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# Diet of *Octopus vulgaris* in False Bay, South Africa

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**Abstract** The diet of *Octopus vulgaris* was analysed using instantaneous daytime observations, midden counts, and stomach contents and a total of 39 prey species were identified. From stomach contents, the most important prey species were *Plagusia chabrus* (64.6% IRI, index of relative importance) and *Haliotis midae* (21.6% IRI). Crustaceans were the most frequently found prey group in octopus stomachs (63.6% frequency of occurrence), followed by molluscs (37.6%), teleosts (11.2%), and polychaetes (10.8%). Prey size and diversity increased with increasing octopus size. From middens, the mean shell lengths of *H. midae* consumed by small, medium, and large *O. vulgaris* were 53.3, 72.6, and 86.0 mm, respectively. Compared with stomach contents, midden counts were 3 times higher for shelled molluscs, but 5 times lower for crustaceans and soft-bodied organisms. Similarly, instantaneous daytime observations were 3 times higher for shelled molluscs, but 5 times lower for crustaceans and 2 times lower for soft-bodied organisms.

## Introduction

*Octopus vulgaris* is a coastal species (Guerra 1981), occurring in tropical, subtropical, and temperate waters of the East Atlantic Ocean and Mediterranean Sea (Mangold 1997). It supports important fisheries along the northwest coast of Africa, Atlantic European coast, Mediterranean Sea, and Japanese waters (Guerra 1997).

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*O. vulgaris* has also been identified as a potential species for commercial exploitation in South Africa (Smith and Griffiths 2002). It is furthermore ecologically important as a generalist predator, feeding on crustaceans, molluscs, polychaetes, and fish (Mangold 1983). *O. vulgaris* is opportunistic, with its diet often reflecting abundance of prey available (Nigmatullin and Ostapenko 1976; Guerra 1978 cited in Mangold 1983; Smale and Buchan 1981). Prey availability, and thus diet, have been shown to vary with depth and habitat type, as these factors determine benthic assemblages (Ambrose 1984). Diets have also been linked to octopus size (Nigmatullin and Ostapenko 1976; Smale and Buchan 1981) and maturity stage (Cortez et al. 1995). Seasonal variation has been shown for *O. mimus* off Chile (Cortez et al. 1995), and has been suggested only for *O. vulgaris* off the east coast of South Africa (Smale and Buchan 1981).

Three methods have generally been used to determine the diets of octopus. Many species consume their prey in shelters and prey remains often accumulate to form middens, which can be collected and identified (Ambrose and Nelson 1983; Vincent et al. 1998; Dodge and Scheel 1999). The second method is the examination of stomach contents (Whitaker et al. 1991; Sanchez and Obarti 1993; Quetglas et al. 1998), and the third is direct observation (Mather 1991; Mather and O'Dor 1991; Forsythe and Hanlon 1997). Stomach contents examination is considered the best method (Nixon 1987), but midden counts are also frequently used. Ambrose (1983) and Mather and O' Dor (1991) observed disparate removal rates of various prey items from middens but failed to provide a comparison of octopus diet as determined by midden counts and stomach contents. In contrast, Smale and Buchan (1981) determined the diet of *O. vulgaris* from both stomach contents and midden counts and found the results to be comparable.

This study determines the diet of *O. vulgaris* in False Bay, South Africa and assesses variation in diet resulting from octopus size. Results obtained from stomach contents, midden counts, and instantaneous daytime observations are compared.

