilities of the parents are fully operative. Thus it may be concluded that brood-size in DCC is not dependent on the present-day food gathering capabilities of the parents and that the high fledging success and first year survival from supernormal broods of 5 and 6 only reflects abundance of food in the breeding season.

In this situation the annual recruitment to the population is limited by the toll of post fledging mortality. The amount of post fledging survival might be related to the availability of food after the breeding season, which might be restricted due to small prey populations or difficult feeding conditions. So availability of food to the fledged young and the skill of the young in catching their prey probably are the ultimate factors controlling recruitment in the population studied.

Thus clutch-size in this DCC-population could be related to availability of food after the breeding season, which will favour genes responsible for largest possible broods, provided that all fledged chicks of normal weight have an equal chance to survive. This hypothesis would not necessarily compromise Lack's view that clutch-size should be adapted to the greatest number of young that parents can normally raise, as the principal point in this statement is the idea that food limits the ability of the parents to raise young and thus food would control recruitment to the population. Considering clutch-size in different subcolonies it was found that in the most recent colony (A) smallest clutch-sizes were more common than in the older subcolonies where small clutches were scanty or absent. Production of young in the most recently founded colony is slightly lower than in the older colonies. The difference was apparently not due to worse breeding in the younger colony but may be attributed to the smaller mean clutch in this colony. As 6 out of 7 three year old birds were observed breeding in the youngest colony it is likely that this colony also has the greatest proportion of young adult birds. Data on breeding of older adult birds showed that these birds were not breeding at random over the island either; a greater fraction of the old breeding birds than might be expected by chance was breeding in the regularly observed parts of the colonies. These data correspond very well with trends discussed by Nelson in his 1970 paper.

One of the least understood phenomena in seabirds is the occurrence of deferred maturity. There is little doubt that this is an adaptation to the exploitation of food resources which are scarce or difficult to prey upon, but this does not explain why birds who are apparently adult and who do survive already for years do not join the breeding population, or, if they start breeding for the first time, why they are less successful than the older breeding birds. In this discussion of deferred maturity Nelson explains deferred recruitment to the breeding population in colonial seabirds by repulsive social behaviour of the older established breeding birds which discourages younger adult birds to start breeding in their vicinity. Otherwise breeding in colonial birds is only possible with the aid of "social stimulation", which appears to be optimal among a great number of conspecifics. So the young birds can also supposed to be attracted to the center of the colony with its great number of conspecifics. Based on quantitative data Nelson suggests that the age composition of

the population will determine at which age the young adult birds will join the breeding part of the population and in the Gannet it was observed that new breeders were most attracted to equally aged breeding birds.

This would also account for the often reported fact that in an expanding seabird population mean age of first breeding is lowered.

The mechanism described above is functionally the same as Wynne-Edwards principle, but the manner of exclusion of young birds from breeding is not by actual repulsion and the mechanism by which this behaviour has evolved is not necessarily group selection. In Nelson's view a subtle social-behavioral mechanism regulates recruitment to the breeding population, relying on age-dependent territoriality. Food can be important in this situation by controlling the amount of time that a bird can spend in display at the colony.

As the data on breeding from the Mandarte DCC-colony fit nicely in this theory it might be suggested to link Lack's view to a functional derivate of the often criticized view of Wynne-Edwards.

In this way absolute recruitment to the DCC-population would be effected by a two-stage mechanism: the annual crop of young produced depends on the ^{number} of birds breeding and hence on the age of first breeding (itself dependent on the age structure of the breeding population), and the number of potential first breeders depends on the mortality rate in the first year (and in the case of deferred breeding the mortality rate in subsequent years). Crucial to the understanding of the population dynamics of this species is knowledge of the manner in which density and age structure of the living population influence age of first breeding on the one hand and juvenile mortality on the other. Research applying ethological methods to this ecological problem is seen as the next step in the cormorant study programme.

6. SUMMARY.

This paper deals with the breeding biology and some aspects of the demography of Mandarte Island's DCC-population. A review of a selection from the literature on breeding of colonial seabirds is presented. Special attention is given to the question "which factors determine clutch-size in seabirds"? and results of experiments on artificially enlarged broods

are briefly discussed. Data on survival from enlarged broods of Mandarte's cormorants are summarized and compared with data from normal broods. Underlying information is mainly based on band reading from living birds. Detailed information and statistics on breeding in 1972 are presented. Age composition of the population, age at first breeding and mean span of adult life are calculated. The results from this study strongly indicate that, in the DCC-population studied, control of absolute recruitment would be exerted by first year mortality, whereas the age of first breeding, which is dependent of the age structure of the breeding population, controls the annual production of the population.

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