



Review of reproduction in the Sacoglossa (Mollusca, Opisthobranchia)

Katbe R. Jensen

KEY WORDS: Sacoglossa, Opisthobranchia, reproductive systems, development patterns, fecundity, distribution.

ABSTRACT A brief summary of functional morphology of reproductive systems in the Sacoglossa is given. Penial morphology appears to have been important in speciation. Loss of penial armature has apparently occurred repeatedly in sacoglossan evolution; it may be a single gene mutation and may serve as a rapid means of reproductive isolation. Extracapsular yolk (ECY) occurs only in the superfamily Plakobranchoidea. Its function and origin are still debated. Reproductive data for 98 species of Sacoglossa are summarized. The correlation between relative capsule size and development type is confirmed. Development pattern is not related to phylogeny, neither at family nor genus level. The fraction of species with non-planktotrophic development appears to be higher in the Caribbean than in any other zoogeographic regions. This is interpreted as an example of local (sympatric) speciation. Cladistic analysis may help to resolve this. Information on mating and spawning behaviour is scarce, as is information on aspects of fertilization. The existing information is summarized and its phylogenetic and evolutionary importance discussed.

RIASSUNTO Viene qui presentata una breve revisione della morfologia funzionale del sistema riproduttivo dei Sacoglossa. La morfologia del pene è un elemento importante nella speciazione: la perdita dell'armatura sembra essere avvenuta ripetutamente nel corso dell'evoluzione del gruppo, probabilmente causata dalla mutazione di un singolo gene e potrebbe essere stata alla base di un rapido isolamento riproduttivo. Il tuorlo extracapsulare (ECY) è presente solo nella superfamiglia Plakobranchoidea e la sua funzione ed origine sono ancora incerte. Vengono qui presentati i dati relativi all'attività riproduttiva di 98 specie di Sacoglossa. Il rapporto tra taglia della capsula e tipo di sviluppo viene confermato. Le caratteristiche dello sviluppo non sono collegate né alla filogenesi, né sono omogenee a livello di famiglia o genere. Il gruppo di specie a sviluppo non planctotrofico appare più comune nel Mare Caraibico che in qualsiasi altra area zoogeografica e può essere interpretato come un esempio di speciazione simpatica. L'analisi cladistica potrebbe aiutare a comprendere questa anomalia. Dati relativi all'accoppiamento e alle tecniche di deposizione sono ancora pochi, tanto quanto quelli relativi alla fertilizzazione. I dati esistenti vengono qui sintetizzati e discussa la loro importanza filogenetica ed evolutiva.

K. R. JENSEN, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark, e-mail: jensen@ait.ac.th
Present address: Asian Institute of Technology, P.O. Box Y Klong Luang, Pathumthani 12120, Thailand.

INTRODUCTION

Sacoglossan opisthobranchs are simultaneous hermaphrodites requiring copulation for transfer of allosperm for internal fertilization. Reproductive systems are highly complex and the function is incompletely understood (JENSEN, 1997b). Data on egg size and development type for Caribbean sacoglossans were reviewed by CLARK & JENSEN (1981). Since then data for a large number of species from other regions have been published. Sacoglossans differ from most other opisthobranchs in that egg size is not a good indicator of development type (CLARK & JENSEN, 1981; DEFRESE & CLARK, 1983; HADFIELD & MILLER, 1987). Instead the relative size of egg capsules may be a more reliable indicator of development type (CLARK & JENSEN, 1981). Sacoglossan egg masses are gelatinous clusters, more or less cylindrical, and coiled into more or less regular spirals (CLARK *et al.*, 1979; HADFIELD & SWITZER-DUNLAP, 1984; JENSEN, 1992, 1997a). The eggs are usually encapsulated singly, though twin embryos are seen in a number of species (JENSEN, 1992). A peculiar feature of many sacoglossan egg masses is the occurrence of extracapsular yolk (CLARK *et al.*, 1979; BOUCHER, 1983). The function of this is still not clear, but it may be nutritional in some species, defensive in others.

