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ANNUAL VARIATION IN GREAT SKUA DIETS: THE IMPORTANCE OF COMMERCIAL FISHERIES AND PREDATION ON SEABIRDS REVEALED BY COMBINING DIETARY ANALYSES

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Abstract. This study combines conventional dietary assessment with stable isotope techniques to describe Great Skua (*Stercorarius skua*) diet. Stable carbon and nitrogen isotope ratios in feathers of Great Skua chicks collected over three years were analyzed in conjunction with pellet and regurgitate collections. A significant drop in trophic status was detected in 1997, which likely resulted from an increase in herring and mackerel in the diet. These items were almost certainly obtained from a commercial trawler, as evidenced by a significant drop in territorial attendance during the ship's absence. Feathers yielded significantly different $\delta^{13}C$ values among years, and part of this may have been related to a period of enhanced phytoplankton growth during 1996. A combined approach, such as the one described here, is likely to become increasingly useful in elucidating the diets of polyphagous birds.

Key words: dietary analyses, fisheries, pellets, regurgitates, seabirds, stable isotopes.

Variación Anual en la Dieta de *Stercorarius skua*: La Importancia de Pesqueros Comerciales y Predación de Aves Marinas Revelada por la Combinación de Análisis de Dieta

Resumen. Este estudio combina evaluaciones de dieta convencionales con técnicas de isótopos estables para describir la dieta de *Stercorarius skua.* Analizamos la proporción de isótopos estables de carbono y nitrógeno en las plumas de pichones de *S. skua* colectadas durante más de tres años, en conjunto con colecciones de pellets y regurjitados. Un descenso significativo en la posición trófica fue detectado en 1997 probablemente como consecuencia del incremento de arenque y caballa en la dieta. Estos ítems fueron casi con seguridad obtenidos de un pesquero de arrastre comercial, como lo sugiere la caída significativa de la presencia en el territorio durante la ausencia del barco. Las plumas generaron valores significativamente diferentes de $\delta^{13}C$ entre años, parte de lo cual puede haber estado relacionado con un período de gran crecimiento del fitoplancton durante 1996. Un enfoque combinado como el descripto aquí será probablemente cada vez más útil para elucidar la dieta de aves polífagas.

INTRODUCTION

More than half of the entire breeding population of Great Skuas (*Stercorarius skua*) nests in Scotland, and the number of breeding pairs there has more than doubled to around 7900 since the early 1970s (Lloyd et al. 1991). One reason for this increase seems to be changes in fishing practices (Furness 1987), with discards from commercial fishing activities forming an important part of the diet (Furness and Hislop 1981, Hamer et al. 1991). However, seabirds, pelagic fish such as sandeels (*Ammodytes* spp.) and herring (*Clupea harengus*), and goose barnacles (*Lepas* spp.) are also commonly taken (Furness and Hislop 1981, Phillips et al. 1997). During the decline in sandeel availability in the 1980s, the numbers of seabirds eaten by Great Skuas in Shetland increased markedly (Hamer et al. 1991). Concern

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has grown over the possible impact that predation by Great Skuas may be having on other seabird populations (Furness 1997, Heubeck et al. 1997, Phillips, Thomson, and Hamer 1999). Likely future reductions in European fishing effort, with its associated decline in discard availability (Furness 1997), and continued growth in Great Skua numbers at some sites (Phillips, Bearhop et al. 1999), may lead to increased predation by skuas on other seabirds.

Until recently, analyses of Great Skua diets have relied almost exclusively on conventional techniques such as direct observation and collection of pellets (regurgitated indigestible remains of prey), regurgitates (regurgitated whole prey items), or stomach contents (Furness and Hislop 1981, Furness 1997). However, there are acknowledged drawbacks to these approaches (Duffy and Jackson 1986). Analyses of pellets tend to overestimate the importance of prey with hard body parts in comparison with soft-bodied prey items, and certain prey types are more likely to appear in regurgitates than others (Duffy and Jackson 1986, Hobson et al. 1994). Furthermore, sampling must take place over an extended period; otherwise short-term fluctuations in diet may obscure longer-term patterns.

