Modelling the Proportion of Sardine and Anchovy in the Diet of Cape Gannets: Some Initial Investigations

C.L. Cunningham* and D.S. Butterworth*

Introduction

The breeding success, and consequently population size, of Cape Gannets has been hypothesised to be strongly dependent on the size of the sardine and anchovy resources in South Africa. The quantification of such relationships is a pre-requisite for attempts to tailor management approaches for these fish resources so as to take adequate account of the needs of predators for which these species provide forage. As a first step towards this end, this document presents the results from some analyses of the relationships between the contributions in percentage (by mass) of sardine and of anchovy in the diet of Cape Gannets to the abundances of these resources.

Data

The contributions of sardine and of anchovy to the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas Island colonies are available from 1978 to 2004 (Table 1). The estimates of spawner stock biomass (SSB) for sardine and anchovy have been taken from the most recent assessments for these resources (Table 2, from Cunningham and Butterworth 2004a,b). Assessment model estimates of abundance have been used for these analyses, rather than the survey estimates themselves, to filter out most (hopefully!) of the measurement errors associated with the survey results.

In addition to pursuing relationships with spawning biomass estimates provided by the assessment models, the use of observed recruitment from the May surveys was also investigated. This is because the colonies considered here are situated on the west coast of South Africa, so that the feeding behaviours of their Cape Gannet populations may be more closely related to the southward run of recruits over the autumn-winter period than to spawner biomass at the end of the year.

Furthermore, the proportion of observed SSB in the November survey west of Cape Agulhus was calculated from biomass per stratum data (updated in 2005). This proportion was applied to the estimates of SSB from the most recent assessments to obtain annual estimates of SSB west of Cape Agulhus. This alternative was investigated in the light of the recent sardine distribution shift to the east. Since the Cape

* MARAM (Marine Resource Assessment and Management Group), Department of Mathematics and Applied Mathematics, University of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa. Email: c.l.cunningham@telkomsa.net, dll@maths.uct.ac.za.

Gannet colonies considered are on the west coast, their feeding behaviour might be linked more closely to the abundance of sardine towards the west, rather than to the abundance of the whole population.

Model

Although one expects a monotonic relationship between the proportion of a species in a predator's diet and the abundance of that species, this relationship cannot be linear throughout as a proportion is bounded above by 1. Assuming further that the contribution of various species to the diet is directly proportional to their abundances, the relationship between proportion of prey in the diet and the abundance (*B*) of that prey would be of the form:

$$prop_{prey}(y)=\frac{B_{prey}(y-1)}{B_{prey}(y-1)+B_{other}(y-1)}$$

where, for example, $prop_{prey}(y)$ denotes the proportion of sardine in the diet of Cape Gannets in year y, $B_{prey}(y-1)$ denotes the SSB of the sardine in November of the previous year y-1 and $B_{other}(y-1)$ is the biomass of other prey species.

In the case of the Cape Gannet diet, a multivariate analysis is desirable as data on both the sardine and anchovy abundances and dietary proportions are available. Thus the model can be elaborated:

$$prop_{sardine}(y)=\frac{B_{sardine}(y-1)}{B_{sardine}(y-1)+B_{anchovy}(y-1)+B_{other}(y-1)}$$

Note that this accounts sensibly for non-linearities: for example, if both sardine and anchovy abundances doubled, the proportion of sardine in the diet would not be expected to be the same as if only the sardine abundance had doubled, as a uni-variate linear relationship would imply.

