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ORIGINAL ARTICLE

Distribution and reproductive biology of the little cuttlefish *Sepiola atlantica* (Cephalopoda: Sepiolidae) around Anglesey, North Wales

N. J. E. Jones · C. A. Richardson

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Abstract *Sepiola atlantica* were captured in seine nets at twelve locations around the coast of Anglesey, UK. Animals were most abundant on the very sheltered shore of Y Foryd Bay and the wave-exposed shore of Traeth Penrhos, and these two locations were further sampled seasonally to examine the seasonal occurrence, population structure and reproductive biology of *S. atlantica*. *Sepiola atlantica* (5–28 mm dorsal mantle length (DML)) migrated inshore seasonally and first appeared in July where they attained peak abundances between July and August at seawater temperatures of 17°C. Numbers declined between September and October as temperatures fell below 15–16°C, and in late October, they migrated offshore. Male *S. atlantica* was significantly smaller and matured at a smaller DML than females. The number of spermatangia on the bursa copulatrix of female *S. atlantica* varied seasonally attaining maximum numbers in October with a mean of 22 spermatangia on the bursa copulatrix of Y Foryd Bay females. At Y Foryd Bay and Traeth Penrhos, the number of spermatophores in male and potential fecundity in female *S. atlantica* ranged between 1 and 147 and 25 and 141, respectively. The spermatophoric complex and gonadosomatic index showed a high degree of variability in individuals of similar wet body weight with the female gonad constituting a far greater percentage of the total wet body weight than the male gonad. It is concluded that *S. atlantica* of all sizes and maturity stages congregate in the shallow waters around Anglesey between July and October when environmental conditions are favourable for enhanced growth and maturation and where the high numbers of animals enhance opportunities for mating.

Keywords *Sepiola atlantica* · Little cuttlefish · Atlantic bobtail squid · Seasonal distribution · Fecundity

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Introduction

An understanding of the reproductive strategy of a cephalopod species is critical in determining its life cycle and ecology (Boyle and Rodhouse 2005). Generally, short life cycle of cephalopods means that regular annual recruitments into populations are necessary in order to successfully sustain the population (Boyle 1990), and a complete understanding of the reproductive strategy of commercially important species is a key fisheries management tool (Pecl 2001). The Sepiolidae (commonly referred to as "bobtail squid") have a global distribution in most tropical, temperate and some Arctic waters (Norman 2000) and are found over the continental shelf from the intertidal zone, to depths of 1,600 m (Nixon and Young 2003). There are few target fisheries for Sepiolids (Jereb et al. 1997), yet the potential exists for members of the family to be exploited since many similar small cephalopods are caught as bycatch in fin fisheries and sold for human consumption (Volpi et al. 1995). The FAO (2009) records that 351,781 tonnes of cuttlefish and bobtail squid were caught in 2007. Cephalopods are also of ecological importance as food for organisms from higher trophic levels, such as cetaceans, seabirds, crustaceans and both demersal and pelagic fishes, as well as being predators themselves (Smale 1996; Lefkaditou and Kaspiris 2005; Rosa et al. 2006). *Sepiola atlantica* has been recorded amongst the stomach contents of the common dolphin, *Delphinus delphis* (Silva 1999; De Pierrepont et al. 2005), the small spotted catshark, *Scyliorhinus canicula* (Lyle 1983), Arctic and common terns, *Sterna paradisaea* and *S. hirundo*, respectively (Pearson 1968), and is an important prey item for whiting, *Merlangius merlangus* in the Irish Sea (Patterson 1985).

Cephalopod populations (other than nautiloids) comprise short-lived semelparous animals at different stages in their life cycle, and they are strongly influenced by, and responsive to interannual changes in environmental conditions such as seawater temperature and the availability and movement of prey species (Semmens et al. 2007; Pierce et al. 2008). In turn, these variables influence population size, distribution and species abundance (Boyle and Boletzky 1996; Semmens et al. 2007; Pierce et al. 2008). Cephalopods are known to migrate over both large-scale (thousands of kilometres), meso-scale (hundreds of kilometres) or local or fine-scale movements of one or more kilometres (Boyle and Boletzky 1996). Squid undertake both horizontal and vertical migrations to areas that offer optimum environmental conditions for spawning, embryonic development, juvenile and adult growth (Nesis 1985) and in turn enhance genetic exchange within a population (Boletzky 1983). Migratory cycles are often tuned to the reproductive cycle of the species and to seasonal cycles, with many neritic cephalopods migrating shoreward in the spring prior to spawning (Boyle and Boletzky 1996).

The distribution and reproductive biology of Sepiolids including members of the genus *Sepiola* have been relatively well studied (see Boletzky et al. 1971; Boletzky 1975, 1983; Gabel-Deickert 1995; Jereb et al. 1997; Salman and Önsoy 2004). *Sepiola atlantica* Orbigny (1839–1842), also known as the little cuttlefish or the Atlantic bobtail squid, occurs in coastal waters on the continental shelf of the north-eastern Atlantic (65 °N to 35 °N) from Iceland, the Faeroe Islands and western Norway south to Morocco (Reid and Jereb 2005) but is absent from the Mediterranean Sea (Naef 1916; Grimpe 1925; Bello 1986, 1992; Mangold and Boletzky 1988) and is one of the most common cephalopods in British waters (Yau and Boyle 1996). However, despite its wide distribution, common occurrence and prominent role in the marine food chain, little is known of its ecology and reproductive biology (see Yau and Boyle 1996; Jones and Richardson 2010; Rodrigues et al. 2010). The aims of the present study were (1) to describe the distribution of *S. atlantica* around the coast of Anglesey (UK), (2) to compare the seasonal distribution of *S. atlantica* between a wave-exposed and sheltered shore on Anglesey and (3) to further our understanding of the population ecology and reproductive biology of *S. atlantica* in order to gather information that would be of benefit to both conservation biologists and aquaculturists.

