The diet of the juvenile cuttlefish *Sepia officinalis* (Cephalopoda: Sepiidae) in the English Channel

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**ABSTRACT**

The diet of *Sepia officinalis* was studied by examining the stomach contents of 119 samples caught across 3 sites (Torbay, Whitsands and Bigbury) along the South-West coast of England. A total of 4 different prey groups were identified (Crustacean, Echinoderm, Cephalopoda and Fish). The heaviest stomach contents weights were recorded at Torbay, the only site inhabited by seagrass beds. A sub-tidal faunal survey of 5 sites at Torbay recorded 26 groups, belonging to 6 major phyla (Mollusca, Crustacea, Echinoderm, Annelida, Bryozoa and Chordata). The highest crustacean density was recorded at Babbacombe Bay, the only algal habitat surveyed. A comparison between *S. officinalis* prey quantities recorded in the stomachs and in the sub-tidal survey showed that fish and crustaceans were positively selected for, with Mollusca, Annelida, Bryozoan and Echinoderm all selectively avoided.

**Key words:** *Sepia officinalis*, Cephalopoda, English Channel, stomach contents analysis, seagrass, sub-tidal.

**INTRODUCTION**

Almost all cephalopods are active predators that feed on mobile living animals (Boucaud-Camou & Boucher-Rodoni, 1983). Independent of diet, cephalopods grow very quickly with growth rates reaching as high as 3-10% of their body weight per day (Lee, 1994). Due to having large energy requirements (Pascual, 1978), cephalopods have developed a very efficient protein digestion system, which is important when feeding is limited to high levels of protein (Lee, 1994).

The common cuttlefish, *Sepia officinalis* has a distribution that ranges from the North Sea to South Africa (Roper et al., 1984). The species is commonly found in shallow inshore waters of the North-East Atlantic (Adam & Rees, 1966) and lives for approximately 2 years in this region (Challier et al., 2005). *S. officinalis* buries itself in sand during the day using its chromatophores as camouflage (Holmes, 1940). The species then emerges at dusk to hunt for prey (Boucher-Rodoni et al., 1987), using its three stage visual attack sequence (Messenger, 1968). It is a highly specialised predator with well-developed eyes and delicate movements controlled by elongated fins (Messenger, 1977).

*S. officinalis* is an important commercial fisheries species within the English Channel (Challier et al., 2005). The fishery in the region provides one of the highest yields in the North-East Atlantic (Royer et al., 2006) and reported English and French annual landings have tripled over the past 10 years in the English Channel. It is an area with little management of the species. *S. officinalis* spawn in the region between spring and midsummer, with the majority of eggs hatching along both north and south coasts in the summer (Challier et al., 2005). Autumn is the main period of recruitment in the region, with *S. officinalis* then spending winter in deeper water at the western end of the English Channel. They migrate inshore during spring, with the adults spawning and the juveniles undergoing early maturation (Boucaud-Camou and Boismery, 1991). *S.*
officinalis's migration is possibly influenced by the strength of the Atlantic currents flowing into the western parts of the region (Wang et al., 2003). *S. officinalis* is an abundant species in the English Channel with annual estimates ranging from 31-74 million young cuttlefish over the period of 1995-2002 (Royer, 2002). Its feeding could have a significant impact on the surrounding prey species inhabiting the region.

Examining stomach contents is commonly used in studies to collect information on the diet and feeding activity of *S. officinalis*. Previous studies have focused on the juveniles in order to determine their diet and foraging behaviour. Once hatched, the young resemble a miniature adult cuttlefish (Nixon & Mangold, 1998; Agin et al., 2006) and for the first 3 months of their life history, the main prey for young *S. officinalis* are amphipods (Pinczon du Sel et al., 2000). Young cuttlefish forage on crustaceans such as decapods and amphipods during the first 2 months of their life-history, before switching predominantly to fish (Guerra, 1985). This was confirmed in the Algarve, South Portugal (Alves et al., 2006) and in the Ria de Vigo, North-West Spain (Guerra, 1985), in which crustaceans were found to be more important in weight for younger cuttlefish, but for larger *S. officinalis*, fish were dominant. During development after hatching, they choose to forage on small crustaceans, especially mysids, *Gammarus* and young shrimp (Wells, 1958; Boletzky & Hanlon, 1983). A 5 month study by Blanc et al., (1998) on the early stages of *S. officinalis* in Morbihan Bay, France, recorded that they had a diet consisting mostly of crustaceans (89%), with other groups including fish (4.6%), annelids (1.2%) and cephalopods (0.7%). A study by Pinczon du Sel et al., (2000) in the Bay of Biscay using stomach contents analysis, recorded that fish were the main component of the diet during the *S. officinalis* growth period in the off-shore regions. For older individuals that were returning to reproduce in coastal waters, crustaceans made up the majority of the diet (Pinczon du Sel et al., 2000). A change in diet was also recorded as the species grew by Castro & Guerra, (1990). This study examined the stomach contents of 1345 *S. officinalis* individuals, recording 40 different items of prey. They comprised of 4 groups: polychaeta, crustacean, cephalopod and bony fish.