However, predators such as Cape Gannets typically have different preferences for different species, favouring some above others. Letting α reflect the relative preference the birds have for sardine over other prey and β the corresponding relative preference the birds have for anchovy, the model becomes:

$$prop_{anchovy}(y)=\frac{\beta B_a(y-1)}{\alpha B_s(y-1)+\beta B_a(y-1)+B_{other}(y-1)}$$

$$prop_{sardine}(y)=\frac{\alpha B_s(y-1)}{\alpha B_s(y-1)+\beta B_a(y-1)+B_{other}(y-1)}$$

If we further assume (apparently reasonably so given inspection of Table 1) that sardine and anchovy are the dominant prey species, so that the combined biomass of other species (which will not vary in synchrony) can be reasonably approximated by a constant, and divide numerator and denominator by β, these equations become:

$$prop_{anchovy}(y)=\frac{B_a(y-1)}{\lambda B_s(y-1)+B_a(y-1)+cst}$$

$$prop_{sardine}(y)=\frac{\lambda B_s(y-1)}{\lambda B_s(y-1)+B_a(y-1)+cst}. \qquad (1)$$

The Holling Type II functional response (Holling 1959) assumes that the rate of prey consumption by a predator increases as prey density increases, but eventually levels off at an asymptote at which the rate of consumption remains constant regardless of further increases in prey density. The equation above is similar to that for the Holling Type II functional response, except that the proportion of prey in the diet, rather than the amount of prey consumed by the predator, is modelled. Thus for ease of notation, equation (1) above is referred to as a "Holling Type II" form or model in this document.

A residual sum of squares minimisation was used to fit the model to the observed data for years $y = 1985, \ldots, 2004$.

Results

The "Holling Type II" model is able to fit the observed time series of percentage mass of anchovy in the diet of Cape Gannets reasonably well (Figure 1). However, there is a clear model mis-specification for sardine. The model continues to predict an increase in the percentage mass of sardine in the diet of Cape Gannets after the proportion observed actually declined in the late 1990s (Figure 2). This results in a systematic trend in the residuals (Figure 2). In terms of the trend in the percentage mass of sardine in relation to SSB, it is evident from inspection of Figure 2 that the model over-predicts the contribution for high SSB and under-predicts for low SSB.

A number of alternatives were pursued in an attempt to achieve a satisfactory fit to the sardine data:

i) "Holling Type III" form: birds tend to dismiss rare prey species, and increase their search activity for that species only when it increases in density. To reflect this it may be more appropriate to square the biomass terms in equation (1), similarly to the form of the Holling Type III functional response model (hence the name accorded here). This form was used first for both anchovy and sardine, and then only for the latter while preserving the "Holling Type II" form for the former.

ii) "Relation to recruitment": use of observed recruitment estimates rather than model estimates of spawning biomass.

iii) "Eastward shift of sardine SSB": use of only the proportion of the sardine SSB west of Cape Agulhas.

However, none of these alternatives was able to resolve the mis-specification problem for sardine noted above, and made at best only minimal improvements to the fits for the basic "Holling Type II" model.

A Simple Approach for Sardine

In an attempt to better understand the reasons for this model-data incompatibility for sardine, a simple model was investigated, excluding consideration of anchovy in case this was leading to some confounding. A linear model forced through the origin (as the contribution of sardine to the Cape Gannet diet would obviously be zero in the absence of sardine) was fit to the observed sardine data, using both the SSB in Table 2 (see Figure 3) and observed estimates of recruitment from the May survey (for which the results were similar to those for SSB and are therefore not shown here). The regression against SSB indicates that the model underestimates the percentage mass of sardine in the Cape Gannet diet at low abundances and overestimates at high abundances (as observed in recent years). It is clear from these results that there is no consistent simple relationship between the contribution of sardine to the Cape Gannet diet and sardine abundance for the full period for which such data are available.

Discussion

Functional relationships between the proportions of sardine and of anchovy in the diet of Cape Gannets to the abundances of these two populations have been explored. A "Holling Type II" form seems to model the relationship between the anchovy abundance and the contribution in mass percentage of anchovy in the diet of Cape Gannets quite adequately. However, no satisfactory (relatively simple) relationship between the proportion of sardine in the Cape Gannet diet and sardine abundance could be found during this initial investigation.