Methods

The distribution of *S. atlantica* around the coast of Anglesey was established opportunistically between June and October 2006 at twelve locations (See Fig. 1) varying in substratum type from mud to fine sand. In addition, between June 2006 and September 2008, two locations, Y Foryd Bay (a very sheltered site) within the Menai Strait and Traeth Penrhos (a south-west facing exposed site), were sampled intensively to study the seasonal occurrence of *S. atlantica*. Sampling was undertaken an hour before low water in order to survey as much of the subtidal zone as possible, on both neap and spring tides using a beach seine net (20 × 2.2 m, cod end mesh diameter = 5 mm), towed initially perpendicular to and then parallel to the shore using a small dinghy. Sampling was restricted to a depth of <1.5 m to ensure that the top of the net was on the surface to prevent animals swimming over the top of the net. Locations Y Foryd Bay and Traeth Penrhos were sampled three times each month, with a standard four tows per session; thus, fishing effort was roughly equal at both sites, with each sampling visit taking ~2 h. A distance of ~40 m was left between tows in order to reduce the chances of disturbance to *S. atlantica* further along the shore. The start and finish of each tow were recorded using a Garmin E-Trex Legend (GPS), and the depth of the tow was estimated from the dinghy using an Eagle CU DA 128 echo sounder. Seawater temperature during sampling was recorded continuously using a Tinytag temperature data logger. The degree of wave exposure at each location (Fig. 1) was assessed using the Ballantine 'Biologically defined Exposure Scale' (Ballantine 1961). Some of the *S. atlantica* caught were killed immediately and placed on ice in preparation for freezing and later study whilst others were transported alive back to the laboratory (see Jones and Richardson 2010).

Dorsal mantle length (DML) and anterior mantle width (MW) from a subsample of thirty *S. atlantica* of a range of sizes collected over the sampling period were measured using vernier callipers (to the nearest 0.1 mm). The reproductive stage of each *S. atlantica* was assessed using the maturity stage scale (juveniles (I) to sexually mature (IV)) devised by Yau and Boyle (1996) and their gender determined. Blotted total wet weight (Ww) and dissected gonad weight (gw) (♀ = ovary; ♂ = spermatophoric complex = spermatophoric sac, vas deferens and spermatophoric glands) of sexually mature (stage IV) animals were determined to the nearest 0.01 and 0.001 g, respectively, using a balance. Digital images of whole gonads of *S. atlantica* placed under a dissecting photo-microscope were taken and the captured images analysed using analySIS® image software to count the number of spermatophores in Needham's sac of mature males. Potential fecundity (PF) in mature females was determined by counting the number of oocytes

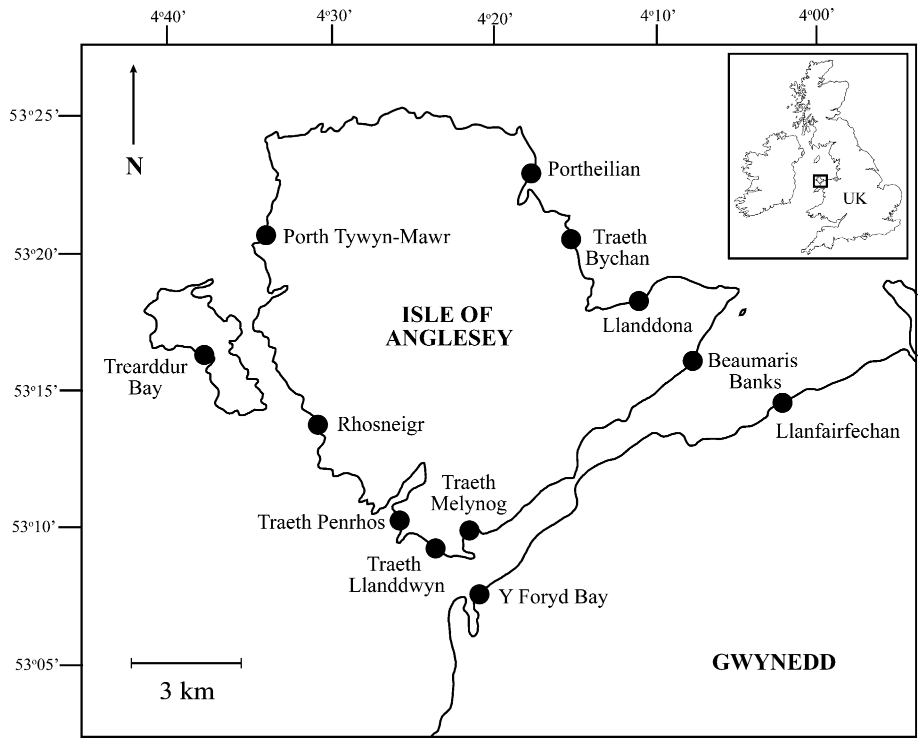

Fig. 1 Isle of Anglesey and the locations where *Sepiola atlantica* were collected. Inset the location of the Isle of Anglesey within the UK

in the ovary and the number of ripe eggs in the oviduct, whilst relative fecundity (RF) was calculated as a ratio of potential fecundity to total wet weight (RF = PF/Ww). A gonadosomatic index (GSI) for females and a spermatophoric complex index (SCI) for males were calculated using the equation: GSI or SCI = 100*[gonad wt (g)/(total wt−gonad wt (g))].

