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Feeding habits and diet composition of *Octopus cyanea* (Gray, 1849) in Zanzibar waters, Tanzania

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Abstract

The octopus fishery in Zanzibar is an essential activity of coastal communities. To assist with developing fisheries management plans, baseline information on the feeding of *Octopus cyanea* (Gray, 1849) was collected in relation to sex and maturity stages. The feeding habits and diet composition of 543 *O. cyanea* were studied over a period of 12 months at Paje, Kizimkazi, Chwaka Bay and Nungwi. Samples at each site were collected on two days per month during spring tide. Digestive tract contents revealed that *O. cyanea* preyed on 36 species of crustaceans, molluscs and fishes, with crabs a major prey item. The number of prey species in a single stomach ranged from one to six. *O. cyanea* in Zanzibar is therefore a generalist predator with a mixed diet. The octopus gonadosomatic index (GSI) indicated a peak breeding season in June to October, which correlated with low prey consumption. Mature octopuses ingested a small amount of food from mainly small sessile prey. Females consumed less food than males of similar maturity stages, suggesting that they ate less or had higher digestion rates. The information is useful for developing fisheries management plans for the octopus fishery in Zanzibar.

Keywords: *Octopus cyanea*, sex, maturity stage, frequency of occurrence, Zanzibar waters

Introduction

The big blue octopus, *Octopus cyanea* (Gray, 1849), is a shallow-water species that spends its life in intertidal and sub-tidal reefs for refuging, hunting, and reproduction (Norman *et al*., 2001). It is found in different parts of the world, from East Africa (Guard and Mgaya, 2002) through Madagascar (Benbow *et al*., 2014), French Polynesia (Scheel *et al*., 2017), India (Nair *et al*., 2018), Australia, and Hawaii (Herwig *et al*., 2012). This octopus is one of the most harvested species in tropical and sub-tropical regions for commercial, subsistence, and recreation purposes (Guard and Mgaya, 2002; Herwig *et al*., 2012). It dominates the octopus catch, accounting for about 99 % of all catches in Tanzania and Zanzibar (Guard and Mgaya, 2002; Rocliffe and Harris, 2016).

Octopuses need sustainable fisheries and appropriate management measures to flourish and increase their population size (Pita *et al*., 2021). Such management undertakings have been introduced in Zanzibar based on size limits and seasonal closures (Rocliffe and Harris, 2016). However, these management measures have currently failed to satisfy the community's expectations (personal observation). It is expected that the underperformance of these management approaches is probably due to a lack of linkage between scientific information and community knowledge. Thus, there is a need to study the trophic ecology of *O. cyanea* to provide baseline information that can aid in the formulation of a management plan for the area.

The management effort needs robust information to make informed decisions about the future preservation of particular species (Herwig *et al*., 2012). Therefore, this knowledge of the trophic ecology of

O. cyanea would be used as a reference point by the managers and practitioners in the formulation of the management strategies. Moreover, the information from this study would also provide insight for the growth assessment of this species in captivity (Rosas-Luis *et al*., 2019). Despite the presence of some studies on growth, fisheries, and reproductive biology (Guard and Mgaya, 2002), catch status (Rocliffe and Harris, 2016), growth, exploitation rate, and recruitment pattern (Silas *et al*., 2021), and the environmental influence on abundance and distribution (Chande *et al*., 2021), the trophic ecology of *O. cyanea* has not yet been studied in Zanzibar.

Materials and methods

Description of study area

This study was conducted in Unguja, one of the two sister islands that form Zanzibar (Fig. 1). Octopus samples were collected at Kizimkazi and Paje (in the southern parts), Nungwi (in the northern part), and Chwaka Bay (in the central part). All samples were collected from the artisanal fishermen, who used both on-foot and diving collection methods.

Biological sampling

The samples of *O. cyanea* were collected monthly for a period of 12 consecutive months. For each month, two

Figure 1. The Map of Unguja Island (Tanzania) showing the four sampled sites.