## Materials and methods

Study sites and sampling techniques

Daytime collections of *O. vulgaris* using SCUBA were undertaken in five sites in False Bay, namely Glencairn, Windmill Beach, Miller's Point, Buffels Bay, and Cape Hangklip (Fig. 1). These sites were chosen as all of them had kelp beds (*Ecklonia maxima*), with reef consisting largely of granite/sandstone boulders, which provided good habitat for *O. vulgaris*. Windmill Beach accounted for 50% of the sampling trips due to its being the most sheltered site. This was followed by Miller's Point (19%) and Buffels Bay (13%). Sampling was conducted between 10.00 a.m. and 3.00 p.m. at 0–10 m depths in the months of February 1997 to January 1998. An attempt was made to capture all octopuses seen on sampling dives using a technique similar to that described by Smale and Buchan (1981). Once the octopus was captured the midden was revisited to collect all midden piles, which were placed with the occupant in collecting bags. Molluscan shells that appeared badly pitted, broken or dull were excluded so as to reduce the probability of including previous inhabitant's prey remains. Any whole or flesh remains dropped by the octopus while fleeing or found in the midden were noted as an instantaneous observation of octopus feeding. All samples were brought to the laboratory and frozen at –20°C. Prior to stomach content analysis, octopuses and midden piles were thawed and weighed, and prey remains from middens were counted. Abalone (*Haliotis midae*) shells from middens were measured to determine prey size selectivity. Abalone shells were used as an index because a large sample size of intact shells was collected. The alimentary canal was removed from each octopus and cut along its length, and all the contents were removed and rinsed through a 500-$\mu$m sieve. The material retained by the sieve was sorted under a dissecting microscope and identified to the lowest possible taxon. In some circumstances prey identification was made possible by observing what octopuses were consuming at time of capture or by certain diagnostic features of prey items. Diagnostic features included the presence of "dense fur" or "fleshy projections" and radula shape, which was used to distinguish *H. midae* from limpets. The presence of three parallel ridges on the nippers distinguished *Plagusia chabrus* from other crabs belonging to the family Grapsidae. The number and volumetric displacement of each prey species remains found in the gut were also determined. The number of each prey item in the gut was assumed to be one unless more than one radula, head, pair of eyes, beak, or operculum were found.

Results from instantaneous daytime observations, midden counts, and stomach contents were compared using frequency of occurrence of prey types. However, $\chi^2$ analyses were performed only for three aggregated groups: (1) small crustaceans (isopods, amphipods, and megalopa larvae) and large crustaceans (crabs and rock lobsters excluding larval stages); (2) shelled molluscs; and (3) soft-bodied animals (octopuses, polychaetes, and teleosts). This was done to ensure that the expected frequency of prey items for any dietary technique did not fall below 5% (Zar 1984). The overall importance of prey species in the diet of *O. vulgaris* was assessed using a modified version of the Pinkas et al. (1971) equation where the index of relative importance (IRI) is calculated as follows:

$$\text{IRI} = (\%\text{ number of prey species in gut} + \%\text{ volume of prey species in the gut}) * \%\text{ frequency of occurrence of prey species in gut}$$

Prey frequencies of occurrence of small (0–300 g), medium (301–1,000 g), and large (>1,000 g) octopuses were submitted to multivariate statistics using PRIMER analysis programmes to test for significant dietary differences between octopuses of various sizes. Data were transformed using the square root and analysed by the Bray-Curtis similarity measure. ANOVA followed by a Tukey test (Zar 1984) was used to compare mean shell lengths of abalone consumed by small, medium, and large octopuses.

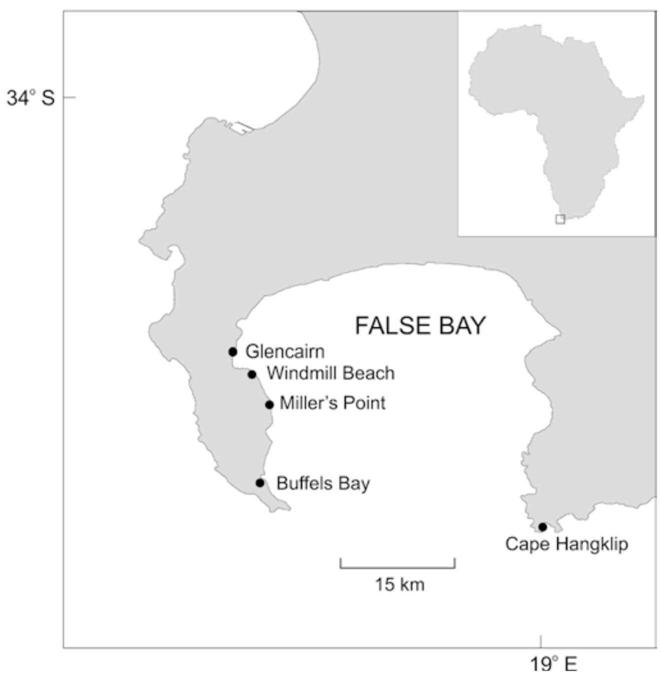


**Fig. 1** Map of Africa with enlarged map of False Bay showing localities of sampling sites

## Results

In total 336 octopus specimens were collected: Windmill Beach (155), Miller's Point (105), Buffels Bay (56), Hangklip (12), and Glencairn (8). An average of 5.3 octopuses were collected per sampling dive lasting 1.5 h on average. The majority of octopuses (83%) were found resting inside shelters. Of the 29 octopuses observed to be feeding at time of capture only 13.7% were found outside shelters. Midden piles were found in 73% of shelters containing an octopus. Of the 336 octopuses, 74.4% contained prey items in the gut.