Potential differences in the DML and MW between male and female *S. atlantica* from Y Foryd Bay and Traeth Penrhos were tested where appropriate using one-way ANOVA or a Student's t test, respectively. Potential significant differences in DML and Ww between males and stage IV females of the same reproductive stage from Y Foryd Bay were investigated using one-way ANOVA. Where sample numbers were too small for ANOVA, the less powerful Student's t test and Mood's median test were used to check whether there were any significant differences in DML and Ww of stage II and III *S. atlantica*. Due to the small sample size of stage III males from Traeth Penrhos ($n = 2$), statistical differences between the sexes at this site could not be established. A Mood's median test was applied to determine differences in gonadosomatic indices as tested pairs were neither normally distributed nor assumed to have equal variance.

Results

Figure 1 shows the locations surveyed off the Anglesey coast and within the Menai Strait. *Sepiola atlantica* were recorded at each location surveyed except Rhosneigr, although they had previously been reported (B. Roberts pers. comm.). The largest number of *S. atlantica* collected from Y Foryd Bay was forty-two in July 2007, whilst twenty-one were collected at Traeth Penrhos in July 2006. No *S. atlantica* were caught when wind speeds exceeded 7 knots.

Figure 2 shows a clear seasonal pattern of abundance of *S. atlantica* at Traeth Penrhos and Y Foryd Bay between 2006 and 2008. At Traeth Penrhos, animals were present only during July and August. With the exception of July 2006 when sampling did not take place in Y Foryd Bay, individuals were present between July and September. A single juvenile was collected in April 2007 during a period of unseasonably clement weather, and three *S. atlantica* were collected in October 2006, although in the following years, they were absent in October. The annual arrival of *S. atlantica* into shallow coastal waters at both locations in July coincided with a seawater temperature of ~17°C. In August, the numbers of individuals decreased and were absent once the seawater temperature fell below 15°C. It is likely that *S. atlantica* left the exposed Traeth Penrhos location slightly earlier than the sheltered site of Y Foryd Bay.

The largest *S. atlantica* collected (28 mm DML) was from Porth Tywyn Mawr in August 2006, whilst the smallest was 5 mm (DML), from Trearddur Bay in July 2006. Two hundred and two *S. atlantica* were collected from Y Foryd Bay between August 2006 and September 2008 and ranged in size between 7 and 24 mm (DML) (Fig. 3a). Sixty-seven *S. atlantica* (size range 7–20 mm DML) were

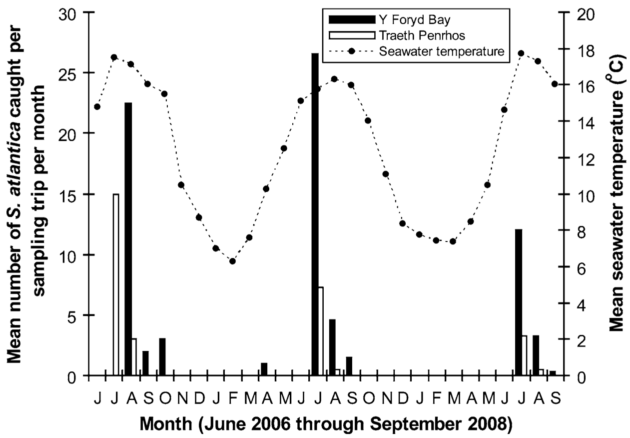

Fig. 2 The seasonal distribution of *Sepiola atlantica* collected from Traeth Penrhos and Y Foryd Bay, Anglesey between June 2006 and September 2008. In 2007 and 2008, sampling was usually only undertaken between April and November

collected from Traeth Penrhos between July 2006 and August 2008 (Fig. 3b). The male/female ratio at Traeth Penrhos and Y Foryd Bay was 1.14:1 ($n = 24{:}21$) and 1:1 ($n = 76{:}76$), respectively. The remaining animals in these populations showed no signs of sexual differentiation and were classed as stage I juveniles. Figure 3 illustrates the size frequency distributions of juvenile, male and female *S. atlantica* from Y Foryd Bay and Traeth Penrhos between 2006 and 2008. Juveniles from Y Foryd Bay ranged in size between 7 and 11 mm (mean = 9.33 ± 1.43 mm SD), whilst males measured between 11 and 22 mm DML (mean = 15.20 ± 2.12 mm SD) and females between 12 and 24 mm in DML (mean = 17.75 ± 2.55 mm SD) (Fig. 3a). One-way ANOVA showed that Y Foryd Bay females were significantly ($P < 0.001$) larger than males. Juveniles at Traeth Penrhos were similar in size (range 7–10 mm DML (mean = 10.28 ± 1.63 mm (SD)) to those at Y Foryd Bay, whilst the size of males (size range, 11–18 mm; mean = 13.82 ± 1.91 mm SD) and females (size range, 10–20 mm; mean = 16.20 ± 2.66 mm SD) was smaller (Fig. 3b). Traeth Penrhos females were also significantly ($P = 0.001$) larger than males.

