DISCUSSION

The populations of most of the species reviewed have increased steadily from a low ebb at the beginning of the 20th century. Some species such as the Alcidae have not regained their former distribution and abundance as sketched by Norton (1923), but others, such as the large gulls, appear to have greatly surpassed their numbers previous to 19th century exploitation. Most seabirds increased all together for several decades after 1900, then others joined in and increased especially rapidly while several lagged behind or failed. Several of the factors involved are discussed below.

A. Factors associated with increasing populations

1. Protection. Protection from predation on the breeding grounds by humans and pet cats and dogs has evidently been a major factor. Of equal importance for Leach’s Petrels and Laughing Gulls has been release from the effects of sheep. Close cropping by sheep removes the rank vegetation that Laughing Gulls require for nesting sites, and produces a dense turf of grasses through which petrels do not readily burrow.

2. Clutch size. One might expect species which lay a larger clutch of eggs (Double-crested Cormorant and Common Eider—up to 6 eggs) to increase more rapidly than those which lay smaller clutches (Herring Gull, terns and Black Guillemot—clutch size 2-3), and this has been generally true. But Laughing Gulls on Muskeget and Great Black-backed Gulls in Maine (clutch size of 3) increased as rapidly as either of the larger-clutched species.

3. Immigration. The unusually rapid increase of the Double-crested Cormorant and Great Black-backed Gull populations in Maine may reflect some immigration of birds from Nova Scotia in the way that Herring Gulls emigrating from Maine contributed to the unusually rapid increase in Massachusetts during the 1940s. There is no evidence whether immigration of Laughing Gulls into Muskeget from southern colonies took place or not.

From what evidence is available, however, it appears that both Great Black-backed Gull and Double-crested Cormorant populations in Nova Scotia were increasing during the same decades as were the populations in Maine, although the rate of growth is not clear. If one suggests that immigration contributed to the rapid increase in Maine, one must account for simultaneous increase of
the breeding population in Nova Scotia in the presence of emigration.

The increases recorded are arithmetically "possible" if there was almost perfect survival of fledged young during the decades involved.

4. Social characteristics. Seabirds which feed close to their nests, nest in small dispersed groups, and those which feed at distances from their nests, nest in large dense groups (Lack, 1966). Among the seabird species nesting in New England, Least Terns, Common Eiders, the large gulls, and Black Guillemots feed close to their nests. Others such as Leach's Petrel, Arctic Tern, Roseate Tern, and Common Puffin feed at relatively longer distances from their nests.

The species that feed at longer distances have fewer colonies and stronger site tenacity or group adherence. Even though Roseate and Arctic terns have shifted colony sites several times, the colony members moved all together in a dense group. Common Puffins have not founded a new colony in Maine since before 1900.

Among the species reviewed here, the less intensely colonial species have had larger population increases and expanded their ranges more than the more intensely colonial species. The more intense site tenacity or group adherence might have inhibited population growth by inhibiting the founding of new colonies.

B. The effects of the increase of the Herring Gull population

Interactions with Herring Gulls have apparently played important roles both in unusually rapid increases of some species and in the sudden reversal of population trends of others.

(1) The three species that have increased most rapidly (Double-crested Cormorant, Common Eider, and Great Black-backed Gull) usually established new colonies in existing Herring Gull colonies. Thus the fact that there has always been a surplus of Herring Gull colonies might have facilitated population growth.

Herring Gulls, terns, and Black Guillemots, whose populations have increased more slowly (Figs. 2 and 4), founded their colonies on their own, without making use of already established seabird colonies. Although Herring Gulls settled on tern or Laughing Gull colonies, most of their colonization was of unoccupied islands.

Double-crested Cormorants occupy a number of rocky ledges where no gulls breed, but most of their colonies are on the edges of existing Herring Gull colonies. They seem to suffer little predation from gulls unless intruders disturb a colony, and they are one of the few species which displace both Great Black-backed Gulls and Herring Gulls from the preferred nesting sites on the tops of islands.