Cannibalism by *S. officinalis* is frequent in the natural environment (Ibanez & Keyl, 2010). *S. officinalis* feed upon a range of molluscs, crustaceans and fish and so is said to be euryphagous (Alves et al., 2006). This flexible diet allows it to survive in locations where its usual prey is not distributed (Pinczon du Sel et al., 2000).

Studies have begun to investigate the diet required to successfully rear juvenile *S. officinalis*. Alternative diets have been used, resulting in low growth rates of fragile individuals (Boletzky & Hanlon, 1983). An abundant supply of enriched live prey appears essential for successful rearing of juvenile cuttlefish (Koueta et al., 2002).

Morbihan Bay is a coastal area in North-West France that is potentially an important nursery ground for *S. officinalis*. Predatory fish prey on the young individuals and the eggs, with the cuttlefish spawning from March to July (Blanc & Daguzan, 1999). Seagrass beds are thought to be an important habitat for many commercially exploited fish and invertebrate species (Jackson et al., 2001), such as *S. officinalis*. Over 80 hectares of the seagrass *Zostera marina* are located at Torbay (Hirst & Attrill, 2008) (Figure 1). Few studies have shown that seagrass beds are important spawning habitats for cuttlefish, but a paper by Jackson et al., (2002) recorded increased numbers of *S. officinalis* inhabiting seagrass beds from St. Catherine Bay, Jersey, English Channel, when compared with numbers in nearby sandy habitats.

![Fig 1. Distribution of seagrass beds in South-West England](http://jncc.defra.gov.uk/page-2409-2409)
The main aims of this study are to record juvenile *S. officinalis*’s diet and to elucidate the prey community structure and abundance within seagrass and non-seagrass habitats inhabited by juvenile *S. officinalis*, to determine their potential diets. These results will be obtained through stomach contents analysis and sub-tidal habitat dive surveys. The prey recorded from both will be compared to deduce which groups are selected for and selectively avoided by juvenile *S. officinalis*.

**MATERIALS AND METHODS**

**Stomach Contents Analysis:**

*S. officinalis* specimens were collected from the 3 sites of Torbay, Whitsands and Bigbury on the South-West coast of England (Figure 2). A fourth site near Itchenor harbour, West Sussex was also investigated but insufficient samples were collected to be of use. The Torbay samples were caught by local fishermen in December, 2010. The Bigbury samples and Whitsands samples were caught by the Marine Biological Association (MBA) scientific trawling vessel on request in August, 2011. For each cuttlefish, the dorsal mantle length (DML) was recorded in centimetres to 3 significant figures and weight to the nearest gram. The body, cuttlebone and stomach were photographed and labelled for further identification. The digestive tract was removed and stomach cut away from the caecum and intestine tissue. The fullness of the stomach was recorded using a subjective scale from 0-5, similar to that used by Castro and Guerra (1990), with zero being empty and 5 fully distended. Empty stomachs were retained to allow repletion quotient (RQ) analysis. The repletion quotient is formulated by the number of stomachs with contents divided by the total number of stomachs examined (Blanc et al., 1998; Pinczon du Sel and Daguzan, 1997).

The inner and outer stomach linings were then carefully removed and the stomach contents washed out onto a white tray. The total stomach contents of each sample were wet weighed to ±0.001g and examined with the hard parts sorted into the major taxonomic groupings of crustacean, echinoderm, cephalopod and fish with the use of a dissection microscope (Alves et al., 2006). Prey were identified as crustacean by the presence of legs, antennae, carapace, rostra, ommatidia, mandibles and other fragments. Fish were recognised through the presence of otoliths, scales and bones. Cephalopod parts identified included beaks, suckers and parts of the cuttlebone; echinoderms were observed as almost fully intact brittle stars.

![Figure 2. Map to show the 3 sites for stomach analysis at Torbay, Whitsands and Bigbury](http://www.picturesofengland.com/mapofengland/south-west-map.html)
To describe the diet of juvenile *S. officinalis*, different quantitative and qualitative methods were used as described by Lima-Junior & Goitein, (2001). These include frequency of occurrence (%F), the volumetric analysis index (%V) and the relative importance (IRI) of each prey item $F_i$. The percentage by weight (%W) was also calculated.