Figures 4a and b show a general trend of increasing maturity stage with increasing body size in *S. atlantica* from both locations (see also Table 1). Considerable overlap in the size ranges of animals from each of the four maturity stages is apparent, with the exception of stage III animals from Traeth Penrhos, where the two males recorded were smaller in size than the smallest of the females collected. At different stages during their development, female *S. atlantica* from Y Foryd Bay and Traeth Penrhos were generally larger than males. Stage II males appeared smaller than stage II females, although the difference was not significant (Y Foryd Bay: Mood's median

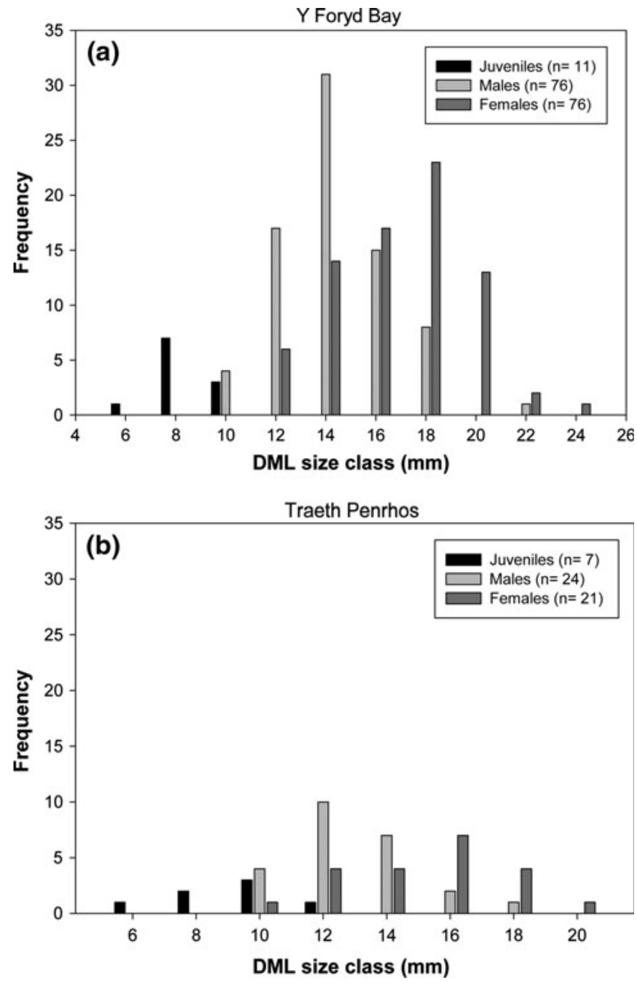

Fig. 3 Length-frequency distributions of juvenile, male and female *Sepiola atlantica* collected between 2006 and 2008 from (**a**) Y Foryd Bay and (**b**) Traeth Penrhos

test, chi-square = 1.76, $P > 0.05$, $df = 25$; Traeth Penrhos: $t = -1.04$, $P > 0.05$, $df = 19$). Stage III males were significantly smaller than stage III females (Y Foryd Bay: Student's t test, $t = 2.58$, $P = 0.014$, $df = 37$), whilst stage IV females were larger than males (Y Foryd Bay: ANOVA, $F = 92.18$, $P \leq 0.001$, $df = 86$; Traeth Penrhos: $t = -3.72$, $p = 0.002$, $df = 14$). In terms of the body mass of some of the maturity stages, total wet weight (Ww) of stage II and III males and females from both locations was not significantly different ($P > 0.05$) (Y Foryd Bay: stage II, $t = -0.82$, $df = 24$, stage III, $t = -1.61$ $df = 37$; Traeth Penrhos: stage II, $t = -1.64$, $df = 19$). Y Foryd Bay stage IV females were significantly heavier ($P \leq 0.001$) than males (ANOVA, $F = 27.68$, $df = 86$), but this difference was not detectable in *S. atlantica* in individuals from Traeth Penrhos ($t = -1.02$, $P > 0.05$, $df = 14$).

Fifty per cent of male *S. atlantica* from Y Foryd Bay and Traeth Penrhos were fully mature at 13.2 mm and

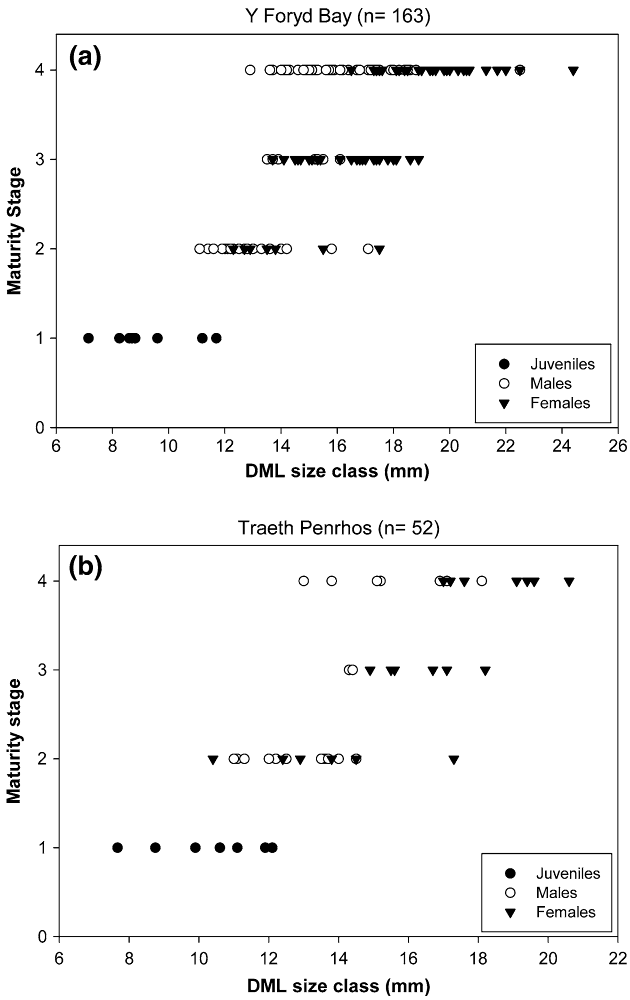

Fig. 4 The relationship between dorsal mantle length (*DML*) and maturity stage of *Sepiola atlantica* collected from (**a**) Y Foryd Bay and (**b**) Traeth Penrhos