Had such a relationship (both reliable and precise) been found with Cape Gannet diet data, these data could now be used to improve assessment precision and/or as substitutes for survey inputs to an OMP in the event of mechanical problems necessitating abortion of a survey. Given this seeming lack of a simple relationship, however, the first priority would seem to be better understand why the proportion of sardine in the Cape Gannet diet (at the two colonies considered) decreased as the sardine abundance increased across the turn of the Century. This is because a plausible model for the relationship between sardine abundance and these diet data throughout the last two decades is a prerequisite for further confident development of any model linking bird dynamics and fish abundance, in particular if this is to be used in the formulation of management advice.

Acknowledgements

Rob Crawford and Leshia Upfold are thanked for providing the data for the annual composition of the Cape Gannet diet for these analyses. Janet Coetzee is thanked for providing the observed biomass per stratum data used to calculate the proportion of SSB west of Cape Agulhus.

References

Cunningham, C.L., and Butterworth, D.S. 2004a. Base Case Bayesian Assessment of the South African Anchovy Resource. Unpublished MCM document WG/PEL/APR04/01.

Cunningham, C.L., and Butterworth, D.S. 2004b. Base Case Bayesian Assessment of the South African Sardine Resource. Unpublished MCM document WG/PEL/APR04/02.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist. **91**:385-398.

Table 1. The contribution by mass percentage of sardine and anchovy in the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas Island (Crawford and Upfold pers. comm.)

	Bird Island Lamberts Bay		Malgas Island	
Year	% anchovy	% sardine	% anchovy	% sardine
1978	49.24	13.87	44.35	8.85
1979	63.02	5.90	46.48	4.22
1980	68.98	2.58	40.22	6.11
1981	82.44	2.54	21.92	9.46
1982	83.05	3.01	41.19	1.85
1983	57.84	10.01	29.80	0.98
1984	37.51	19.56	27.18	5.41
1985	26.47	27.15	15.84	15.14
1986	62.73	23.54	23.57	19.08
1987	36.57	48.80	29.99	39.56
1988	51.42	26.35	18.31	46.60
1989	23.15	59.35	9.12	47.65
1990	11.90	57.44	5.00	64.13
1991	43.28	31.86	18.58	40.52
1992	53.08	29.68	26.02	34.85
1993	37.31	45.59	7.58	53.50
1994	10.48	66.03	4.15	47.77
1995	26.85	64.00	9.02	47.70
1996	9.03	64.52	0.84	50.66
1997	22.47	57.74	3.21	53.62
1998	24.41	48.14	2.80	49.07
1999	33.39	41.39	7.14	54.68
2000	53.96	35.62	20.41	33.62
2001	52.07	18.46	26.74	33.59
2002	41.65	15.75	23.71	35.77
2003	27.28	48.57	15.80	34.75
2004	13.51	24.21	5.25	12.08

Table 2. Estimates of sardine and anchovy SSB in millions of tonnes (Cunningham and Butterworth 2004a,b).

Year	anchovy	sardine
1984	1155.9	105.7
1985	1003.0	137.3
1986	1742.0	185.8
1987	1451.4	227.8
1988	1113.3	293.7
1989	651.3	436.3
1990	590.7	513.5
1991	1566.4	621.5
1992	1379.7	687.9
1993	912.0	1047.3
1994	524.0	1269.7
1995	433.6	1210.4
1996	401.0	1238.8
1997	909.7	1206.0
1998	1025.4	1588.2
1999	1501.9	2829.9
2000	3227.3	3424.7
2001	4532.4	3444.8
2002	3565.4	4694.8
2003	2907.6	4672.7

