The incidence of plastic pollution was shown to be increasing during the 1980s. Both large- and small-scale geographic variation in plastic loads occurred as a function of variable plastic density in the environment. Intergenerational transfer of plastic particles was identified as an important pathway for plastic flow in those species that accumulate plastic particles and feed their chicks by regurgitation. This pathway can account for higher plastic loads in nonbreeders and failed breeders than in birds that breed successfully, and such results need not indicate adverse effects from plastic ingestion. Intergenerational transfer resulted in annual cycling of plastic loads in successfully breeding birds. In species that do not regurgitate indigestible stomach contents, immature birds have the largest plastic loads and are most likely to exhibit adverse effects from plastic ingestion.

Key words: Plastic pollution; seabirds; southern Africa.

METHODS

The incidence of plastic in 60 seabird species was determined from regurgitations (Ryan 1988). Most sampling took place at sea off the southwestern cape, South Africa, and at Inaccessible Island (37°50'S, 12°30'W), Gough Island (40°21'S, 9°53'W), and the Prince Edward Islands (46°45'S, 37°50'W).

All plastic particles found in seabirds were oven-dried at 30°C and weighed to the nearest 0.1 mg. No attempt was made to score the degree of wear of individual particles (cf. Day 1980), because the original shape and state of wear of particles at the time of ingestion could not be inferred with accuracy. Industrial pellets (virgin plastic particles) from seabird stomachs seldom showed surface crazing typical of pellets at sea (Gregory 1978); pellet wear in seabird stomachs eventually results in smooth pellets, the original shapes of which are often obscure.
Nonparametric statistics (Chi-square, log-likelihood ratios, Spearman’s rank correlations, Fisher’s exact tests, and Mann-Whitney U-tests) were used to test the significance of all comparisons made (Zar 1984), except for differences between mean particle mass, which were tested using Student’s t-tests (normality of data first tested with F-tests; Zar 1984).

RESULTS AND DISCUSSION

LONG-TERM (INTERANNUAL) VARIATION

Plastic and related artificial products were first recorded in seabird stomachs in the early 1960s (Bennett 1960, Rothstein 1973, Harper and Fowler 1987), following the rapid growth of the plastics industry in the 1950s (Colton 1974). Since then the incidence of plastic in seabirds has increased to its present ubiquitous level (Day et al. 1985, Ryan 1988). Day (1980) and Day et al. (1985) showed a general increase in the incidence of plastic in Short-tailed Shearwaters (Puffinus tenuirostris) up until the study ended in 1977. Similar increases in plastic loads have been documented for three species of prion (Pachyptila) between 1960 and 1977 (Harper and Fowler 1987).

This trend has continued into the 1980s in at least one seabird species off southern Africa. A comparison of the incidence of plastic in Antarctic Prions (P. desolata) collected during 1979 to 1980 with those collected during 1983 to 1985 showed an increase in the frequency of occurrence of plastic (four of 12 and 42 of 60, respectively, \( G = 5.64, df = 1, P < 0.05 \)) and in the number and total mass of plastic particles per bird \( (U_{12,60} = 475.5, 472.5 \) respectively; 1-tailed \( P < 0.05 \)).

Local decreases in plastic pollution and ingestion by some marine organisms have occurred as a result of improved handling and processing systems in specific plastics industries (Kartar et al. 1973, 1976). However, seabirds ingest plastic from widespread and diverse origins (Ryan 1986), decreasing the effectiveness of local reductions in plastic losses into the ocean. International legislation may reduce the amount of plastic at sea (Horsman 1982, Dixon and Dixon 1983, van Franeker 1985), but there are problems associated with implementation and enforcement of dumping restrictions (Carvell 1985). Also, growth of plastic industries in developing countries is likely to maintain the increase in the amount of plastic pollution at sea for some time, and the levels in birds presumably also will continue to rise.

GEOGRAPHIC VARIATION

Day (1980) and Day et al. (1985) demonstrated differences between plastic loads in seabirds collected from different regions, attributing them to varying densities of plastic pollution at sea. Similar geographic differences in plastic loads have been recorded by Furness (1985b) and van Franeker (1985). Any demonstration of geographic variation in plastic loads should, however, be based on comparisons of plastic loads in similarly-aged birds at the same time of year, because other sources of variation may mask or create spurious geographic patterns (see below).