Analyses of stable carbon and nitrogen isotope ratios in consumer tissues do not suffer from these biases and are a powerful dietary assessment technique, particularly when used in conjunction with conventional methods (Hobson et al. 1994, Schmutz and Hobson 1998). This approach is now well established (Michener and Schell 1994). It has been widely demonstrated that the ratio of stable nitrogen isotopes in consumer proteins (^{15}N:^{14}N, expressed as $\delta^{15}N$) yields information on trophic position, exhibiting a stepwise enrichment of between 3‰ and 5‰ at each trophic level (e.g., DeNiro and Epstein 1981, Hobson and Welch 1992, Bearhop et al. 1999). The ratio of stable carbon isotopes (^{13}C:^{12}C, $\delta^{13}C$) can be used to assess the relative importance of different carbon pools to a consumer, such as marine versus freshwater, or inshore versus pelagic feeding habits (Chisholm et al. 1982, Hobson et al. 1994, Bearhop et al. 1999).

A further advantage of stable isotope analyses is that, depending on the turnover rate of the tissue chosen, dietary information spanning different temporal scales can be obtained (Hobson and Clark 1992). For example, it has been demonstrated that isotopic signatures in feathers provide information on diet at the time of feather growth (Hobson and Clark 1992). Thus, the feathers of chicks can provide dietary information integrated over the period during which the feathers were growing. Although chicks do not produce pellets, their diet is broadly similar to adults (S. Votier, unpubl. data). Therefore the pellets produced by adults and the isotope signatures of chick feathers should reflect similar dietary intake.

Several studies using pellet analyses of Great Skua diet have shown marked annual changes in the relative consumption of different prey types (Hamer et al. 1991, Phillips et al. 1997). These dietary shifts generally resulted from changes in prey abundance and commercial fishery activities. However, given the biases associated with conventional techniques, it is possible that under certain conditions only large scale changes in diet would be distinguished using these methods and more subtle changes would be left undetected. This is particularly likely for soft-bodied prey items or fish with small or delicate otoliths such as mackerel (*Scomber scombrus*) and herring (Jobling and Breiby 1986). (Although pellets also contain some of the larger fish bones, otoliths are by far the easiest means of identifying species.)

We investigated the diet of breeding Great Skuas over a three-year period at the St. Kilda archipelago, UK. Given the nature of the fishery operating in the waters around the islands, we predicted that herring and mackerel should feature more heavily in the diet of skuas when trawlers were present. We also predicted that pellets would be less likely to detect such changes than regurgitates or stable isotope analyses. Pellet and regurgitate data can sometimes produce equivocal results in terms of the relative importance of particular types. By adding the dimension of stable isotope analyses we hoped to resolve some of the uncertainties. Using this integrated approach, we provide evidence for annual variation in diet composition. Our results have important implications for studies estimating the impact of Great Skuas on their prey, particularly in light of recent concerns that predation may have resulted in the local decline of some seabird populations (Furness 1997, Heubeck et al. 1997).

METHODS

SAMPLE COLLECTION AND PREPARATION

Body feathers (8–10 per individual) were clipped from 4–6-week-old Great Skua chicks at Hirta, St. Kilda archipelago (57°49′N, 08°05′W) in the summers of 1995, 1996, and 1997, and stored in sealed plastic bags.

Pellet collections were made at least once every 10 days from breeding territories in 1996 and 1997, following the methods described by Furness and Hislop (1981). Additionally, prey samples in the form of regurgitates were collected from adults (mostly from birds trapped at their nests during late incubation and early chick rearing) and chicks. Regurgitates from 1997 were stored frozen in sealed plastic bags in preparation for isotope analyses. In 1996 and 1997, pellet collections were made during most of the breeding season. In 1995 St. Kilda was visited for only two weeks during chick rearing. Pellets from that year include those collected during this period plus some *ad hoc* collections by the warden earlier in the season. No regurgitates were sampled in 1995. Pellets were assigned to one of five categories: bird (mostly Hydrobatidae, Alcidae, and Procellariidae), herring or mackerel, whitefish (all fish except mackerel and herring, mostly Gadidae), goose barnacle (*Lepas* spp.), and other (including squid, sheep, rabbit, and crustacea). Temporal distribution of the three most common types of pellet (bird, whitefish, and goose barnacle) in 1996 and 1997 was recorded on a weekly basis, starting three weeks prior to median hatching date.

ISOTOPIC ANALYSES

Isotopic analyses, including cleaning, drying, and powdering of feathers and regurgitate soft-tissue samples, followed the methods described by Bearhop et al. (2000). Lipids were extracted from the soft tissue of regurgitated prey items using a Soxhlet apparatus with refluxing solvent (1:1 mix of methanol and petroleum ether). Precision and accuracy was ≤0.2‰ for δ^{13}C measurements, and ≤0.4‰ for δ^{15}N.