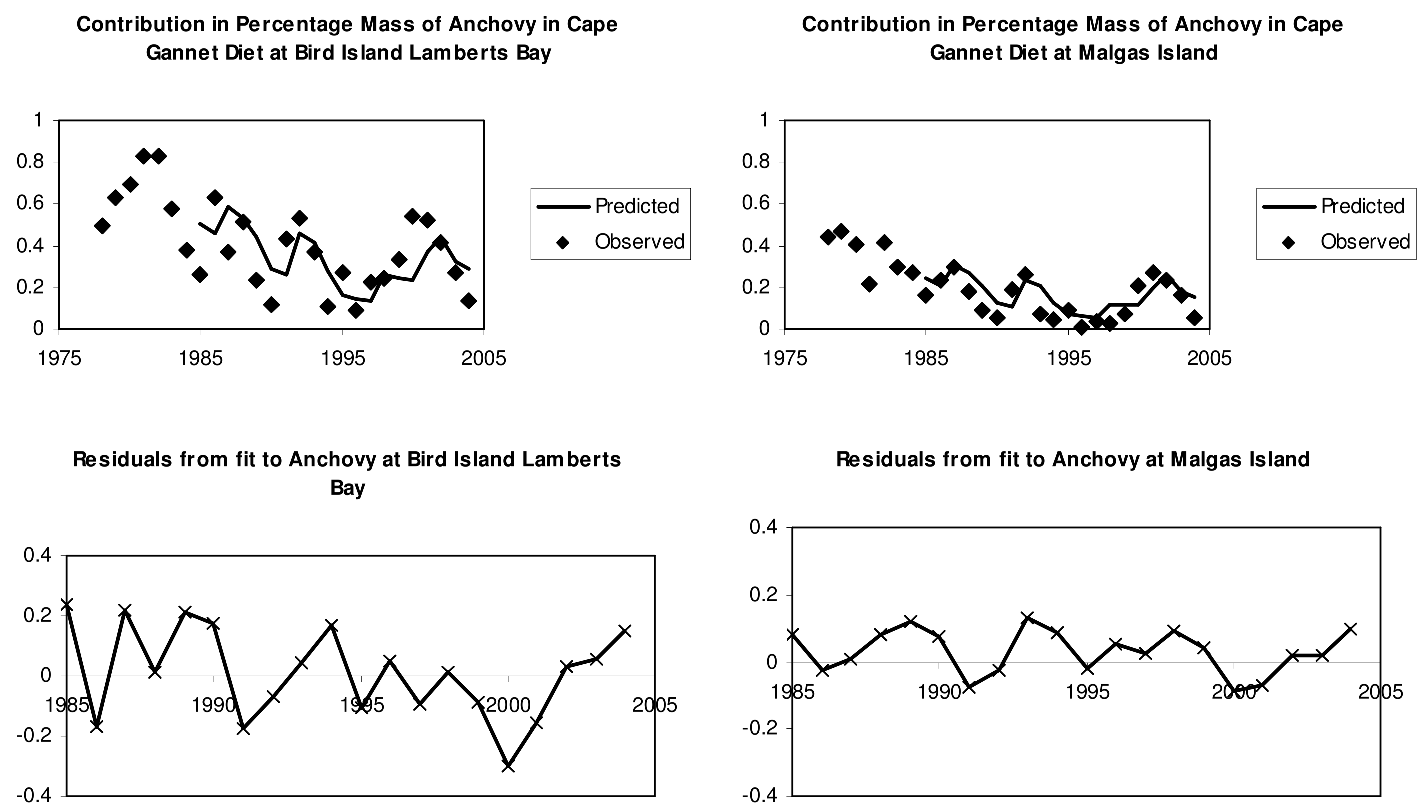

Figure 1. Observed and predicted contributions by mass percentage of ***anchovy*** *in the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas island, using the "Holling Type II" model and assessment model estimates of SSB. The residuals from the fit of the models to the data are shown in the lower panels.*

