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RESEARCH ARTICLE

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Relationship between egg features and maternal body size in the simultaneous hermaphrodite *Oxynoe olivacea* (Mollusca, Opisthobranchia, Sacoglossa)

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Abstract This paper provides information on spawn morphology and egg features of the stenophagous planktotrophic Mediterranean sacoglossan *Oxynoe olivacea*. Smith and Fretwell's hypothesis, predicting that individuals of the same population growing in the same environmental conditions and varying in size should spawn eggs of a constant size, was tested in a population of *O. olivacea* living in the Straits of Messina. To determine whether (a) spawn mass size, (b) total egg number per spawn, and (c) egg size were related to parent size of *O. olivacea*, 21 egg masses (seven egg masses deposited by seven different 20 mm animals, seven egg masses deposited by seven different 25 mm animals and seven egg masses by seven different 30 mm animals) were randomly chosen and examined. Results showed that both spawn mass width and number of eggs per spawn mass increased across *O. olivacea* body size and apart from the significant variation of the short capsule diameter, there was no consistent variation of egg features in *O. olivacea*. In conclusion the species allocates constant amounts of energy to individual embryos and thus supports the prediction designed by Smith and Fretwell.

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Introduction

Phenotypic variation among reproductive traits (egg size, spawn mass, embryonic development rate, and larval success) is fundamental to evolutionary ecological studies (Marshall and Keough 2005). This variation, observed among and within a wide range of taxa, provides the raw material on which natural selection operates (Bernardo 1996; Roff 2002).

The investigation of the evolution of life histories requires an accurate knowledge of the trade-offs that govern reproductive strategy (Kaplan and Cooper 1984; Lloyd 1987). Trade-offs occur because no simultaneous maximization of all life-history traits is possible, thus optimization of reproductive traits entails a compromise in the allocation of resources between the size and number of descendants (Roff 2002; Stearns 1992).

Many theoretical studies (Smith and Fretwell 1974; Christiansen and Fenchel 1979; Begon and Parker 1986; Parker and Begon 1986; McGinley et al. 1987; Lalonde 1991; Levitan 2000; Sakai and Sakai 2001; Hendry and Day 2003; Sakai and Harada 2004, 2005) have analysed optimal offspring size assuming a size-number trade-off. Furthermore, the effects of environmental variation on optimal offspring size have been explored in both empirical and theoretical studies (Einum and Fleming 1999; Moran and Emlet 2001; Marshall and Keough 2005). Within this framework, there has been particular interest in examining the compromise between the size and number of offspring produced and maternal body size (Lack 1947; Roff 2002; Sakai and Harada 2004, 2005).

One of the first attempts to understand the evolution of offspring size was the graphical model of Smith and Fretwell (1974), in which it is assumed that offsprings are produced using a fixed amount of endogenous reserves and that no current income is available during reproduction. A central assumption of this and others models (see Marshall and Keough 2005) is that offspring size and fitness is not maternal size dependent, but constant among individuals of the same population growing in the same environmental conditions.

Despite the fact that the aforementioned principles could be applied to numerous taxa (Stearns 1992) the linear size number trade-off model of Smith and Fretwell (1974) is not universally supported among marine gastropods. For prosobranch species, the general trend is that the number of eggs increases with female size and that egg size is independent of female size (Miloslavich and Defresne 1994; Chaparro et al. 1999; Ilano et al. 2004), whereas many empirical contradictions are present within opisthobranch species (Eyster 1979; Hadfield and Miller 1987; Yusa 1994; Jones et al. 1996; Ito 1997).

Although the opisthobranch order Sacoglossa (=Ascoglossa) is a relatively widespread group of marine herbivore molluscs, approximately 250 species described (Jensen 1997a), there is a surprising paucity of information on their developmental features for the Mediterranean Sea (Gonor 1961; Marin and Ross 1993; Thibaut and Meinesz 2000; Gianguzza et al. 2001; Jensen 2001). Most temperate species of sacoglossans have planktotrophic larvae and, as a consequence, culturing the slugs through their planktotrophic larval stages is particularly difficult (Clark et al. 1979; Trowbridge 2000; Jensen 2001).

