Vertical distribution, behavior, chemical composition and metabolism of *Stauroteuthis syrtensis* (Octopoda: Cirrata) in the northwest Atlantic

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ABSTRACT: The cirrate octopod *Stauroteuthis syrtensis* is a mesopelagic species commonly collected in the North Atlantic. Individuals were observed at depths >600 m and typically within 100 m of the bottom in three ~900 m deep canyons indenting the southern edge of Georges Bank. When first sighted, most octopods were floating passively with their webbed arms gathered into a small ball. When disturbed, they expanded their webs to form a 'balloon' shape, swam slowly by sculling their fins, pulsed their webs like medusae and, in some cases, streamlined their arms and webs and moved away smoothly by rapidly sculling their fins. The bodies of 9 octopods comprised 92 to 95% water, with tissue containing 9 to 22% carbon (C) and 2 to 4% nitrogen (N). These values were similar to those reported for medusae and ctenophores. Oxygen (O_2) consumption rates of 4.6 to 25.8 µmol O_2 g^{-1} C h^{-1} were within ranges reported for medusae, ctenophores, and deep-water cephalopods. The stomachs of *S. syrtensis*, dissected immediately after capture, contained only the calanoid copepod *Calanus finmarchicus*. Calculations indicated that *S. syrtensis* need 1.3 to 30.1 ind. d^{-1} of *C. finmarchicus* to meet their measured metabolic demand. Excretion rates (0.3 to 12.4 µg NH_4^+ g^{-1} C h^{-1} and 0.06 to 4.83 µg PO_4^{3-} g^{-1} C h^{-1}) were at least an order of magnitude lower than rates reported for other octopods or gelatinous zooplankters. O:N ratios (11 to 366) suggested that *S. syrtensis* catabolized lipids, which may be supplied by *C. finmarchicus*. Vertical distribution, relatively torpid behavior and low metabolic rates characterized *S. syrtensis* as a benthopelagic and relatively passive predator on copepods.

KEY WORDS: *Stauroteuthis syrtensis* · Respiration · Excretion · Chemical composition · Vertical distribution · Behavior

INTRODUCTION

Stauroteuthis syrtensis Verrill, 1879 is a deep-water octopod that occurs throughout the North Atlantic (Collins & Henriques 2000, Collins et al. 2002, Collins & Villanueva 2006). Most specimens have been collected at depths of 500 to 4000 m, with many speci-

mens caught in bottom trawls and higher abundances reported at depths of 1500 to 2500 m (e.g. Collins & Henriques 2000, Collins et al. 2001, 2002, Vecchione & Galbraith 2001, Vecchione & Pohle 2002). Specimens captured at depths of 250 to 500 m off Greenland and Iceland provided evidence that the vertical distribution of this species was influenced by water temperature as

Iceland provided evidence that the vertical distribution of this species was influenced by water temperature as much as, or more so than, depth (Collins 2002).

Stauroteuthis syrtensis has been observed to display a variety of behaviors, including swimming by sculling its paired fins, swimming via medusoid contractions of its web complex, inflating its web to varying degrees, and inverting its arms and web to expose suckers that differ from those of most octopods in that they contain bioluminescent photophores and are not adhesive (Vecchione & Young 1997, Johnsen et al. 1999, Collins et al. 2002, Collins & Villanueva 2006). Inflation and inversion of the web have been hypothesized to be defensive responses to disturbance or behaviors involved in capturing small crustacean prey attracted by the bioluminescence emanating from the suckers (Vecchione & Young 1997, Johnsen et al. 1999, Collins et al. 2002). A secondary web that links the arms to the primary web in *S. syrtensis* and other Cirroteuthidae facilitates behaviors such as medusoid swimming, inflation and inversion.

Similar to other members of the suborder Cirrata, *Stauroteuthis syrtensis* possesses a fragile, semi-gelatinous body (Collins & Henriques 2000, Collins et al. 2002), which suggests that the metabolic rates of *S. syrtensis* should resemble those of medusae and ctenophores, rather than the higher respiratory demands of more muscular cephalopods. In addition, if *S. syrtensis* ambushes prey, perhaps by using its bioluminescent suckers as lures, then its O_2 consumption rates should be relatively low and similar to other deep-water cephalopods that have replaced visually guided pursuit of prey with an ambush strategy (Childress & Mickel 1985, Seibel et al. 2000, Seibel & Carlini 2001).

The present study provides the first measurements of O_2 consumption and NH_4^+ and PO_4^{3-} excretion for *Stauroteuthis syrtensis* collected in Oceanographer Canyon, a deep-water canyon that indents the southern boundary of Georges Bank. Furthermore, *in situ* observations from crewed submersibles documented the vertical distribution and behavior of these octopods in this and 2 adjacent canyons, Hydrographer and Lydonia Canyons.