A total of 39 species were recorded as prey of *O. vulgaris*. Of these 30 were identified from middens, 14 from stomach contents, and 8 from direct observations (Table 1). The frequency of occurrence of prey items in the diet of *O. vulgaris* as obtained by the three dietary techniques (Fig. 2) differed significantly ($\chi^2 = 260.04$, $df = 4$, $P < 0.05$) and was largely attributed to stomach contents having a relatively higher frequency of crustaceans (large 28.4%, small 23.2%) and soft-bodied organisms (polychaetes 8.2%, teleosts 8.5%), but a lower frequency of shelled molluscs (abalone 13.4%, limpets 7.6%, winkles 7.6%). Middens had a relatively lower frequency of crustaceans (large 12.1%, small 0%) and soft-bodied organisms (<3.6% in total), but a higher frequency of shelled molluscs (abalone 29.5%, winkles 21.5%, limpets 20.5%, bivalves 12.8%). Although the frequency of abalone was extremely high (63%) for daytime observations it contributed little to the overall

**Table 1** Raw dietary data of *Octopus vulgaris* in False Bay based on three methods: instantaneous daytime observations, midden counts, and stomach contents. The number of octopuses consuming prey at time of capture was 29, the number of dens with midden piles was 206, and the number of octopuses with food in the gut was 250

