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Biochemical content, energy composition and reproductive effort in the broadcasting sea star *Asterias vulgaris* over the spawning period

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Abstract

To assess sex differences in reproductive effort, we examined the biochemical composition and energetic content of the principal body components of the broadcast spawning sea star *Asterias vulgaris* in the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada. The body wall was the most stable body component, showing no variations in mass or in lipid and protein content (and total energetic content) between sexes or during spawning. Patterns in the gonads differed between sexes and with spawning. The lipid, protein and carbohydrate content of the ovary dropped during spawning, while only the protein content of the testis decreased significantly. Reproductive effort, expressed as loss of energy in the gonads during spawning for an individual weighing 10 g in underwater mass (8.2 cm in radius), was six times greater in females (49.5 kJ) than males (7.9 kJ). The energetic content of the pyloric caeca also decreased during spawning, by 17.7 kJ in females and 21.5 kJ in males, mainly due to a decrease in lipids. If this decrease is included as reproductive effort, it lessens the gender difference. The caecum decrease possibly represented expenditures due to formation of aggregations or the expulsion of gametes during spawning. Effectively, we observed aggregations during a massive spawning in this population. The sex ratio did not differ from 1:1 in all size classes sampled. This suggests that, unless males suffer higher mortality, females manage to allocate as much energy to somatic growth as males, possibly by feeding at higher rates to compensate for their higher reproductive effort. Stomach protein content tended to be higher in females than males and may indicate greater muscular development to facilitate digestion.

Keywords: Gamete spawning; Gulf of St. Lawrence; Proximate biochemical composition; Reproductive effort; Sea star *Asterias vulgaris*

1. Introduction

As reproduction usually entails major energetic costs, insights into reproductive strategies can often be obtained by examining how energy is allocated to different processes (Giesel, 1976; Grime, 1979; Todd, 1979; Lawrence, 1985; Lawrence and McClintock, 1994; Doughty and Shine, 1997). Ingested energy must be partitioned among reproduction, growth and maintenance, and this allocation may vary between sexes as well as changing during the reproductive cycle (Giesel, 1976; Lawrence, 1985; Reznick, 1992; Lawrence and McClintock, 1994; Carey, 1999). Often reproduction is restricted to a particular period when food intake is maximal (MacGinitie and MacGinitie, 1949; Giese, 1959). If reproductive effort (costs) differs between sexes, one would predict the

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energetic content and growth of somatic tissues to be lower in the sex with the greater reproductive effort. An analysis of how reproduction changes the allocation of energy to various organs can indicate their importance in reproduction, maintenance and somatic growth (Giese, 1966; Williams, 1966; Lawrence, 1973, 1985; Stearns, 1976; Charlesworth, 1980; Hirshfield, 1980).

Many studies of the biology of shallow-water sea stars report on their reproduction, population dynamics and energetics (e.g., Menge, 1974; Lawrence and Lane, 1982; Harrold and Pearse, 1987; Chia and Walker, 1991). One of the best studied species is the common North Atlantic sea star, *Asterias vulgaris* (Verrill) (Walker, 1974; Lowe, 1978; Lowe and Dearborn, 1979; Walker and Larochelle, 1984; Smith, 1985; Smith and Walker, 1986; Watts et al., 1990; Himmelman and Dutil, 1991; Claereboudt and Bouland, 1994; Gaymer et al., 2001a,b,c), which occurs from southern Labrador to North Carolina (Smith, 1940; Bousfield, 1960). Several workers consider it to be synonymous to *Asterias rubens* of European waters (Tortonese, 1936; Franz et al., 1981; Nichols and Barker, 1984). Both are broadcast spawners that release gametes from late spring to early summer. The planktotrophic larvae develop into juveniles that settle from mid summer to early autumn (Smith, 1940; Lacalli, 1981; Nichols and Barker, 1984). For *Asterias* species and other free-spawning asteroids that do not provide parental care, the energy allocated to the production of gametes can be considered as their reproductive investment (Thorson, 1950; Mileikovsky, 1971).

Although numerous studies quantify seasonal changes in the relative size or biochemical composition of different body components in sea stars (Pearse and Giese, 1966; Vance, 1973; Crisp, 1974; Chia, 1974; Menge, 1974; Graham, 1977; Harrold and Pearse, 1980; Lawrence and Moran, 1992; McClintock et al., 1995), often males and females are not considered separately. Instead they are pooled without first being shown to be similar. This approach has often been used for *Asterias* spp. (Gemmill, 1914; Vevers, 1949; Jangoux and Vloebergh, 1973; Walker, 1974; Barker and Nichols, 1983; Franz, 1986), but there are exceptions where the sexes are treated separately (Lowe, 1978; Lowe and Dearborn, 1979). On the other hand, several studies of *Asterias* spp. only deal with specific organs in one sex (Oudejans and Van der Sluis, 1979; Oudejans et al., 1979; Smith and Walker, 1986).

Although male and female *A. vulgaris* have similar reproductive behaviour, both releasing gametes directly into the water, reproductive effort could vary between sexes, given the differences in size, morphology and chemical composition of male and female gametes. If this were true, reproductive effort could be higher for one sex than the other. This in turn could cause differences between sexes in the energy available for somatic growth and could change growth rates leading to a change in the sex ratio with increasing body size.

In this study, we compare energy allocation to different body components in male and female *A. vulgaris* to provide insights into the reproductive strategy of this species. We first compare the size and biochemical and energetic composition of different body components in males and females at two contrasting points in the reproductive cycle, before and after spawning. We then estimate reproductive effort for each sex, and finally we examine whether sex ratio varies with size.

2. Methods

2.1. Sea star sampling

We used SCUBA diving to collect adult *A. vulgaris* (Fig. 1) measuring >2 cm in radius (distance from the centre of the oral opening to the extremity of an average-sized arm) on 25 June 1998, just prior to spawning, and on 26 July 1998, when spawning was finished (Fig. 2). That these sampling dates represented times before and after spawning was confirmed by additional sampling on 19 June, 4 July and 13 August 1998. Gonadal and caecum indices (organ mass as a percentage of total body mass) were determined for each of these sampling dates. Sampling was done between 5 and 10 m in depth on bedrock substratum at Île aux Goélands, in the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada. On 23 and 25 June, two animals were seen releasing gametes, and some were in tight aggregations. Also, some of individuals collected on 25 June released

Fig. 1. A sea star *Asterias vulgaris* in spawning position.