MATERIALS AND METHODS

Observation and collection. *Stauroteuthis syrtensis* were observed from 'Johnson-Sea-Link' submersibles, which operate to a depth of 914 m (Youngbluth 1984). Visual observations were made in Hydrographer, Oceanographer and Lydonia Canyons during June 1995, September 2001, June 2002, September 2003, September 2004, and October 2005 (Fig. 1). Individuals for studies of respiration and excretion were collected
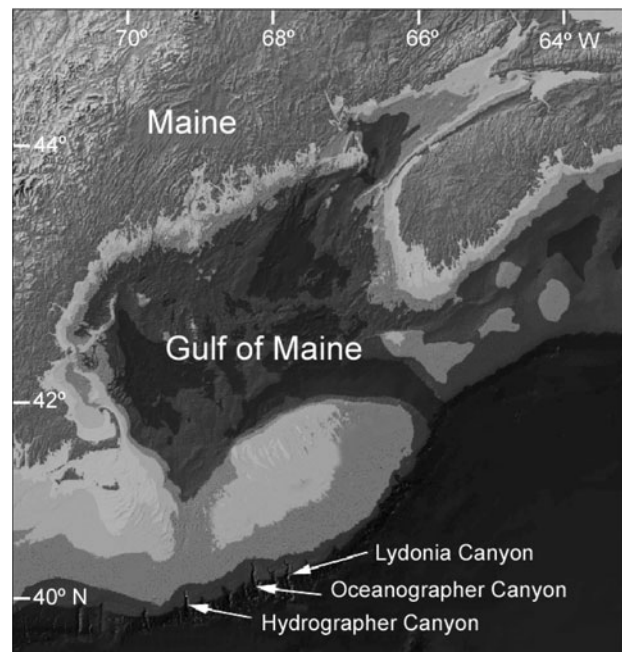

Fig. 1. Locations of sampling for cirrate octopods *Stauroteuthis syrtensis*

in Oceanographer Canyon during September 2004. At the sampling stations, dates, times, depths, temperatures, salinities, and concentrations of dissolved O_2 were recorded with Seabird SBE 25 Sealoggers.

Octopods and water samples without visible organisms (i.e. controls) were collected in 6.5 l acrylic samplers that had been washed with a 1 mol l^{-1} HCl solution prior to use (Tietze & Clark 1986). An individual sampler contained either 1 individual of *Stauroteuthis syrtensis* or a control water sample.

Measurements of respiration and excretion. Upon return to the surface, samplers were transferred quickly from the submersible to a dark room maintained at an air temperature of 4 to 5°C, which mimicked *in situ* conditions. Within 28 h of capture, all octopods except the largest individual (wet weight, WW = 158 g) were transferred gently into 0.5 to 2.2 l acrylic chambers. These smaller chambers, which acted as respirometers, were filled and sealed in a manner that avoided the formation or trapping of air bubbles. When additional water was needed to fill a smaller chamber, seawater collected in Niskin bottles from 800 to 900 m water depth was added. The largest individual was too large for the smaller chambers, so it was incubated in the original 6.5 l sampler, which served as a respirometer.

An experiment consisted of one or more respirometers, each holding a single octopod, and a respirometer that contained water without visible organisms, which yielded measures of background changes in concen-

trations of dissolved O_2, NH_4^+ and PO_4^{3-}. Antibiotics were not added to any of the respirometers. During experiments, all respirometers were kept in darkness at 4 to 5°C and ambient pressure (1 atm) for 9 to 22 h.

O_2 consumption was measured concurrently in control and experimental respirometers with a noninvasive, micro-optode system (PreSens; http://microoptode.com/html/start.html). O_2 concentrations (µmol O_2 l^{-1}) were logged at 1 s intervals. In some experiments, recordings were conducted for 30 min periods, separated by 30 to 60 min intervals, so that O_2 consumption could be tracked in multiple respirometers using a single micro-optode system. Records from the initial 2 to 6 h were excluded from estimates of O_2 consumption to eliminate periods of equilibration and acclimation. Rates of O_2 consumption were calculated using least-squares linear regression, and only the results of statistically significant regressions were used. If controls yielded statistically significant rates of O_2 consumption, these values were subtracted from the appropriate experimental rates to account for respiration by organisms other than *Stauroteuthis syrtensis*.

Winkler titrations were performed on duplicate water samples removed from representative respirometers (Wetzel & Likens 2000). When compared to records from micro-optodes, these measurements provided a check on the reliability of the time series.

Duplicate samples for estimating NH_4^+ excretion and either duplicate or single samples for estimating PO_4^{3-} excretion were extracted from an acrylic sampler at the beginning of an experiment, i.e. an initial control, and from control and experimental respirometers at the end of the incubation periods. Due to a contaminated filtering apparatus and unavoidable delays in obtaining a replacement bulb for the spectrophotometer, these samples were not filtered, and they were frozen at −20°C for up to 11 d before analysis. Concentrations were determined by standard spectrophotometric methods using a Spectronic Genesys 8 spectrophotometer, with a 10 cm cuvette at 640 nm for NH_4^+ and 882 nm for PO_4^{3-} (Strickland & Parsons 1972, American Public Health Association 1989). Rates of NH_4^+ and PO_4^{3-} excretion not attributable to *Stauroteuthis syrtensis* were calculated using concentrations in the appropriate initial and final controls, and these values were subtracted from rates calculated using final concentrations in experimental respirometers and initial concentrations from the appropriate controls. Only positive differences were reported.

Following experiments, *Stauroteuthis syrtensis* were transferred to tared pans and frozen (−20°C). In a shore-based laboratory, each frozen specimen was thawed and its WW was recorded to the nearest 0.1 g. After determination of WW, specimens were dried at 60°C until a consistent dry weight (DW) was obtained

to the nearest 0.1 g over a period of 2 to 4 d. Each dried specimen was thoroughly homogenized, and aliquots were sent to the Analytical Laboratory of the Marine Science Institute at the University of California, Santa Barbara, where proportions of C, H and N were determined using a Perkin-Elmer Model 240 elemental analyzer and an acetanilide standard.