The close association of Common Eiders, Herring and Great Black-backed gulls appears to be complex. Gull predation has frequently been observed on Common Eider chicks and eggs (Mendall, 1968), yet field experience of the last 10 years indicates that very few Common Eider females nest on islands that are not gull colonies. Finnish observers (Nyström, 1927; Olsoni, 1928; Bergman, 1939;
von Haartman, 1945) have reported that many diving ducks favor islands with nesting gulls, and have suggested that one selective advantage in the Baltic area is avoidance of predation by crows.

A puzzling aspect of the species interactions is the apparently successful coexistence of Great Black-backed and Herring gulls throughout their ranges despite obvious competition. Black-back predation on Herring Gull chicks is frequent (Paynter, 1949; Harris, 1964, 1965; Weaver, 1970). Erwin (1971) found a positive correlation between Herring Gull nesting success and increasing distance from Black-back nests in a mixed colony. But measurements of breeding success for all members of a colony showed no simple correlation between the breeding success of Herring Gulls and the number of Black-back pairs on the island (Kadlec and Drury, 1968a). Increase in the Great Black-backed Gull population might be partially responsible for the slower increase in Herring Gull population after 1950.

(2) Common Puffins, Razorbills, and Common Murres suffer from gull interference. Nettleship (1972c) measured the impact on Common Puffins, which was serious even in a large colony. One should expect such predation and piracy to have an exaggerated impact on small populations. Prospecting has been seen at several former alcid colonies in Maine, but gulls now occupy all of them and gull interference may have inhibited or prevented recolonization.

Laughing Gulls and the large terns have declined for several decades and the decline seems to have been associated with their being displaced from traditional breeding grounds (Gross, 1948b; Norton, 1924b, 1925a; Wetherbee et al., 1972).

The censuses of terns made in the first three decades of this century are scattered, variable, and strongly influenced by one or two critical estimates, so they can be interpreted several ways. Nisbet (1973) concluded that the tern population in Massachusetts reached its peak before 1920 and Norton (1925a) reported that the tern population in Maine had already reached its peak. Allen and Norton (1931) repeated this opinion. Nisbet's conclusion suggests that the decline began in the south before the impact of gull interference could have been felt.

Later censuses in Maine (Allen and Norton, 1931; Palmer, 1949) indicate that terns continued to increase together with gulls into the early 1940s in spite of being driven from most of their traditional colonies by gulls.

Nevertheless, the numbers of terns breeding on Muskeget declined abruptly after 1935 coincident with the spectacular increase there of Laughing Gulls. Terns left Penikese and Tern Island soon after gulls arrived and a similar litany might be said for about 20 islands.

The mechanism by which the growing gull population displaces the smaller species appears to be straightforward. Some immatures of the larger gulls are apparently excluded from existing colonies and upon reaching breeding age these are evidently attracted by social stimuli provided by an established colony of smaller larid species. The first Herring Gull colonists are joined by others and after the
gull colony grows for several years, the terns suddenly leave. Apparently once terns left the traditional colonies, several unfavorable environmental factors affected them, including predation and human disturbance (Norton, 1924c) and food shortage (Nisbet, 1973).

(3) One might ask what are the differences between those species that apparently thrive in the presence of Herring Gulls and those that suffer from their presence. What went wrong between Herring Gulls, Laughing Gulls, and the terns? The smaller species have been displaced from critical breeding grounds when no "ecological" competition for resources was detectable.

If one takes contemporary theories of community ecology (Odum, 1969) seriously, one should expect community processes (mutual selection pressures) to have adjusted the species within the coastal bird communities to maintain maximum species diversity. But these theories suggest the operation of group selection within closed systems (Drury and Nisbet, 1971).

Should it not be a matter of indifference to Herring Gulls as individuals whether Laughing Gulls and terns are exterminated or remain? The obvious difference between the species that coexist and those that do not is body size. The larger ones can repel interfering gulls. Darwin noted that no species can be selected for the benefit of another.

Darwin also noted that the most closely related species must compete most intensely. The more closely related, the less easily one species can drive the other out. Weaver (1970) reported that well motivated adult Herring Gulls can drive Great Black-backed Gulls out of the larger gull's territory in defense of a small Herring Gull chick; hence the long-continuing competition between Herring and Great Black-backed gulls should not seem unreasonable in open systems.