**IRI**

This indicates the relative importance that food item $i$ had in *S. officinalis*’s diet.

$$IRI = F_i \times V_i$$

IRI: Importance Index of food item $i$ in the sample;
$F_i$: Occurrence Frequency of the item;
$V_i$: Volumetric Analysis Index of the item. (Lima-Junior & Goitein, 2001)

$F_i$ This is the frequency of occurrence (%F) of the prey item in the cuttlefish stomachs. If 2 or more food items are found, the total will not add up to 100%. Below is the formula used by Hyslop (1980).

$$\%F_i = \frac{100n_i}{n}$$

$F_i$: frequency of occurrence of the $i$ food item in the sample; $n_i$: number of stomachs in which the $i$ item is found; $n$: total number of stomachs with food in the sample.

$V_i$ To calculate this, you must work out $M_i$:

$$M_i = \frac{\Sigma i}{n}$$

$M_i$: mean of ascribed points for the $i$ food item
$\Sigma i$: sum of the ascribed points for the $i$ food item;
$n$: total number of stomachs with food in the sample (Lima-Junior & Goitein, 2001). This value is converted into a percentage.

$$V_i = 25 M_i$$

$V_i$: Volumetric Analysis Index of the $i$ food item in the sample;
25: multiplication constant to obtain a percentage;

This indicates the relative abundance of a food item found in the stomach samples, with the method used by Lima-Junior & Goitein, (2001).

$$\%W = \frac{W_i}{T_i} \times 100$$

$W_i = \text{total weight of prey item } i \text{ in site } i$
$T_i = \text{Total weight of stomachs in site } i$

The repletion quotient (RQ) was calculated for Torbay, Whitsands and Bigbury using the formula:

$$RQ = \frac{\text{number of stomachs with contents}}{\text{total number of stomachs}} \times 100$$

A chi-squared test was used to test the frequency occurrence (%F) of prey groups recorded at Torbay and Whitsands. It was also used to test for significance between stomach contents weights compared against size of *S. officinalis* samples from Whitsands. A Kruskall-Wallace non-parametric test compared the total and full stomach population’s stomach contents weights recorded at all 3 sample sites.

**Sub-tidal cuttlefish habitat survey:**

The other aspect of the investigation was to study the prey faunal assemblage and habitat within the Torbay area. Surveys conducted in the area, as part of a current PhD project confirmed that there were seagrass beds sited and that the species had spawned in these areas in previous years (Isobel Bloor, pers.comm). Five dive sites were chosen in the Torbay area, with varying *S. officinalis* egg densities and habitat (Table 1).
On the 15th and 16th of August 2011, using a University of Plymouth Dive Centre dive boat and 6 divers, all having the HSC qualification, 5 locations in the Torbay area (Figure 3) were surveyed for their faunal compositions. Divers obtained samples of seagrass and marine fauna, to provide information on the choice of prey that juvenile cuttlefish have at each dive site. A comparison was then made to determine sites used for spawning and to what egg density.

A random sampling method was designed, with 16 seagrass faunal samples collected at each of the 5 sub-tidal sites. 4 separate patches were sampled, with four replicates sampled at each patch. This gave a total of 80 separate faunal samples collected over the two days of diving. Before releasing the anchor, a drop camera was used to confirm that the divers were placed in the correct location. Each sub-tidal site had a depth of 1-10 metres. Each dive pair took a 0.125 m² quadrat with a mesh bag securely attached, cable ties, scissors, slate, pencil and a camera; conducting two replicates at each dive site region. They were also asked to record all marine fauna seen whilst diving in the area, giving a record of the more mobile species that were unlikely to be caught within the quadrat net. They were asked to record a 5 minute video at each dive region to give a visual record of each dive site habitat. Once the samples were returned to the surface, the quadrat nets were washed out; all samples were sorted, with 5 seagrass blades taken as a sub-sample, along with all collected marine fauna. The sorted samples were then transferred to a labelled, protective plastic

Table 1. The habitat and egg densities found at each of the 5 sub-tidal dive sites surveyed.

<table>
<thead>
<tr>
<th>Dive Site</th>
<th>Habitat</th>
<th>Egg density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Torre Abbey Sands</td>
<td>Seagrass</td>
<td>High</td>
</tr>
<tr>
<td>Thatchers Gut</td>
<td>Seagrass</td>
<td>Low/none</td>
</tr>
<tr>
<td>Millstones Bay</td>
<td>Seagrass</td>
<td>High</td>
</tr>
<tr>
<td>Hope Cove</td>
<td>Seagrass</td>
<td>Low/none</td>
</tr>
<tr>
<td>Babbacombe Bay</td>
<td>Seagrass</td>
<td>High</td>
</tr>
</tbody>
</table>

Fig 3. Map showing the 5 sub-tidal sites surveyed within the Torbay area.

Available (online): http://edina.ac.uk/digimap/
The quadrat nets were then returned to the divers to collect the next samples. The samples were transferred to storage jars and fixed in formalin that evening, with the use of safety goggles, gloves and lab-coat.