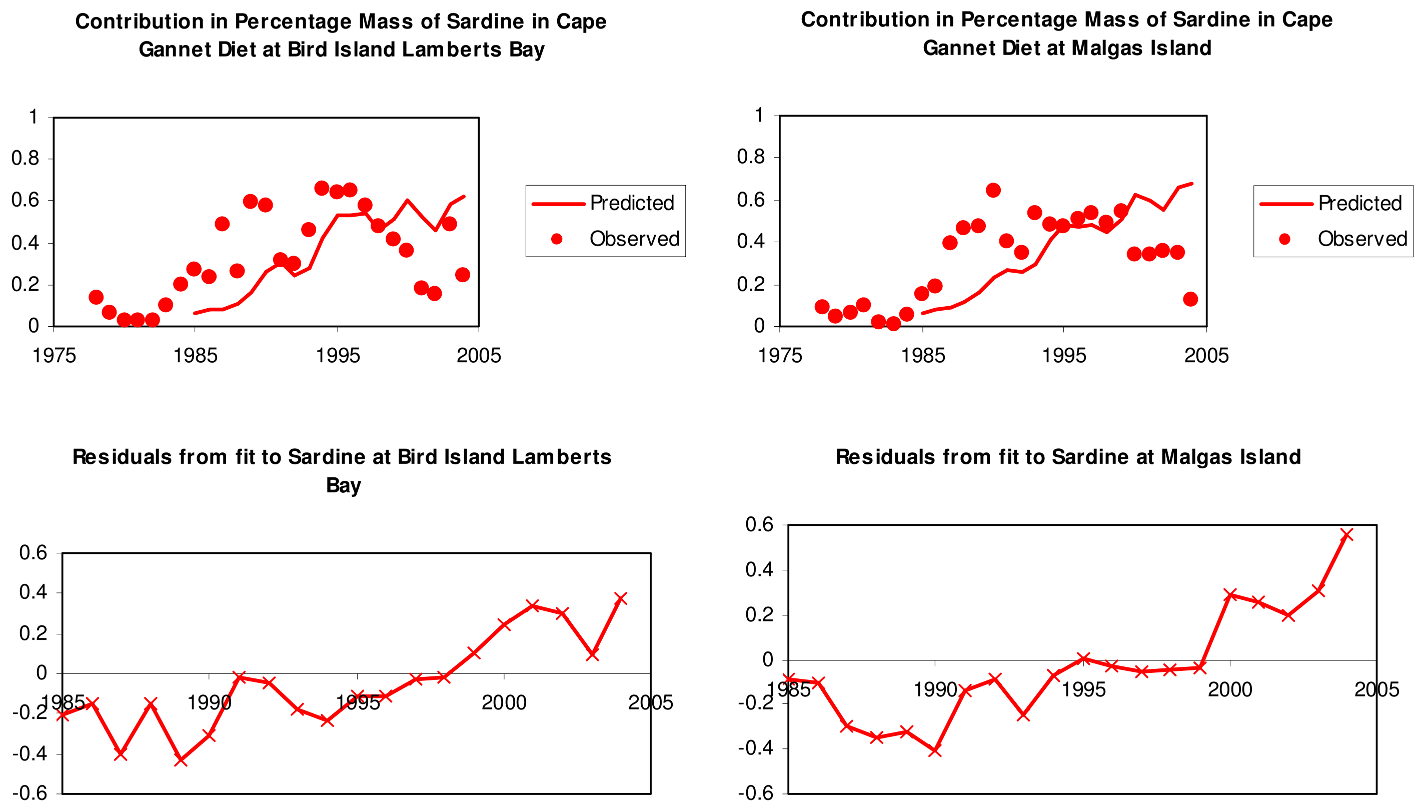

*Figure 2. Observed and predicted contributions by mass percentage of **sardine** in the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas island, using the "Holling Type II" model and assessment model estimates of SSB. The residuals from the fit of the models to the data are shown in the lower panels.*