The observed interactions among gulls and terns during the last 75 years are more consistent with Darwinian natural selection than with classical or contemporary succession theory (Drury and Nisbet, 1973a). Unfortunately much of classical community ecology theory has been taken over into the philosophical structure of the "conservation establishment" and is complicating the human aspects of the search for a valid environmental conservation.

C. Habitat contamination with toxic chemicals

(1) DDE. Three of the species considered here (Double-crested Cormorants, Herring Gulls, and Common Terns) spend more of their time feeding at the heads of bays than the rest of the seabirds. The graphs of their population histories (Figs. 2, 3, 4) suggest marked decreases in the rate of growth after 1940. In contrast, most of the species feeding farther offshore have continued to increase, whereas several aquatic species (not considered here) that feed primarily in fresh waters and estuaries began sharp population declines during the 1940s (Great Blue Heron, Black-crowned Night Heron, Osprey, and Bald Eagle). The major factor responsible for the population decline in these inland species is now generally believed to be the effects of DDE on reproduction (Ames, 1966; Ames and Mersereau,
Although Double-crested Cormorants doubled their numbers every 5-7 years between 1930 and 1945, they have not doubled their numbers in the 20 years since the cormorant control program was stopped in 1953 (Fig. 2). Postupalsky (1971) found an inverse correlation between levels of DDE and reproductive success in the western Great Lakes region. Anderson et al. (1969) found 2-11 ppm (wet weight entire eggs) of stationary populations of Double-crested Cormorants in five localities in Minnesota and North Dakota; they found 20+ ppm of DDE (wet weight entire eggs) taken from a population in Wisconsin whose eggshell thickness has decreased 25% and whose population has decreased to nearly zero. Zitko et al. (1972) reported 8.6-29.4 ppm of DDE (wet weight entire eggs) in Double-crested Cormorant eggs taken in the Bay of Fundy area. Kury (1969) reported 6.2 ppm DDE (wet weight entire eggs) in Double-crested Cormorant eggs taken from Muscongus Bay, Maine, and 7.6 ppm in eggs from the Isles of Shoals. Kury suggested that the Double-crested Cormorants in Muscongus Bay appeared to be unaffected by DDE and in the course of about 150 visits to Double-crested Cormorant colonies during the last 10 years we have seen only a few (perhaps 1%) collapsed eggs with rubbery shells. However, the fledging success Kury reported (“only one young to survive per nesting pair”) is scarcely larger than that in the reportedly stationary or declining populations in the Lake Superior-Lake Nipigon area (Anderson et al., 1969; Postupalsky, 1971).

These reports suggest that DDE contamination might be one factor in the slow increase of Double-crested Cormorants in the Gulf of Maine in recent years (Fig. 2, Table 1).

A change in slope similar to that shown by breeding Double-crested Cormorants occurs in the graph of the Christmas Counts of Herring Gulls (Fig. 3). Growth was rapid in 1920-1940 as compared to 1948-1970. When analysed for DDE content, eggs of Herring Gulls nesting on the outer islands of Maine and Rhode Island were found to contain the lowest levels of gull eggs examined by Hickey and Anderson (1968). Reproductive success measured on these colonies was in some cases high (Block Island) and in others low (Little Green Island, Matinicus Island—Kadlec and Drury, 1968a). The causes of low reproductive success in Maine’s outer islands is probably the greater effort required in food-finding (Hunt, 1973).

Hickey and Anderson (1968) reported “generally normal” reproduction on gull colonies in Minnesota where 60 ppm DDE was found in the eggs. But Keith (1966) found high egg mortality at gull colonies in Green Bay, Lake Michigan (97 ± 11 ppm DDE in 1963 and 202 ± 34 ppm DDE in 1964, wet weight entire eggs). In the course of counting over 30,000 gull nests between 1962 and 1969, many of which were close to industrialized areas, we saw very few (< 2%) collapsed, rubbery eggs, and we have found no indication of hatching failure.

The evidence is inadequate to draw any conclusions, but it is doubtful that DDE contamination has had a significant effect on
Herring Gull population growth. However, contamination levels of gulls feeding in metropolitan areas and in the estuaries of large industrialized rivers are being tested.