On the 22\textsuperscript{nd} of August 2011, with the use of a formalin fume cupboard, formalin was washed off all samples and then transferred into labelled pots containing 70\% ethanol for further preservation.

On the 6\textsuperscript{th} of October 2011, ethanol was washed off each sample and all marine fauna in each sample was separated into phyla in small vials. The seagrass blades were put back into 70\% ethanol for possible future study.

Using a microscope and identification books such as Hayward & Ryland, (1995), the separated marine fauna were identified to the lowest possible taxon (Castro & Guerra, 1990). The abundance of species found in each replicate and the density of each individual species per 0.125m\textsuperscript{2} was recorded.

Using Primer software, an MDS plot was produced, with ANOSIM showing the similarities of the faunal composition recorded at each of the 5 sites. A 1-way ANOVA was used to investigate crustacean densities recorded at all 5 sites, and a Tukey post-hoc test assessed the differences. IVLEVS electivity index was used to compare the percentage compositions of prey recorded in the stomachs with what was recorded in the sub-tidal habitats. The formula used is:

$$E = \frac{r_i - p_i}{r_i + p_i}$$

Resulting values for E range from -1 and +1, where -1 indicates complete avoidance for the group, 0 no active selection, and +1 complete selection for the group (Strauss, 1979). $r_i$ is the percentage of the particular fauna group found in the S. officinalis stomachs and $p_i$ is the percentage of the same group found in the sub-tidal habitats.

### RESULTS

#### General diet composition

A total of 119 stomachs were sampled, with 55 *Sepia officinalis* from Torbay, 55 from Whitsands and 9 from Bigbury. Across the three sites 78 contained food items (65.5\%) and 41 were empty (35.5\%). The individual repletion quotients for each site are shown in Table 2. A total of 4 major groups were identified within the stomach contents, with the general diet consisting of crustacean, fish, echinoderm and cephalopod.

<table>
<thead>
<tr>
<th>Site</th>
<th>Torbay</th>
<th>Whitsands</th>
<th>Bigbury</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of stomachs examined</td>
<td>55</td>
<td>55</td>
<td>9</td>
</tr>
<tr>
<td>Mean cuttlefish weight</td>
<td>43.15</td>
<td>83.73</td>
<td>102.67</td>
</tr>
<tr>
<td>Repletion quotient (RI %)</td>
<td>69.1</td>
<td>65.6</td>
<td>55.6</td>
</tr>
</tbody>
</table>

#### Diet in relation to site

Crustaceans were the most dominant and important prey for each of the 3 sites, with the largest IRI values (Table 3). This prey group occurred in over 80\% of stomachs (%F) that had contents for all 3 sites. Crustaceans were followed by fish, with its highest frequency (%F) found at Torbay. The volume (%V) of crustaceans and fish recorded were very similar at Torbay and Whitsands. Crustacean had the highest contribution by weight (%W) in the stomach contents, followed once again by fish, which had its highest %W at Torbay. Small amounts of echinoderm were discovered in the Torbay stomach samples; one individual cuttlefish stomach contained 3 whole brittlestars. Small amounts of cephalopod were also recorded in the Torbay stomach samples. Neither echinoderm nor cephalopods were recorded in the Whitsands or Bigbury stomach samples.
It was hypothesised that the same frequency occurrence (%F) of prey items would occur at the sites of Torbay and Whitsands, both with an equal sample size. A chi squared test showed that the %F recorded for Torbay and Whitsands were significantly different (n=4, df=3, p<0.05).

**Table 3.** Dietary composition by prey group of *S. officinalis*, according to indexes of occurrence (%F), volumetric analysis index (%V), index of relative importance (IRI) and weight (%W) for the sites of Torbay, Whitsands and Bigbury.

<table>
<thead>
<tr>
<th>SITE</th>
<th>Food Item</th>
<th>Occurrence Frequency (%F)</th>
<th>Volumetric Analysis Index (%V)</th>
<th>Importance Index (IRI)</th>
<th>% Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>TORBAY</td>
<td>Crustacean</td>
<td>81.6</td>
<td>85.156</td>
<td>6948.75</td>
<td>71.9</td>
</tr>
<tr>
<td></td>
<td>Echinoderm</td>
<td>2.63</td>
<td>0.408</td>
<td>1.074</td>
<td>0.321058</td>
</tr>
<tr>
<td></td>
<td>Cephalopod</td>
<td>5.26</td>
<td>0.759</td>
<td>3.992</td>
<td>2.834211</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>42.1</td>
<td>13.676</td>
<td>575.743</td>
<td>24.94211</td>
</tr>
<tr>
<td>WHITSANDS</td>
<td>Crustacean</td>
<td>91.4</td>
<td>85.442</td>
<td>7809.36</td>
<td>81.87148</td>
</tr>
<tr>
<td></td>
<td>Echinoderm</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Cephalopod</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>40</td>
<td>14.558</td>
<td>582.356</td>
<td>18.12857</td>
</tr>
<tr>
<td>BIGBURY</td>
<td>Crustacean</td>
<td>100</td>
<td>92.961</td>
<td>9256.056</td>
<td>85.72</td>
</tr>
<tr>
<td></td>
<td>Echinoderm</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Cephalopod</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>20</td>
<td>7.039</td>
<td>140.789</td>
<td>14.28</td>
</tr>
</tbody>
</table>

