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INFLUENCE OF SAMPLE SIZE AND SAMPLING FREQUENCY ON THE QUANTITATIVE DIETARY DESCRIPTIONS OF A PREDATORY FISH IN THE BENGUELA ECOSYSTEM

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Spatial and temporal variation in the diet and feeding intensity of snoek, *Thyrsites atun*, a top predator of the southern Benguela, was investigated to provide information on data requirements for accuracy of annual diets as inputs to ecosystem models. Appropriate sample sizes to produce accurate daily or event-scale diet descriptions were investigated by means of *a posteori* tests. Cumulative prey diversity curves showed that 55 (± 25) stomachs containing food are required to accurately quantify presence and absence data of prey species. Differences in the percentage contribution of dominant prey in consecutive and cumulative 10-stomach classes, indicates that a minimum of 75–80 (± 25) stomachs containing food are necessary to describe the proportion by weight of primary prey. Diets of snoek (proportions by weight) sampled inshore (shallower than 50 m and within 25 km of the coast) off the Cape Peninsula during six consecutive weeks (i.e. one day per week) in autumn 2001 were highly variable. Comparing diet for the six-week period with that of diets from consecutive 10-sample weekly units revealed 95% similarity at 70 samples per week. Seasonal diets between Cape Columbine and Cape Hangklip also varied, but there was no evidence of a predictable seasonal pattern in diet that could be related to prey life history; two-way nested ANOSIM revealed that seasonal prey proportions across years were statistically less similar than those within years. Snoek spawn offshore in winter/spring. Statistical differences between inshore (<50m) and offshore (>150m) prey composition were largely influenced by the absence of anchovy *Engraulis encrasicolus* and much larger proportions of Cape hake *Merluccius* spp. and lanternfish *Lampanyctodes hectoris* in the offshore diet. Feeding intensity (in terms of proportions of fish with prey and mean stomach fullness) was strongly seasonal and highest during the spawning season. Sampling programmes for the southern Benguela should account for spatial and temporal variation in diet and feeding intensity of predators if accurate annual dietary descriptions are to be achieved. The results of this study indicate that a minimum of 70 snoek stomachs (containing food) should be collected at each sampling event.

Key words: diet, feeding intensity, snoek, South Africa, temporal variation, *Thyrsites atun*

Increasingly, holistic ecosystem approaches are being developed for fisheries management purposes, incorporating multispecies models as potential tools for quantifying and predicting trends in the biota of whole ecosystems (Hollowed *et al*. 2000, Whipple *et al*. 2000, Shannon and Moloney 2004). Most models combine input data such as fishing, environmental forcing and ecological interactions (predator-prey, competition) to produce possible representative iterations of exchanges in the ecosystem. Trophic interactions within ecosystems play a large role in multispecies modelling, so diet and feeding data are of primary importance (Bogstad *et al.* 1995). Knowledge of predator diets can also be used to draw conclusions on prey distribution and biomass. Changes in predator diet can be related to concomitant changes in prey movements and abundance in an ecosystem and thus aid in the greater understanding of ecosystem functioning (e.g. Crawford *et al.* 1992).

The recent upsurge in ecosystem modelling has focused largely on the models themselves rather than on improving the biological data on which the models depend. Dietary data are often garnered from sources that are inaccurate or of limited use because of poor spatio-temporal coverage. Given the complexity of ecosystem models, inaccurate dietary descriptions for important predators are likely to bias outputs and lead to poor management decisions.

In this study, empirical data from snoek *Thyrsites atun*, an important pelagic predator in the Benguela ecosystem, is used to investigate the influence of sample size and sampling frequency on quantitative dietary descriptions for this species.

MATERIAL AND METHODS

Specimens used in this study were caught between Cape Columbine and Cape Hangklip by both handline

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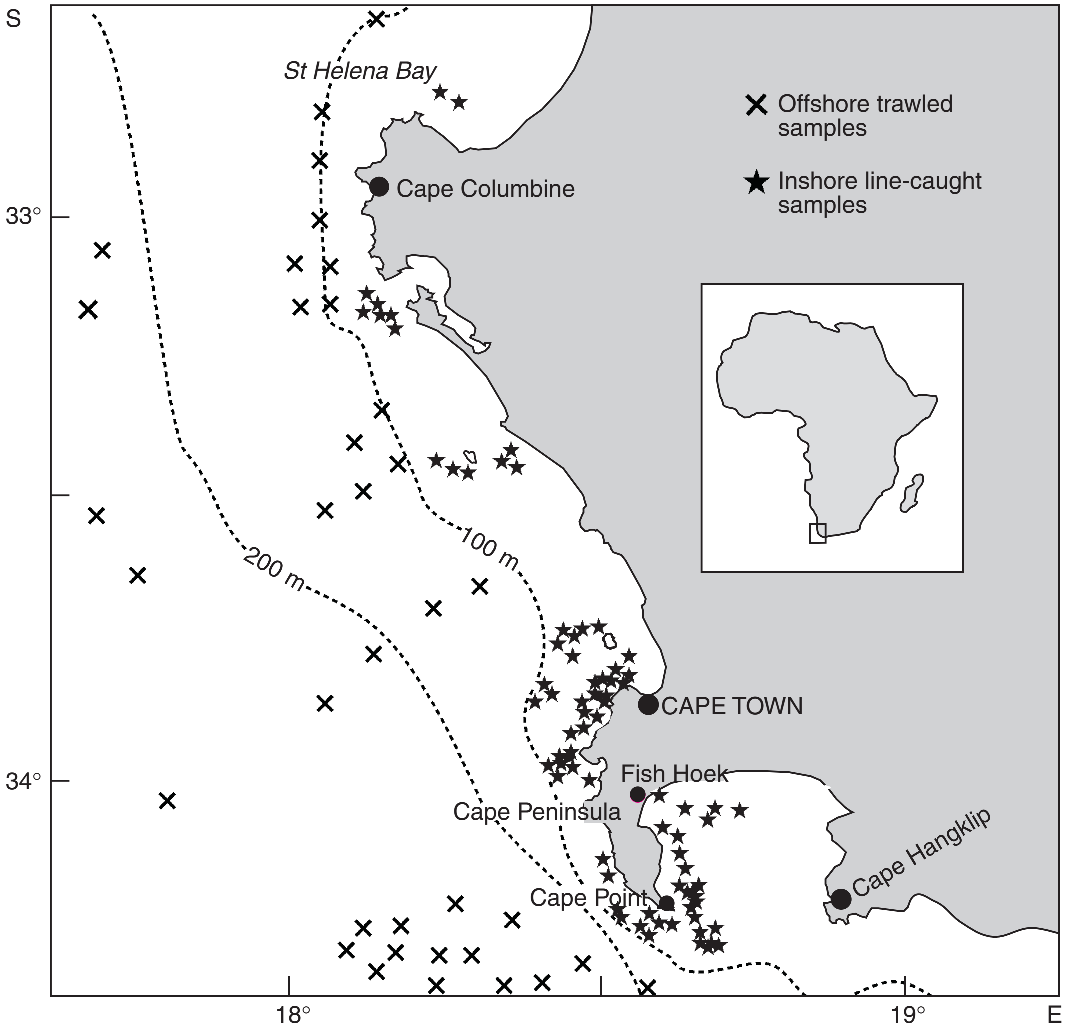