Moreover, studies revealing importance of body size in determining offspring traits are recent and still rare (Angeloni 2003; Krug 2001). Like most opisthobranchs, sacoglossans are simultaneous hermaphrodites requiring cross-fertilization. In most species male gametes mature first and animals can function as males at a small size. Apparently, they can also receive and store allosperm at this stage (Jensen 1999, 2001; Angeloni 2003). Furthermore, many sacoglossans have extended spawning periods, lasting for their entire adult lives (i.e. at least several months). This naturally complicates a simple relationship between maternal size and clutch size, and further investigation is needed to understand whether sacoglossans present a relationship between parental size and offspring traits.

The overall aim of this work was to provide information on the morphology of spawn masses and egg features of the planktotrophic highly stenophagous *Oxynoe olivacea* (Rafinesque, 1819) in light of the effect of maternal body size. In this study the hypothesis that individuals of *O. olivacea*, varying in size and growing in the same environmental conditions, should spawn eggs of a constant size (Smith and Fretwell 1974) was tested.

Material and methods

Study animal

The shelled sacoglossan *O. olivacea* is a suctorial feeder characterized by an extreme stenophagy, as feeding is restricted just to the green, siphonalean algal genus *Caulerpa* (Jensen 1994; Williams and Walker 1999). In the Mediterranean Sea this species, that previously lived and foraged exclusively on the native *Caulerpa prolifera* (Forskål) Lamouroux, is now found on stands of invasive species of *Caulerpa* (Thibaut and Meinesz 2000; Gianguzza et al. 2002). The simultaneous hermaphrodite *O. olivacea* can reach 45 mm in length; it has a penis without any armature such as spines or hooks and requires allosperm transfer for internal fertilization (Jensen 2001).

Like many opisthobranchs this species becomes sexually mature at a small size (15–20 mm length) (Trowbridge 1992, 1993, 1995; Todd et al. 2001) and can mate in different roles: sperm donor, sperm recipient, and both donor and recipient at the same time (Gianguzza et al. 2004). During the autumn months it produces benthic egg masses on *C . taxifolia* fronds (Gianguzza 2001) and in the laboratory its spawning frequency was of 0.25 egg masses/day (Thibaut and Meinesz 2000).

Collection and maintenance in the laboratory

One hundred *O. olivacea* individuals were collected, by scuba-diving, between February 1999 and November 2001 from a stand of *C. taxifolia* in the Straits of Messina at the Torre Faro's Marina (38°15.95′N; 15° 39.10′ E Italy, Sicily, western Mediterranean) at a depth of 8 m. When not used for observations, the animals were maintained in 35 l aquaria with circulated natural seawater, at ambient light and temperature regimes (22°C). Lighting inside the laboratory was programmed to an alternating cycle of 12 h light and 12 h dark. *C. taxifolia* was supplied daily *ad libitum* to ensure continuous access to food. All the animals were measured for body length at full extension, while they were crawling on the clean flat bottom of a 20 cm petri dish filled with filtered seawater (Gianguzza et al. 2004). Each sea slug was measured to the nearest 1.0 mm on a Leika MZ APO compound microscope with an ocular micrometer. The precision of measuring *O. olivacea* was 2.8% (Gianguzza et al. 2004).

Spawn mass production and egg patterns

A laboratory experiment was carried out in order to observe if the spawn mass production and egg patterns of *O. olivacea* are related to maternal body size. Pairs of different sizes were considered for a total of three different treatments (S1, S2, S3).

Treatment S1– This treatment involved one pair of *O. olivacea* of about 20 mm.

Treatment S2– This treatment involved one pair of *O. olivacea* of about 25 mm.

Treatment S3– This treatment involved one pair of *O. olivacea* of about 30 mm.