Diet in relation to size

Fish made up a greater proportion of the diets found in Torbay than those found in Whitsands. At Torbay, its composition was 100% for the weight range of 0-20g and over 50% for 60-80g (Figure 4a). Crustaceans made up a greater proportion of the diet at Whitsands (Figure 4b), with every weight range having a composition of over 50%. Cephalopods were only eaten at Torbay in the 20-40g and 60-80g weight ranges, with very small percentage compositions. Echinoderms were only eaten at Torbay at the 20-40g weight range, at an even smaller composition. There was no clear trend for either site of diet changing with an increasing *S. officinalis* body weight. A chi squared test showed that the crustacean and fish mean averages (%) recorded were significantly different (n=2, df=1, p<0.05) between the weight ranges of 0-120g and 120-220g at Whitsands (Table 4).

![Fig 4](image)

Fig 4. The diet composition (%) of *Sepia officinalis* caught at Torbay and Whitsands, at various weight intervals.
Mean stomach contents weights were recorded heaviest at Torbay, for the total and full stomach population (Table 5) (Figure 5). The stomach contents weights for Torbay, Whitsands and Bigbury were tested for normality using the Kolmogorov-Smirnov test, with all 3 sites found not to have a normal distribution at $p<0.01$. The relationship between the total population stomach contents weights recorded at Torbay, Whitsands and Bigbury was not significant (Kruskal-Wallis $H = 0.68$, d.f = 2, $P = 0.712$). The relationship between the population of full stomach contents weights at Torbay, Whitsands and Bigbury was also not significant (Kruskal – Wallis $H = 0.80$, d.f = 2, $P = 0.670$). Bigbury had the greatest percentage of empty stomachs, with Torbay having the lowest.

Stomach contents weight in relation to site

The stomach contents weights at Torbay and Whitsands had a significant negative Pearsons correlation with length to weight ratio, but a non-significant positive Pearsons correlation at Bigbury (Table 6). A large amount of the stomachs weighed between $0>x<0.04g$, with the empty stomachs removed from the data (Figure 6). An exceptionally heavy stomach recorded at Torbay with a weight of 0.2g and length to weight ratio of 0.21 was removed as an outlier.

Table 5. Mean stomach contents weights for the total and full stomach population at Torbay, Whitsands and Bigbury ± standard error.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total $\pm$ SE</th>
<th>Full $\pm$ SE</th>
<th>% empty</th>
</tr>
</thead>
<tbody>
<tr>
<td>Torbay</td>
<td>0.015 ± 0.006</td>
<td>0.028 ± 0.006</td>
<td>50.9</td>
</tr>
<tr>
<td>Whitsands</td>
<td>0.014 ± 0.002</td>
<td>0.022 ± 0.003</td>
<td>36.4</td>
</tr>
<tr>
<td>Bigbury</td>
<td>0.008 ± 0.003</td>
<td>0.014 ± 0.004</td>
<td>44.4</td>
</tr>
</tbody>
</table>

Table 6. Pearson correlation and p-values for the sites of Torbay, Whitsands and Bigbury for stomach contents weights against length to weight ratios.

<table>
<thead>
<tr>
<th>Site</th>
<th>Pearson correlation</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Torbay</td>
<td>-0.377</td>
<td>$p&lt;0.05$</td>
</tr>
<tr>
<td>Whitsands</td>
<td>-0.438</td>
<td>$p&lt;0.05$</td>
</tr>
<tr>
<td>Bigbury</td>
<td>0.636</td>
<td>$p=0.249$</td>
</tr>
</tbody>
</table>
Stomach contents weight in relation to size

Torbay had a small sample weight distribution of 15-99g, with a large majority of the full stomachs from Torbay recorded in samples weighing between 20-60g (Figure 7a). A larger weight distribution was collected from Whitsands, 34-210g, with most full stomachs in samples between 40-80g (Figure 7b). Bigbury also had a large weight distribution, from 50-190cm (Figure 7c) and had very spread out data.