ATTENDANCE

In most seabirds, time spent away from the colony can be taken as an index of foraging effort, and this has been shown to be the case for Great Skuas in Shetland, UK (Furness and Hislop 1981, Caldow and Furness 2000). On St. Kilda in 1997, we recorded and averaged the number of adults present at a minimum of 30 randomly selected territories every one to two days. Attendance data were only recorded between 09:00 and 13:00 (BST) to control for diurnal variation in foraging effort. These data were compared to those collected in 1996 (Phillips et al. 1997). During 1997, a large factory trawler operated in the waters close to St. Kilda and periodically processed fish within 2 km of the colony. Adult attendance data collected while the trawler was present were compared to attendance while the boat was absent. On most days visibility was good, with the mainland (75 km distant) regularly discernable. Trawler presence or absence was assessed visually and subsequently confirmed by the ship's operators (A. Sinclair, pers. comm.). It is unlikely that other trawlers could have been operating near the colony without being noticed and no trawlers were noted close to the colony during the 1995 and 1996 collections.

STATISTICAL ANALYSES

Differences among isotopic values of feathers and dietary samples were tested using Multivariate Analyses of Variance (MANOVA). In these models, δ^{15}N and δ^{13}C values of tissues were the dependent variables and year or dietary category were factors. In all cases, Scheffé tests were used to indicate groups that differed significantly. Chi-square tests and Fisher exact tests were used to check for among-year differences in diet assessed via conventional means. The effects of time of season and year on the proportion of bird pellets were investigated using a Generalized Linear Model (GLM) with binomial error distribution and logit link function, which was run with an adjustment for overdispersion (Crawley 1993, GLIM version 4.0). Since attendance is known to decline as the breeding season progresses, the effect of trawler presence was also tested using a GLM (in this case with a normal error distribution) with date (expressed in days after 30 May) as a covariate and trawler presence or absence as a factor. Unless stated otherwise, values presented are means ± SD. In all cases a significance level of $P < 0.05$ was used.

RESULTS

Isotope signatures of Great Skua chick body-feathers differed significantly among the three years (Fig. 1). Mean δ^{15}N values in 1997 (11.5 ± 0.5‰) were significantly lower than those

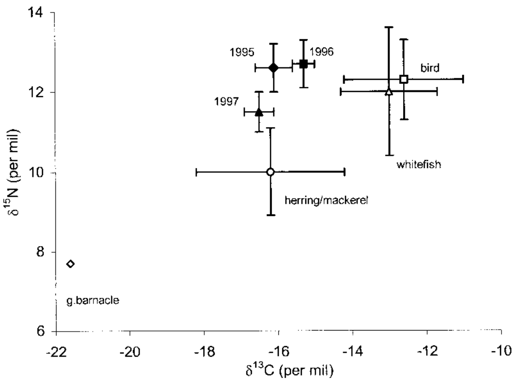

FIGURE 1. Mean ± SD stable carbon and nitrogen isotopic compositions of Great Skua chick feathers collected at St. Kilda in 1995, 1996, and 1997, and those of the main Great Skua dietary categories collected in 1997.

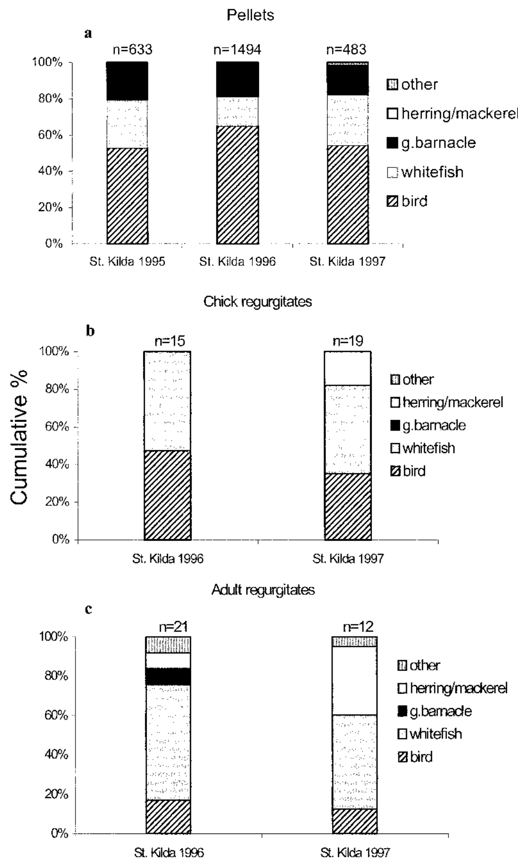

FIGURE 2. Percentage composition of the main prey categories in the diet of Great Skuas assessed via conventional techniques. Sample sizes appear above bars.