In the African sector of the Southern Ocean, northerly seabird populations tend to eat more plastic than do southerly populations. The incidence of plastic in Wandering Albatross chick regurgitations is higher at the more northerly Gough Island (six of 100) than at the Prince Edward Islands (two of 354, \( G = 1.60, df = 1, P < 0.001 \)). Also, Broad-billed Prions (P. vittata) breeding at Inaccessible Island, north of the Sub-tropical Convergence, apparently contain higher plastic loads than those at Gough Island, which lies farther south (Ryan and Fraser 1988). These results probably reflect the higher densities of plastic at sea in the northern part of the Southern Ocean (e.g., Gregory et al. 1984).

On a much smaller scale, local differences in foraging area also influence the incidence of ingested plastic in seabirds. Kelp Gulls (Larus dominicanus) feeding at garbage dumps in South Africa have a higher frequency of occurrence of plastic (seven of 33) than those feeding elsewhere (one of 29, \( G = 4.88, df = 1; P < 0.05 \)). Such differences are less likely to be observed in species that do not regularly regurgitate indigestible stomach contents.

SEX-RELATED VARIATION

No sex-related variation in plastic incidence in seabirds has been recorded (Day 1980, Day et al. 1985). Such a sexual difference is unlikely in birds lacking marked sexual dimorphism, Giant-petrels have the greatest sexual dimorphism of any seabird species (Hunter 1983), and a greater incidence of plastic might be expected in the smaller, more marine-foraging females (Hunter 1983). No such trend was observed, although
sample sizes were small (Southern Giant-Petrel [M. giganteus]: six of 70 males and three of 53 females; $P > 0.5$; Northern Giant-Petrel [M. halli]: zero of 25 males and two of 16 females; $P > 0.1$; G-tests).

AGE-RELATED VARIATION

Day (1980) and Day et al. (1985) reported larger plastic loads in immature than in adult Parakeet Auklets (Cyclorhynchus psittacula) and Tufted Puffins (Fratercula cirrhata). These differences were attributed to hypothesized broader foraging niches and perhaps greater dietary experimentation by young, inexperienced birds (e.g., Porter and Sealy 1982). This apparently is the case in Kelp Gulls foraging at garbage dumps in southern Africa: the frequency of occurrence of ingested plastic in immature birds (four of 12 birds, identified by at least some brown, immature plumage) was significantly greater than that in adults (one of 18 birds; $G = 4.03$, df = 1, $P < 0.05$). Kelp Gulls regularly regurgitate indigestible stomach contents as pellets (Ryan 1988), so there is no plastic accumulation, and particles found in the stomach have been ingested recently. However, most Procellariiformes (and most auks; Harris 1984; R. H. Day, in litt.) seldom regurgitate pellets, allowing plastic particles to accumulate in the stomach (Furness 1985a, 1985b; Ryan, in press). This fact, coupled with the intergenerational transfer of plastic from parents to chicks, allows an alternative interpretation of age-related variation in the incidence of plastic in many seabird species.

Plastic particles frequently are found in the stomachs of seabird chicks (Kenyon and Kridler 1969, Rothstein 1973, Pettit et al. 1981) and occasionally in meals fed to chicks (Day 1980, pers. observ.). With the exception of Laysan Albatross (Diomedea immutabilis) chicks, which sometimes eat plastic objects lying around their nests (Fry et al. 1987), all the plastic in seabird chicks derives from meals from their parents. I suggest that the larger plastic loads found in immatures than in adults can be partially explained by this intergenerational transfer of plastic particles, at least in those species that regurgitate food to their chicks. For example, all 15 Blue Petrel (Halobaena caerulea) chicks collected at the Prince Edward Islands contained plastic particles, and both the number and total mass of particles were significantly larger in chicks than in adults (Table 1; $U_{15,53} = 605.5$, 537, respectively; $P < 0.001$, 0.02, respectively). Plastic also was more frequent in White-chinned Petrel (Procellaria aequinoctialis) and Kerguelen Petrel (Pterodroma brevirostris) fledglings (seven of seven and eight of 26, respectively) than in adults (108 of 193 and two of 23, respectively, excluding beached birds; $G = 7.93$, 3.90, respectively; df = 1; $P < 0.05$, 0.01, respectively).