Fig. 1: Map of the west coast of South Africa showing sampling locations of offshore and inshore samples

and bottom trawl (Fig. 1). Handline catches were made during scientific and commercial fishing operations, at bottom depths of <50 m and within 5 nautical miles of the coast (hereafter referred to as inshore samples). Offshore samples were taken by bottom trawls, from both research and commercial vessels, at depths of between 150 and 450 m and distances >50 km from the coast.

Each fish was measured for fork length (*FL*, to the nearest mm) and total mass (to the nearest g). It was then cut open, the sex determined and the gonads and stomach contents removed and chilled on ice (maximum 12 h) or frozen for later processing ashore. Gonads were weighed to the nearest 1 g, and prey items identified to the lowest possible taxon and weighed (wet weight) to the nearest 0.1 g. Bait (in line-caught stomachs) and items consumed in the codend (from trawled fish) were easily recognized and omitted from the analysis.

Dietary contributions of each prey type were expressed as percentage by weight. This provides a measure of the prey's energy contribution (Macdonald and Green 1983), a preferred measurement in ecosystem modelling. Given that snoek diet changes ontogenetically (Griffiths 2002), and that juveniles were not sampled consistently, only fish >70 cm *FL* were used for the analysis. For all statistical comparisons of prey composition, prey items contributing <5% were combined to form a so-called "other" group, to reduce the likelihood of Type 1 errors (Cortés 1997).

Sample size

The objective here was to empirically determine the minimum number of stomachs required to provide a clear, precise description of the diet of snoek on a given day (sampling event). To this end, two simple *a posteori* tests – one based on prey diversity and the other on the proportion of the dominant prey item – were used to investigate the relationships between sample size and dietary accuracy for each of 20 samples (10 inshore and 10 offshore).

Inshore samples, each with between 60 and 110 stomachs containing food, were collected in 1996 (n = 2, July and September), 1998 (n = 2, August and September) and 2001 (n = 6, March/April). Offshore samples, each with between 60 and 115 stomachs containing food, were obtained during the winters of 1998 and 2000.

In the case of prey diversity curves, the total number of species appearing in the diet is plotted against the cumulative number of stomachs analysed. Generally, as the number of stomachs examined increases, so the rate of new or unique prey types appearing declines, until eventually an asymptote is reached (Ferry and Cailliet 1996). The median, range and mean at which asymptotes were attained for offshore and inshore snoek samples were calculated (samples in which an asymptote could not be confirmed were not included in these calculations).

Cumulative diversity curves are most suitable for presence/absence diet descriptions, i.e. measurements of diet diversity (Ferry and Cailliet 1996), and are consequently not suitable for estimating sample sizes for diets based on prey proportions. However, relative proportions of prey would theoretically also stabilize with increasing sample size. To estimate the event-scale sample size at which stabilization occurred for snoek, the difference in the proportional contribution of the dominant prey item between consecutive 10-sample size-classes was calculated as:

$$D_{(n)} = P(i)_{(n+10)} - P(i)_{(n)} \quad ,$$

where D is the percentage difference between consecutive classes (n and n + 10) and P is the relative percentage of prey type i for the specified class. The asymptote was taken to correspond with the size-class beyond which D was <1%. The dominant prey item was defined as that species constituting the highest proportion by mass for the entire sample collected during that sampling event.

Mean values of D (i.e. at corresponding size-classes) were then plotted for the inshore and offshore samples, and the standard deviation (*SD*) per class was calculated in each case. The average asymptotic level of the curves was taken as the size-class after which the mean D was <1%.

Weekly and seasonal variation in diet

The southern Benguela is characterized as a productive but variable ecosystem, biota undergoing major shifts in abundance over time (Shannon *et al.* 1992). The variation in relative prey proportions in the diet of snoek was examined at two temporal scales, week and season. It was hoped that, by observing the scale and degree of variation in diet, a sampling frequency could be determined that would suitably encompass the changes in diet over time.