Prey community structure and abundance within different known habitats

26 groups were identified across the 5 subtidal survey sites and these have been condensed into 6 major phyla to allow for comparison with stomach contents. Mollusca had the highest density across all 5 sites (Table 7) and also the highest percentage composition (Figure 8). Crustacea had the second highest density in the natural habitat and were found at highest quantities at Babbacombe Bay and Torre Abbey Sands (Figure 9), where both have a high Sepia officinalis egg density. The greatest percentage composition of crustaceans was found at Babbacombe Bay at 43.2%, the only site surveyed that had an algal dominated habitat. Only one individual fish was found across all 5 sites, the Shore Clingfish, Lepadogaster lepadogaster at Thatchers Gut. Low densities of Echinoderms, Annelidas and Bryozoans were apparent across the 5 sites. Millstones Bay had the lowest total faunal abundance with only the 3 groups recorded (Mollusca, Crustacean and Annelida), each having a low density compared to the other sites. Hope Cove had the highest total faunal abundance, with 5 groups recorded (Mollusca, Crustacea, Echinoderm, Annelida and Bryozoa).

A 1 way ANOVA with a Tukey post-hoc test showed that there is a significant difference at p<0.001 (d.f = 4, F = 5.90, P=0.000) between crustacean densities recorded at the dive sites of Torbay (Figure 6). The Tukey test showed that Babbacombe Bay is significantly different to all sites at p<0.001, apart from Torre Abbey Sands.
The MDS plot shows clustering for the 5 dive sites at Torbay (Figure 10), showing that they all have a very different species assemblage between each other. ANOSIM showed that all of the 5 surveyed dive sites are significantly different from each other at p<0.001, except for when comparing Thatchers Gut (TG) and Millstones Bay (MB), which was significant at p<0.05 (p=0.013).

The densities per 0.125m² x ± SE for each major phyla recorded at the 5 dive sites of Torre Abbey Sands (TAS), Thatchers Gut (TG), Millstones Bay (MB), Hope Cove (HC), Babbacombe Bay (BB).

**Table 7.** The density per 0.125m² x ± SE for each major phyla recorded at the 5 dive sites of Torre Abbey Sands (TAS), Thatchers Gut (TG), Millstones Bay (MB), Hope Cove (HC), Babbacombe Bay (BB).

<table>
<thead>
<tr>
<th>Site</th>
<th>Mollusca</th>
<th>Crustacea</th>
<th>Echinoderm</th>
<th>Annelida</th>
<th>Bryozoa</th>
<th>Chordata</th>
<th>Total Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAS</td>
<td>17.6±1.43</td>
<td>3.8±0.71</td>
<td>0.6±0.05</td>
<td>2.1±0.48</td>
<td>0.06±0.05</td>
<td>0</td>
<td>32.7±1.58</td>
</tr>
<tr>
<td>TG</td>
<td>9.6±2.79</td>
<td>2.8±0.51</td>
<td>2.8±0.61</td>
<td>0.6±0.20</td>
<td>0.06±0.05</td>
<td>0.06±0.06</td>
<td>16.0±0.59</td>
</tr>
<tr>
<td>MB</td>
<td>5.6±2.05</td>
<td>0.9±0.17</td>
<td>0</td>
<td>0.5±0.18</td>
<td>0</td>
<td>0</td>
<td>7.1±0.48</td>
</tr>
<tr>
<td>HC</td>
<td>28.8±0.51</td>
<td>1.5±0.41</td>
<td>0.08±0.06</td>
<td>0.8±0.14</td>
<td>0.13±0.09</td>
<td>0</td>
<td>31.4±1.31</td>
</tr>
<tr>
<td>BB</td>
<td>6.6±2.03</td>
<td>6.3±1.76</td>
<td>0.5±0.26</td>
<td>1.0±0.31</td>
<td>0.13±0.09</td>
<td>0</td>
<td>14.7±1.53</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>13.7±1.79</strong></td>
<td><strong>3.1±0.44</strong></td>
<td><strong>0.6±0.17</strong></td>
<td><strong>1.0±0.14</strong></td>
<td><strong>0.08±0.03</strong></td>
<td><strong>0.01±0.01</strong></td>
<td></td>
</tr>
</tbody>
</table>

Fig 8. Faunal percentage composition (%) recorded at the 5 dive sites of Torre Abbey Sands (TAS), Thatchers Gut (TG), Millstones Bay (MB), Hope Cove (HC), Babbacombe Bay (BB).

Fig 9. Crustacean densities found at each of the 5 dive sites per 0.125m² quadrat area, with their corresponding egg densities. The letters correspond to a Tukey post-hoc test, with sites not sharing a letter being significantly different from eachother.

Fig 10. MDS plot showing how different the species assemblages were between the 5 surveyed sub-tidal habitats at Torbay.