O. cyanea is a generalist predator feeding on fish, molluscs, annelids, and arthropods (Armendáriz Villegas *et al*., 2014). Like most octopus species, its feeding preference reflects the prey composition in a given environment (Scheel *et al*., 2017). Since Zanzibar is home to a variety of marine species, *O. cyanea* is expected to exhibit a feeding pattern that reflects the prey population and composition in the environment (Scheel *et al*., 2017). The goal of this study was to examine the feeding habit and diet composition of *O. cyanea* using stomach content analysis in relation to sex and gonadal maturity stages in Zanzibar.

days of the spring tide were spent collecting samples at each site. Once landed, all samples were taken to a laboratory where the dorsal mantle length (DML) and the total body weight (TW) were measured and the sex determined. The DML was measured using a measuring tape to the nearest 0.5 cm, while the TW was measured using an electronic digital balance to the nearest 0.5 g. Sex was determined by observing the presence of spermatophoric grooves (a whitish-gray line on the ventral surface) on the third right arm of males and their absence in females (Herwig *et al*., 2012). Once measured, octopuses were dissected, their gonads and

stomachs extracted, and preserved in a 10 % freshwater formalin solution.

Diet analysis and prey identification

The stomachs were weighed after extraction, and the prey items were identified and counted. To make them clear, all contents were flushed with fresh water and put on a tray ready for sorting. The prey items extracted from each octopus were recorded monthly. The empty stomachs were also recorded. All data pertaining to feeding was recorded by sex and maturity stage. The stomach fullness was determined and grouped into five levels (empty, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$ and bloated) based on the distension and amount of prey in the stomachs. The bloated level denoted a swollen stomach, which was completely filled with food, while the empty level denoted a stomach devoid of food. The following indices were calculated:

- Fullness weight index (FWI) was calculated as the ratio of the digestive tract content to the total weight of organisms less the empty digestive tract weight (Villegas *et al*., 2014).
- The digestive tract weight index (DTWI) was calculated as the ratio of digestive tract weight to total weight (Quetglas *et al*., 2005).
- Gonadosomatic index (GSI) was calculated as: GSI = $\text{Wo}/(\text{Wt} - \text{Wo})$ *100 Where 'Wo' is the weight of ovary and 'Wt' is the total wet weight (Guard and Mgaya, 2002).

The importance of each prey category was determined using the frequency of occurrence (FO) method. FO was calculated as the percentage ratio between the number of stomachs containing a given prey item with respect to the total number of stomachs containing food (Cortez *et al*., 1995). The digestive tract weight index (DTWI) and the fullness weight index (FWI) were used to determine the amount of food consumed. To determine the prey species in the diet, the number of prey species was counted and recorded by the sexes and maturity stages. In order to relate feeding with maturity, GSI was used to define the peak and least breeding of *O. cyanea* in the area.

The prey items were identified to the lowest possible taxonomic group using a specialized identification key. Crustaceans were identified by the colour of their carapaces and shells and the shape and colour of their chelae (Quetglas *et al*., 2005). Fish were identified using remaining parts of their bodies, while octopus were identified by physical observation when not

under intensive digestion or by the presence of beaks in the octopus body. The foods in an advanced state of digestion were recognized as 'unidentified' but were not included in the calculation of the index. A dissecting microscope was used to examine small prey items from the octopus stomachs. All the data were grouped by sex and maturity stage.

Determination of maturity stages

The gonadal development of male octopuses was classified into three (3) maturity stages: stage I (immature), stage II (maturing) and stage III (mature), while females were classified into five maturity stages: stage 1 (immature), stage II (maturing), stage III (mature), stage IV (spawning), and stage V (spent). This classification was used as per Guard and Mgaya (2002) with a minimal modification. In males at stage III, spermatids and spermatozoa are abundant and there are no empty spaces between cells and in females at stage IV is seen when there is a significant increase in oocyte size, deeper infoldings of the follicular epithelium, as well as increased yolk production. At stage V, female oocytes have been discharged. All individual octopuses staged as stage III, IV and V were classified as mature and those with maturity stages I and II were classified as immature.

Data analysis

To analyze feeding habits and diet composition, all 543 samples of *O. cyanea* were used. The identified prey items were grouped according to taxonomic affinities, resulting in three putative groups: molluscs (bivalves, gastropods, and cephalopods), crustaceans, and fish. The comparison of the sizes of male and female octopuses was determined by means of a t-test. An analysis of the influence of maturity stages on the diet between groups was made by means of a t-test. The comparisons of fullness levels among maturity stages, sexes, and sites were made by means of a one-way analysis of variance (ANOVA). The level of statistical significance used was $p < 0.05$.