14.2 mm DML, respectively, and 50% of females from both locations were fully mature at 16.9 mm and 15.7 mm, respectively. All males and females from Y Foryd Bay and Traeth Penrhos were mature at 18 mm and 19.9 and 15.9 and 20 mm DML, respectively. The number of *S. atlantica* from Traeth Penrhos and Y Foryd Bay between June and October in different stages of gonad development is shown in Table 2. At Y Foryd Bay, the abundance of stage I juveniles remained low throughout the season (between July and October), whilst low numbers of subadult stage II and stage III *S. atlantica* were only present in July and August. Fully mature animals (stage IV) were present throughout the season, being most numerous in July and August during which time they were the dominant group within the population. Lower numbers of *S. atlantica* were collected from Traeth Penrhos, although the population structure was similar in several respects to the population from Y Foryd Bay. Stage I juveniles and stage II subadults were only present in July and September, and in July almost half of the *S. atlantica* caught were stage II animals. Stage III *S. atlantica* were present in low numbers at Traeth Penrhos during July and August only, whilst fully mature animals were found in comparatively low numbers in July, yet later they constituted a large proportion of the population in August and September.

Between July and October, >50% of stage IV females present at Y Foryd Bay had previously mated ($n = 38$) as evident from the presence of spermatangia on the *bursa copulatrix*. There was a consistent monthly increase in the number of spermatangia on the *bursa copulatrix* of females collected from Y Foryd Bay. The mean number of spermatangia observed on the *bursa copulatrix* of Y Foryd Bay females between 2006 and 2008 was 22.0 (±13.83 SD), range 2–48 spermatangia ($n = 24$). Interestingly, only one mated female was recorded at Traeth Penrhos with 51 spermatangia on the *bursa copulatrix*.

Figure 5 shows the relationships between total wet weight and male SCI and female GSI from Y Foryd Bay and Traeth Penrhos (see also Table 3). At both locations, there was a high degree of variability in both SCI and GSI of animals of similar weight; the female gonad constituted a significantly greater proportion of the total wet weight than the male gonad (Y Foryd Bay: $P \leq 0.001$, chi-square = 40.97; Traeth Penrhos: $P = 0.001$, chi-square = 10.97).

The relationship between potential fecundity and size (DML) of *S. atlantica* at Y Foryd Bay and Traeth Penrhos is shown in Fig. 6 (see also Table 4), where there appears to be a large degree of variability in potential fecundity amongst animals of a similar size. The relative fecundity of female *S. atlantica* ranged between 15.8 and 59.7 eggs g^{-1} (mean 26.6 ± 8.8 (SD) eggs g^{-1}) at Y Foryd Bay and between 24.5 and 51.8 eggs g^{-1} (mean 34.0 8 ± 8.37 (SD) eggs g^{-1}) at Traeth Penrhos. By comparison, Fig. 7 shows the relationship between size (DML) and the number of spermatophores present in Needham's sac of male *S. atlantica* from both sites. There is a high degree of variability in the number of spermatophores in mature male *S. atlantica* of similar size. A comparison of the relationship between DML and numbers of spermatophores for both sites showed significant, but weak correlation (Y Foryd Bay: Pearson's correlation coefficient of 0.33, $P = 0.03$; Traeth Penrhos: Pearson's correlation coefficient of 0.73, $P = 0.02$) between the two variables. The mean number of spermatophores of male *S. atlantica* ($n = 42$) from Y Foryd Bay was 42.86 (±31.59 SD), with a range of between 1 and 147 spermatophores, whilst a mean of 56.8 (±35.80 SD) spermatophores were found in *S. atlantica* ($n = 9$) from Traeth Penrhos (range 3–106 spermatophores).

Table 1 Mean dorsal mantle length (*DML*) and wet weight (*Ww*) at each maturity stage for juvenile, male and female *Sepiola atlantica* collected from Y Foryd Bay and Traeth Penrhos

Maturity stage	*N*	Mean ♂ DML (mm) ± SD	*N*	Mean ♀ DML (mm) ± SD	Significant difference between ♂ & ♀
DML Y Foryd Bay					
II	19	12.97 ± 1.4	7	14.02 ± 1.8	Not significant***
III	8	14.81 ± 0.9	31	16.22 ± 1.4	Significant**
IV	49	16.13 ± 1.7	38	19.68 ± 1.6	Significant*
DML Traeth Penrhos					
II	14	12.70 ± 1.2	7	13.45 ± 2.1	Not significant**
III	2	14.35 ± 0.07	6	16.33 ± 1.2	n/a
IV	8	15.63 ± 1.7	8	18.50 ± 1.3	Significant**
Maturity stage	***N***	**Mean ♂ Ww (g) ± SD**	***N***	**Mean ♀ Ww (g) ± SD**	**Significant difference between ♂ & ♀**
Ww Y Foryd Bay					
II	19	0.81 ± 0.1	7	0.88 ± 0.1	Not significant**
III	8	1.19 ± 0.2	6	1.38 ± 0.3	Not significant**
IV	49	1.58 ± 0.4	38	2.15 ± 0.5	Significant*
Ww Traeth Penrhos					
II	14	0.75 ± 0.1	7	0.93 ± 0.3	Not significant**
III	2	0.88 ± .09	6	1.33 ± 0.1	n/a
IV	8	1.54 ± 0.6	8	1.84 ± 0.5	Not significant**