**Comparison of diet composition (%) and sub-tidal habitat composition (%)**

Mollusca, Annelida and Bryozoa all have an electivity value of -1 (Table 8). Crustaceans were the dominant prey item recorded in the stomachs and their electivity rating confirms that the group is positively selected for. Fish have a high electivity rating due to a relatively high percentage composition in the stomachs, but a small percentage found in the sub-tidal habitat. This is likely to be exaggerated by the
lack of fish being caught in the samples. Echinoderm are also selectively avoided in the wild, with a large negative electivity value due to a much smaller amount found in the stomachs than from the sub-tidal habitat surveys.

**DISCUSSION**

The *Sepia officinalis* samples that were caught for stomach contents analysis were beginning their autumn off-shore migration and would have been spawned in the spring of that year.

**Diet of Sepia officinalis**

This study showed that *S. officinalis* feed mainly on crustaceans and fish. This has been recorded in other studies investigating the diet of *S. officinalis*, such as Guerra, (1985) Castro & Guerra, (1990), Pinczon du Sel, (2000) and Alves et al., (2006).

Annelids are shown to be part of the *S. officinalis* diet, in studies by Blanc et al. (1998), Blanc & Daguzan, (1999) and Alves et al. (2006), however none were found in this study. There were also no Molluscs recorded, but Alves et al. (2006) recorded high frequency occurrence (%F) values of bivalve molluscs, particularly in the diet of the smaller individuals. Bivalve molluscs and small gastropods were not taken into account by Castro and Guerra (1990).

Crustacean %F at the 3 sites (Torbay = 81.6%, Whitsands = 91.4%, Bigbury = 100%) were higher than other studies, such as by Castro & Guerra, (1990). They recorded a %F of 57.8%, but had a much larger sample size of 1345 *S. officinalis* stomachs.

Fish %F (Torbay = 42.1%, Whitsands = 40%, Bigbury = 20%) are similar to that of other studies by Castro & Guerra, (1990) and Alves et al., (2006), 38.7% and 44.84% respectively.

Cannibalism was only recorded at one site and at much lower levels than found in studies by Guerra, (1985), Castro and Guerra, (1990), Pinczon du Sel, (2000) and Alves et al., (2006). The high %F of cephalopods may be caused by *S. officinalis* biting each other when trapped inside fishing nets or by fights during mating (Pinczon du Sel, 2000). High levels of cephalopod %F are a sign of food scarcity (Ibanez & Keyl, 2010), possibly showing that the sites chosen provide a plentiful supply of prey for the juveniles.

*S. officinalis* are opportunistic predators (Boucher-Rodoni et al., 1987) but the diet recorded from our stomach contents samples was not as diverse as expected.

**Diet in relation to site**

Significant differences were recorded between the frequency occurrences of prey groups recorded in the stomachs at Torbay and Whitsands. The fact that the habitats at these sites are different provides a good habitat comparison as seagrass beds are found in Torbay (Hirst & Attrill, 2008), but not at Whitsands. Also, Torbay and Whitsands have equal *S. officinalis* sample sizes with greater capability for comparison.

Seagrass beds are an important habitat for many species (Jackson et al. 2011), in particular for mobile macrofauna (Larkum et al. 2006). Torbay recorded the highest %F and %W of fish, but a greater %F of crustaceans was recorded at Whitsands, which was a surprising result. A study by Hirst & Attrill, (2008) discovered that *Zostera* seagrass patches in Torbay supported a greater amount of biodiversity compared to the bare sand. Seagrass increases the predation efficiency of ambush predators (Heck & Orth, 1980) and *S. officinalis* falls into this category. The habitat provides greater ambush cover for such predators, due to a...

**Table 8.** Values for IVLEVS electivity for all 6 major phyla recorded across the 5 surveyed sub-tidal habitats.
higher structural complexity found (Heck & Orth, 1980).

Echinoderms were only recorded at Torbay, with fully intact brittlestars encountered in a S. officinalis weighing only 29g. This possibly was accidental prey, with no recording of the species foraging on Echinoderms in any previous S. officinalis dietary studies by Guerra, (1985) Castro & Guerra, (1990), Pinczon du Sel, (2000) and Alves et al., (2006). Castro & Guerra, (1990) did not record any fully intact prey fauna, as the species breaks up its prey during ingestion (Guerra et al., 1988).