RESULTS

Vertical distribution

Eighty-one *Stauroteuthis syrtensis* were sighted in 4 canyons during 24 dives conducted during 6 cruises. Approximately 90% of the octopods were recorded as single individuals in a field of view that encompassed approximately 400 m^3 of water. The maximum number of individuals sighted in a single field of view was 5; this observation took place at approximately 14:00 h on 7 September 2002 at a depth of 848 m in a water column of 1000 m in Oceanographer Canyon.

Stauroteuthis syrtensis were sighted at depths of 603 to 908 m (mean ± SE: 780.9 ± 8.3 m; Table 1). The octopods were observed from ~0.5 to 258 m above the bottom (100.1 ± 7.2 m). The 35 individuals observed during daytime dives (14:00 to 17:00 h) and the 46 individuals observed during nighttime dives (20:00 to 00:30 h) were sighted at similar, but significantly different distances above the bottom (daytime 81.2 ± 10.6 m, nighttime 114.4 ± 9.2 m, $t = -2.37$, df = 73, p < 0.05). Octopods were collected or sighted in water with temperatures ranging from 4.20 to 6.14°C (4.67 ± 0.06°C), salinities ranging from 34.86 to 35.03 psu (34.96 ± 0.01 psu), and dissolved O_2 concentrations ranging from 3.00 to 5.54 ml l^{-1} (4.83 ± 0.16 ml l^{-1}) (Table 1).

Behavior

When first sighted, most *Stauroteuthis syrtensis* were floating passively, with their arms contracted, webs curled into a small ball and eyes hooded. When disturbed, seemingly by light, noise, or turbulence from the submersible, octopods would expose their eyes and unfold their webs, which they often inflated. Initially, octopods tended to move away from the submersible by sculling their fins or pulsing their webs like a medusa. Eventually, some octopods streamlined their webbed arms behind their bodies and increased the rate at which their fins sculled to move away from the submersible smoothly and more rapidly.

Neither hunting nor feeding behavior was observed, which was expected given the response of the octopods to disturbance from the submersibles. The guts of

Table 1. *Stauroteuthis syrtensis.* Details for collections and sightings of cirrate octopods from Oceanographer Canyon for use in metabolic experiments. Salinity was consistantly 35 psu. –: data not applicable

Octopod	Date	Latitude, Longitude	Time of collection (h)	Depth of collection or sighting (m)	Depth of bottom (m)	Temperature (°C)	Dissolved O_2 (ml l^{-1})
1	17 Sep 2004	40° 20.182 N, 68° 08.277 W	14:45	888	930	4.30	5.52
2				807		4.37	5.48
3		40° 20.427 N, 68° 08.291 W	22:42	784	910	4.60	5.35
4			22:53	725		4.80	5.25
5			21:48	821		4.59	5.36
6			21:25	908		4.44	5.42
7	22 Sep 2004	40° 19.996 N, 68° 07.997 W	14:45	741	913	4.74	5.28
8		40° 20.363 N, 68° 08.250 W	21:35	857	910	4.86	5.21
9	23 Sep 2004	40° 20.057 N, 68° 07.890 W	21:38	861	912	4.67	5.30
–	All collections & sightings (mean ± SE)	–	–	780.9 ± 8.3	881.0 ± 6.4	4.66 ± 0.063	4.829 ± 0.155

3 individuals captured during 3 different dives were dissected immediately after completion of the dives. The stomachs contained 8 to 25 intact or partially digested *Calanus finmarchicus.* The calanoids exhibited no evidence of dismemberment, and they were mostly Stage V copepodites along with a few adults. These crustaceans were never observed in water samples used as controls in metabolic experiments, so it was unlikely that the octopods fed after capture. *C. finmarchicus* occurred in all of the canyons and, in 2002, a series of 26 samples taken at depths of 430 to 750 m with a suction sampler mounted on the submersible yielded a mean abundance (±SE) of 31.2 ± 3.4 ind. m^{-3} across the 3 canyons.

Chemical composition, O_2 consumption, and excretion

Nine *Stauroteuthis syrtensis* were used in experiments (Table 1). All octopods were captured within 185 m of the sea floor in a water column of 910 to 930 m. WW and DW of these octopods varied by an order of magnitude (Table 2). Water comprised 92 to 96% of the entire bodies of all octopods (Table 2). C:N ratios ranged from 4.57 to 7.60, with a mean (±SE) of 5.77 ± 0.31. WW, DW and C contents were normally distributed and homoscedastic after log$_{10}$ transformation (Ryan-Joiner tests for

WW = 0.98, df = 8, p > 0.10; DW = 0.98, df = 8, p > 0.10; and C content = 0.98, df = 8, p > 0.10; Cochran's tests for DW versus WW = 0.54, df = 2, 8, p > 0.05; C content versus WW = 0.24, df = 2, 8, p > 0.05; and C content versus DW = 0.60, df = 2, 8, p > 0.05). Statistically significant linear regressions that explained > 80% of the variation in the data revealed that all 3 measures of size were related and reliable (Fig. 2).