For inshore snoek, a six-week sampling programme was undertaken around the Cape Peninsula in autumn 2001, with the aim of collecting once weekly a total of 100 snoek stomachs that contained food. Because five of the six samples taken were large enough to give an accurate description of the diet, data from the third week of sampling was excluded from this analysis.

The diet for each week was plotted, as was the average diet over the six-week period. Prey proportions were subjected to multivariate analysis using PRIMER® for Windows™ (release 5.0). To detect similarities between diets from week to week, and similarities between each week's diet and the overall diet for the six-week period, a one-way ANOSIM was performed on the data. Graphic representations of the similarity between samples were produced by means of Bray–Curtis similarity matrices, from which multidimensional scaling (MDS) plots and dendrograms (cluster analysis) were drawn (Clarke and Warwick 1994).

The database used to describe seasonal diet was collected between September 1994 and January 1998. For that period, samples were collected monthly between Cape Columbine and Cape Hangklip (Fig. 1) in all consecutive seasons, but were limited to the inshore area. The year was divided into seasons: autumn, March – May; winter, June – August; spring, September – November; summer, December – February (of the following year). Seasonal prey proportions were subjected to MDS and cluster analysis. To de-

Table I: The cumulative number of prey types listed against sample sizes for the 10 inshore and 10 offshore datasets. The shaded blocks show the points at which maximum prey diversity was reached for each sample, the circled numbers indicate samples where the asymptote may not have been reached and shaded circles are where diversity continued to increase during the last 10 stomachs examined

Number of stomachs examined	Number of prey species encountered									
	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6	Sample 7	Sample 8	Sample 9	Sample 10
Inshore										
1	1	1	1	1	1	1	1	1	2	4
2	3	2	1	2	1	1	1	1	5	5
3	3	3	1	2	1	3	1	1	5	5
4	3	4	2	3	1	3	1	1	5	5
5	3	5	3	3	1	3	2	1	5	5
10	3	6	3	3	2	4	3	1	6	5
20	5	6	3	4	3	5	4	1	6	7
30	5	6	4	5	6	7	5	3	7	7
40	5	6	5	5	6	7	5	3	7	7
50	5	6	5	5	7	7	5	3	7	7
60	6	6	5	5	7	7	5	3	8	7
70	6	6	5	6	7	7	5	5	8	
80	6		5	6	7	7	5	6		
90	6		5	6	7	7	5			
100	6		5	6		7				
110	6		6	6		7				
120										
Offshore										
1	1	1	1	1	1	2	1	1	1	1
2	2	2	1	1	2	2	3	2	2	1
3	2	2	2	3	2	3	3	3	4	2
4	3	2	2	5	2	3	4	3	5	2
5	3	2	2	6	3	4	4	3	5	3
10	4	3	4	6	4	5	5	3	6	6
20	5	5	6	6	5	6	5	4	6	7
30	6	6	6	6	5	6	5	5	6	7
40	6	6	6	7	6	6	6	5	6	7
50	6	6	6	7	6	6	6	5	8	7
60	6	7	9	8	6	6	6	6	8	8
70	6	7	9	8	6	6	6	6	8	8
80	6	7	9	9	7		6	6	8	8
90		7	9	9	7		6		8	8
100		7	9	9	7		6		8	8
110				9					9	8
120				9					9	8

tect seasonal variation and possible grouping of similar prey proportions within like seasons, a two-way nested ANOSIM was performed on the seasonal data.

Combining sample size and sampling frequency

Infrequent large samples can lead to dietary bias, often termed "intra-haul correlation" (Bogstad *et al.* 1995, Tirasin and Jørgensen 1999). Consequently, a sampling strategy consisting of frequent small samples has been advocated (e.g. Bogstad *et al.* 1995). Here, the minimum weekly samples necessary to describe the diet of snoek inshore around the Cape Peninsula over a five-week period is investigated, using the same samples used to determine weekly diet variation. Diets calculated from weekly samples increasing in units of 10 samples were compared with the overall diet for the sampling period, using the Bray–Curtis index (Clarke and Warwick 1994).

Spatial variation in diet

In the southern Benguela, snoek move offshore to spawn in winter/spring (Griffiths 2002). The diet of snoek sampled simultaneously, inshore and offshore, off the Cape Peninsula during the winter 1995, 1996 and 1997 and spring 1996 were compared for spatial (depth-related) differences. Differences in diet (proportions by weight) were investigated through a one-way ANOSIM.

Variation in feeding intensity

Snoek used for this analysis were those used in the seasonal diet variation study. The seasonal rate of prey consumption for snoek was estimated by calculating the percentage of snoek with food in their stomachs, as well as the mean meal size of all fish with stomachs containing food.

The percentage of fish with stomachs containing food was determined from the proportions of empty stomachs for the whole dataset. Data were pooled over years, as χ^2 tests revealed no significant difference in seasonal proportions between years (female: spring $p = 0.60$; summer $p = 0.06$; autumn $p = 0.69$; winter $p = 0.90$, male: spring $p = 0.06$; summer $p = 0.07$; autumn $p = 0.45$; winter $p = 0.78$).

The mean meal size, or "stomach fullness", was calculated by means of a consumption index:

$$\text{Stomach fullness} = \frac{SM}{FM - GM} \times 100 \quad ,$$

where SM is the total mass of the stomach contents, FM the total fish mass and GM the gonad mass. Subtraction of the gonad mass reduced the variation caused by changing gonad size and weight throughout the year. Stomach fullness was calculated only for fish with stomachs containing food, and males and females were analysed separately so that they could be tested for differences in feeding intensity.

Stomach fullness data were normalized by log-transformation prior to comparisons based on ANOVA. Initial analysis revealed that variance between seasons was significantly higher than that between years for both females ($F = 7.85$, $p = 0.00437$) and males ($F = 4.52$, $p = 0.004$), so data were pooled over years to test for differences in stomach fullness between seasons.