| Prey category | Dietary assessment method | | | | | | |
|---|---|---|---|---|---|---|---|
| | Daytime observations | | Midden counts | | Stomach contents | | |
| | Occurrence | Number | Occurrence | Number | Occurrence | Number | Volume |
| Crustaceans | | | | | 159 | | |
| Large crustaceans | 3 | 3 | 47 | 56 | 93 | 119 | 129.1 |
| *Jasus lalandii* | – | – | 2 | 2 | 2 | 2 | 34 |
| *Paguristes gamianus* | – | – | – | – | 13 | 16 | 7 |
| *Plagusia chabrus* | 2 | 2 | 42 | 50 | 62 | 75 | 79 |
| Other crabs | 1 | 1 | 4 | 4 | 28 | 26 | 9.1 |
| Small crustaceans | – | – | – | – | 76 | 397 | 61.7 |
| Amphipods (*Paramoera capensis*) | – | – | – | – | 19 | 69 | 4.2 |
| Amphipods (other) | – | – | – | – | 17 | 57 | 2.7 |
| Isopods | – | – | – | – | 5 | 15 | 1.8 |
| Megalopa larvae (*P. chabrus*) | – | – | – | – | 45 | 256 | 53 |
| Other crustaceans | – | – | 1 | 1 | – | – | – |
| *Austromegabalanus cylindricus* | – | – | 1 | 1 | – | – | – |
| Molluscs | | | | | 94 | | |
| Abalone | 17 | 17 | 115 | 288 | 44 | 48 | 350.7 |
| *Haliotis midae* | 17 | 17 | 114 | 287 | 43 | 47 | 347.2 |
| *H. spadicea* | – | – | 1 | 1 | 1 | 1 | 3.5 |
| Bivalves | – | – | 50 | 108 | 2 | 2 | 2.8 |
| *Choromytilus meridionalis* | – | – | 25 | 52 | 1 | 1 | 0.3 |
| *Donax serra* | – | – | 2 | 2 | – | – | – |
| *Dosinia lupinsus orbignyi* | – | – | 2 | 2 | – | – | – |
| *Lutraria lutraria* | – | – | 10 | 22 | 1 | 1 | 2.5 |
| *Macoma litoralis* | – | – | 1 | 1 | – | – | – |
| *Mytilus galloprovincialis* | – | – | 14 | 17 | – | – | – |
| *Tivela compressa* | – | – | 1 | 2 | – | – | – |
| *Venurupis corrugatus* | – | – | 1 | 1 | – | – | – |
| *Venus verrucosa* | – | – | 8 | 9 | – | – | – |
| Limpets | – | – | 80 | 177 | 25 | 25 | 44.2 |
| *Dendrofissurella scutellum* | – | – | 2 | 2 | – | – | – |
| *Patella barbara* | – | – | 9 | 14 | – | – | – |
| *P. cochlea* | – | – | 1 | 1 | – | – | – |
| *P. compressa* | – | – | 59 | 120 | – | – | – |
| *P. granularis* | – | – | 1 | 1 | – | – | – |
| *P. longicosta* | – | – | 4 | 4 | – | – | – |
| *P. miniata miniata* | – | – | 19 | 28 | – | – | – |
| *P. tabularis* | – | – | 6 | 7 | – | – | – |
| Unidentified | – | – | – | – | 25 | 25 | 44.2 |
| Octopus | 2 | 2 | – | – | 7 | 7 | 135.1 |
| *Aphrodoctopus schultzei* | – | – | – | – | 1 | 1 | 6 |
| *Octopus vulgaris* | 2 | 2 | – | – | 6 | 6 | 129.1 |
| Winkles | 4 | 4 | 84 | 146 | 25 | 33 | 5.2 |
| *Oxystele sinensis* | 2 | 2 | 25 | 29 | 17 | 22 | 0.8 |
| *Gibbula zonata* | – | – | 2 | 5 | 5 | 5 | 0.2 |
| *Turbo cidaris* | 2 | 2 | 64 | 110 | 6 | 6 | 4.2 |
| *T. sarmaticus* | – | – | 2 | 2 | – | – | – |
| Other molluscs | 2 | 2 | 6 | 7 | 1 | 1 | 0,1 |
| *Burnepena lagenaria* | – | – | 1 | 1 | – | – | – |
| *Choronia lampas pustulata* | – | – | 2 | 2 | – | – | – |
| *Conus mozambicus mozambicus* | – | – | 1 | 1 | – | – | – |
| *Cymatium cutaceum africanum* | – | – | 2 | 2 | – | – | – |
| *Phalium labiatum zeylanicum* | – | – | 1 | 1 | – | – | – |
| *Phyllodesmium serratum* | 1 | 1 | – | – | – | – | – |
| *Tambja capensis* | 1 | 1 | – | – | – | – | – |
| *Volvarina zonata* | – | – | – | – | 1 | 1 | 0.1 |
| Polychaetes | – | – | 2 | 2 | 27 | 38 | 56.2 |
| Errantia spp. | – | – | – | – | 19 | 26 | 20.1 |
| Sedentaria spp. | – | – | 2 | 2 | 8 | 12 | 36.1 |
| Teleosts | 1 | 1 | 1 | 1 | 28 | 28 | 39 |
| *Liza richardsoni* | 1 | 1 | – | – | – | – | – |
| Unidentified | – | – | 1 | 1 | 28 | 28 | 39 |
| Other | – | – | 4 | 4 | – | – | – |
| *Parechinus angulosus* | – | – | 4 | 4 | – | – | – |