collected in 1995 (12.6 ± 0.6‰) and 1996 (12.7 ± 0.6‰; ANOVA: $F_{2,77} = 36.5$, $P < 0.001$). In these two earlier years, δ^{15}N values did not differ significantly. The mean δ^{13}C values of feathers from all years differed significantly from one another (1995 = −16.1 ± 0.5‰, 1996 = −15.3 ± 0.3‰, 1997 = −16.5 ± 0.4‰; $F_{2,77} = 67.1$, $P < 0.001$). Among the main dietary categories (goose barnacle not included because $n = 1$), there was also some significant isotopic segregation. The δ^{15}N values of herring/mackerel regurgitates ($n = 9$) differed from those of bird ($n = 5$) and whitefish ($n = 5$), the latter two not differing significantly ($F_{2,16} = 7.3$, $P = 0.005$). A similar pattern was detected for δ^{13}C ($F_{2,16} = 9.5$, $P = 0.002$).

In the case of pellets, herring/mackerel and "other" dietary categories were combined to reduce the number of expected counts that were below 5. Sampled diet differed from expected distributions of pellets ($\chi^2_6 = 63.7$, $P < 0.001$), with more bird and less whitefish than expected in 1996 (Fig. 2a). Pellet data from 1995 were similar to those from 1997 ($\chi^2_3 = 6.1$, $P = 0.19$). Small sample sizes meant it was not possible to test for differences in the representation of herring and mackerel in pellets among years.

There were no detectable annual differences in the composition of chick regurgitates ($\chi^2_2 = 4.3$, $P = 0.12$; Fig. 2b); however the number of expected counts less than five was high (two out of six). There was no significant difference in the occurrence of mackerel and herring in chick regurgitates between the two years (Fisher exact test, $P = 0.09$, whitefish and bird categories combined).

Most regurgitates produced by adults were of whitefish (Fig. 2c). As with chicks, there was no significant difference in the occurrence of mackerel and herring in adult regurgitates between the two years (Fisher exact test, $P = 0.21$, whitefish and bird categories combined). However, the trend in both adult and chick regurgitates was for increased proportions of mackerel and herring in 1997 compared to 1996 (Fig. 2b, c).

The percentage of pellets representing bird prey at St. Kilda in 1997 increased as the season progressed, while the occurrence of fish remained relatively constant and goose barnacle abundance declined over the same period (Fig. 3). A GLM indicated that the increase in the production of pellets composed of bird remains as the season progressed was significant and

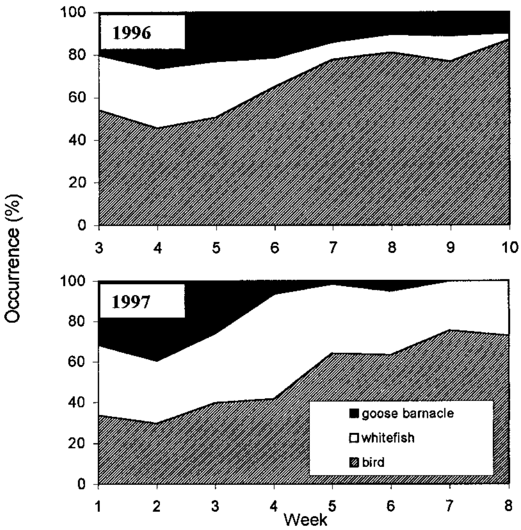

FIGURE 3. Temporal changes in the occurrence of the three main dietary categories in the pellets produced by Great Skuas at St. Kilda in 1996 and 1997. Week 1 begins three weeks prior to median date of hatching; pellet sampling was two weeks later in 1996 than 1997.

consistent across years (time of season effect, $F_{1,15} = 13.9$, $P < 0.01$, year effect, $F_{1,15} = 0.1$, $P > 0.05$; season × year interaction, $F_{1,15} = 0.02$, $P > 0.05$).