RESULTS

The number of stomachs containing food in each sample ranged between 60 and 115, with a mean of 89 (± 21.7). The stomachs in inshore samples contained a mean of 6.4 (± 0.84) prey species per sample and those in offshore samples a mean of 7.3 (± 1.33). The median level at which the diversity asymptote was reached was 30 stomachs (range 10–70 stomachs) for inshore and 60 stomachs (range 20–80 stomachs) for offshore samples (Table I). The mean asymptotic values were 38.6 and 53.7 stomachs examined for the inshore ($n = 7$) and offshore ($n = 8$) samples respectively (three inshore and two offshore samples did not attain an asymptote). These asymptote values were not significantly different between inshore and offshore samples (Mann–Whitney U–test, $p > 0.05$).

The marginally higher asymptote values for offshore samples could be attributable to a greater prey diversity (16 vs 12 species in 10 samples) and the larger number (10 vs 6) of "rare" species (i.e. those contributing <1% by weight) offshore (Appendix).

The mean sample size at which the asymptotic level (i.e. $D \leq 1\%$ between classes) was reached was 74 associated with the calculation of prey proportions as sample size increases.

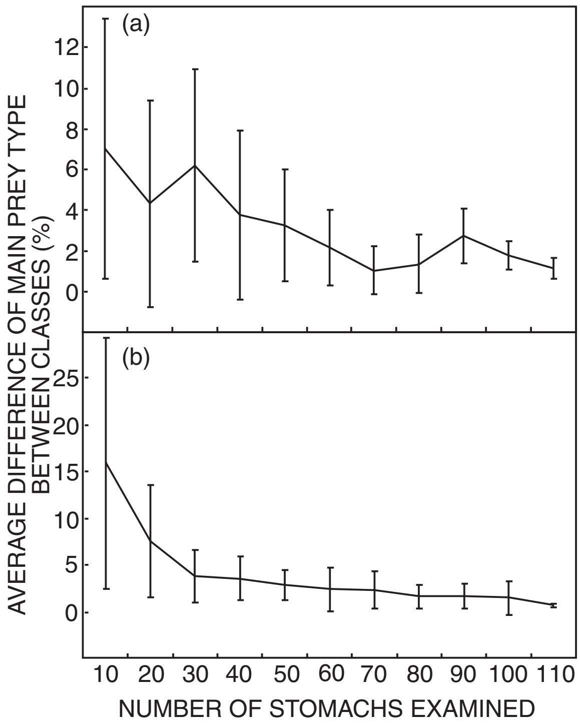


Fig. 2: Variation in the mean percentage difference between 10-stomach classes for the main prey type for the (a) inshore and (b) offshore datasets. Vertical bars denote *SD*