All treatments were performed simultaneously with ten replicates. To ensure the independence of data and to avoid pseudo-replication, each encounter consisted of a unique combination of animals and thus *O. olivacea* individuals were not used more than once (Underwood 1981). Prior to the treatments, all animals were kept for 24 h in separate glass vessels filled with food to avoid the possibility of spawning from sperm stored during field copulations (Gianguzza et al. 2004). Food was removed 5 h before the treatments began to ensure similar levels of hunger/satiation (Jensen 1987; Gianguzza et al. 2001). Then, all animals were separated into pairs and maintained in a 20 cm dish filled with seawater at stable temperature and controlled light as previously described. All pairs were observed through a Leitz M3C dissection microscope, until copulation occurred, to make sure that allosperm transfer had taken place.

Method

To determine whether (a) spawn mass size, (b) total egg number per spawn, and (c) egg size were related to parent size, 21 egg masses (seven egg masses deposited by seven different 20 mm animals, seven egg masses deposited by seven different 25 mm animals, and seven egg masses by seven different 30 mm animals) were randomly chosen and examined from those spawned by the pairs of *O. olivacea* used in treatments S1, S2, and S3. The egg masses were carefully detached from the substratum to avoid damage to the basal capsules. The width and the total number of eggs per spawning event were determined in all egg masses using a binocular microscope. Afterwards, the long capsule diameter (LCD), short capsule diameter (SCD), and uncleaved egg diameter (UD; Fig. 1) were independently measured for each of the three maternal body sizes on a subsample of 150 uncleaved eggs, randomly selected from each of the 21 egg masses. All diameters were measured to the nearest 1.0 μm using a Leika MZ APO compound microscope with an ocular micrometer.

Statistical analysis

Variations of spawn mass width, total egg number per spawning, and length of *O. olivacea* LCD, SCD, and UD egg diameters were analysed by ANOVA (Analysis of Variance) considering the fixed factor Maternal Size (MS) with three levels: 30 mm, 25 mm, and 20 mm ($n=7$). All data were tested for homogeneity of variance with Cochran's C-test (Winer 1971) and results showed that the homogeneity of variance assumption was not violated. After ANOVA, means were compared (at $\alpha=0.05$) with Student-Newman-Keuls (SNK) tests (Underwood 1997). The GMAV 5.0 software (University of Sydney, Australia) was used to perform the statistical tests.

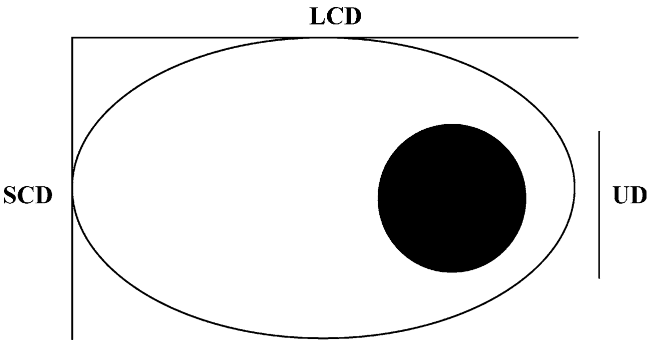

Fig. 1 Measurements used on *Oxynoe olivacea* eggs. Long Capsule Diameter (LCD); Short Capsule Diameter (SCD) and Uncleaved egg Diameter (UD)

Results

The majority of copulations were successful and a total of 44 egg masses were produced: 12 in the S1 treatment, 15 in the S2, and 17 in the S3. In the laboratory *O. olivacea* individuals laid gelatinous egg masses varying in colour from white to yellow. These spawn masses form a regular spiral ribbon from two to five whorls on a *C. taxifolia* frond a few hours or, at most, one day after copulation.