Three developmental patterns are usually distinguished in opisthobranchs (THOMPSON, 1967). Planktotrophic larvae have a long pelagic phase during which they feed. Lecithotrophic larvae have a short swimming phase, lasting from several hours to a few days, during which no feeding takes place; the pelagic phase may be extended and feeding initiated if a suitable sub-

strate is not located in a few days (KEMPFF & TODD, 1989). In species with direct development fully formed juveniles hatch from the egg mass. In most opisthobranchs, including the Sacoglossa, a veliger stage is actually formed within the egg capsule, but metamorphosis is completed prior to hatching (CLARK *et al.*, 1979; CLARK & JENSEN, 1981; JENSEN, 1997b). It is generally assumed that the incidence of direct development increases with latitude; this is known as Thorson's rule, and it has been claimed that this rule does not apply to the Sacoglossa (CLARK & GOETZFRIED, 1978).

In the present study reproductive anatomy of the Sacoglossa is summarized, and data on egg size, capsule size and development type are reviewed. This is correlated with phylogeny, latitudinal and regional distribution. Other aspects of reproductive biology, such as mating behaviour and fecundity, are also discussed.

MATERIALS AND METHODS

Most data have been taken from information scattered in the taxonomic literature. Some unpublished observations made during international marine biological workshops in Hong Kong and Western Australia are also included. The sources of the data, including authorship for species, are shown in Appendix 1.

Measurements of egg diameters are for uncleaved eggs, and measurements of capsule size in most cases include the longest diameter, and a short diameter perpendicular to this (Fig. 1). In cases where ranges have been given, the median value has been used in calculations.



Table 1. Data on egg diameter and development type in relation to geographical latitude of shelled Sacoglossa (Oxynoacea).

Taxon	Latitude	Egg diam.	Dev. type
Family Volvatellidae			
<i>Ascobulla</i>			
<i>fischeri</i>	35S	?	P
<i>A. ulla</i>	25N	60µm	ED
<i>Volvatella</i>			
<i>australis</i>	25S	100.8±6.2µm	L?
<i>V. bermudae</i>	32N	66µm	P
<i>V. ventricosa</i>	35S	97.2±10.5µm	P?
Family Juliidae			
<i>Julia japonica</i>	30-35N	65µm	P
<i>Berthelinia</i>			
<i>australis</i>	38S	54µm	P?
<i>B. caribbea</i>	25N	100µm	L
<i>B. darwini</i>	25S	102.8±5.9µm	L?
<i>B. ganapati</i>	10-20N	50µm	P
<i>B. limax</i>	30-35N	250µm	L
<i>B. rotnesti</i>	35S	?	L?
Family Oxynoidae			
<i>Oxynoe</i>			
<i>antillarum</i>	25N	63µm	P
<i>O. azuropunctata</i>	25N	120µm	L
<i>O. olivacea</i>	40N	62-69µm	P
Same	28N	250µm	?
<i>O. panamensis</i>	10N	?	P
<i>O. viridis</i>	25S	72µm	P
Same	35S	56µm	P
<i>Lobiger</i>			
<i>sagamiensis</i>	22N	?	P?
<i>L. souverbiei</i>	25N	56µm	P

Abbreviations: ED, encapsulated direct; L, lecithotrophic; P, planktotrophic

RESULTS

Review of reproductive systems (from JENSEN, 1996, 1997b):

The sacoglossan gonad is hermaphroditic, though a few species have separate male and female follicles. Gamete formation has not been studied, and ultrastructure of spermatozoa has only been described in one species (HEALY, 1993). Oocytes usually mature after spermatocytes, so animals may copulate as males before they are able to spawn. The genital system is either androdiaulic or triaulic; that is, there is a vas deferens separated from the female system, which again may have a separate route for transporting allosperm. The hermaphroditic duct usually forms an ampulla where autosperm is stored. The male system consists of an internal closed vas deferens, a prostate gland, and an eversible penis enclosed in a penial sheath. The prostate is a glandular part of the vas deferens in the shelled Oxynoacea, but a separate gland opening into the vas deferens in the non-shelled Plakobranchacea. In

the cerata-bearing Limapontioidea the prostate is composed of a number of short lobes; in the parapodia-bearing Plakobranchidae it is highly branched throughout the visceral mass. The function of the prostatic secretion is unknown. At least 3 possibilities exist: (1) nutrition for maturing sperm, (2) nutrition for allosperm storage, (3) "nuptial present" to induce sperm recipient to utilize that particular sperm for fertilization. The penis is usually muscular and highly extensible. Often it is equipped with a cuticular stylet. Size and shape of stylets show great variation (GASCOIGNE, 1974). Penial armature is absent in only two families, Oxynoidae and Hermaeidae; but it is also rare in the Plakobranchidae. In most species the penial opening is located below the base of the right rhinophore.