In 1997, attendance declined significantly as the season progressed (GLM $F_{1,32} = 7.5$, $P = 0.01$, adjusted $r^2 = 0.8$, slope = 0.01) but this was strongly influenced by the presence of the factory trawler. Attendance was significantly lower when the vessel was not operating in St. Kilda waters (1.8 ± 0.1 birds per 30 territories, trawler present; 1.4 ± 0.1 birds per 30 territories, trawler absent; GLM, $F_{1,32} = 68.6$, $P < 0.001$). Median attendance in 1996 (median = 1.85, 95% CI = 1.79–1.90 birds per 30 territories, $n = 29$ days) was not significantly different from 1997 (median = 1.75, 95% CI = 1.69–1.85 birds per 30 territories, $n = 36$ days; Mann-Whitney $U = 638$, $P > 0.05$).

DISCUSSION

The significant decrease in δ^{15}N signatures of chick feathers collected in 1997 (Fig. 1) suggests that there was an increase in occurrence of lower-trophic-status prey in the diets of these birds in that year. Other studies report fractionations of around 3–5‰ (e.g., DeNiro and Epstein 1981, Hobson and Welch 1992, Bearhop et al. 1999) for δ^{15}N between consumer tissues and their diets. In this study the differences between feather δ^{15}N signatures and those of the main dietary items as indicated by conventional analyses (birds and whitefish), are much smaller. This suggests that lower-trophic-status prey comprise a larger part of Great Skua diet than would be predicted from pellet collections alone.

Much of the evidence for the drop in trophic status points to an increase in the consumption of herring and mackerel in 1997. These fish species tend to consume prey of lower trophic status than do whitefish and seabirds (Moller-Buchner et al. 1984, Whitehead 1984, Furness 1997), and this is evidenced by the significantly lower δ^{15}N value of herring/mackerel (Fig. 1). Although not statistically significant, probably because of the small sample sizes, the increased occurrence of herring and mackerel in regurgitates collected in 1997 compared to 1996 supports the idea that the importance of this dietary category changed between the two years (Fig. 2b, c). In addition, the significant decline in Great Skua attendance during the absence of a large fish-processing trawler suggests that the birds were utilizing discards from this vessel either directly or via kleptoparasitism of other species such as Northern Gannets (*Morus bassanus*). During this absence the ship had returned to a port over 200 km from the colony, so the drop in attendance almost certainly reflects birds having to spend more time seeking alternative prey, rather than following the trawler as it moved further away. Large numbers of seabirds were observed feeding around this trawler, which was landing between 50 and 100 metric tons of fish per haul, the bulk of which were herring and mackerel (A. Sinclair, pers. comm.). The implications of long-term drops in territorial attendance in Great Skuas were first noted during the Shetland sandeel crisis. During this period, low sandeel availability correlated with longer foraging trips, low territorial attendance, and low breeding success (Hamer et al. 1991). More importantly, the age structure of the breeding population changed with 28% of adults failing to return to breed and large numbers of immature birds recruiting into the colony (Hamer et al. 1991). In the case of the St. Kilda skuas, attendance never dropped below 1 bird per 30 territories during the absence of the trawler. This suggests that although discards provided a convenient food source, alternatives were fairly easy to come by.

Despite the small sample size, it could be argued that an increase in goose barnacle consumption (Fig. 1), during 1997 could have produced the drop in $\delta^{15}N$ values in the feathers of Great Skua chicks. In fact, goose barnacle pellets are particularly conspicuous because of their hard calcareous plates and are unlikely to be under-represented in pellet collections. Since there was no significant change in the numbers of goose barnacle pellets across the three-year study period (Fig. 2a), it is unlikely that any significant change in their consumption occurred.

The annual differences among our pellet data are likely a product of variation in the timing of pellet collections and a seasonal increase in the importance of birds in the diet (Fig. 3). Compared with 1997, pellet collection in 1996 began when chicks on average were two weeks older and finished two weeks later than in 1997. It should be noted that isotope signatures of chick feathers represent the same period each year. A GLM indicated a significant seasonal increase in the amount of bird consumed, and there was no year effect once the seasonal trend had been accounted for. Seasonal changes in the proportion of bird in the diet of Great Skuas are probably in response to the fledging of auks and increases in the numbers of nonbreeding storm-petrels (*Oceanodroma leucorhoa* and *Hydrobates pelagicus*) and Manx Shearwaters (*Puffinus puffinus*) attending the colony.