ANOVA results showed that spawn mass width varied significantly according to animal size ($F_{2;\ 18}=83.16$; $P=0.00001$). SNK results reveal that spawn masses increased across all the three body sizes (20 mm < 25 mm < 30 mm) ranging from a minimum of 20.08 ± 0.7 (SE) mm (laid by 20 mm long pairs; Fig. 2) to a maximum of 30.33 ± 0.5 (SE) mm (laid by 30 mm long pairs; Fig. 2). Moreover, the number of eggs per spawn mass (Fig. 3) varied considerably depending on the size of the animals ($F_{2;\ 18}=61.24$; $P=0.00001$). SNK results showed that number of eggs per spawn mass increased across all the body sizes (20 mm < 25 mm < 30 mm).

The egg capsules were ovoid and each capsule contained a single ovum with a transparent albumen. The long capsule diameter (LCD) was 120 ± 0.4 (SE) μm in eggs from pairs 20 mm long, 121 ± 0.5 (SE) μm in eggs from pairs 25 mm long and 122 ± 0.8 μm in eggs from

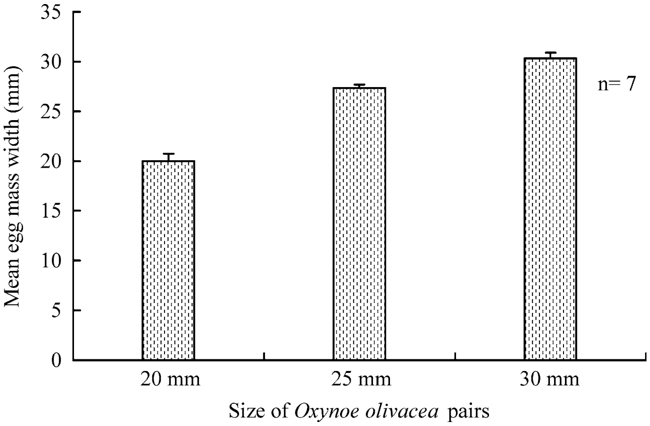

Fig. 2 Mean values + standard error of egg mass width laid by *Oxynoe olivacea* animals of 20 mm, 25 mm, and 30 mm ($n=7$)

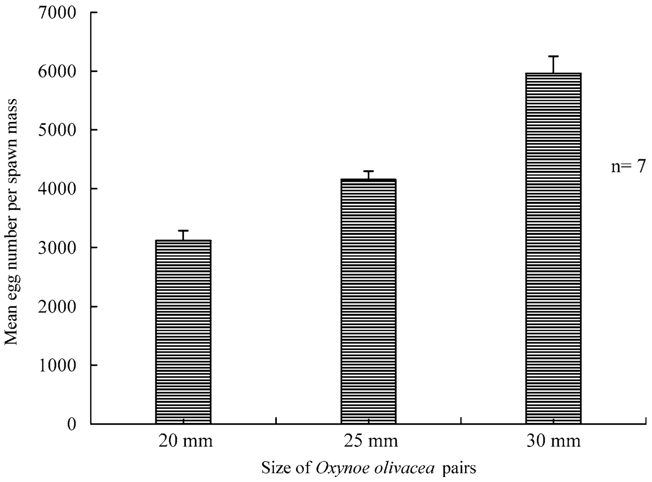

Fig. 3 Mean values + standard error of total number of eggs per spawn mass laid by *Oxynoe olivacea* animals of 20 mm, 25 mm, and 20 mm

pairs 30 mm long. The value of short capsule diameter (SCD) was maximum in eggs from pairs 30 mm long (90 ± 0.7 μm) and minimum in eggs from pairs 20 mm long (69 ± 1.1 μm). The uncleaved egg diameter (UD) ranged from 65.4 ± 0.9 μm in eggs laid by 20 mm long animals to 67 ± 1.1 μm in eggs from pairs 30 mm long.

ANOVA results revealed significant differences just in the length of the short capsule diameter ($F_{2;\ 18} = 83.1$; $P = 0.00001$). SNK test results emphasized that the short capsule diameter increased significantly with maternal body size (20 mm < 25 mm < 30 mm).