The female system consists of a small oviduct, a fertilization chamber, an albumen gland, and a mucus gland surrounding the large oviduct. Nothing is known about formation of yolk and albumen. The eggs are fertilized and covered with albumen in the



Table 2. Data on egg diameter and development type in relation to geographical latitude of superfamily Plakobranchoidea.

Taxon	Latitude	Egg diam.	Dev. type	Taxon	Latitude	Egg diam.	Dev. type
Family Plakobranchoidea							
<i>Elysia</i>				<i>E. timida</i>	40N	120µm	L/ED
<i>atroviridis</i>	22N	54±6µm	P?	<i>E. trisinuata</i>	30-35N	46µm	P
<i>E. australis</i>	35S	64µm	P	<i>E. tuca</i>	25N	111µm	L
<i>E. bangtawaeensis</i>	7N	?	P?	<i>E. viridis</i>	40N	60-70µm	P
<i>E. canguzua</i>	25N	?	P	Same	50-55N	66µm	P
<i>E. catulus</i>	42N	75.3±3.1µm	P	Same	60N	66-76µm	P
<i>E. chlorotica</i>	42N	96±8µm	ED	<i>Plakobrancheus</i>			
2nd population	42N	79±3µm	P	<i>iauthobapsus</i>	20N	?	P?
<i>E. cornigera</i>	25N	105µm	L?/ED?	<i>Thuridilla</i>			
<i>E. elisiae</i>	20N	ca.80µm	?	<i>bayeri</i>	10N	80µm	?
<i>E. evelinae</i>	25N	104µm	L/ED	<i>T. bopei</i>	40N	200µm	L
<i>E. expansa</i>	25-35S	?	P	<i>T. ratna</i>	10N	80-85µm	?
<i>E. gordanae</i>	40N	?	L?	<i>T. vatae</i>	10N	55-65µm	P
<i>E. hamatani</i>	30-35N	68µm	P	<i>Tridachia</i>			
<i>E. bedgpethi</i>	30N	?	P?	<i>crispata</i>	25N	205µm	L/ED
<i>E. japonica</i>	22N	91±4µm	P?	Family Boselliidae			
<i>E. leucolegnote</i>	22N	?	?	<i>Bosellia leve</i>	28N	64µm	?
<i>E. maoria</i>	35S	70µm	P?	<i>B. mimetica</i>	25N	59µm	P
<i>E. ornata</i>	25N	?	P	Same	40N	60-75µm	P?
<i>E. papillosa</i>	25N	92µm	L	Family Platyhedylidae			
<i>E. patagonica</i>	46S	?	P?	<i>Gascoignella</i>			
<i>E. patina</i>	25N	63µm	P	<i>aprica</i>	22N	?	P?
<i>E. serca</i>	25N	61µm	P	Abbreviations as in Table 1.			
<i>E. subornata</i>	25N	120µm	ED				
<i>E. thompsoni</i>	25S	62µm	P?				

fertilization chamber. Probably also capsules are secreted here, or in the proximal part of the mucus gland. The eggs do not pass through the albumen gland, which in the non-shelled sacoglossans is highly branched, and usually closely associated with tubules of the digestive gland. Eggs are usually encapsulated singly, though twin embryos occur in some species. During spawning eggs usually pass single-file through the oviducal opening, and organisation of eggs within the surrounding mucus may be completed by the mouth area (some Oxynoacea), or in the spawn groove (some Plakobranchoidea). The chemical and ultrastructural composition of egg masses are unknown. Extracapsular yolk (ECY) is present in one superfamily, Plakobranchoidea. It may form a continuous string or consist of numerous small clumps. It may have the same colour as the eggs or it may have a different colour (BOUCHER, 1983; JENSEN, 1992). Its function and site of production are unknown.