Asterisks denote the statistical tests used to determine significance at $P < 0.05$. * One-way ANOVA. ** Student's *t* test, *** Mood's median test

n/a Not applicable

Table 2 Monthly variation in the number (percentage) of *Sepiola aNStlantica* from Traeth Penrhos and Y Foryd Bay in different stages (I to IV) of gonad development

Site	July (%)	August (%)	September (%)	October (%)
Stage I				
Traeth Penrhos	6 (13.9)	0	1 (25)	n/d
Y Foryd Bay	8 (8.6)	2 (3.1)	0	1 (25)
Stage II				
Traeth Penrhos	20 (46.5)	0	1 (25)	n/d
Y Foryd Bay	17 (18.2)	9 (14.2)	0	0
Stage III				
Traeth Penrhos	7 (16.2)	1 (20)	0	n/d
Y Foryd Bay	24 (25)	15 (23.8)	0	0
Stage IV				
Traeth Penrhos	10 (23.2)	4 (80)	2 (50)	n/d
Y Foryd Bay	44 (47.3)	37 (58.7)	3 (100)	3 (75)

n/d No data

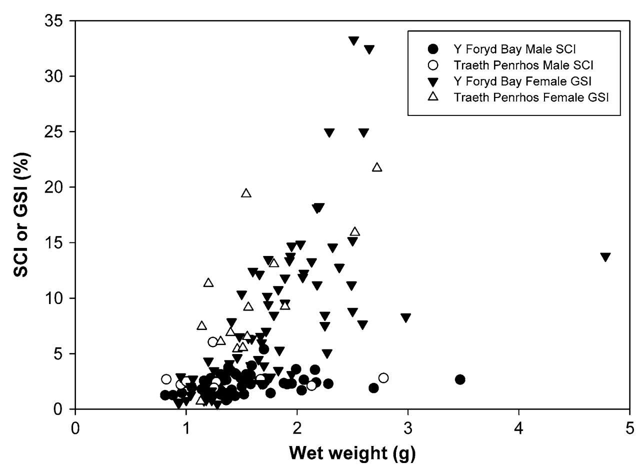

Fig. 5 The relationship between wet weight (*Ww*), spermatophoric complex index (*SCI*) and gonadosomatic index (GSI) for male and female *Sepiola atlantica* collected from **(a)** Y Foryd Bay and **(b)** Traeth Penrhos between 2006 and 2008

Discussion

Both exposed and sheltered sand and mud shores around Anglesey were suitable habitats for *S. atlantica*. During windy weather conditions (winds >7 Knots) when waves and swash occurred along the shores, little cuttlefish were not caught in shallow water, and it has even been suggested that they might be eradicated during extreme weather events and rough seas (see Yau and Boyle 1996). Heavy swells generated during storms disturb inshore sediments and Boletzky (1983) noted that large *S. robusta* moved offshore in the advance of storms and only returned inshore when conditions were favourable.

In 1996, Yau and Boyle reported that *S. atlantica* were present annually between December and August in the shallow sublittoral waters of Firemore Bay, Loch Ewe, Scotland, and they suggested that the continued presence of

Table 3 A comparison of body weight (Ww) and the spermatophoric complex index (SCI) and gonadosomatic index (GSI) of mature male and female *Sepiola atlantica* collected from Y Foryd Bay and Traeth Penrhos between 2006 and 2008

Site	Sex	*N*	Mean Ww (± SE) (g) of *Sepiola*	Range (g)	Mean SCI or GSI (±SE) (%)	Range (%) min (max)	Sig. diff in SCI or GSI (%) between ♂ & ♀
Y Foryd Bay	♂	57	1.52 (±0.05)	0.81–3.47	2.35 (±0.11)	0.81 (5.39)	Significant
Y Foryd Bay	♀	68	1.81 (±0.07)	0.93–4.78	8.70 (±0.85)	7.08 (33.29)	
Traeth Penrhos	♂	10	1.41 (±0.19)	0.82–2.78	2.78 (±0.37)	1.92 (6.04)	Significant
Traeth Penrhos	♀	14	1.62 (±0.12)	1.13–2.72	9.88 (±1.56)	5.84 (21.70)	

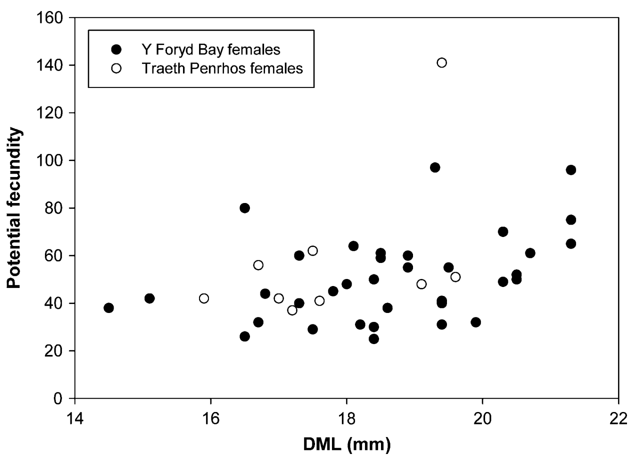

Fig. 6 The relationship between potential fecundity (*PF*) and dorsal mantle length (*DML*) in female *Sepiola atlantica* collected from Y Foryd Bay and Traeth Penrhos between 2006 and 2008