Duplicate Winkler titrations from 8 of the 9 experiments had coefficients of variation < 5%. These data were homoscedastic and normally distributed (Cochran's test = 0.55, df = 2, 7, p > 0.05; Ryan-Joiner tests for Winkler values = 0.94, df = 7, p > 0.10; and microoptode values = 0.92, df = 7, p > 0.05). A statistically significant linear regression indicated that measure-

Table 2. *Stauroteuthis syrtensis.* Weights and elemental composition of cirrate octopods. DW: dry weight

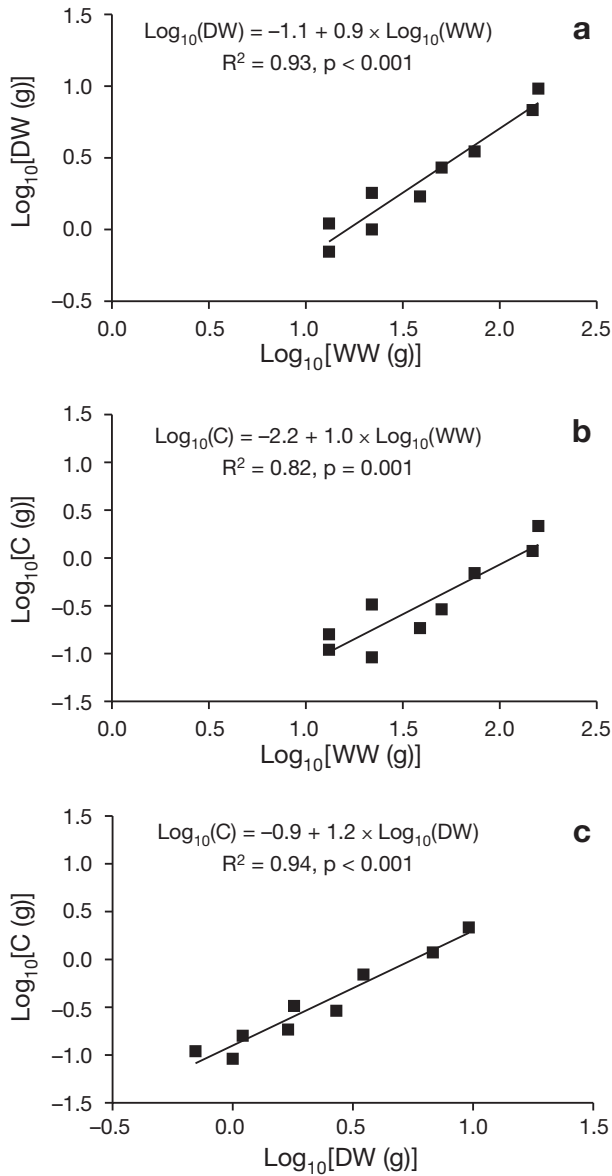| Octopod	Weight (g) Wet	Weight (g) Dry	Proportion of water	Proportion of DW C	Proportion of DW H	Proportion of DW N	C content (g)
1	74.2	3.5	0.95	0.198	0.033	0.032	0.69
2	13.2	1.1	0.92	0.144	0.026	0.024	0.16
3	147.7	6.8	0.95	0.174	0.029	0.031	1.18
4	21.9	1.0	0.95	0.091	0.020	0.018	0.09
5	38.8	1.7	0.96	0.108	0.021	0.024	0.18
6	13.2	0.7	0.95	0.156	0.026	0.021	0.11
7	21.9	1.8	0.92	0.181	0.030	0.028	0.33
8	50.2	2.7	0.95	0.107	0.020	0.022	0.29
9	158.1	9.6	0.94	0.224	0.039	0.042	2.16
Mean	59.91	3.21	0.943	0.1537	0.0271	0.0269	0.577
± SE	±18.76	±1.01	±0.005	±0.0151	±0.0021	±0.0024	±0.230

Fig. 2. *Stauroteuthis syrtensis.* Linear regression of $\log_{10}$-transformed dry weight (DW, in g) (a) on wet weight (WW, in g), (b) C content (in g) on WW, and (c) C content on DW for cirrate octopods

ments. Weight-specific and C-specific rates of O_2 consumption varied among octopods, with ranges of 0.031 to 0.243 μmol O_2 g^{-1} WW h^{-1}, 0.576 to 3.192 μmol O_2 g^{-1} DW h^{-1}, and 4.631 to 25.788 μmol O_2 g^{-1} C h^{-1} (Table 3). With the values for Octopod 9 excluded, weight-specific and C-specific rates of O_2 consumption decreased as body size increased, with the models fit to WW and C content explaining a larger amount of variation in the data (Fig. 3). Octopod 9 was the largest individual and, although there was no evidence of unusual behavior, this individual may have had an imperceptible injury resulting in stress and greater O_2 consumption. As expected, data standardized to DW varied more than data standardized to C content due to the difficulty of removing bound water from gelatinous tissue (Youngbluth et al. 1988).

Concentrations of NH_4^+ and PO_4^{3-} in 4 or 5 respirometers containing *Stauroteuthis syrtensis* were distinguishable from changes in controls (Table 4). However, most concentrations were near detection limits regardless of holding times. A small individual, Octopod 6 (Table 2), excreted 3 to 45 times as much NH_4^+ as the other octopods (Table 4). With this individual included, the weight-specific and C-specific excretion rates for NH_4^+ decreased for larger *S. syrtensis*, with the curves explaining 92 to 96% of the variation in the data (Fig. 4). Similar decreasing relationships explained 47 to 70% of the variation in the PO_4^{3-} data when the values recorded for Octopod 3 were excluded (Fig. 5). This octopod was one of the largest (Table 2), and it excreted more PO_4^{3-} than predicted by the model, perhaps due to an imperceptible injury. Atomic ratios for O:N, O:P and N:P, calculated from values measured during single experimental runs, ranged from 11.01–365.83, 376.52–11471.99 and 1.03–135.84, respectively (Table 5). Removing Octopod 3, which had a relatively low rate of NH_4^+ excre-

ments taken by micro-optodes were reliable measures of relative O_2 consumption, with micro-optodes consistently yielding higher concentrations than the Winkler titrations (micro-optode value = 1.35 × Winkler value, $F = 3541.35$, df = 1,7, $p < 0.001$, $R^2 = 0.91$).