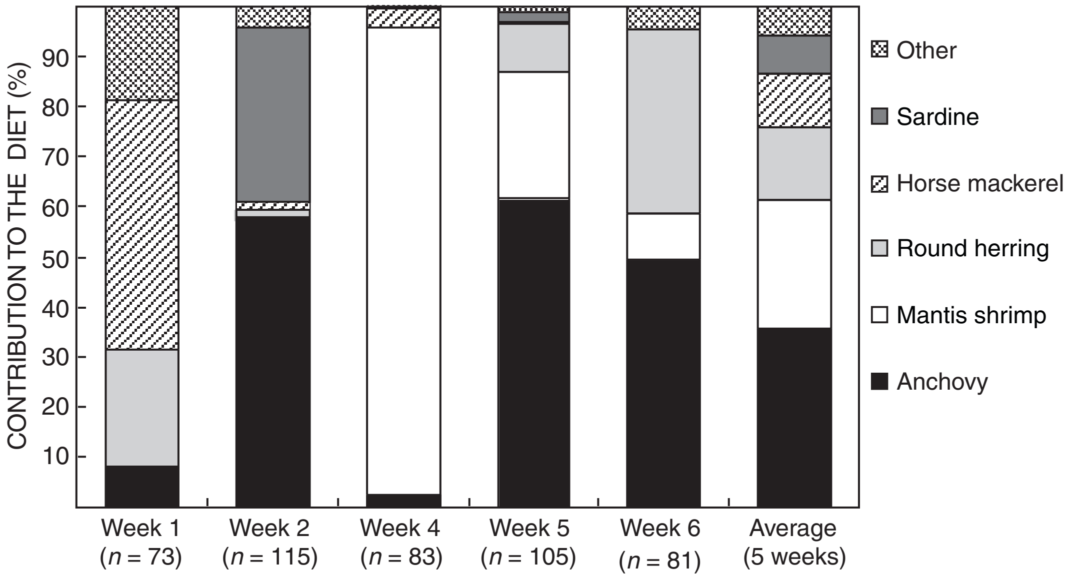


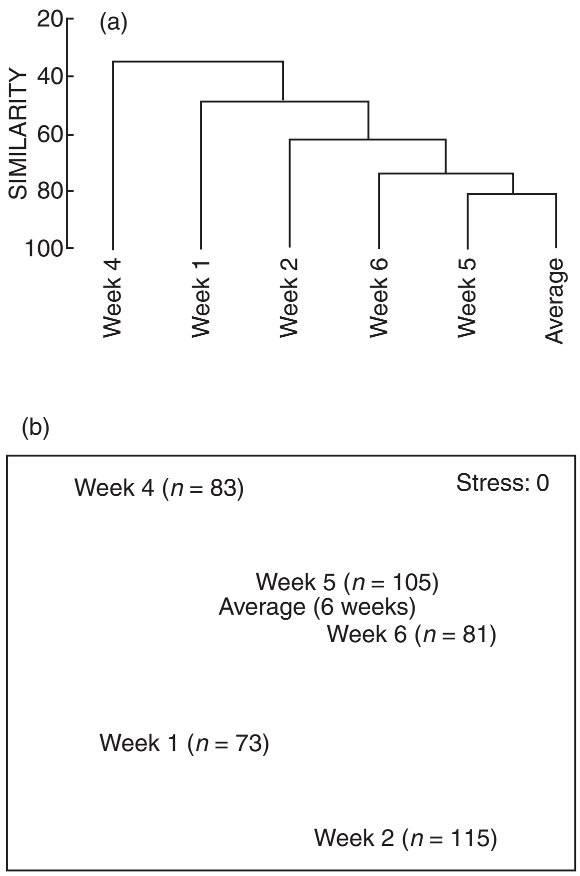
Fig. 3: Weekly variation in the inshore diet of snoek during a six-week period (in April 2001). Owing to poor availability of snoek, insufficient data for analysis were collected in Week 3

Weekly and seasonal variation in diet

Snoek diet varied considerably over the six-week sample period (Fig. 3). The diet in Week 1 was dominated by horse mackerel *Trachurus t. capensis*, which appeared infrequently in the other weeks. Weeks 2, 5 and 6 were dominated by anchovy *Engraulis encrasicolus*. Sardine *Sardinops sagax* was the secondmost prevalent prey in the diet in Week 2, the only time that it appeared in any substantial quantity in the diet. Week 3 was completely dominated by mantis shrimp *Pterygosquilla armata capensis*. That prey was present in subsequent weeks, but in declining quantities. The diets in Weeks 5 and 6 were similar, but more round herring *Eutrumeus whiteheadi* were found in Week 6 than in any other week. The "average" diet for the six-week period is most similar to Week 5, but is not closely mirrored by the diet in any one of the weeks over the sampling period.

Multivariate analyses revealed that the diets in Weeks 5 and 6 were most similar to the overall diet (Fig. 4). Apart from those weeks, there seemed to be no temporal correlation between diets, i.e. the similarity does not diminish with increasing time between samples. The zero stress value indicated that the MDS plot was a good representation of the data (Clarke and Warwick 1994). A one-way ANOSIM indicated no significant degree of similarity between any of the samples, or the samples and the average diet ($R = -0.68$, $p = 0$).

From the seasonal analyses of diet, snoek found inshore and offshore between Cape Columbine and Cape Hangklip fed on a wide variety of species between September 1994 and November 1997. These included 11 species of pelagic teleost, 11 demersal teleosts, 1 reef fish, 8 crustaceans, 4 cephalopods and 1 annelid (see Griffiths 2002). Despite the high overall prey diversity, the inshore diet was generally dominated by two pelagic species, sardine and anchovy, which occurred in almost equal proportions in spring and summer 1994, in winter, spring and summer 1995, and in autumn 1996 (Fig. 5a). Sardine dominated the diet in autumn 1995 and from winter 1996 through spring 1997. Anchovy were only dominant in winter 1995, and were almost absent from the diet in autumn 1995 and from spring 1996 to autumn 1997 (Fig. 5a). Round herring, another pelagic shoaling fish, were prominent in the diet between summer 1994 and autumn 1995, but appeared only in small amounts thereafter. Horse mackerel and mantis shrimp appeared sporadi-



cally in small amounts in the diet. Juvenile Cape hake (*Merluccius* spp.) also featured in the inshore diet, albeit rarely, but hake were prominant on the offshore diet (Fig. 5b).

A two-way nested ANOSIM, with diets grouped according to season, showed no significant relationship between season and diet composition (R = 0.143, p = 0.17, with 35 permutations and 999 data simulations). Cluster analysis and a MDS plot supported this finding, neither revealing clear seasonal grouping of prey proportions (Fig. 6). The low stress value (0.16) for the MDS plot indicated that it was a good representation of the data (Clarke and Warwick 1994). The only seasons showing any notable grouping were spring 1995, winter 1996 and spring 1997, perhaps the consequence of scarcity of anchovy during those seasons (Barange *et al*. 1999).

Combining sample size and sampling frequency

The similarity of the subsamples to the overall diet was highly variable with weekly samples of <70 stomachs containing food (Fig. 7). Diets were consistently greater than 95% similar where weekly samples were greater than or equal to a sample size of 70 stomachs.

Spatial variation in diet

The prey of snoek caught offshore between Cape Columbine and Cape Hangklip consisted mainly of Cape hake, sardine, horse mackerel, lanternfish *Lampanyctodes hectoris* and round herring. Like the inshore diet, the relative proportions of primary prey varied substantially between seasons.

A one-way ANOSIM showed a significant difference in species composition between the inshore and offshore diets between Cape Columbine and Hangklip during similar seasons (R = 0.885, p = 0.029, with 35 permutations and 999 data simulations). The difference was characterized mainly by the high prevalence of hake and lanternfish and the absence of anchovy in the offshore diet (Fig. 5b).

Variation in feeding intensity

The proportion of snoek with stomachs containing food was highest in winter and spring (the spawning season), and lowest in summer (Fig. 8), and proportions between seasons were significantly different (χ^2 = 236.65, df = 3, p < 0.001). The percentages of females with stomachs containing food were marginally higher than males in autumn and winter, but not significantly so (χ^2 = 4.3, df = 2 , p = 0.6).

The mean stomach fullness depicted a similar pattern to that of food consumption (Fig. 8). The highest degree of stomach fullness was in winter and spring. There was no significant difference in fullness between males and females, except in winter, when females had significantly fuller stomachs than males (F = 3.9, p = 0.05). However, seasonal differences were highly significant, being more pronounced in females (female: F = 7,85, p = 0.0004; male: F = 4.52, p = 0.0041).