S. atlantica in the Loch was probably dependent on the annual recruitment of individuals from outside the Bay. A distinct seasonal pattern of the occurrence of *S. atlantica* was observed at both Y Foryd Bay and Traeth Penrhos between July and October and was related to seasonal changes in seawater temperature. Little cuttlefish (size range between 5 and 28 mm DML) arrive into shallow waters once seawater temperatures reach 17°C. By contrast, Yau and Boyle (1996) collected *S. atlantica* of a range of sizes (between 3 and 21 mm DML; a maximum size smaller than around Anglesey) from Loch Ewe, Scotland, over a more extended period (between December and August, 1988–1992). They found highest abundances in July and unusually collected three animals in December 1988, although the majority of individuals were netted between March and August when sampling was undertaken. However, they did not sample between September and February, so individuals may have persisted in the Loch at other times of the year. *Sepiola atlantica* appeared seasonally in the spring and summer on three Flemish Banks (Oost Dyck, Buiten Ratel and Kwinte Bank) between 1981 and 1986 (Maertens 1988). Kristensen (1959) noted that *S. atlantica* were present in Dutch coastal waters during the summer, whereas during the winter, they were found 10 km from the coast and Beyst et al. (2001) collected juvenile *S. atlantica* in May in the surf zone off the Belgian coast, although they were absent throughout the rest of the year. Large (>22 mm DML) *Sepietta oweniana* migrate from deep (400 m) to shallower water (40 m) off the north-eastern Greek coast between the early summer and the autumn to spawn (Lefkaditou and Kaspiris 2005), in a similar manner to those from the northern Catalan Sea (Mangold-Wirz 1963). Around the British Isles, small (2–4 mm DML) and mature *S. atlantica* up to 20 mm DML have been caught in offshore plankton hauls collected during the autumn and winter (October to January) (Collins et al. 2002), indicating that spawning takes place shortly before this time in populations around the British Isles.

Sepiola atlantica enters the shallow subtidal zone (depth 1–2 m) in the spring and summer for a number of reasons. They probably seek prey species, e.g. shrimp *Crangon crangon*, that are plentiful during the summer in the warm

Table 4 The relationship between size (DML) and female fecundity in *Sepiola atlantica* collected from Y Foryd Bay and Traeth Penrhos between 2006 and 2008

Site	*N*	Mean DML (mm) (±SD)	Mean potential fecundity (±SD)	Range min (max)	Probability (Pearson's correlation coefficient)	Mean no. oocytes in ovary (±SD)	Range min (Max)	Mean no. ova in oviduct (±SD)	Range min (max)
Y Foryd Bay	35	18.62 (±1.67)	43.61 (±2.40)	25 (97)	0.015* (0.408)	11.91 (±10.77)	0 (42)	38.74 (±13.64)	14 (80)
Traeth Penrhos	9	17.77 (±1.29)	48.5 (±12.9)	37 (141)	0.169 (0.501)	10.22 (±9.43)	0 (25)	47.60 (±35.50)	26 (141)

The correlation analysis between DML (mm) and potential fecundity is shown

* Significant at $P < 0.05$

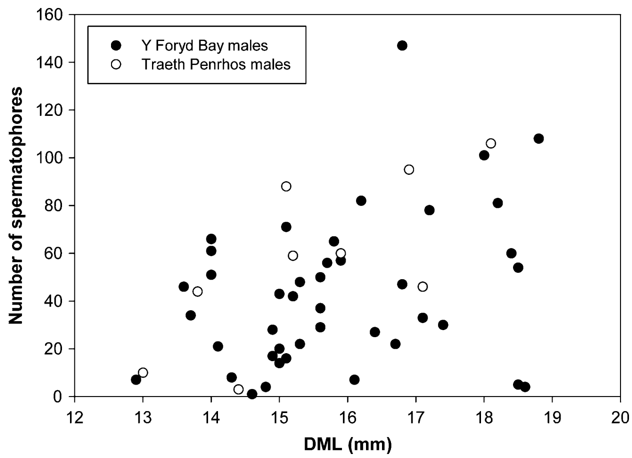

Fig. 7 The relationship between dorsal mantle length (*DML*) and the number of spermatophores in male *Sepiola atlantica* collected from Y Foryd Bay and Traeth Penrhos between 2006 and 20

shallow waters around Anglesey (pers. obs.), and an inshore migration into shallow water offers the opportunity for locating a suitable mate. However, the presence of animals of all maturity stages throughout the summer season suggests that the sole purpose for the annual migration may not be for mating. Evidence for shallow water mating was obtained when a mating pair of *Sepiola atlantica* was observed following collection in 2008 from the seine net. Also, individuals captured in the seine net and transferred to aquaria readily mated during the summer months (see Jones and Richardson 2010). Egg laying in inshore waters following mating and fertilisation may occur. However, despite extensive trawling in the shallow subtidal in a range of locations around Anglesey, no egg masses were found. *Neorossia caroli* prefers to lay its egg masses in deep water off Sardinia in the Mediterranean rather than in shallow water (Cuccu et al. 2007), and *S. atlantica* may adopt a similar strategy. Interestingly, *S. atlantica* appeared to leave the more exposed shore at Traeth Penrhos earlier in the season than the sheltered Y Foryd Bay probably because at the exposed location storms and inclement weather tended to be more frequent towards the end of the summer.