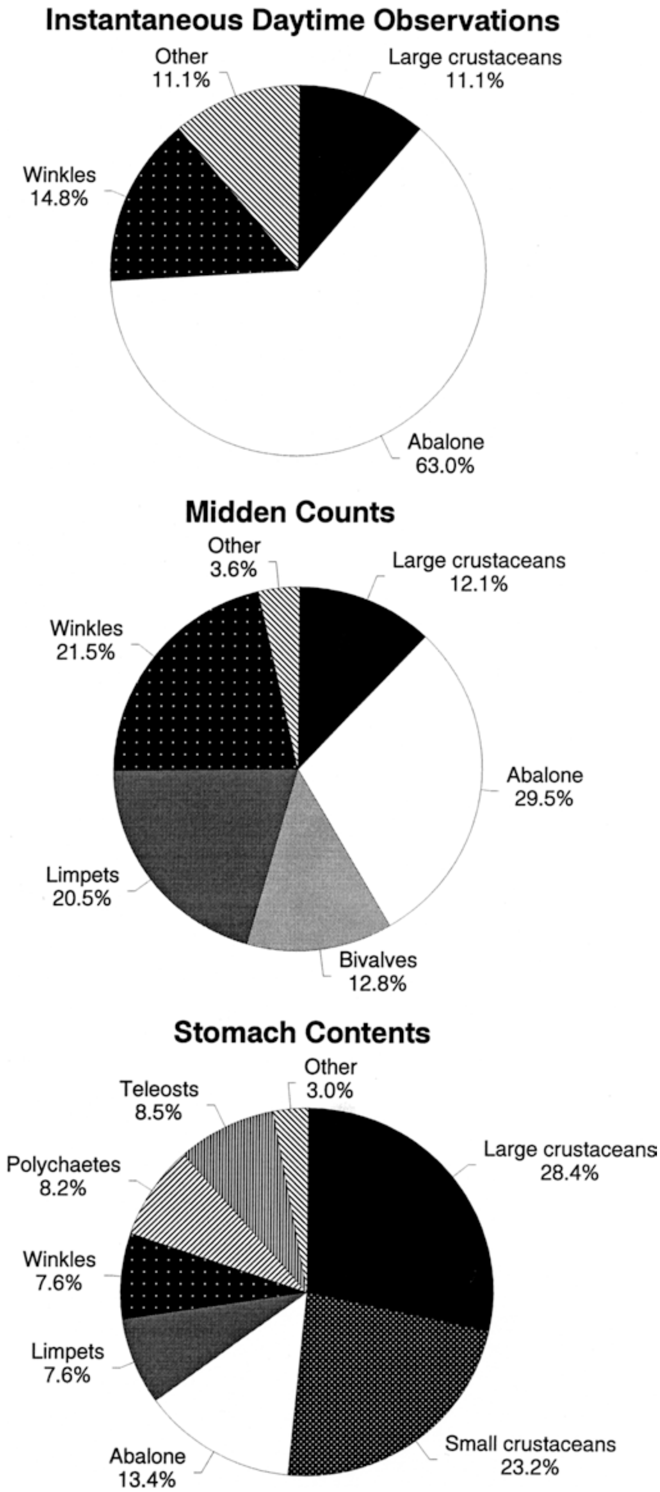


**Fig. 2** Diet of *Octopus vulgaris* in False Bay using frequency of occurrence of prey items for three assessment techniques, namely, instantaneous daytime observations, midden counts, and stomach content analysis

difference between dietary assessment techniques due to a small sample size.

The most important prey species of *O. vulgaris* in False Bay was *P. chabrus* (with a mean carapace width of 41 mm for post-settlement larvae), contributing 64.6% to the total IRI, followed by *H. midae* (21.6%), the amphipod *Paramoera capensis* (2.0%), and *O. vulgaris* (1.0%; Fig. 3). Certain limpets and teleosts are potentially important but could not be quantified, as they were not identified to species level. In terms of prey groups, the crustacean group was the most dominant, occurring in 63.6% of octopuses' stomachs containing food. This was followed by molluscs (37.6% frequency of occurrence), teleosts (11.2%), and polychaetes (10.8%). These figures are calculated from Table 1, using the figure for each group found in column 5 divided by 250 (i.e. the number of octopuses with food in gut), and are expressed as a percentage. Although Table 1 displays summation figures for prey groups, the summed frequency of occurrence figures appear to be incorrect. This is because Table 1 provides prey data on the lowest possible taxonomic level, with frequency of occurrence for prey groups calculated independently of this table as opposed to straight summations of number and volume figures. For example, if an octopus contained the following crustaceans in the gut: one amphipod, one isopod and one crab, then the frequency of occurrence of crustaceans as a group would be recorded as one and not three. This indicates that crustaceans were present in the gut irrespective of number of crustacean species.

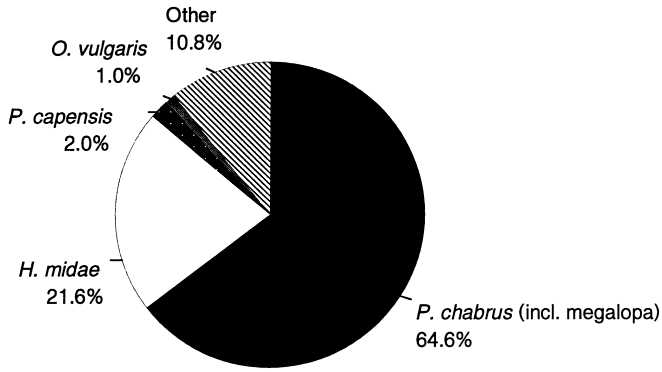


**Fig. 3** The most important prey species in the diet of *O. vulgaris* from False Bay expressed as percentage IRI (index of relative importance; total IRI = 2,818)