These results indicate that snoek feed more frequently and consume larger meals during their spawning season. Given that sampling was not restricted to any specific time of day (e.g. when the fish

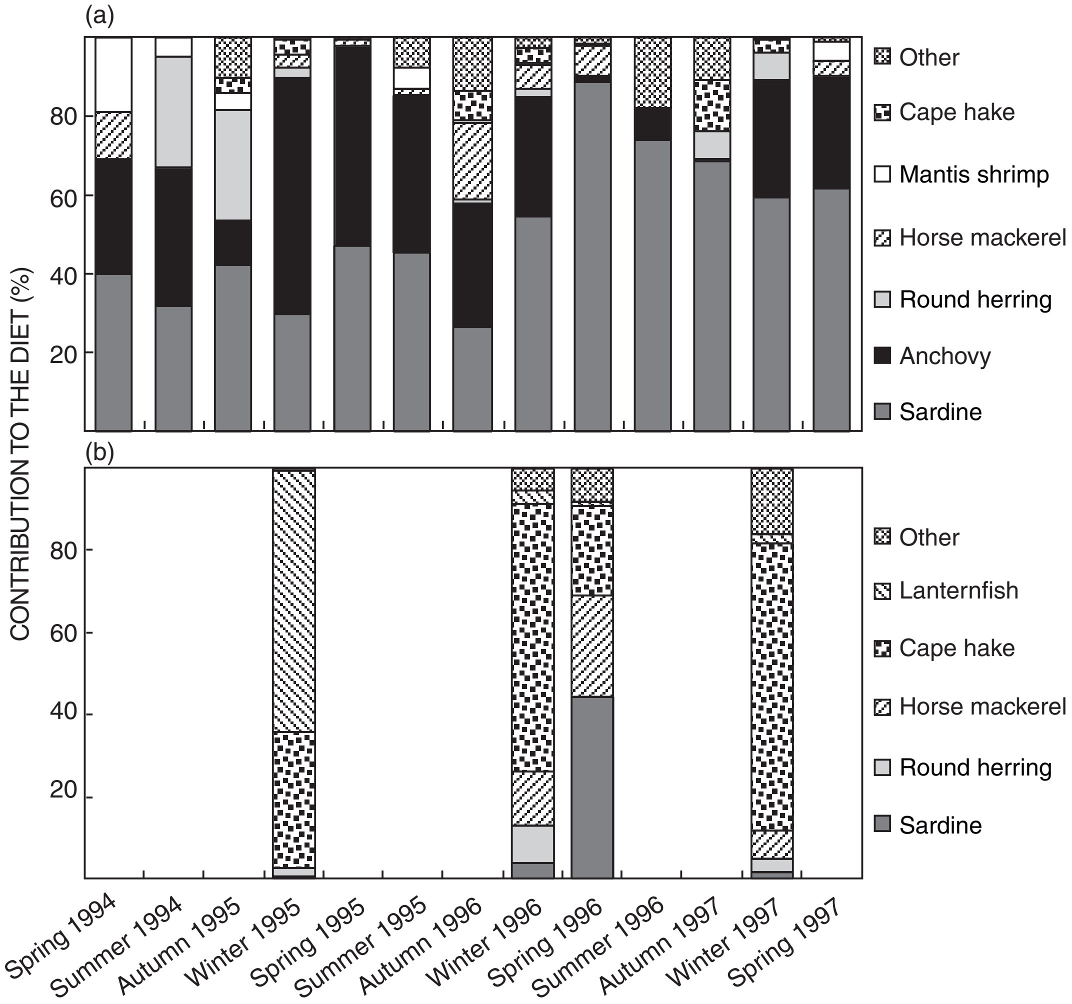


Fig. 5: Seasonal contributions of each of the prey types to the diets of snoek (a) inshore and (b) offshore

were feeding) and was essentially random throughout the years, these results clearly show a seasonal pattern in food consumption or feeding intensity.

DISCUSSION

In a review of some 200 studies of diet, Ferry and Cailliet (1996) concluded that the majority lacked sufficient data to make statistically sound comparisons and therefore failed to draw tenable conclusions. In addition, none of the studies so reviewed contained any estimates of the precision of samples used. Cumulative diversity curves were first employed by Pielou (1966), and they have since been recommended and described in many studies (Elliot 1971, Hurturbia 1972, Baltz and Morejohn 1977, Cailliet 1977, Hoffman 1979, Calliet *et al.* 1986, Duffy and Jackson 1986, Cortés 1997, Griffiths 1997). In the present study, the diversity asymptote was mostly (90%) attained before all stomachs were included, thus indicating that most