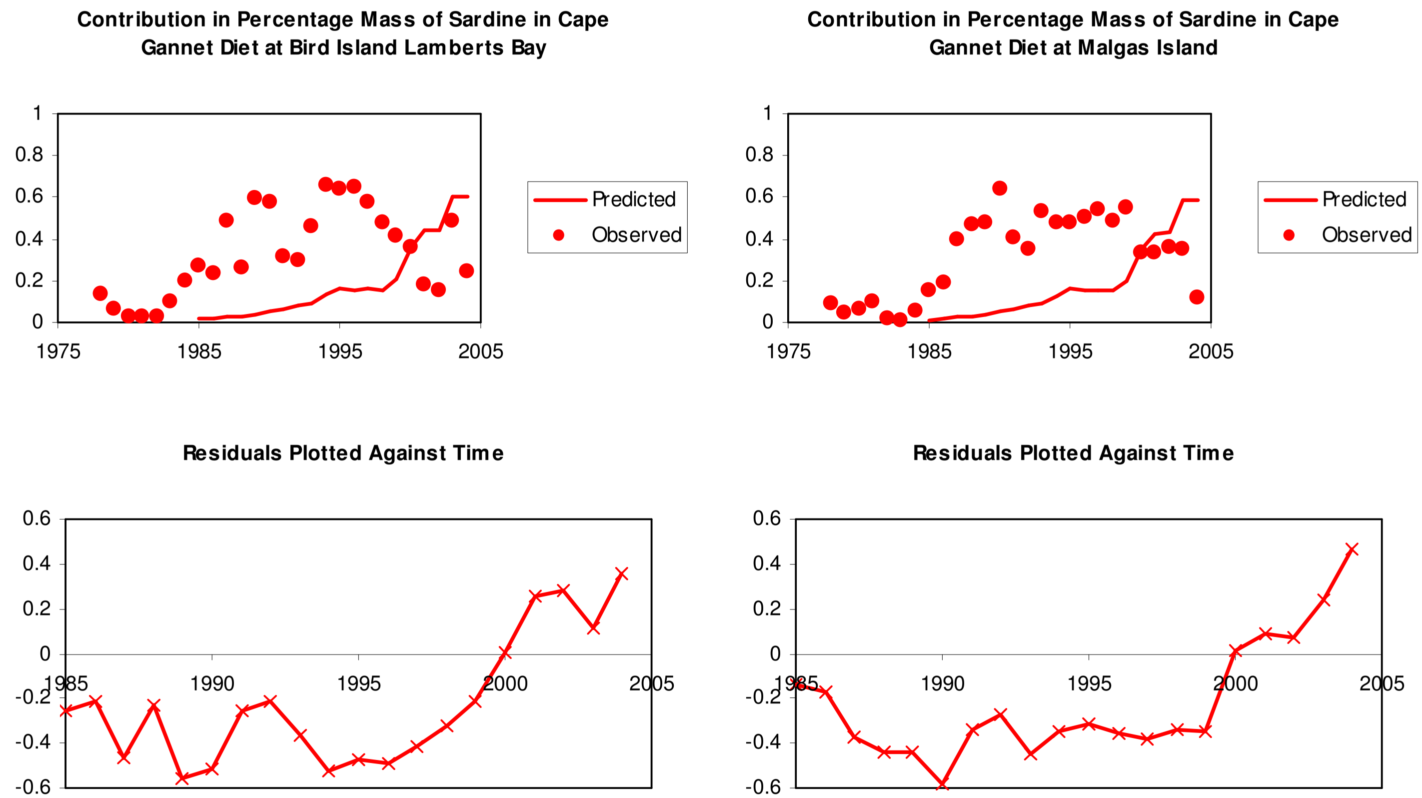

Figure 3a. Observed and predicted contributions by mass percentage of ***sardine*** *in the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas island against time, applying a linear regression through the origin against sardine SSB. The residuals from the fit of the models to the data are shown in the lower panel*