Results

Five hundred and forty-three (543) *O. cyanea* individuals were collected, with 294 (54.1 %) females and 249 (45.9 %) males. Females measured from 5 to 29 cm DML and weighed between 73 and 6300 g TW, while males measured from 4 to 24 cm DML and weighed between 64 and 3630 g TW. Based on monthly data, larger octopuses (13–15 cm DML) peaked from June to July and from October to November (Fig. 2). In the sample, the smallest individual observed to mature

Figure 2. Monthly population size (based on DML) of *O. cyanea* in Zanzibar.

measured 7 cm DML for males and 8 cm DML for females. These smallest mature individuals were caught in October. There was no significant difference in DML between male and female individuals ($t = 0.87$, $df = 22$, $p = 0.197$).

Prey consumption and breeding season

The prey consumption by *O. cyanea* peaked in February (110 prey items) and May (100 prey items), while the lowest prey consumption occurred in June (37 prey items) and October (33 prey items). A sharp decline in the prey consumption occurred from May to June (Fig. 3). In comparison to average size based on DML (Fig. 2), large octopuses were caught in June and October, where a small amount of prey was consumed (Fig. 3). Based on the GSI, the breeding season peaked in June and October (Fig. 4). The least breeding season was found to be from January to March, and December for females. In males, lowest breeding was observed in May (Fig. 4).

Dietary analysis

The fullness level varied significantly between the maturity stages in females ($F = 4.18$, df = 3, p = 0.02) but not in males ($F = 1.01$, df = 3, p = 0.42). All five levels of fullness (empty, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$ and bloated) appeared in males only at stages I and II. At stage III, no male octopus appeared with a bloated level of fullness (Fig. 4 B). In females at stages I, II, and III, all five levels of fullness appeared. But females at stages IV and V did not appear with bloated levels of fullness (Fig. 4 A). However, the number of empty stomachs increased with maturity stages and was higher in females than males.

Digestive tract weight index (DTWI) and fullness weight index (FWI)

The DTWI showed a decreasing mode with maturation stages in both sexes. The value of DTWI increased slightly from stage I but reached very minimal levels at stages III in males and stages V in females (Fig. 6).

Figure 3. The monthly percentage occurrence of prey items consumed by *O. cyanea* in Zanzibar coastal waters.

Figure 4. Monthly Gonadosomatic index (GSI) of male and female *O. cyanea* from Zanzibar.

There was no significant difference in DTWI between the sexes (t = 0.20 , df = 3 , p = 0.46). Between the maturity stages, significant differences were detected between stages I and III in males ($p = 0.04$), stages I and IV ($p = 0.01$), and stages II and V ($p = 0.01$).

The value of the fullness weight index (FWI) decreased along with maturity stages. The rate of decrement was higher in males than females. The FWI decreased from stage II to stage III in males and from stage III to stage V in females (Fig. 7). No significant difference in FWI between the sexes was detected $(t = 1.94,$ $df = 3$, $p = 0.45$).

A total of 36 prey species were identified from three major taxonomic groups: crustaceans (83.4 %), mol-
luses (0.2 %) and fish (7.2 %) (Table 1) luscs (9.3 %), and fish (7.3 %) (Table 1).

Crabs were the preferred prey items in the diet*,* contributing over 63 % of all prey items. Sessile (mussels and barnacles) and slow-moving (sea snails) prey items appeared as the lowest prey groups and were only consumed at the final maturity stages (Fig. 8). Unidentified prey materials were higher, accounting for 55 % (58 % for females, 42 % for males) of all food contents. Most of the unidentified materials were a mixture of crabs, fish scales, fish eggs, and other soft-bodied prey, indicating that the octopus has high prey diversity. Cannibalism accounted for 5.32 % of all prey items and was detected in all maturity stages except at stage I in both sexes.

Diet composition

The findings from this study showed that the *O. cyanea* included up to six different prey types in its diet.

Figure 5. The stomach fullness levels of female (A) and male (B) *O. cyanea* with maturity stage.

--Female Male

0.0 0.5 1.0 1.5 Stage I Stage II Stage III Stage IV Stage V **FWI**

2.0 2.5

3.0

Figure 6. Digestive tract weight index (DTWI) by sex and maturity stage.

However, most of the individuals included between two and three prey species in varying quantities (Fig. 8). Mature individuals (stage III for males, stages IV and V for females) consumed a single or few sessile or slow-moving prey species in variable amounts. Single prey consumption was also observed in all maturity stages, especially when the octopus consumed large prey types or a group of prey of a single species.

Frequency of occurrence (FO)

The frequency of occurrence (FO) was presented at the family level. Portunidae (31.88 %) and Grapsidae (15.96 %) were the two most popular prey families appearing in the diet of *O. cyanea*. The most preferred prey family was Portunidae (31.88 %), followed by the family Grapsidae (15.96 %) which are a family of crabs. The least consumed prey were from families Iblidae, Muraenidae, Odontodactylidae, Oziidae, Phasianellidae, and Strombidae, each contributing only 0.25 % of the total diet of *O. cyanea.* All families are summarized in Table 2.