All octopods became quiescent and ventilated calmly after an initial period of acclimation. All experiments yielded statistically significant regressions, with O_2 consumption in respirometers containing octopods being 1 to 2 orders of magnitude greater than O_2 consumption in controls. *Stauroteuthis syrtensis* consumed 5 to 35% of the O_2 available at the start of the experi-

Table 3. *Stauroteuthis syrtensis*. Weight-specific and C-specific O_2 consumption rates for cirrate octopods. WW: wet weight; DW: dry weight

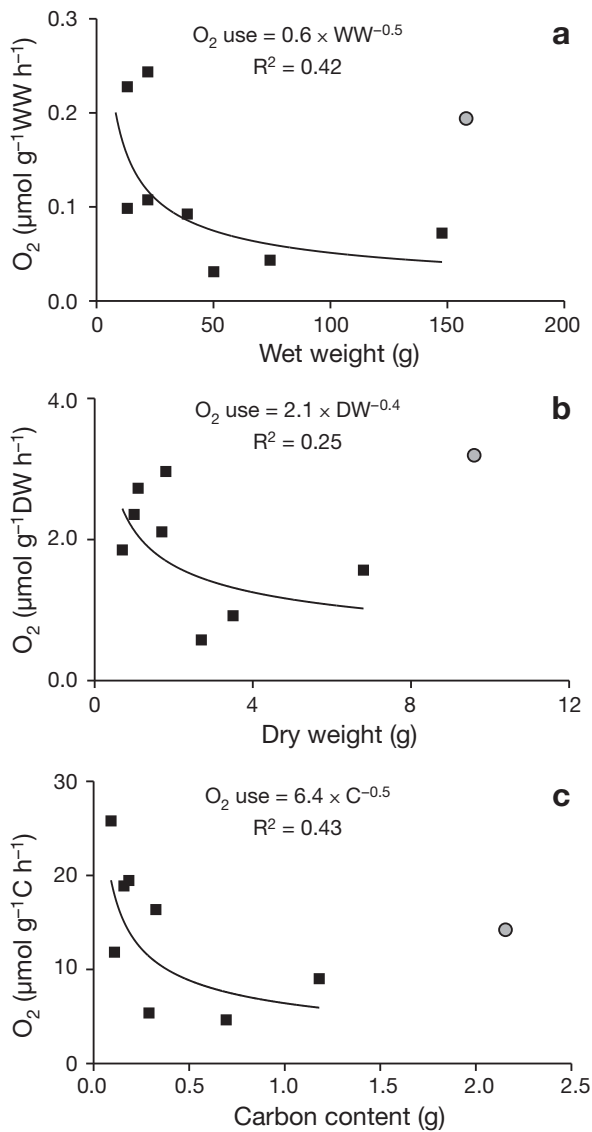| Octopod | μmol O_2 consumed | | |
	g^{-1} WW h^{-1}	g^{-1} DW h^{-1}	g^{-1} C h^{-1}
1	0.043	0.918	4.631
2	0.228	2.726	18.881
3	0.072	1.565	9.013
4	0.107	2.354	25.788
5	0.092	2.108	19.448
6	0.098	1.851	11.830
7	0.243	2.963	16.363
8	0.031	0.576	5.363
9	0.194	3.192	14.220
Mean	0.123	2.028	13.949
± SE	± 0.026	± 0.299	± 2.327

Fig. 3. *Stauroteuthis syrtensis*. Rates of O_2 consumption versus (a) WW, (b) DW, and (c) C content for cirrate octopods. Values for Octopod 9 (grey circle) excluded from data used to fit the curve. Definitions as in Fig. 1
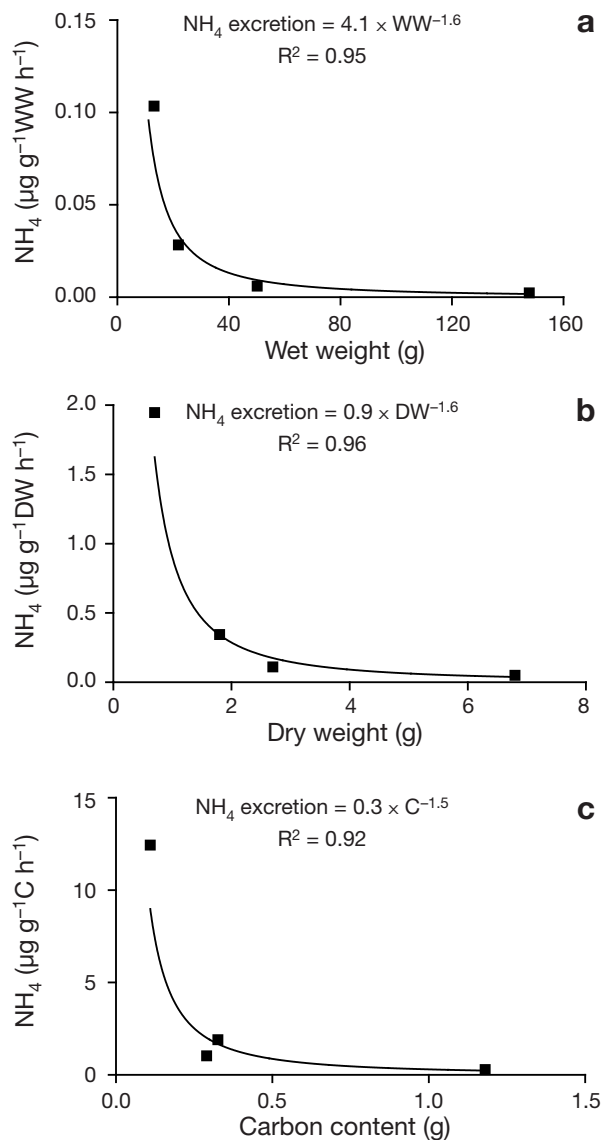
Fig. 4. *Stauroteuthis syrtensis*. Rates of NH_4^+ excretion versus (a) WW, (b) DW, and (c) C content for cirrate octopods. Definitions as in Fig. 1