Plastic in seabird chicks comes from their parents; this allows insight into plastic flux through seabird populations. If particles fed to chicks derive solely from particles ingested on foraging trips during chick rearing, the rate of accumulation in chicks gives a minimal estimate of the natural ingestion rate. Coupled with the known incidence of ingested plastic, these data would allow calculation of the rate of wear of plastic particles in seabird stomachs. Alternatively, if particles fed to chicks derive both from particles stored in the parents' gizzards and from those ingested during the chick-rearing period, loss to chicks would form an additional mechanism for the removal of accumulated plastic particles in species that regurgitate indigestible stomach contents only when feeding chicks.

Evidence from Blue Petrels suggests that the latter explanation is correct; plastic particles in chicks were significantly smaller than were those in adults (Fig. 1; $\chi^2 = 42.35$, df = 5; $P < 0.001$). This result is consistent with the hypothesis that chicks are fed particles that have been stored in the parents' gizzards for some time, and thus are smaller as a result of wear within the parents' stomachs. In addition, if plastic loads fed to chicks represented only that plastic ingested by adults during the chick-rearing period, adult Blue Petrels would have to ingest a plastic particle approximately once every 2 days, giving a particle turnover time through wear (during the non-breeding season) also measured in days. Albatrosses are known to retain indigestible objects in the stomach for up to 6 weeks (Pettit et al. 1981, Furness et al. 1984), and plastic particles fed to White-chinned Petrels were little changed after 12 days in their stomachs (Ryan and Jackson 1987).

However, intergenerational transfer of plastic particles cannot explain the larger plastic loads reported for immature Tufted Puffins and Parakeet Auklets (Day 1980, Day et al. 1985), because puffins feed their chicks whole prey carried in the bill and do not regurgitate stored food, and Parakeet Auklets feed chicks food stored in blind,
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successfully indicated an adverse effect of plastic ingestion. In general, however, inference that plastic ingestion causes reduced breeding success from observations of larger plastic loads in non-breeding birds must be interpreted with caution.

SUBLINGUAL POUCHES (Bédard 1969), with little if any transfer of stored plastic (R. H. Day, in litt.). The age-related difference in plastic loads of these species probably is related to feeding-niche differences between age groups, as suggested by Day (1980) and Day et al. (1985).

A consequence of the transfer of accumulated plastic particles from parents to chicks is that it should produce smaller plastic loads in successfully breeding birds than in nonbreeders or failed breeders (i.e., pairs that failed before egg hatching). Among Broad-billed Prions collected at Gough Island during the chick-rearing period (October/November), birds with well-developed brood patches contained plastic significantly less frequently (six of 38) than did those lacking a well-developed brood patch (five of 10; \(G = 4.66, df = 1; P < 0.05\)).

Day (1980) and Day et al. (1985) demonstrated larger plastic loads in nonbreeding than in breeding Parakeet Auklets, a species which has little if any transfer of plastic between generations (R. H. Day, in litt.). It was suggested that the failure of auklets with large plastic loads to reproduce

successfully indicated an adverse effect of plastic ingestion. In general, however, inference that plastic ingestion causes reduced breeding success from observations of larger plastic loads in non-breeding birds must be interpreted with caution.

SHORT-TERM (INTRA-ANNUAL) VARIATION

The intergenerational transfer of plastic particles from parents to chicks has a major impact on short-term variation in plastic loads in some seabird species. Breeding adults of species that accumulate plastic particles and feed their chicks by regurgitating stored food will exhibit an annual cycle in the incidence of plastic, with plastic loads at their lowest levels immediately after the breeding season, gradually increasing throughout the nonbreeding season, and peaking before hatching in the following breeding season. Losses of accumulated particles to chicks reduce adult plastic loads to the postbreeding minimum. This provides an alternative explanation to that of Day (1980) and Day et al. (1985), which was attributed to changes in the ingestion rate of plastic particles.