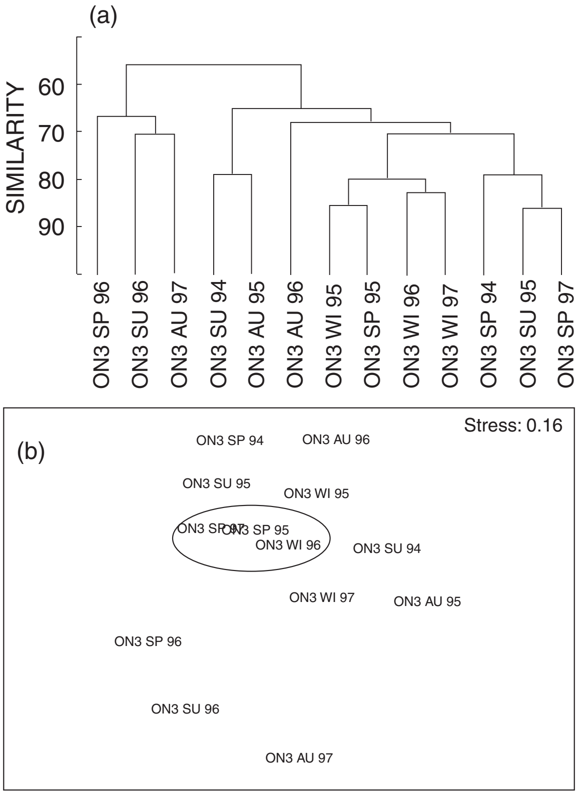


Fig. 6: (a) Cluster analysis and (b) MDS plot of the similarity of seasonal inshore diet samples, based on the Bray–Curtis index. The codes are: ON = inshore; SP = spring; SU = summer; AU = autumn; WI = winter; 96, 97, etc. = the year

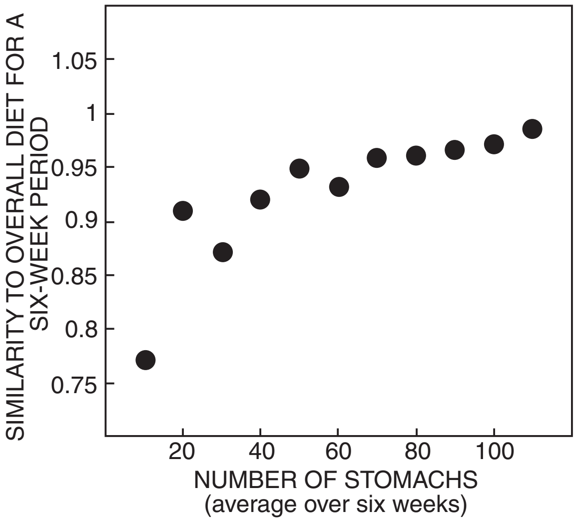


Fig. 7: The Bray–Curtis similarity of each 10-sample class to the total diet over the six week period

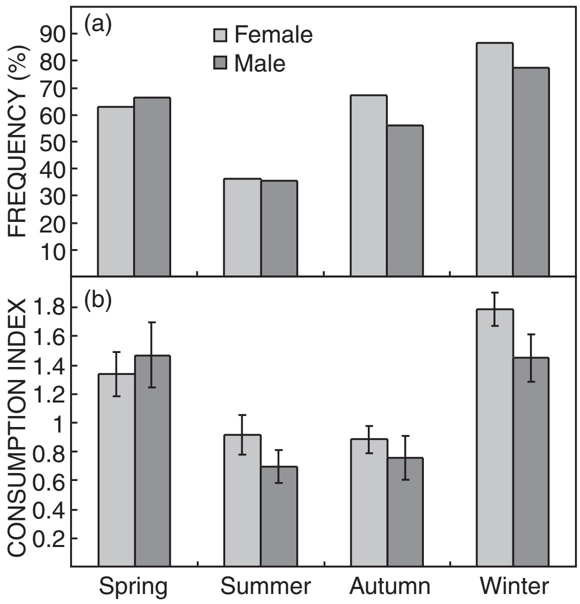


Fig. 8: (a) Seasonal frequency of snoek with stomachs containing food for the period 1994–1997; (b) seasonal stomach fullness as a percentage of fish mass (minus gonad mass), per season over all years combined. The vertical bars indicate the variance of each sample

samples were large enough to accurately describe diet diversity in snoek. The results here suggest that at least 60 stomachs containing food per sample are needed in order to describe the total diversity or niche breadth of snoek in South African waters at the event scale.

Despite its wide support, prey diversity curves are only suitable for describing the presence and absence of prey types in a diet (Ferry and Cailliet 1996), as opposed to prey proportions, which are more useful for ecosystem models. In this study, plotting the percentage differences in prey proportions between successive 10-stomach classes was found to be a quick and effective method for establishing whether samples were large enough to accurately determine the proportion of the dominant prey species in the diet during

Table II: Range and mean of sample sizes at which the diversity asymptote (prey diversity curves) and the prey proportion asymptote (cumulative prey percentage curves) were reached

Sample	Location	Range		
		Minimum	Maximum	Mean
Cumulative prey diversity	Inshore	10	70	52 ± 30.5
	Offshore	20	80	56 ± 27.9
Cumulative prey percentages	Inshore	30	100	74 ± 26.7
	Offshore	60	110	79 ± 21.3

a given sampling event. As expected, the percentage difference of the main prey type between successive classes declined as sample size increased. According to the current dataset of 20 samples, the mean minimum sample size at which the difference between successive classes was <2% was 74 (± 26.7) stomachs containing food inshore and 79 (± 21.8) stomachs containing food offshore. Mean minimum sample size predicted using this method was 42% larger than that predicted by the prey diversity curves (Table II). The exercise of combining sample size and frequency over a six-week period also suggested a minimum sample size of at least 70 stomachs containing food: Bray-Curtis similarity attained an asymptote at 70 stomachs (Fig. 7).

It should be emphasized that the above minima are for stomachs containing food, and that because some fish have empty stomachs (see below), the necessary number of fish to be sampled would be substantially larger, depending on feeding intensity at the time of capture.

Caution should be taken against extrapolating the present results to other predators within the southern Benguela or to predatory fish in other ecosystems. The reason is that, in situations where prey diversity is substantially lower – e.g. Cape gannets *Morus capensis* within the southern Benguela (Crawford *et al.* 1992) – smaller minimum samples sizes are anticipated to provide an accurate description of the diet. The converse would be true of populations with higher prey diversity.