Diets of small, medium, and large octopuses differed significantly (ANOSIM: Global $R = 0.076$, $P < 0.05$). The diet of small octopuses differed significantly from both medium ($R = 0.082$, $P < 0.05$) and large octopuses ($R = 0.138$, $P < 0.05$), with approximately 60% of the average dissimilarity between small and medium, and small and large octopuses being attributed to small crustaceans, large crustaceans, and abalone. The diet of small octopuses was largely attributed to small crustaceans (41.8%), large crustaceans (20.4%), and winkles (17.3%; Fig. 4). In contrast, the diet of medium and large octopuses consisted largely of four prey groups, namely, large crustaceans (26.5% and 28%, respectively), small crustaceans (21.4% and 17.8%), abalone (17.1% and 16.1%), polychaetes (12% in medium

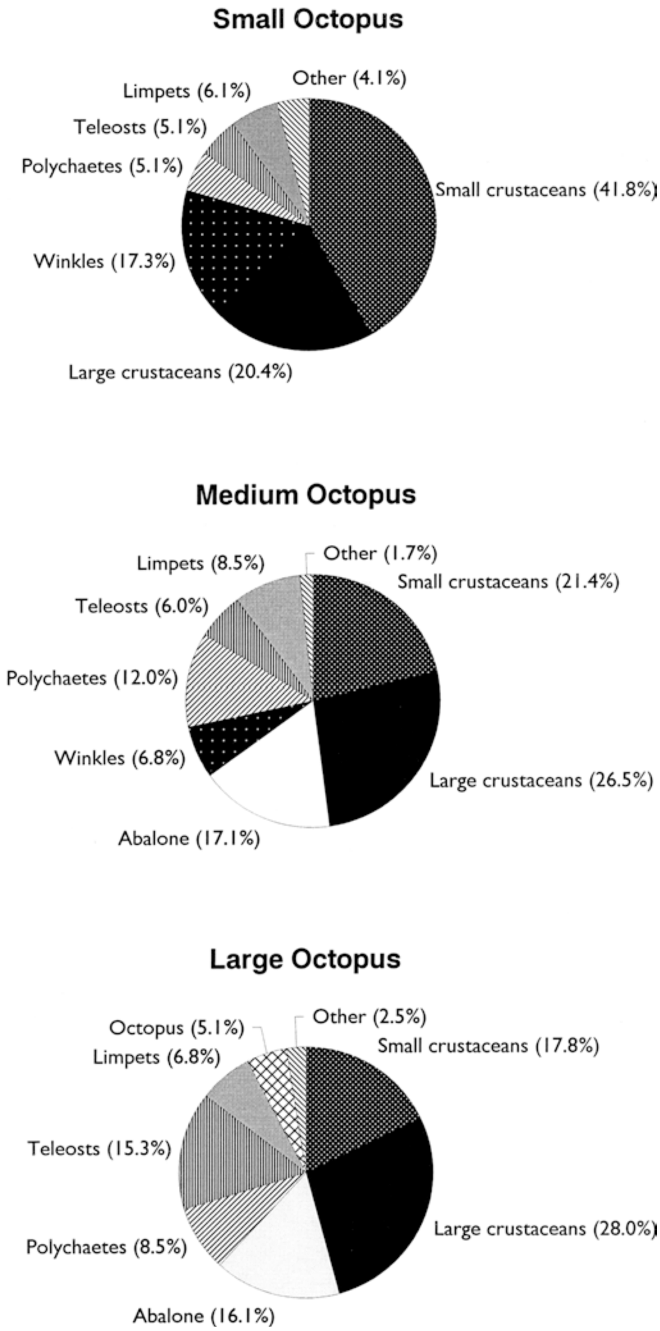


**Fig. 4** Contribution of prey items to the diet of small (0–300 g), medium (301–1,000 g), and large (> 1,000 g) *O. vulgaris* in False Bay using frequency of occurrence of prey items in stomachs. Number of octopuses containing food in stomachs for small, medium, and large octopuses was 54, 87, and 109, respectively