Fertilization is internal, and allosperm may be stored for variable time periods. Animals with no mature oocytes may receive allosperm, thus animals are functionally simultaneous hermaphrodites. Hypodermic impregnation is common, even in species without penial armature. Sperm transfer is usually reciprocal, though not always simultaneously so. Allosperm is stored either in the seminal receptacle or in secondary copulatory butsaes formed after

the first copulation. These structures are connected to the fertilization chamber. Apparently a mixture of mature, motile sperm and immature, non-motile sperm is delivered during copulation (JENSEN, 1986b, 1995). Most sacoglossans also have a large, spherical structure, homologous to the gametolytic sac or bursa copulatrix of other opisthobranchs. In the Sacoglossa this structure is usually called genital receptacle (GASCOIGNE, 1976) because it contains various "surplus" material (albumen, capsule material, sperm in various stages of degradation). It may have a distal connection to the large oviduct, or a more proximal connection to the fertilization chamber. In a few species both connections exist (GASCOIGNE, 1979). In a few species the duct of the genital receptacle connects directly to the vaginal opening. The vaginal opening, where present, may also connect to the seminal receptacle, a functional (secondary?) bursa copulatrix (not homologous with genital receptacle), the fertilization chamber, or the pericardium. The actual route taken by allosperm during copulation is unknown. It is also unknown how allosperm injected by hypodermic impregnation finds its way to the sperm storing structure.

Life history data (see Appendix 1 for references):

Data on egg size, development type and geographical latitude are listed in Tables 1-3. In the Oxynoacea (shelled Sacoglossa) and the



Table 3. Data on egg diameter and development type in relation to geographical latitude of superfamily Limapontioidea.

Taxon	Latitude	Egg diam.	Dev. type	Taxon	Latitude	Egg diam.	Dev. type
Family Polybranchiidae				Same	25N	70µm	P
<i>Caliphylla</i>				Same	40N	60µm	P?
<i>mediterranea</i>	25N	89µm	P	<i>E. emarginata</i>	22N	63.4±2.4µm	P
Same	40N	50-70µm	P?	Same	same	58±4µm	P
<i>Cyerce</i>				<i>E. endophytophaga</i>	35S	77±1.4µm	P?
<i>antillensis</i>	25N	112µm	L	<i>E. felina</i>	40S	56µm	?
<i>C. cristallina</i>	40N	60µm	P?	<i>E. funerea</i>	25N	59µm	P
<i>Mourgona</i>				Same	40N	75-90µm	P
<i>germaineae</i>	25N	62µm	P	<i>E. fuscata</i>	25N	60µm	P
<i>Polybranchia</i>				Same	42N	64.5±2µm	P?
<i>pallens</i>	38S	?	ED?	<i>E. gopalai</i>	10-20N	70µm	P
<i>P. viridis</i>	25N	?	P	<i>E. nigra</i>	56N	70µm	P
Family Hermaeidae				<i>E. nigrovittata</i>	10-20N	70µm	P
<i>Hermaea bifida</i>	40N	48µm	P?	<i>E. translucens</i>	35S	?	P?
<i>H. cruciata</i>	25N	77µm	P	<i>Ercolania</i> n.sp.	35S	58.5±2.6µm	P?
Same	37N	100µm	P?	<i>Limapontia</i>			
<i>Aphysiopsis</i>				<i>capitata</i>	50-55N	82µm	P
<i>maculosa</i>	40N	50µm	P?	<i>L. depressa</i>	50-55N	80µm	P
<i>A. smithi</i>	30N	?	P	<i>L. senestra</i>	50-55N	200µm	AD
<i>A. zebra</i>	25N	71µm	P	<i>Olea</i>			
Family Limapontiidae				<i>bansineensis</i>	50N	?	P?
<i>Alderia</i>				<i>Placida</i>			
<i>modesta</i>	42N	70µm	P?	<i>cremoniana</i>	40N	50-60µm	P?
Same	50-55N	78-87µm	P?	<i>P. daguilaensis</i>	22N	56µm	P
Same	56N	62µm	P	<i>P. dendritica</i>	42N	72±5.1µm	P?
<i>Calliopaea</i>				Same	50-55N	47-67µm	P
<i>oophaga</i>	56N	61.7µm	P	Same	35N	?	P?
<i>Costasiella</i>				<i>P. kingstoni</i>	25N	60µm	P
<i>ocellifera</i>	25N	98µm	ED	<i>P. viridis</i>	40N	40-60µm	P?
<i>C. nonatoi</i>	32N	69µm	L	<i>Stiliger</i>			
<i>C. pallida</i>	22N	84.6±7.7µm	P?	<i>aureomarginatus</i>	35S	56±1.6µm	P?
<i>Ercolania</i>				<i>S. bergbi</i>	30-35N	65µm	P
<i>boodlae</i>	30-35N	65-100µm	P	<i>S. fuscovittatus</i>	25N	66.5µm	P?
<i>E. coerulea</i>	22N	?	P	<i>S. llerai</i>	28N	122µm	?
				<i>S. verticillata</i>	28N	130µm	?