Short-tailed Shearwaters exhibited a gradual increase in the number of ingested plastic particles off Alaska during the austral winter, with levels much greater than those found in breeding birds in Australia during the austral summer (Day 1980, Day et al. 1985). This pattern is consistent with the annual cycle hypothesis outlined above. The smaller average plastic loads in breeding birds is reinforced by the scarcity of nonbreeding individuals around breeding grounds, because many remain in the North Pacific Ocean (Harrison 1983). Skira (1986) demonstrated a gradual decrease in plastic incidence in breeding Short-tailed Shearwaters throughout the breeding season, although she did not identify chick feeding as the major mechanism for losing plastic.

The only trend in plastic incidence in Short-tailed Shearwaters recorded by Day (1980) and Day et al. (1985) not predicted by the annual cycle hypothesis is the decrease in plastic loads in September, just before the breeding season. This observation was based on a small sample of birds (12), however, and none of the monthly changes in the number of particles/bird departs significantly from the overall frequency for birds collected off Alaska (\(G = 5.69, 1.31, 3.51, 4.11,\) and \(4.56,\) respectively; \(df = 3; P > 0.1;\) for May, June, July, August, and September, respectively).
TABLE 1. Seasonal changes in plastic and pumice loads in Blue Petrels collected at the Prince Edward Islands and off the southwestern cape, South Africa, with those in chicks for comparison. Postbreeding birds were sampled during April, prebreeding birds during August and September, and chicks during December and January.

<table>
<thead>
<tr>
<th>Period</th>
<th>Plastic:</th>
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<th>Pumice:</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Frequency of occurrence</td>
<td>Mean no. particles per bird</td>
<td>Mean mass per bird (mg)</td>
<td>Frequency of occurrence</td>
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<tr>
<td></td>
<td>Proportion %</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Postbreeding</td>
<td>11/15  73</td>
<td>4.87</td>
<td>65.1</td>
<td>8/15  53</td>
</tr>
<tr>
<td>Prebreeding</td>
<td>37/38  97</td>
<td>9.16</td>
<td>115.9</td>
<td>14/15  93</td>
</tr>
<tr>
<td>Chicks</td>
<td>15/15  100</td>
<td>16.07</td>
<td>146.0</td>
<td>15/15  100</td>
</tr>
</tbody>
</table>

Day (1980) and Day et al. (1985) supported the explanation of seasonal variation in plastic loads based on seasonal changes in plastic ingestion rate with data on the wear state of particles in Short-tailed Shearwaters. I have reservations about the accuracy of wear data (see Methods), especially because particles at sea exhibit a range of wear states (Ryan 1986). In fact, none of the monthly wear frequencies reported by Day (1980) and Day et al. (1985) departs significantly from the summed data for birds collected off Alaska ($G = 3.19, 4.72, 0.77, 2.04, and 2.52$, respectively; $df = 3; P > 0.1$; for May, June, July, August, and September, respectively).

The seasonal variations in plastic loads in seabirds collected off southern Africa also support the annual cycle hypothesis. Plastic loads in Blue Petrels collected in April (postbreeding) were significantly smaller than were those in birds collected during August to September, just prior to the breeding season (Table 1; $U_{15.38} = 389, 367.5; P < 0.05, 0.1$; for number and mass of plastic particles, respectively). There also was significantly more pumice in adult Blue Petrels collected prior to the breeding season than in birds collected after the breeding season (Table 1; $U_{15.13} = 321.5, 322; P < 0.001$; for number and mass of pumice, respectively).

Similarly, the frequency of occurrence of plastic in White-chinned Petrels and Sooty Shearwaters (Puffinus griseus) was greater during the prebreeding period than during the postbreeding period (Table 2), although the difference was significant only for Sooty Shearwaters ($P = 0.03$, Fisher's exact test). The greatest frequencies of occurrence of plastic in these two species off the southwestern coast of South Africa occurred during the breeding season (Table 2), when only non-breeding birds were present. The annually cyclical fluctuations presumably are damped in these data sets because of the inclusion of immature birds, which cannot readily be distinguished from adult birds during the nonbreeding season.