Discussion

The commercial value and ongoing efforts to manage octopus fisheries has increased the need to investigate various aspects of their lives. This study examines the feeding behaviours of *O. cyanea* at various stages of maturity. This information will contribute to a better understanding of the feeding ecology, nutritional profile, and energy balance of this species in relationship to their stages of maturity.

Figure 7. Fullness weight index by sex and maturity stage.

The maturity of octopuses varies with size, and the smallest mature male and female octopuses found in this study were 360 g (7 cm DML) and 610 g (8 cm DML), respectively. Guard and Mgaya (2002) reported the smallest mature male and female in mainland Tanzania, weighing 320 g and 600 g, respectively. However, the smallest mature male and female *O. cyanea* reported in other geographical areas are 350 g and 520 g in Australia (Herwig *et al*., 2012) and 400 g and 450 g in Madagascar (Raberinary and Benbow, 2012). The largest individual of 6300 g differs from the 11700 g octopus caught in mainland Tanzania (Guard and Mgaya, 2002), the 6400 g in Madagascar (Raberinary and Benbow, 2012), the 6500 g in Hawaii, and the 1900 g in Australia (Herwig *et al*., 2012). These variations might be due to effects of geographic location, environmental plasticity, dietary availability, and the management status of the area (Guard and Mgaya, 2002; Semmens *et al*., 2004). The monthly size variations of *O. cyanea* (Fig. 3) could be due to the timing of reproductive onset in the cohorts.

O. cyanea in Zanzibar spawns throughout the year, with June and October being the peak breeding seasons (Fig. 4). June and October are also the months during which the octopus population is characterized by larger individuals compared to other months (Fig. 2). Simply put, June and October are the periods when large individuals experience peak breeding season in Zanzibar. Similar breeding seasons have been reported by Guard and Mgaya (2002) in mainland

Table 1. Frequency of occurrence (%) of the major taxonomic prey groups in the diet of *O. cyanea*.

Figure 8. The occurrence of prey items consumed at various maturity stages of female (A) and male (B) *O. cyanea* in Zanzibar.

Figure 9. Percentage number of prey species found in individual stomachs during laboratory analysis for both females (A) and males (B). The prey included in the diet ranges from one species to six species in the stomach.

Frequency of occurrence, FO (%)						
Family	Stage I	Stage II	Stage III	Stage IV	Stage V	Total
Portunidae	12.4	11.39	6.84	1.01	0.25	31.89
Grapsidae	7.09	5.57	2.02	0.6	0.6	15.88
Octopodidae	Ω	3.52	1.02	0.5	0.25	5.29
Penaeidae	2.79	0.51	0.76	1.23	Ω	5.29
Alphaeidae	1.52	1.78	1.04	0.25	0.25	4.84
Cancridae	1.77	1.52	1.26	0.25	$\mathbf{0}$	4.8
Congridae	2.28	1.27	0.72	0.51	$\mathbf{0}$	4.78
Sergestidae	1.27	0.75	0.25	1.27	$\mathbf{0}$	3.54
Raninidae	1.52	1.26	0.25	0.25	$\mathbf{0}$	3.28
Plagusiidae	2.28	0.25	0.51	$\overline{0}$	$\mathbf{0}$	3.04
Diogenidae	0.25	1.26	0.76	0.25	0.25	2.77
Gecarcinidae	0.76	0.76	$\mathbf{0}$	$\mathbf{0}$	$\boldsymbol{0}$	1.52
Macrophthalmidae	0.25	1.26	$\mathbf{0}$	\mathbf{O}	$\overline{0}$	1.51
Mitridae	0.25	0.52	0.25	0.25	0.25	1.52
Xanthidae	0.76	$\overline{0}$	0.76	$\mathbf{0}$	Ω	1.52
Littorinidae	0.25	Ω	$\mathbf{0}$	1	0.25	1.5
Sesarmidae	0.2	1.26	$\mathbf{0}$	$\mathbf{0}$	$\mathbf{0}$	1.46
Anguillidae	0.76	0.51	$\mathbf{0}$	\mathbf{O}	$\boldsymbol{0}$	1.27
Trapeziidae	0.52	$\overline{0}$	Ω	0.25	$\boldsymbol{0}$	0.77
Calcinidae	$\mathbf{0}$	0.51	Ω	0.25	$\overline{0}$	0.76
Porcellanidae	Ω	0.51	$\mathbf{0}$	$\overline{0}$	$\mathbf{0}$	0.51
Mytilidae	0.26	$\overline{0}$	Ω	$\mathbf{0}$	0.25	0.51
Iblidae	$\mathbf{0}$	$\overline{0}$	Ω	$\boldsymbol{0}$	0.25	0.25
Muraenidae	$\mathbf{0}$	Ω	0.25	$\boldsymbol{0}$	0.25	0.5
Odontodactylidae	$\mathbf{0}$	0.25	$\mathbf{0}$	$\mathbf{0}$	$\overline{0}$	0.25
Oziidae	$\mathbf{0}$	$\overline{0}$	Ω	$\boldsymbol{0}$	0.25	0.25
Phasianellidae	Ω	$\overline{0}$	0.25	$\boldsymbol{0}$	$\mathbf{0}$	0.25
Strombidae	Ω	0.25	Ω	$\overline{0}$	$\overline{0}$	0.25
TOTAL	37.18	34.91	16.94	7.87	3.1	100