Abbreviations: AD, ametamorphic direct; others as in Table 1.

Plakobranchoidea (parapodia-bearing Sacoglossa) about 30-40% of the species have non-planktotrophic development. In the Limapontioidea (cerata-bearing Sacoglossa) only 13% of the species have non-planktotrophic development (Table 4). Except for the Hermaeidae, non-planktotrophic development occurs in all families.

In the tropical zone, here broadly designated as 25N-25S, one third of the species have non-planktotrophic development (Table 5). North of 25N 20% of the species have non-planktotrophic development, and south of 25S only 15% of the species have non-planktotrophic development. The tropical zone has the highest number of species, but also the largest fraction (32.5%) of non-

planktotrophic development.

In Table 6 species and development type are listed for different zoogeographical regions. Very few species from other regions have known development type. With the exception of Hong Kong, all regions have species with non-planktotrophic development. The Caribbean region apparently has a much larger proportion of non-planktotrophic species.

Egg and capsule size distributions are shown in Fig. 2. Egg size has a skewed, but unimodal distribution, whereas capsule size seems to have a bimodal distribution, corresponding to feeding and non-feeding larvae. In Table 7 egg size and capsule size are correlated with development type. Egg diameter ranges between 40 and



Table 4. Correlation between development type and taxonomic group in the Sacoglossa.

Taxon	Planktotrophic	Non-planktotrophic
Oxynoacea	12 species	7 (8) species
	6 genera	4 genera
Plakobranchoidea	22 species	9 (10) species
	6 genera	3 genera
Limapontioidea	33 species	5 species
	14 genera	4 genera

Table 5. Correlation between development type and latitude in the Sacoglossa (number of species).

Latitude	Planktotrophic	Non-planktotrophic	Total
25N-25S	28	13	41
>25N	24	6	30
>25S	11	2	13
Total	62	21	83

100µm in species with planktotrophic development (mean±s.d. = 59.5±23µm; N=58), and capsule diameters range between 75 and 300µm (mean±s.d. for short diameter = 112.3±30.7µm, and for long diameter = 134.8±36.5µm; N=60). In species with lecithotrophic development egg diameter ranges between 69 and 250µm (mean±s.d. = 122.7±51.4µm; N=12), and capsule diameters range between 107 and 422µm (mean±s.d. for short diameter = 254.7±58.3µm, and for long diameter 313.4±72.6µm; N=12). For species with encapsulated direct development egg diameters range between 60 and 205µm (mean±s.d. = 125.4±51.1µm; N=8), and capsule diameters range between 190 and 456µm (mean±s.d. for short diameters = 288±70.5µm, and for long diameter 329.9±60.4µm; N=7). Only one species of Sacoglossa, *Limapontia senestra*, has ametamorphic direct development (CHIA, 1971). This clearly shows that variability is great for all parameters, and there is great overlap in egg and capsule sizes for all development types. In fact, there is very little difference between egg and capsule sizes of the two non-planktotrophic development types. Relative capsule size seems to be a reliable indicator for distinguishing between feeding and non-feeding larval development. Out of 41 planktotrophic species, 34 have ratios of egg / short capsule diameter greater than 0.5, and 14 of 19 non-planktotrophic species have ratios much smaller than 0.5.