2. **PCBs and heavy metals.** On the whole, the coastal seabirds discussed here seem to have small body burdens of industrial chemicals, but there are regions where high levels of PCBs have been found, such as at Passamaquoddy Bay (Zitko et al., 1972) and Long Island Sound (Hays and Risebrough, 1972). Keith and Gruchy (1971) reported DDE and PCBs in Leach’s Petrels from the Atlantic. Yet Huntington (pers. comm.) has not found any effects on Leach’s Petrels at Kent’s Island (Grand Manan).

3. **Oil.** Tuck (1957, 1960) believed that chronic spills from ships pumping bunker oil at sea are a major hazard to seabirds, especially murres, off Newfoundland. Until now, seabird censuses in the western Atlantic have not been adequate to assess seabird mortality resulting from even a major spill in quantitative terms. For example, two oil tankers (*Fort Mercer* and *Pendleton*) broke up on the shoals off Monomoy (Nantucket Sound) in February 1952. The wintering flock of Common Eiders reportedly decreased from 500,000 to 150,000 (Burnett and Snyder, 1954). If the kill reported was even approximately accurate, it should have had an observable impact on breeding populations. But the size of the wintering flock was only a guess and the breeding ground of the Common Eiders involved was unknown. No censuses of breeding Common Eiders on the coast of Maine were available at the time.

D. **The present populations**

The relative importance of the seabird populations of the Gulf of Maine has been consistently underestimated. The sandy shores of southern New England support major populations of Herring Gulls, Common Terns, and Roseate Terns. In the course of this review it has become clear that major populations of Leach’s Petrels, Double-crested Cormorants, Common Eiders, Great Black-backed Gulls, Arctic Terns, Razorbills, Black Guillemots, and Common Puffins breed on the Maine islands. The Laughing Gulls are of special interest because their habitat includes waters that are markedly colder than those in the species’ central area.

Comparing the results of our recent survey with those of Lock’s pilot census (1971), the Maine populations of all these species (except Double-crested Cormorants and Great Black-backed Gulls) are considerably larger than those breeding on the Atlantic shore of Nova Scotia. Nova Scotia has twice as many miles of shoreline as Maine.

Systematic censuses are not available for Newfoundland’s coast, which is at least four times as long as that of Maine, but it appears that the Gulf of Maine populations of Double-crested Cormorants, Herring and Great Black-backed gulls, and Common, Arctic, and Roseate terns are larger.

The importance of subpopulations. A species’ local numbers is probably not an adequate single measure of the condition of that population. In addition to its numbers, certain population charac-
Characteristics such as age structure, reproductive performance, and division into successfully reproducing subpopulations affect the population's vitality. Even in an increasing species, the fewer the productive colonies, the more vulnerable the species may be to local catastrophes. This appears to be illustrated by the comparative history of the Laughing Gull populations in Massachusetts and Maine.

Between 1900 and 1940, the Nantucket Sound population of Laughing Gulls grew rapidly and reached a level exceeding 20,000 pairs, all on one colony (Wetherbee et al., 1972). The habitat quality on and around this colony (Muskeget) has evidently become gradually less favorable as time has passed, and by 1972 the Nantucket Sound population has been reduced to 150-200 pairs (Andrews, AB, 1972). Between 1900 and 1940, the Maine coastal population grew slowly and reached only 250-300 pairs, about 1% of that in Massachusetts. Since 1940, the Maine population has also decreased, but slowly, and still amounted to about 150 pairs in 1972. Now it is essentially equal to the Nantucket Sound population. One reason for less spectacular population changes and better survival since 1940 might be that the Laughing Gulls in Maine have shifted around among about seven islands.

The decline of the Common Tern population around Cape Cod has also been associated with (among other things) their concentration into one or two major colonies.

The importance of the Maine seabird colonies lies not only in the total numbers but also in the fact that the colonies of the Gulf of Maine make up a number of subpopulations and together constitute an important areal subunit of the western Atlantic population of those species.