Discussion and conclusions

Several optimality models have been developed to predict the optimal maternal investment per offspring on the basis that reproductive strategies evolve to maximize the number of viable offspring and thus parental fitness (Lack 1947; Stearns 1992). One of the most common predictions is that, in females, both the number and size of eggs laid decrease over the course of their lives (Roff 2002). Our results showing that spawn mass size and number of eggs per spawn mass increase across *O. olivacea* body size are in contrast with the above predictions and appear in agreement with some opisthobranch studies supporting the hypothesis that egg production is consistently correlated with maternal body size (Switzer-Dunlap and Hadfield 1979; Switzer-Dunlap et al. 1984; Yusa 1994, 1996; Krug 2001; Angeloni 2003).

For what regards the traditional trade-off model of offspring size and/or number designed by Smith and Fretwell (1974), predicting that under similar environmental conditions egg size should be constant within a population, very often a strong, empirical contradiction has been observed within opisthobranch populations (Eyster 1979; Hadfield and Miller 1987; Yusa 1994; Jones et al. 1996; Ito 1997). For example, Eyster (1979) has shown that in the nudibranch *Tenellia pallida* (Alder and Hancock, 1842) egg size varied among individuals within a population, while Yusa (1994) reported that there was no egg size variation in the sea hare *Aplysia kurodai* (Baba, 1937) related to maternal body size.

Several adaptive intra-population models have been proposed for explaining variation in egg size and all are founded on the basic assumption that an adaptive maternal phenotypic plasticity exists and may influence the offspring traits (Parker and Begon 1986; Sargent et al. 1987). In general, it can be assumed that egg size is a good indicator of reproductive investment (nutritional content, yolk quantity etc.), which affects opisthobranch larval fitness (Gibson and Chia 1995; Ito 1997).

Concerning sacoglossan species, several studies have examined the relationship between egg size, capsule size, presence or absence of extra-capsular yolk, and development type (Kress 1971, 1972; Clark et al. 1979; Clark and Jensen 1981; DeFreese and Clark 1983; West et al. 1984; Jensen 2001, 2003). The result of these studies was that capsule size seems to be the best indicator for the type of development found in a certain species. Egg size generally did not show large intra-specific variation, and egg capsules did not change volume during embryonic development (as opposed to the case for many species of nudibranchs). Only the few species known to have poecilogony show intra-specific variation in egg, and capsule size (West et al. 1984; Krug 1998).

In spite of the high number of studies on egg size and development type (Chia 1971; Clark and Goetzfried 1978; Clark et al. 1979; Clark and Jensen 1981; DeFreese and Clark 1983; Jensen 1986a, b; Trowbridge 1995; Havenhand and Todd 1999; Krug 2001), these studies have not looked at the influence of maternal size. There are some remarks that larger animals produce larger egg masses containing more eggs, but the present study is the first to actually analyze the relationship between egg mass size, number of eggs and maternal size.

Egg mass morphology of marine gastropods has been classified in several studies (Hurst 1967; Soliman 1987; Wägele 1996). Sacoglossan egg masses show rather uniform morphology, namely a more or less cylindrical, sometimes slightly flattened, gelatinous mass of varying length, diameter, and pattern of coiling (Clark et al. 1979; Clark and Jensen 1981; Jensen 1992, 1997b). The arrangement of egg capsules inside the egg mass is usually a more or less irregular spiral, but intra-specific variation in this pattern has not been studied. In the few species where spawning has been observed, the foot and/or the mouth area usually plays a role in the shaping of the egg mass, hence it is not surprising that the width of the egg mass in *O. olivacea* differs with the size of the spawning animal.

In the present study, apart from the significant variation of the short capsule diameter, there was no consistent variation of egg features in *O. olivacea* animals present in the Straits of Messina. In conclusion, the species allocates constant amounts of energy to individual embryos and thus supports, under laboratory conditions, the prediction designed by Smith and Fretwell (1974).

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