FLUX OF PLASTIC THROUGH SEABIRD POPULATIONS

The annual cycle hypothesis assumes that the intergenerational transfer of plastic is the most important pathway for plastic flux in those species of seabird that feed their chicks regurgitated meals. The ingestion-regulated model of Day (1980) and Day et al. (1985), in which variable ingestion rates, balanced by fairly constant erosion, determine plastic loads, can be replaced for these species by a new model in which a more constant ingestion rate is countered by fairly constant erosion plus a regular dumping of accumulated particles into chicks by successful breeding birds (and birds that at least reach the chick-rearing stage). I do not doubt that temporal variations in ingestion rate occur, but feel that these are negligible compared to transfer to chicks, given that the lifespan of plastic particles subject to erosion within seabird stomachs is of the order of years (Ryan and Jackson 1987). However, individual differences in diet and/or foraging area could account for much intraspecific variability in plastic loads.

The addition of another variable to the model does not improve understanding of the magnitude of the pathways involved. Assuming that all accumulated plastic is passed onto chicks during chick rearing (as suggested by data in Skira 1986) and that ingestion and erosion rates are constant, the amount of plastic in fledglings rep-
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FIGURE 2. A conceptual model of plastic pathways through seabirds. The magnitudes of these pathways in each species determine the rate of plastic accumulation.

represents the difference between ingestion and erosion in the parents since the last successful breeding season. The magnitudes of the rates of ingestion and erosion are unknown. Only when the rate of particle wear is determined experimentally from captive birds can this equation be resolved. The conservative estimate of a half life for polyethylene pellets of approximately a year (Ryan and Jackson 1987) suggests that the lifespan of plastic particles in seabird stomachs is considerably longer than Day’s estimate of 6 months (Day et al. 1985). However, as Day et al. (1985) observed, the rate of particle wear is likely to vary greatly in relation to the size, number and types of plastic particles, as well as to the amount and nature of other retained items (e.g., cephalopod beaks, pumice).

There is one further flow pathway for plastic particles through seabirds: egestion of plastic along with other indigestible stomach contents in pellets (Fig. 2). In species in which this occurs frequently, other pathways presumably are of little importance and plastic accumulation presumably is limited (Ryan 1988). Plastic egestion is tacitly omitted from the above model, because egestion of indigestible gizzard contents has not been recorded for procellariiform birds (excluding albatrosses and giant-petrels; Furness 1985a, 1985b, pers. observ.), the group with the highest levels of accumulated plastic pollution (Day et al. 1985, Ryan 1988). The fact that petrels apparently can regurgitate accumulated plastic particles along with chick meals suggests that infrequent egestion of pellets by these species may occur: the behavior of procellariiforms at sea is still largely unknown (Brown 1980). However, it is unlikely that egestion occurs in most procellariiforms. If egestion were an important pathway for the loss of indigestible stomach contents, there should be a positive relationship between the amount of plastic and other indigestible items in bird stomachs. Furness (1985a) found no correlation between the amount of plastic and other indigestible remains in the gizzards of several petrel species and I found no correlation between the amount of plastic and pumice in prebreeding Blue Petrels ($r = 0.23, 0.11; df = 13$; for number and mass, respectively). However, there was a significant correlation between plastic and pumice in postbreeding Blue Petrels, ($r = 0.55, 0.38; df = 13; P < 0.05, 0.1$; for number and mass, respectively), due to the influence of intergenerational transfer of indigestible stomach contents.

The annual cycle hypothesis alters our understanding of the flux of plastic through seabird populations. In species that do not regurgitate indigestible stomach contents and that are fed regurgitated plastic along with their meals as chicks, immature birds up to their first successful breeding attempt will have the highest plastic loads. Thus immatures are more likely to suffer adverse effects from ingested plastic than are breeding adults. Also, the annual cycle hypothesis does not require the rapid erosion of plastic particles within seabird stomachs required by the ingestion-regulated model (cf. Day 1980, Day et al. 1985), which concurs with the considerably longer estimates of the lifespan of plastic particles reported elsewhere (Ryan and Jackson 1987).

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LITERATURE CITED