Table 2. Frequency of occurrence (FO) of prey families in *O. cyanea* diet by maturity stages. At stages I, II, and III, the value is the average of the male and female individuals.

Tanzania at Mafia, where the peak breeding season of *O. cyanea* is June. The peak breeding season for this species has also been documented in October– November in Rodrigues (Sauer *et al*., 2011) and April– June in Madagascar (Raberinary and Benbow, 2012). Other species like *O. vulgaris* in Kenya exhibit their peak breeding season in June and August (Kivengea *et al*., 2015). Thus, geographical differences and the type of species influence peak spawning time.

By linking the monthly octopus population size (Fig. 2), monthly feeding schemes (Fig. 3), and monthly spawning pattern (Fig. 4), it is revealed that the large and mature individuals are associated with low prey consumption. In other words, the large and mature animals that dominate the population in June and October consume a very minimal amount of prey. Meanwhile, in February and May, the months of small-sized octopuses, the *O. cyanea* experiences its lowest GSI, indicating that the population of octopuses is dominated by immature individuals that consume more prey items. This supports the notion that small, non-spawning octopuses consume more prey to invest more energy required for the spawning process in the following months (Archer *et al*., 2022). A similar situation has been reported for immature *O. mimus* in China that experiences high feeding intensity in April and June (Bo *et al*., 2020). This is probably because each octopus species experiences different feeding patterns depending on the period of availability and prey abundance in a particular geographical location. In Zanzibar, prey abundance is higher in February and May.

The food content in the octopus stomach is affected by their maturity stages. The studies conducted by Cortez *et al*. (1995) and Armendáriz Villegas *et al*. (2014) revealed that the average number of empty stomachs increases as animals mature, which suggests a subsequent decrease in food intake with maturity. The current results show that empty stomachs in females ranged between 11 and 18 % for immature individuals

and 22 and 92 % for mature individuals (Fig. 5A). In males, empty stomachs ranged between 10 and 16 % for immature specimens, while mature specimens had about 53 % empty stomachs (Fig. 5 B). These results provide an indication that octopuses modify their feeding with their stage of maturity. Such changes in food intake have been observed in various species in both captivity and the wild (Ernesto *et al*., 2010). For example, Quetglas *et al*. (2005) observed a high incidence of empty stomachs in ripe *O. salutii,* while Bo *et al*. (2020) noticed the presence of more than half of adult *O. minor* females with empty stomachs.

The feeding modification with maturity stages aims to accommodate the physiological requirements of octopuses (Bo *et al*., 2020). For example, during the spawning stage, octopuses stop feeding while focusing exclusively on laying and caring for eggs (Anderson *et al*., 2002). During this period of no or less feeding, octopuses rely on energy in the form of adenosine triphosphate (ATP) from body reserves (Domínguez-Estrada *et al*., 2022). Because an excessive amount of ATP is required throughout the brooding period, their muscles deteriorate and animals become physically less active, hence unable to hunt (Meza-Buendía *et al*., 2021). However, the observed empty stomachs during immature and mature stages are because the octopuses maximize digestion rate to provide energy required for growth and other metabolic activities (Archer *et al*., 2022). The reason why immature octopuses eat more food (87 % for females, 85 % for males) than mature ones is the need to accelerate their body growth and stimulate gonadal development (Villanueva *et al*., 2004; André *et al*., 2009). The observation of more bloated stomachs at immature stages indicates a high food intake. The low values of DTWI (Fig. 6) and FWI (Fig. 7) emphasize that mature individuals consume less food than immature ones.