Snoek is a generalist predator capable of consuming a wide range of demersal and pelagic prey, including teleosts, crustaceans and cephalopods (Griffiths 2002). The southern Benguela is a dynamic environment with high spatio-temporal variation in primary productivity and the relative biomass of individual prey species (Smale 1992). This is reflected in the high weekly variation in the diets of snoek sampled inshore off the Cape Peninsula.

Seasonal changes in prey abundance and biomass are often a result of movements and changes in distribution associated with the life cycle (e.g. spawning migrations in fish, breeding aggregations in squid, periods of dormancy in invertebrates; Keast 1979). Although the feeding intensity of snoek in the southern Benguela, based on stomach fullness and proportions with food, followed a strongly seasonal cycle, being highest during the winter/spring spawning season, seasonal diet composition was highly variable and without a regular pattern.

Onshore–offshore differences in diet were much greater than seasonal differences. The main difference was the absence of anchovy and the higher proportions of hake and lanternfish in the offshore diet. Prey species that were not present in the offshore diet either have much wider distributions than anchovy (e.g. sardine, round herring), or prefer deeper offshore waters (e.g. Cape hake; Payne and Punt 1995).

Given the high spatial and temporal dietary variation of snoek, it is clear that samples of sufficient size and spatio-temporal resolution are necessary to provide accurate descriptions of annual diet. Current data indicate that at least 75 stomachs containing food are necessary to accurately describe diet at the event scale. It is assumed, however, that, if the main prey items are measured with a reasonable degree of precision at each sampling event, the proportions of the most important prey items in the overall diet (by season or year) will be reasonably accurate. Clearly, increasing the precision of lesser prey items at the event scale would require larger samples on account of their lower frequency of occurrence. However, the principle prey items are of primary importance in ecosystem modelling. Given the degree of dietary variation found in this study, an optimum sampling frequency of once a week is considered reasonable for evaluating seasonal diets. Annual diets based on this approach would require 75 × 52 = 3890 stomachs containing food. A review of previous studies of inshore snoek diet in the southern Benguela reveals that annual samples were generally very small (88% of $n \leq 100$) and were often collected during one or two seasons of each year (Table III), bringing into question their accuracy as descriptors of diet for the respective years.

Table III: An overview of previous feeding studies of snoek caught inshore in the southern Benguela, showing the number of stomachs examined containing food (n) and their temporal and spatial coverage

Year	n	Months sampled	Region	Data Source
1958	186	May–Sep.	CC–CH	1958–1974: Nepgen (1979) and origional data housed at MCM
1959	48	Mar.–May	CC–CH	
1960	32	May–Jun.	CC–CH	
1961	33	Feb., May/Jun.	CC–CH	
1962	6	May, Jul.	CC–CH	
1963	56	May/Jun.	CC–CH	
1965	44	Jun./Jul.	CC–CH	
1966	83	Apr.–Jun.	CC–CH	
1967	95	May–Jul.	CC–CH	
1968	19	May–Jul.	CC–CH	
1970	215	Mar.–Aug.	CC–CH	
1971	83	May/Jun.	CC–CH	
1972	94	Mar., May–Nov.	CC–CH	
1973	85	May–Aug.	CC–CH	
1974	96	May–Aug.	CC–CH	
1979	1 068	All months	False Bay	Nepgen (1982)
1985	51	Jun./Jul.	CC–CH	Dudley (1987)

CC–CH = Cape Columbine to Cape Hangklip

The strong seasonal pattern of snoek feeding intensity has two important ramifications for future sampling programmes. First, because minimum sample size for feeding purposes refers to the number of stomachs with food, the total number of fish sampled should vary with season in order to maintain similar dietary precision, i.e. more snoek need to be sampled in summer and fewer in winter. Second, in order to construct a realistic annual diet, seasonal prey composition should be weighted according to feeding intensity in that season.

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APPENDIX

Prey items in the stomachs of inshore and offshore snoek caught between Cape Columbine and Cape Hangklip and their percentage contribution to the diet

Common name	Taxonomy	Contribution to the diet by wet mass (%)	
		Inshore	Offshore
Teleost			
Anchovy	*Engraulis encrasicolus*	46.23	3.05
Sardine	*Sardinops sagax*	18.63	50.04
Round herring	*Etrumeus whiteheadi*	5.74	19.41
Horse mackerel	*Trachurus trachurus capensis*	4.70	8.42
Clinidae	Unidentified species	0.82	
Cape hake (shallow-water)	*Merluccius capensis*		
Cape hake (deep-water)	*Merluccius paradoxis*		12.51
Fingerfin	*Chyrodactylus pixi*	0.42	
Sandlance	*Gonorynchus gonorynchus*	0.23	
Saury	*Scomberesox saurus scomberopides*		0.13
Lanternfish	*Lampanyctodes hectoris*	0.03	0.02
Lightfish	*Maurolicus muelleri*		<0.01
Sand eel	*Gnathophis capensis*	0.01	
Buttersnoek	*Lepidopus caudatus*		0.69
Rattail	*Coelorinchus fasciatus*		0.55
Chub mackerel	*Scomber japonicus*		0.08
Jacopever	*Helicolenus dactylopterus*		0.04
Unidentified pelagic fish remains		5.20	4.26
Crustacea			
Mantis shrimp	*Pterygosquilla armata capensis*	17.95	
Spiny lobster puerulae	*Jasus lalandii*	0.04	
Hermit crab	Unidentified species		0.04
Unidentified Crustacea			0.01
Cephalopoda			
Chokka squid	*Loligo vulgaris reynaudii*		
Flying squid	*Todaropsis eblanae*		0.75
–	*Lycoteuthis* spp.		
Cuttlefish	*Sepia australis*		