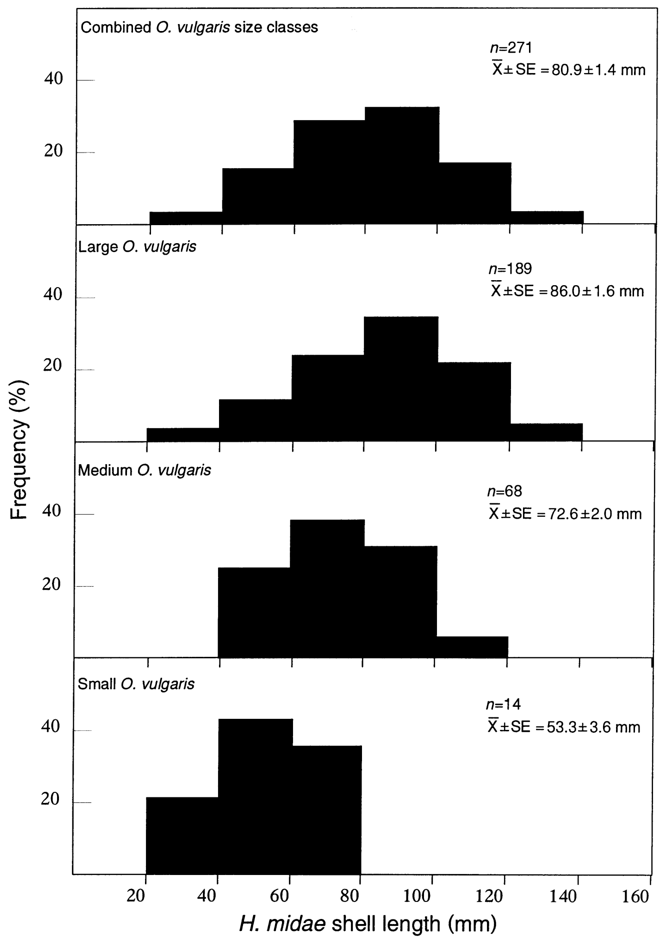


**Fig. 5** Percentage frequency distribution of *Haliotis midae* size classes found in dens occupied by small (0–300 g), medium (301–1,000 g), and large (> 1,000 g) *O. vulgaris* in False Bay, as obtained by midden counts

octopuses), and teleosts (15.3% in large octopuses; Fig. 4). No significant differences were found between the diets of medium and large octopuses ($R = 0.023$, $P > 0.05$).

Middens revealed that *O. vulgaris* in False Bay consumed *H. midae* with shell lengths ranging from 30 to 131 mm (mean 80.9 mm; Fig. 5). Significant differences existed between the mean size of *H. midae* consumed by small, medium, and large *O. vulgaris* (ANOVA: $F_{268} = 23.71$; $P < 0.05$): the mean shell length of abalone consumed by small octopuses (53.3 mm) was significantly smaller than that taken by medium octopuses (72.6 mm, $P < 0.05$) and large octopuses (86.0 mm, $P < 0.05$; Fig. 5). Medium octopuses also consumed significantly smaller abalone than large octopuses ($P < 0.05$).

## Discussion

Using all three diet assessment techniques simultaneously is useful, as it provides the most complete picture of octopus diet, both qualitatively and quantitatively. However, the importance of prey items differed between assessment techniques and these differences are probably due to the time scale over which diet is analysed by each technique. For example, instantaneous observations reveal only what octopuses are eating at time of capture. Sampling at night using this technique may have yielded different results as octopuses may target different prey items at night (Nigmatullin and Ostapenko 1976; Hatanaka 1979).

Instantaneous observations are useful for verifying whether species remains found in middens were actually consumed by an octopus or whether they were solely used for the modification of the midden. As digestion rates in *O. vulgaris* are assumed to be approximately 16 h (Boucaud-Camou et al. 1976), this technique is useful to determine what octopuses consumed the previous night without having to sample at night. The problem with this method is that hard parts (such as bones, setae, exoskeletons) are likely to have a longer gut retention time, thereby emphasizing the importance of teleosts, polychaetes, and crustaceans. Also prey size is difficult to estimate. The distinct advantage with stomach content analysis is that it can assess the importance of small prey items of octopus, such as amphipods, isopods, and megalopa larva. As these prey items are ingested whole they are not found in middens (Smale and Buchan 1981; personal observation). These prey items are also too small to be detected by instantaneous observations. Midden counts provide dietary data over a number of days. The disadvantage of this method is that lighter material is easily removed by biotic and abiotic factors (Ambrose 1983; Mather 1991), thereby emphasizing the importance of heavy shelled prey, such as abalone, bivalves, and limpets. The advantages of this method are (1) it offers the least disturbance to octopuses; (2) a diverse number of prey items can be identified to species level; and (3) prey size is easily measured. Understanding the strengths and weaknesses of each technique is important for interpreting the diet as well as comparing results of dietary studies.