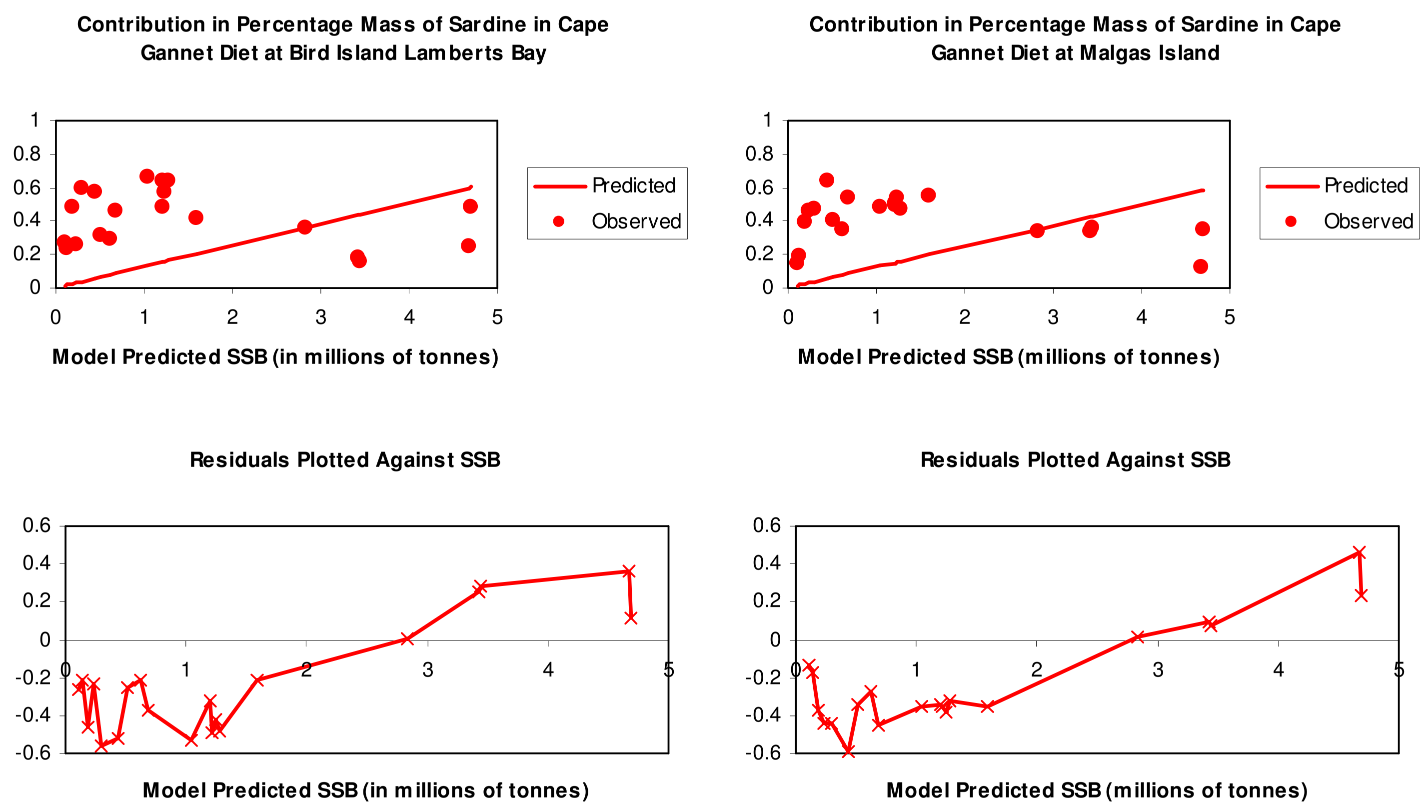

*Figure 3b. Observed and predicted contributions by mass percentage of **sardine** in the diet of Cape Gannets at the Bird Island Lamberts Bay and Malgas island against sardine SSB, applying a linear regression through the origin. The residuals from the fit of the models to the data are shown in the lower panels.*