In general, this study found more food in male *O. cyanea* than females throughout the maturity stages (Fig. 5). This could be explained by two scenarios: first, the male *O. cyanea* maximizes their food and energy investment for searching mates, attraction of females, courtship, fighting, and sperm competition so as to achieve early reproductive success (Bonduriansky *et al*., 2008; Archer *et al*., 2022; Omedes *et al*., 2022). Second, female *O. cyanea* grow to a larger body size (Fig. 2) than males, so they need an extended time to allocate resources needed to produce offspring, and in doing so, they double their physiological processes faster than males (Archer *et al*., 2022). Due to this,

their food is digested more quickly than that of males (Omedes *et al*., 2022), and they invest it in the development of the vitellus (Bo *et al*., 2020). This may explain why more unidentified food remains was found in females than in males in this study, showing that their rapid digestion rates have an immediate impact on the prey they eat.

Octopuses are well-known generalist and opportunistic predators of a variety of prey species (TAFIRI unpublished data), having very high metabolic rates compared to many other benthic predators (Song *et al*., 2019). Their high metabolic processes enable them to consume more prey per unit of time in an efficient manner (Onthank and Cowles, 2011). This generalist predation assures them of their ability to search, capture, and handle a diverse range of prey types to meet their energy and nutrient demands (Scheel *et al*., 2017; Portela *et al*., 2014). The diet of *O. cyanea* in this study was composed of 36 prey species (Table 2). This finding was unsurprising because such generalist feeding has been documented in *O. cyanea* in French Polynesia (Scheel *et al*., 2017). Other octopus species, such as *O. bimaculatus* (Armendáriz Villegas *et al*., 2014), *O. vulgaris* (Smith, 2003), *O. insularis* (Rosas-Luis *et al*., 2019), *O. mimus* (Cortez *et al*., 1995), and *O. minor* (Bo *et al*., 2020), have been described as generalist predators. *O. cyanea* can include up to six different prey species in the stomach at a time, but the inclusion of 2–3 prey species in the diet is common (Fig. 9).

Crustaceans were the most abundant prey consumed by *O. cyanea* (83.4 %), followed by molluscs (9.3 %) and fish (7.3 %) (Table 1). The importance of crustaceans in the octopus diet has been reported by Smith (2003), Rosas-Luis *et al*. (2019), and Bo *et al*. (2020) in the wild, but also proved by Prato *et al*. (2010), Martnez *et al*. (2014), Caamal-Monsreal *et al*. (2016), Maselli *et al*. (2020), and Urrutia-Olvera *et al*. (2021) in captivity. Crab was the most preferred prey in *O. cyanea* (63.75%) , followed by shrimp (13.75 %). Fish and octopus contributed (7.25 %) and (5.25 %) to the diet, respectively. *Charybdis* sp. and *Grapsis* spp. dominated the diet, suggesting their suitability to satisfy the energy demand of *O. cyanea*. *Charybdis* sp., *Grapsus* sp., and *O. cyanea* are coral-associated species (Urrutia-Olvera *et al*., 2021), so the likelihood of an octopus encountering these prey species is higher during foraging time.

Crabs and shrimp were consumed at all maturity stages of the octopus, representing their important role in the energy needs of the octopus (Martínez *et al*.,

2014; Caamal-Monsreal *et al*., 2016; Urrutia-Olvera *et al*., 2021). Most sedentary and slow-moving prey species, such as sea snails, mussels, and barnacles, are consumed by mature (mainly spawning) individuals (Fig. 8). Because of the time and energy investment in egg brooding, it becomes difficult for the spawning individuals to obtain crabs; instead, they adopt an energy-saving technique by relying on these sessile animals found within their habitats or dens (Leite *et al*., 2009; Maldonado *et al*., 2019). This was evidenced in the present study, where the intake of primary prey (*Charybdis* sp. and *Grapsus* sp.) was almost nill (Table 2). Cannibalism is common in octopuses, and it was found in all maturity stages except in stage I individuals (Table 2), demonstrating that the larger individuals consume the smaller ones. In general, data from this study can be included in the management plan for this species, especially when deciding the periods for implementation of management measures.

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Suplementary material

Table S.1. The prey species consumed by *O. cyanea* in Zanzibar.