Data on duration of embryonic period is given in Table 8. Temperatures have in most cases been "room temperature" of the laboratory in question, which means that it will be higher than natural for temperate species and slightly lower than natural for tropical species. Range for species with non-planktotrophic development is 11-28 days (mean±s.d. = 19.2±6.3 d), and for species with planktotrophic development 4-16 days (mean±s.d. = 8.1±3.2 d); the means differ significantly.

Fecundity differs with size of the parent animal and possibly also

with food assimilation. Most species produce one egg mass per day, and spawning begins a few days after copulation. It is unknown how long allosperm can be stored, and how often copulation has to be repeated. Table 9 summarizes information on fecundity in the Sacoglossa. Whether fertilization is controlled by the sperm recipient, i.e. through sperm selection, or the sperm donor, through sperm competition, is also unknown.

DISCUSSION

Planktotrophy is assumed to be ancestral in the Mollusca (STRATHMANN, 1985). Whether it is also ancestral in the Opisthobranchia remains to be determined. The presence of a veliger stage, whether freeswimming or encapsulated, even in species which are shell-less as adults, indicates that the opisthobranch ancestor was planktotrophic. Evolution of non-feeding larvae is seen as an adaptation to stable supplies of adult food and/or high predatory losses in the planktonic stage (STRATHMANN, *op. cit.*; HADFIELD & MILLER, 1987).

In the Sacoglossa non-feeding larvae occur in all major clades; often different development types are found in species of the same genus, and it is not possible to deduct whether planktotrophy is ancestral. True cases of poecilogony are, however, rare; in most cases a species can change between the two non-feeding types, which should not be called poecilogony (BOUCHET, 1989). The only experimentally corroborated case where planktotrophic and encapsulated development occur in one species is *Elysia chlorotica* (WEST *et al.*, 1984). The case of *Elysia subornata* (= *E. cauze*) (CLARK *et al.*, 1979) has been shown to be two or three sibling species (JENSEN & CLARK, 1983; CLARK, 1984).

It is generally assumed that the incidence of non-planktotrophic development in marine invertebrates increases with latitude. This is known as Thorson's Rule. However, it has been claimed that



Table 6. Geographic variation in development patterns.

A. Japan, 30-35N

Taxon	Development
<i>Julia japonica</i>	P
<i>Berthelinia limax</i>	L
<i>Elysia bamatanii</i>	P
<i>Elysia trisinuata</i>	P
<i>Ercolania boodlea</i>	P
<i>Stiliger bergbi</i>	P

Total number: 6; 1 non-planktotrophic

B. Florida, 25N, and Bermuda, 32N

Taxon	Development
<i>Ascobulla ulla</i>	ED
<i>Volvatella bermudae</i>	P
<i>Berthelinia caribbea</i>	L
<i>Lobiger souverbiei</i>	P
<i>Oxynoe antillarum</i>	P
<i>Oxynoe azuropunctata</i>	L
<i>Bosellia mimetica</i>	P
<i>Elysia canguzua</i>	P
<i>Elysia cornigera</i>	L?/ED?
<i>Elysia evelinae</i>	L/ED
<i>Elysia ornata</i>	P
<i>Elysia papillosa</i>	L
<i>Elysia patina</i>	P
<i>Elysia serca</i>	P
<i>Elysia subornata</i>	ED
<i>Elysia tuca</i>	L
<i>Tridachia crispata</i>	L/ED
<i>Polybranchia viridis</i>	P
<i>Caliphylia mediterranea</i>	P
<i>Cyerce antillensis</i>	L
<i>Mourgona germaineae</i>	P
<i>Hermaea cruciata</i>	P
<i>Aplysiopsis zebra</i>	P
<i>Costasiella ocellifera</i>	ED
<i>Costasiella nonatoi</i>	L
<i>Placida kingstoni</i>	P
<i>Ercolania coerulea</i>	P
<i>Ercolania funerea</i>	P
<i>Ercolania fuscata</i>	P

Total number: 29; 12 non-planktotrophic

C. Mediterranean, 40N

Taxon	Development
<i>Oxynoe olivacea</i>	P
<i>Bosellia mimetica</i>	P?
<i>Elysia gordanae</i>	L?
<i>Elysia timida</i>	L/ED
<i>Elysia viridis</i>	P
<i>Thuridilla hopei</i>	L
<i>Caliphylia mediterranea</i>	P?
<i>Cyerce cristallina</i>	P?
<i>Hermaea bifida</i>	P?
<i>Aplysiopsis maculosa</i>	P?
<i>Ercolania coerulea</i>	P?
<i>Ercolania funerea</i>	P
<i>Placida cremoniana</i>	P?
<i>Placida viridis</i>	P?