**Diet in relation to size**

At Whitsands, crustaceans recorded the greatest percentage composition of the diet across the entire sample distribution. Previous studies by Castro & Guerra, (1990) and Alves et al., (2006) found that as a cuttlefish grows, greater amounts of fish are eaten in relation to crustaceans. A chi-squared test on the weight ranges at Whitsands showed a significant difference between 0-120g and 120-220g juvenile S. officinalis. Whitsands samples were chosen for comparison because these juveniles had the largest weight distribution, and so were the samples with the greatest range of maturity. The smaller S. officinalis were preying on greater amounts of crustacean than fish, perhaps due to crustaceans being the easiest prey to catch (Alves et al., 2006). A stronger trend of dietary changes correlated with size was expected to be found in this study. It is possible that the S. officinalis sampled were too young for a useful comparison to be made with previous studies. In this study, the variety of prey recorded in the diet was similar across the entire sample weight distribution. Castro & Guerra, (1990) recorded that the variety of prey in the diet decreased with an increasing S. officinalis size.

**Stomach contents weight in relation to site**

For the total and full stomach population, Torbay recorded the highest average stomach contents weights. The seagrass beds at this site possibly provided the highest prey densities for juvenile S. officinalis. Torbay also recorded the highest repletion quotients. The repletion quotients across all 3 sites (mean average of 62.8%) were similar to those recorded in a study by Alves et al., 2006, at 64.9%. Empty stomachs found could be due to cephalopods having high food conversion rates (Boletzky, 1983; Lee, 1994).

At Torbay and Whitsands, the stomach contents weight had a negative Pearsons correlation with S. officinalis length to weight ratio. This indicates that the shorter and fatter S. officinalis were foraging on a greater amount of prey than the longer and thinner S. officinalis. It is possible that the shape of an individual affects its foraging ability, or that perhaps their shape affects the rate at which they are required to grow. These are hypotheses that require further investigation.

**Stomach contents weight in relation to size**

The majority of the full stomachs recorded at Torbay and Whitsands were from smaller S. officinalis, weighing between 20-60g and 40-80g respectively. This suggests that younger individuals eat a greater quantity of prey, perhaps to grow as fast as possible. It is possible that many young cephalopods have an early phase of rapid exponential growth (Semmens et al. 2004) to ensure a smaller time period of being very vulnerable to predation.

**Prey community structure and abundance within different known habitats**

Across the 5 sub-tidal dive sites Mollusca had the highest abundances, but were not recorded in the diet of S. officinalis. The sampling method chosen was biased towards immobile and slow moving organisms. Mobile fauna such as fish and cephalopods had time to escape, resulting in only few numbers recorded. Crustaceans are the preferred prey of S. officinalis (Guerra, 1985) with the highest densities recorded at Torre Abbey Sands and Babbacombe Bay, which are a seagrass and algal habitat respectively. Both of these sites
have high egg densities, so possibly S. officinalis recognise the best habitat for its juveniles. 4 of the dive sites were seagrass habitats, which are common areas inhabited by ambush predators (Schultz et al., 2009), such as S. officinalis. They have the potential to exclude certain prey species, lowering the diversity recorded (Schultz et al., 2009). An ANOSIM showed that all the chosen sub-tidal sites had a significantly different faunal assemblage. The sites had varying egg densities, but seagrass inhabited the first 4 sites. These were expected to have very similar faunal assemblages, with just the algal habitat of Babbacombe Bay to be significantly different.

The seagrass habitat of Hope Cove recorded the highest mean abundance of species, due to huge amounts of Mytilus edulis sprats inhabiting the site. To the south is a mussel farm, north-west of Fishcombe Cove. Mussels compete for space as they grow (Griffiths & Hockey, 1987) and so are possibly in direct competition with S. officinalis prey for space and nutrients, and with the S. officinalis themselves for locations to lay their eggs. M. edulis were not recorded in any of the sampled stomachs.

**Comparison between stomach contents diet composition (%) and sub-tidal habitat composition (%)**

Mollusca, Annelida and Bryozoa all had an electivity rating of -1, with these phyla selectively avoided in the environment by juvenile S. officinalis. Echinoderm also had a low electivity rating, due to a greater amount recorded in the environment than in the diet. This shows that they are also selectively avoided by S. officinalis. Fish and crustaceans were positively selected by S. officinalis, as found in previous studies by Guerra, (1985) Castro & Guerra, (1990), Pinczon du Sel, (2000) and Alves et al., (2006). Cephalopoda was not included in IVLEVS as the group produced a biased figure of almost +1 due to only a small amount recorded in the stomachs and none in the environment.

**Further study**

1. More stomach contents analysis samples collected at Torbay, Whitsands and Bigbury.
2. Determine the gender of each individual for dietary comparison between males and females.
3. Collect samples over a period of 5 months (Blanc et al., 1998) to investigate diet with size.
4. More sites sampled along the South-West coast and compare with French studies.
5. Investigate faunal assemblages at Whitsands and Bigbury, using a similar method to the sub-tidal survey conducted at Torbay.
6. Investigate survival rate of juveniles at each sampled site. This would allow us to select the best spawning grounds for S. officinalis and advise on which areas are most important for protection and conservation.

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