Table 4. *Stauroteuthis syrtensis*. Weight-specific and C-specific NH_4^+ and PO_4^{3-} excretion rates. –: data unavailable

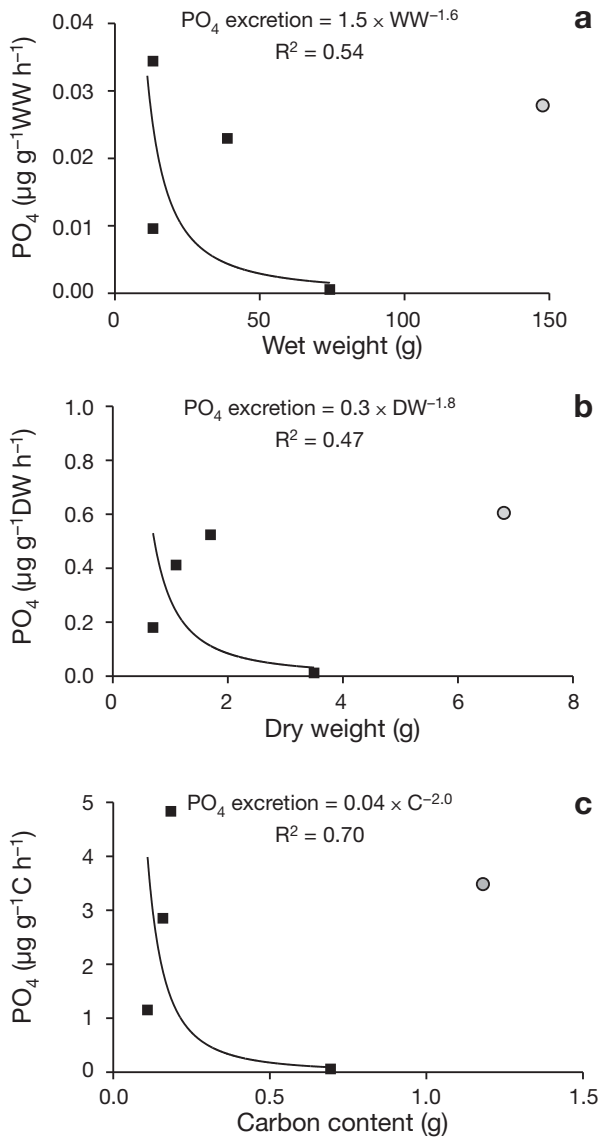| Octopod | μg NH_4^+ excreted | | | μg PO_4^{3-} excreted | | |
	g^{-1} WW h^{-1}	g^{-1} DW h^{-1}	g^{-1} C h^{-1}	g^{-1} WW h^{-1}	g^{-1} DW h^{-1}	g^{-1} C h^{-1}
1	–	–	–	0.0005	0.0117	0.0588
2	–	–	–	0.0344	0.4118	2.8518
3	0.0023	0.0495	0.2851	0.0278	0.6049	3.4846
4	–	–	–	–	–	–
5	–	–	–	0.0229	0.5239	4.8335
6	0.1034	1.9459	12.4339	0.0096	0.1802	1.1515
7	0.0282	0.3437	1.8979	–	–	–
8	0.0059	0.2615	2.4352	–	–	–
9	–	–	–	–	–	–
Mean	0.0350	0.6124	3.9110	0.0191	0.3465	2.4760
± SE	± 0.0235	± 0.4490	± 2.8600	± 0.0062	± 0.1101	± 0.8460

Fig. 5. *Stauroteuthis syrtensis*. Rates of PO_4^{3-} excretion versus (a) WW, (b) DW, and (c) C content for cirrate octopods. Values for Octopod 3 (grey circle) excluded from data used to fit the curve. Definitions as in Fig. 1

Table 5. *Stauroteuthis syrtensis*. Ratios of oxygen (O) consumed to nitrogen (N) and phosphorus (P) excreted. –: data unavailable

Octopod	O:N	O:P	N:P
1	–	11471.99	–
2	–	963.75	–
3	365.83	376.52	1.03
4	–	–	–
5	–	585.70	–
6	11.01	1495.55	135.84
7	99.76	–	–
8	60.43	–	–
9	–	–	–
Mean ± SE	134.26 ± 79.30	2978.70 ± 2131.82	68.43 ± 67.41
Without Octopod 3			
Mean ± SE	55.07 ± 25.68	–	135.84
Without Octopod 1			
Mean ± SE	–	855.38 ± 245.56	–

son, *Stauroteuthis syrtensis* were composed of >90% water, 3 to 7% C, and 0.6 to 1.4% N. In addition, the chemical composition of *S. syrtensis* was more similar to values reported for various gelatinous zooplankton than to values reported for crustaceans or fishes (Bailey et al. 1995). *S. syrtensis*, various medusae and ctenophores have water contents >90%, C contents <25% of DW, and N contents <5% of DW. In contrast, crustaceans and fishes typically have water contents <90%, C contents >35%, and N contents >5%. Thus, the metabolic rates of *S. syrtensis* would be expected to be similar to those of gelatinous zooplankton.