As with *O. vulgaris* elsewhere (Mangold 1983), the population in False Bay consumes a wide range of prey, including crustaceans, molluscs, polychaetes, and teleosts. *O. vulgaris* mainly consumes *P. chabrus* in False Bay as opposed to the brown mussel *Perna perna* off the east coast of South Africa (Smale and Buchan 1981). The dietary difference between study sites is indicative of the opportunistic nature of *O. vulgaris* with diet reflecting prey availability at the different sites. As octopuses are known to cause problems in a number of crustacean and molluscan fisheries (Rees and Lumby 1954; Boyle 1997; Kojima 1992) it is worth noting their interactions with *H. midae* and the rock lobster *Jasus lalandii*, which supports important fisheries in the Western Cape. All three dietary techniques indicate that abalone is an important prey item of *O. vulgaris* in False Bay. Consequently, substantial predation of *H. midae* can exacerbate already declining recruitment caused by recent ecological shifts in the environment east of Cape Hangklip (Tarr 2000). In contrast, *J. lalandii* is an insignificant component in the natural diet of *O. vulgaris* in False Bay. However, when presented with the opportunity *O. vulgaris* frequently prey on *J. lalandii* caught in traps (personal observation). This opportunistic feeding behaviour has also been observed for other similar octopus species, namely *O. maorum* (Ritchie 1972), *O. tetricus* (Joll 1977), and *O. magnificus* (personal observation). The frequency of occurrence of crustaceans and teleosts in the diet in False Bay was similar to other shallow-water (< 15 m) *O. vulgaris* populations in the western Mediterranean (Sanchez and Obarti 1993) and along the east coast of South Africa (Smale and Buchan 1981), but the contribution of teleosts was markedly less when compared to deeper-water (> 15 m) populations in the western Mediterranean (Quetglas et al. 1998), off South Carolina (Whitaker et al. 1991), and off the northwest coast of Africa (Nigmattulin and Ostapenko 1976; Hatanaka 1979). These comparisons probably reflect the difference in prey availability with depth.

When comparing diet as a function of octopus size, small octopuses were found to be more specialized predators consuming mainly amphipods, isopods, and megalopa larvae and to a lesser degree crabs and winkles. Medium and large octopuses had a more diverse and generalist diet with importance being more evenly distributed among large crustaceans, small crustaceans, abalone, polychaetes, and teleosts. Smale and Buchan (1981) also observed an increase in prey diversity with increasing octopus size. Cannibalism occurred in large octopuses (> 1,000 g), in accordance with other reports for *O. vulgaris* along the South African east coast (Smale and Buchan 1981), *O. dofleini* (Hartwick et al. 1978 cited in Nixon 1987; Hartwick 1983), and *O. magnificus* (Villanueva 1993).

The mean shell length and range of *H. midae* consumed by *O. vulgaris* increased with increasing octopus size. A similar result was found for *O. vulgaris* feeding on the mussel *P. perna* by Smale and Buchan (1981). In both studies it was assumed that shells in octopus dens are prey remains and not material used solely for the modification of dens. As many octopuses were observed eating abalone in their dens, this assumption is most likely valid in False Bay.

Unlike the high frequency of boreholes in *H. discus discus* shells reported by Kojima (1992), *H. midae* shells in middens were seldom bored (percentage frequency of occurrence = 3.4, $n = 236$). This absence may indicate that octopuses are ineffective at boring through thicker molluscan shells, as reported by Ambrose et al. (1988), and that *O. vulgaris* can overpower *H. midae*. As strength increases with octopus size, it explains why larger octopuses are capable of overpowering and consuming larger *H. midae*. This study supports the suggestion made by Kojima (1992) that bored abalone shells yield a minimal estimate of octopus predation on abalone. It is also noteworthy that abalone shells less than 30 mm in length were not found in middens. Abalone less than 30 mm may be protected against octopus predation, as they shelter under sea urchins (Day and Branch 2000). However, in the area east of Cape Hangklip where sea urchins have been eradicated by invading west coast rock lobsters (Tarr et al. 1996; Tarr 2000), octopuses may play a significant role in the high mortality of juvenile abalone. Consequently, recruitment failure will negatively impact upon the sustainability of the abalone fishery. Abalone larger than

130 mm were not found in middens. This may be attributed to stronger adhesion and thicker shells of larger specimens.

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