Other biases in conventional assessment techniques lead to variation in the apparent importance of different prey in the diet. One is related to the time of day when samples are collected. Storm-petrels, which are the most common seabirds in Great Skua diet at St. Kilda (Phillips et al. 1997), and shearwaters tend not to be seen in the waters close to St. Kilda during daylight hours (Leaper et al. 1988). The difficulty of locating and capturing such mobile prey items makes it likely that the skuas catch petrels while they attend the colony during darkness or early dawn. This is supported by the presence of large numbers of Manx Shearwater carcasses on the slopes where many of the shearwaters nest (Manx Shearwaters are much larger than the two storm-petrel species and are therefore not swallowed whole). Pellets produced on territories after consumption of these petrels can be easily detected several days later. By comparison, any item consumed during the hours of darkness would have been in the digestive tract for a considerable period and would be less likely to be found in regurgitates, because regurgitates were not collected until at least 5 hr after dawn. This factor may therefore explain some of the disparity between pellets and regurgitates in their respective estimates of bird consumption.

There were significant differences among $\delta^{13}C$ signatures of chick feathers among the three years (Fig. 1). Some of this variation is likely to be a consequence of trophic enrichment, as $\delta^{13}C$ values increase by about 1‰ on average at each trophic level (Rau et al. 1983, Fry and Sherr 1984, Hobson and Welch 1992). The difference between 1995 and 1997 $\delta^{13}C$ values (0.4‰) is consistent with the difference of $\delta^{15}N$ measurements (1‰). However, in 1996 $\delta^{13}C$ signatures in chick feathers were 0.8‰ higher than in 1995 (Fig. 1) and there are several possible explanations for this. The change could be a result of increased intake of prey with high $\delta^{13}C$ values, but since there was no difference in $\delta^{15}N$ between these two years, this seems unlikely. It has been demonstrated that the carbon isotope signatures of inshore-foraging seabirds are enriched in ^{13}C when compared to those foraging offshore (Hobson et al. 1994). Conceivably, Great Skuas may simply have been foraging closer to the colony in 1996. If this were the case then lower adult attendance would be anticipated in other years and this was not recorded. A final possibility may be that there were changes in the carbon pool at the food web base in 1996. Isotopic enrichment may occur in phytoplankton and organic matter during periods of elevated primary productivity due to increased carbon demand (Deuser et al. 1968, Rau et al. 1992, Pancost et al. 1997). Continuous plankton recorder surveys for the waters to the north of St. Kilda indicate that primary productivity in 1996 was considerably higher than in 1995 or 1997 (Sir Alister Hardy Foundation for Ocean Science, unpubl. data) and this could have resulted in the elevated $\delta^{13}C$ signatures observed in chick feathers grown in 1996.

It follows from this that the drop in $\delta^{15}N$ signatures of feathers during 1997 might also be interpreted as a change in oceanographic conditions. For example upwelling nitrate from deep oxygen-depleted water can elevate $\delta^{15}N$ values of marine organisms (Michener and Schell 1994). A weakening of any upwelling in the waters around St. Kilda during 1997 could conceivably have produced the drop in $\delta^{15}N$ values.

However, if this phenomenon did explain the drop in $\delta^{15}N$ during 1997 we would not necessarily expect the corresponding fall in $\delta^{13}C$ because nitrogen and carbon isotope signatures are effectively uncoupled at the nutrient level. Moreover, all of the other evidence points to a real change in trophic status during this year rather than a change in the $\delta^{15}N$ signatures of nutrients.

It is clear from the results of this study that stable isotopes can add useful additional information to conventional dietary analyses. A combined approach to dietary assessment is likely to become increasingly important when assessing the diets of species where control or conservation is an issue. In particular, the integrated approach adopted here provided strong evidence that herring and mackerel were considerably more important in some years than would have otherwise been suggested. In general, the reliance of Great Skuas on these fish (which are rarely found in pellets) may be greater than currently realized. Great Skuas have been turning increasingly to feeding by killing seabirds as the quantities of discards provided by trawl fisheries in the northeast Atlantic have declined (Furness 1997). Discarding is a wasteful practice that the European Union Common Fisheries Policy and the FAO Code of Conduct for Responsible Fisheries seek to reduce to near zero. Over recent decades the quantities of trawl fishery discards has fallen, but largely as a result of reduced catches due to stock depletion and reducing fishing effort rather than to improved fisheries management. Discarding by pelagic fisheries is generally less than from demersal fisheries, but may also provide scavenging seabirds with feeding opportunities. With respect to potential future reductions in fishing effort and reductions in the availability of discard fish, the predicted impacts of Great Skuas on other seabird populations may have to be carefully assessed, with attention to indirect (forensic) methods to complement direct studies of skua diet composition.

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