C-specific rates of O_2 consumption recorded for *Stauroteuthis syrtensis* were higher than values reported for gelatinous zooplankton after scaling to a temperature of 4.5°C using a Q_{10} of 2 (148 to 825 µl O_2 g^{-1} C h^{-1} in the present study versus 1 to 181 µl O_2 g^{-1} C h^{-1} in Bailey et al. 1995). In contrast, scaled, weight-specific respiration rates for *S. syrtensis* were at the lower end of ranges reported for cephalopods from shallow and deep water (0.9 to 7.8 µl O_2 g^{-1} WW h^{-1} in the present study versus 0.3 to 190.2 µl O_2 g^{-1} WW h^{-1} in Seibel et al. 1997, Daly & Peck 2000, Seibel & Childress 2000). Rates of O_2 consumption for *S. syrtensis* were most similar to those reported for the vampire squid *Vampyroteuthis infernalis* and 2 deep-water octopods, *Japetella heathi* and *J. diaphana* (1.9 to 2.4 µl O_2 g^{-1} WW h^{-1}, 3.5 µl O_2 g^{-1} WW h^{-1}, and 5.4 to 19.4 µl O_2 g^{-1} WW h^{-1}; Seibel et al. 1997). The similarity between the metabolic demands of *S. syrtensis* and *V. infernalis* may be related to the replacement of visual identification and pursuit of prey with a more passive strategy. It has been hypothesized that both

tion, and Octopod 1, which had a relatively low rate of PO_4^{3-} excretion, yielded a single value of 135.84 for N:P and mean ratios (± SE) of 55.07 ± 25.68 for O:N and 855.38 ± 245.56 for O:P (Table 5).

DISCUSSION

Water (73 to 87%) and protein (8 to 20%) represent the primary components of cephalopod bodies, which yield estimates of 4 to 10% C and 2 to 4% N relative to WW (Croxall & Prince 1982, Krzynowek & Murphy 1987, Moltschaniwskyj & Semmens 2000). In compari-

species use bioluminescence to lure prey (Childress & Mickel 1985, Johnsen et al. 1999, Collins & Henriques 2000, Seibel et al. 2000, Seibel & Carlini 2001, Robison et al. 2003). In addition to differential activity, some of the observed differences in O_2 consumption may be related to allometric scaling, with larger animals consuming proportionally less O_2, as observed in the present and previous studies (e.g. Seibel et al. 1997). Another consideration is that rates of O_2 consumption measured at *in situ* pressures would be expected to be higher than the rates measured at sea level in the present and other studies (Bailey et al. 1994, 1995). Previous comparisons and those in the present study are related to measurements made at surface pressures.

NH_4^+ and PO_4^{3-} excretion rates for *Stauroteuthis syrtensis* were low. The rates were at least an order of magnitude lower than those reported for 2 species of ctenophores, a trachymedusan and a benthopelagic holothurian, i.e. 0.22 to 9.67 µg NH_4-N g^{-1} C h^{-1} and 0.02 to 1.58 µg PO_4-P g^{-1} C h^{-1} recorded in the present study versus 55.4 to 1 389.5 µg NH_4-N g^{-1} C h^{-1} and 11.6 to 443.5 µg PO_4-P g^{-1} C h^{-1} reported in Bailey et al. (1994). In addition, rates of NH_4^+ excretion for *S. syrtensis* were approximately 3 orders of magnitude less than rates reported for the Antarctic octopod *Pareledone charcoti* and the shallow-water octopod *Octopus ocellatus*: 0.04 to 1.51 µg NH_4-N g^{-1} DW h^{-1} and 0.002 to 0.080 µg NH_4-N $µg^{-1}$ WW h^{-1} in the present study versus 2521.2 µg NH_4-N g^{-1} DW h^{-1} in Daly & Peck (2000) and 3 to 40 µg NH_4-N $µg^{-1}$ WW h^{-1} in Segawa & Nomoto (2002). The unavoidable need to store the samples before analysis may have resulted in lower concentrations, but excretion rates should have remained valid unless the loss of NH_4^+ or PO_4^{3-} was unequal across samples. The relatively low rates of N excretion also could be related to storage of NH_4^+ or other nitrogenous cations as an evolutionary adaptation to increase buoyancy (Seibel et al. 2004).

The relatively low excretion rates translated into relatively high atomic ratios compared to values reported for other zooplankton. The O:N and O:P ratios for *Stauroteuthis syrtensis* (11 to 366 and 376 to 11 472, respectively) typically were higher than those reported for a variety of Antarctic zooplankton (7 to 20 and 43 to 304, respectively; Ikeda & Mitchell 1982) and 2 species of ctenophores, a trachymedusan and a benthopelagic holothurian (9 to 24 and 50 to 317, respectively; Bailey et al. 1994). In addition, the O:N ratios for *S. syrtensis* were higher than those reported for *Octopus vulgaris* (3 to 15; Katsanevakis et al. 2005). Given the observed O:N ratios, *S. syrtensis* seemed to metabolize lipids (Mayzaud & Conover 1988). In addition, the high O:P and N:P ratios indicated that most octopods were not leaking phosphorus due to injury (Mayzaud & Conover 1988).