Despite the assertion that female cephalopods are generally more numerous than males (Mangold-Wirz 1963), in shallow coastal waters, members of the family Sepiolidae have almost equal male to female ratios. In our study, *S. atlantica* had an approximately equal male/female ratio (1.14:1 for Traeth Penrhos and 1:1 for Y Foryd Bay) that is not dissimilar from other *S. atlantica* populations, e.g. a 1.4:1 ratio in Loch Ewe (Yau and Boyle 1996), and of other members of the Sepiolidae (see Orsi Relini and Bertuletti 1989; Zumholz and Frandsen 2006; Rosa et al. 2006; Jereb et al. 1997).

Fecundity in female cephalopods is estimated by counting the number of oocytes in the ovary and ripe eggs in the oviduct of wild specimens or by counting the number of eggs laid by females in captivity. However, conditions in captivity are often different to those in the wild. Counts of ova in wild-caught specimens may give an underestimation of fecundity as spawning may have already been initiated prior to capture (Mangold-Wirz 1963). Jones and Richardson (2010) recorded five female *S. atlantica* that had been collected from the wild and held in captivity that laid between 8 and 161 eggs, whilst Rodrigues et al. (2010) recorded twelve female *S. atlantica* laying between 31 and 115 eggs under laboratory conditions, numbers similar to the range in potential fecundity of wild-caught females from the present study (range of 25–141 eggs) and from Loch Ewe = 42–146 (Yau and Boyle 1996). Salman and Önsoy (2004) reported a potential fecundity of 117–245 (mean of 159), 163–191 (mean of 177) and 111–407 (mean of 231) eggs in *S. robusta*, *S. steenstrupiana* and *S. intermedia,* respectively.

A mean of forty-two and fifty-six (range 1–147 ($n = 51$)) spermatophores were counted in males from Y Foryd Bay and Traeth Penrhos, respectively, estimates considerably lower than those of individuals from Firemore Bay, Scotland (Yau and Boyle 1996), from which between 59 and 338 spermatophores were recorded. It is possible that the difference between the two populations is that males from Anglesey may have mated several times during their migration into shallower water prior to capture since the fecundity of females was similar in both the Scottish and Anglesey populations, or that those *S. atlantica* from Firemore Bay were collected closer to spawning or in fact closer to the spawning grounds. The number of spermatophores found in male *S. atlantica* is similar to other members of the Sepiolinae. Salman and Önsoy (2004) recorded between 98 and 217 (mean of 156) spermatophores in male *Sepiola intermedia* and 109–386 (mean of 143) spermatophores in *S. robusta*.

Yau and Boyle (1996) found that the ovary of fully mature females accounted for as much as 22% of the residual body weight, whilst in males, the spermatophoric sac complex and testis accounted for a smaller proportion, ~7.8% of residual body weight. The ovary of fully mature females from Anglesey accounted for up to 33% (mean of 8.7%) and 21% (mean of 9.8%) of the residual body weight at Y Foryd Bay and Traeth Penrhos, respectively. In males from Y Foryd Bay, the spermatophoric sac complex and testis accounted for up to 5% (mean of 2.4%) of the residual body weight, whilst a maximum SCI of 6% (mean of 2.8%) was determined for mature males from Traeth Penrhos, similar to the Firemore Bay population. Once again, these findings are similar to those made for other Sepiolids (see Salman and Önsoy 2010).

During mating, male *S. atlantica* transfer spermatophores to females, which are subsequently stored in the *bursa copulatrix*, a large pouch located near the female genital opening that facilitates the attachment of the spermatangia (Reid and Jereb 2005; Rodrigues et al. 2009), where they can be stored for up to 1 month (Yau 1994). Therefore, the presence of spermatangia in a number of female *S. atlantica* from Y Foryd Bay throughout the season suggests that females mate in or close to the shallow waters of Y Foryd Bay over a prolonged period in the summer and early autumn. The numbers of spermatangia recorded in the present study are similar to those found in other Sepiolidae. Önsoy et al. (2008) observed mated female *S. patagonica* with between 2 and 19 (mean = 9) spermatangia, Hoving et al. (2008) recorded between 6 and 21 (mean = 14 $\pm$ 5) spermatangia female^{-1} in *R. moelleri*, whilst Cuccu et al. (2007) recorded between 5 and 24 spermatangia in mated female *N. caroli*.

Our study has demonstrated that the little cuttlefish, *S. atlantica*, has a seasonal distribution in the shallow subtidal zone around the coast of Anglesey where it is likely to be an important prey species of fishes as well as being a predator of coastal invertebrates. Animals of all sizes and maturity stages congregate in the shallow waters around Anglesey between July and October when environmental conditions are favourable for enhanced growth and maturation and where the high numbers of animals in the shallow subtidal zone enhance opportunities for mating and genetic exchange. From observations and anecdotal evidence, it appears that *S. atlantica* mate whilst in the shallow subtidal zone of Y Foryd Bay and possibly spawn in the area soon afterwards. No egg masses were found at low water of spring tides or in the shallow subtidal perhaps suggesting that *S. atlantica*, having mated in shallow water, spawns in deeper water offshore. The study has highlighted the importance of Y Foryd Bay as an area of scientific and conservation importance to *S. atlantica*.

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