E. Future censuses

Although the available data have shown major population changes between 1900 and 1970, the techniques are not adequately rigorous for future censuses. The counts have been sporadic, carried out opportunistically without funding or coordination. Precise scientific investigations of the trends in these populations might have contributed important information toward the resolution of public policy issues, but the opportunity to do so has been lost because of the indifference or failure to realize the value of such data on the part of many people including public and private organizations and the scientific community. More precise censuses are required if we are to make the best possible use of bird populations as indicators of environmental quality. For such censuses, the Gulf of Maine from Cape Cod to Cape Sable should be considered a minimum geographic unit.

In order to establish a valid baseline census, several requirements should be met. The most important is that the people taking the census should use similar techniques and have the time and facilities to do a good job (Bach, 1970). Instructions for those taking seabird censuses have been prepared (Operation Seafarer, 1969; Nettleship, 1972a). Techniques include photographic records, properly timed surface counts, and mapping sample plots.
SUMMARY

This paper reviews the last 75 years of history and the present status of 15 species of seabirds in New England. With several exceptions this history has been one of steady increase of numbers and expansion of ranges, but the large gulls (Herring and Great Black-backed gulls) are the only species that have continued to increase since 1940 in the urbanized areas of southern New England.

Not enough is known about Leach's Petrels to ascertain whether the steady decline since 1900 reported by Allen and Norton has continued or been reversed. The populations of Double-crested Cormorants, Common Eiders, Great Black-backed Gulls, and Laughing Gulls (at Muskeget) have grown most rapidly. The increase of Double-crested Cormorants has been much slower since 1945 although they are now breeding on the coast of Connecticut. Common Eiders have extended their breeding range as far south as Cape Porpoise, Maine. Subpopulations of the Herring Gull have grown rapidly during periods of population shifts, but the New England population as a whole has increased slowly. The center of abundance of Herring Gulls has shifted from Maine to southeastern New England. The increase of Herring Gulls, Great Black-backed Gulls, and Double-crested Cormorants was slowed between about 1945 and about 1958 by the effects of a special control program on the coasts of Maine and Massachusetts. Laughing Gulls, after a period of remarkable growth in Nantucket Sound extending into the 1940s, have declined at a steep rate and have been almost eliminated from that area. The New England population of Common Terns increased steadily until about 1940 and has decreased steadily since then. With the decrease, the population center has shifted west from Cape Cod to Block Island Sound and the southern shore of Long Island. Roseate Terns in southern New England and New York, and Arctic Terns that replace them to the northeast, have fluctuated less than, but parallel with, Common Terns. Least Terns have steadily extended their range northward and westward in the last 30 years. They have almost reached Portland, Me. Black Skimmers have recolonized the southern shores of Long Island and Massachusetts.

If the estimates for 1899 are correct, Black Guillemots have increased at a rate similar to that of Herring Gulls, but their range has not been extended beyond its limits in 1950. Common Puffins probably reached a population plateau in their two colonies on the Gulf of Maine in the mid-1950s. Razorbills recolonized the coast of Maine about 1950; their numbers are small and restricted to four colonies. The Maine islands now support major elements of several seabird species including Leach's Petrels, Double-crested Cormorants, Common Eiders, Great Black-backed Gulls, Arctic Terns, Razorbills, Black Guillemots, and Common Puffins. The sandy shores of southeastern New England support major populations of Herring Gulls, Common Terns, and Roseate Terns, and the two areas support a small population of Laughing Gulls adapted to a cold water habitat. According to Lock's pilot census, these populations are considerably larger than those found along the much longer Atlantic shoreline of...

Limitations in the available census data, which are probably adequate only to detect population changes of 25-35%, result from lack of systematic coverage and of uniform census techniques. Proper systematic censuses are needed for the seabird populations of New England’s coast because these species are sensitive to changes in the quality of the coastal waters and might be useful to monitor such changes in the future. The species that will most accurately reflect localized effects nest in small numbers evenly distributed along the coast.

Two major forces have influenced seabird numbers during these 75 years: (1) protection from predation by humans and domestic animals; and (2) expansion of the numbers of Herring Gulls. Among the seabirds considered, Double-crested Cormorants may have suffered from DDE contamination. Although the Herring Gull population growth is lowered in a similar way beginning about 1950, it is not clear what factors are responsible. The patterns of interaction observed among these colonial seabirds while they were increasing are discussed in relation to contemporary informal theories of community development.

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