Converting O_2 consumption to C consumption by applying a respiratory quotient of 0.8 yielded estimates of metabolic demand expressed as % body C d^{-1} that ranged from 0.11 to 0.59 % d^{-1}, with a mean (± SE) of 0.32 ± 0.05 % (Table 6). Examinations of gut contents from *Stauroteuthis syrtensis* expanded on previous reports that the octopods fed on unidentified copepods (e.g. Johnsen et al. 1999) and on the hypothesis that mucus secreted by buccal secretory glands entrapped prey that were then handled by the cirri (Vecchione & Young 1997). In this case, only *Calanus finmarchicus* was found in the stomachs of *S. syrtensis*, with the condition of the prey indicating that they were swallowed whole. In addition, *C. finmarchicus* captured in the canyons during September 2004 had accumulated lipid stores (Miller et al. 1998), which *S. syrtensis* could have assimilated and stored, as reported for a species of *Opisthoteuthis* (Rosa et al. 2005), and eventually metabolized to produce the observed O:N ratios. Converting the C requirements of *S. syrtensis* to daily maintenance rations by assuming a contribution of 0.234 mg C $ind.^{-1}$ of *C. finmarchicus* yielded rations of 1.3 to 30.1 ind. d^{-1}, with a mean (±SE) of 6.7 ± 3.1 ind. d^{-1} (Table 6). Thus, the metabolic demands of relatively inactive *S. syrtensis*, which often float passively according to observations made during the present and previous studies (Vecchione & Young 1997, Collins et al. 2002), would be met by the prey available in <1 m^3 of water, given the mean abundance of *C. finmarchicus* measured across all 3 canyons in 2002.

The *in situ* observations made during the present study confirmed and expanded on knowledge of the distribution of *Stauroteuthis syrtensis*. This species has often been captured in bottom trawls (Collins & Henriques 2000), and the octopods observed and captured during our study were, on average, approximately

Table 6. *Stauroteuthis syrtensis.* Metabolic demand, calculated from O_2 consumption using an assumed respiratory quotient of 0.8, and inferred maintenance ration based on the assumption that a single *Calanus finmarchicus* contained 0.234 mg of C

Octopod	Metabolic demand (% body C d^{-1})	Maintenance ration (no. of copepods d^{-1})
1	0.11	3.2
2	0.43	2.9
3	0.21	10.4
4	0.59	2.3
5	0.45	3.5
6	0.27	1.3
7	0.38	5.2
8	0.12	1.5
9	0.33	30.1
Mean	0.32	6.7
± SE	± 0.05	± 3.1

100 m off the bottom during the day and at night. The ecological importance of the statistically significant difference in mean depth between daytime and nighttime sightings remains uncertain. This difference represented approximately 4% of the total average depth of the water column. Observations of up to 5 octopods in a 400 m^3 field of view indicated that trawl surveys yielding octopod abundance estimates of 8 to 9 ind. km^{-2} swept area may have integrated small-scale patches of octopods (Collins et al. 2001).

Although octopods may have sensed the submersible before they were sighted, *in situ* observations revealed that many individuals drifted in a 'sleeping mode,' with their bodies contracted into a relatively compact ball and their eyes hooded. In this posture, the octopod was difficult to distinguish from floating debris. This quiescent behavior was not exhibited by captive octopods. In response to disturbance caused by the submersibles, *Stauroteuthis syrtensis* inflated its web complex and exhibited the ballooning behavior noted previously (Vecchione & Young 1997, Johnsen et al. 1999, Collins et al. 2002). Thus, observations in the present study supported the hypothesis that these behaviors may function as an alarm response to deter or confuse predators, such as Cuvier's beaked whales *Ziphius cavirostris* and blue sharks *Prionace glauca* (Vecchione & Young 1997, Johnsen et al. 1999, Santos et al. 2001, Collins et al. 2002, Kubodera et al. 2007). Observations also indicated that slow sculling of the paired fins, medusoid contractions of the web, and rapid fin sculling were similar to patterns of locomotion reported for another deep-water cephalopod, *Vampyroteuthis infernalis* (Seibel et al. 1998). *S. syrtensis* seemed to employ this sequence of behaviors in response to increased levels of disturbance. The behaviors of *S. syrtensis* also resemble those described for other cirrate octopods (Boletzky et al. 1992, Hovland 1992, Villanueva et al. 1997).

In summary, the results of the present study confirmed that *Stauroteuthis syrtensis* is a deep-water species that often lives near the bottom. The octopods typically floated passively, and they responded to increasing disturbance by inflating their webs and employing progressively faster modes of locomotion to escape. *S. syrtensis* fed on the copepod *Calanus finmarchicus*, with relatively few prey needed to meet their basal metabolic demands. In general, the chemical content of *S. syrtensis* was more similar to gelatinous zooplankton than to more muscular cephalopods, but its O_2 consumption was greater than that of gelatinous zooplankton and similar to other deep-water cephalopods that have been reported to be ambush predators. In addition, *S. syrtensis* excreted relatively little NH_4^+ or PO_4^{3-}, and the octopods seemed to catabolize lipids, which could have been derived from *C. finmarchicus*.

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