Total number: 14; 2(3) non-planktotrophic

D. Hong Kong, 22N

Taxon	Development
<i>Lobiger sagamiensis</i>	P?
<i>Elysia atroviridis</i>	P?
<i>Elysia japonica</i>	P?
<i>Elysia leucolegnote</i>	?
<i>Gascoignella aprica</i>	P?
<i>Ercolania coerulea</i>	P
<i>Ercolania emarginata</i>	P
<i>Placida dagnilarensis</i>	P
<i>Costasiella pallida</i>	P?

Total number: 9; none non-planktotrophic

E. Western Australia, 25-35S

Taxon	Development
<i>Ascobulla fischeri</i>	P
<i>Volvatella australis</i>	L?
<i>Volvatella ventricosa</i>	P?
<i>Berthelinia darwini</i>	L?
<i>Berthelinia rotnesti</i>	L?
<i>Oxynoe viridis</i>	P?
<i>Elysia australis</i>	P
<i>Elysia expansa</i>	P?
<i>Elysia thompsoni</i>	P?
<i>Stiliger aureomarginatus</i>	P?
<i>Ercolania endophytophaga</i>	P?
<i>Ercolania translucens</i>	P?
<i>Ercolania n.sp.</i>	P?

Total number: 13; 3 non-planktotrophic



this rule does not apply to the Sacoglossa (CLARK & GOETZFRIED, 1978). This has been confirmed by the present study. Though few species have been studied from the southern hemisphere, the fraction of species with non-planktotrophic development is distinctly higher in the tropical zone than in temperate zones (Table 5). Unfortunately no sacoglossan species has an exclusively polar distribution.

The high incidence of non-planktotrophy in the Caribbean (Table 6B) can be interpreted as an adaptation to temporally stable, but spatially restricted adult food sources, i.e. offspring should be retained in the area of the parents (CLARK & GOETZFRIED, 1978), and sufficient nutritional material can be allocated to developing embryos to suppress the feeding planktonic stage. In fact, the number of green algal species of suitable morphology (see JENSEN, 1997b) is very high in the Caribbean, but also in Western Australia (WOMERSLEY, 1984). Whether the high incidence of non-planktotrophic development in the Caribbean is due to local, sympatric speciation can be clarified by application of cladistic analysis. One working hypothesis would be that each of the non-planktotrophic species of e.g. *Elysia* have planktotrophic sister-species in neighbouring areas; an alternative hypothesis, also supporting local speciation, would be that the non-planktotrophic species are more closely related to one another than to any congener from other regions. Unfortunately the anatomy of the Caribbean species of *Elysia* has not been described in detail, and a preliminary cladistic analysis based on literature information, and including several Indo-West Pacific species of *Elysia* did not give meaningful results.

It has been claimed previously that relative capsule volume is a better indicator of development type in the Sacoglossa than egg diameter (CLARK & JENSEN, 1981). The present study has confirmed this. Although average egg diameter is significantly smaller in planktotrophic species than in non-planktotrophic species, ranges overlap considerably (Table 7). Only 7 planktotrophic species have short capsule diameters greater than twice the egg diameter. One of these species is *Elysia chlorotica* in which populations with different development types have been described (WEST *et al.*, 1984). This indicates that speciation may be in progress. Capsule size may be a plastic character which can adapt locally to food availability, and increasing capsule size to include more nutritional material (albumen) may reduce the need for a post-hatching feeding veliger. Three of the 7 planktotrophic species with large capsules are congeners of the apparently cosmopolitan *Placida dendritica*, and they may be recent speciations, one in the Caribbean, *P. kingstoni*, one in the Mediterranean, *P. viridis*, and one in the South China Sea, *P. daguilarensis*. Again application of cladistic analysis may clarify whether widely separated populations of *P. dendritica* gave rise to the other 3 species. Two of the 7 species belong to the genus *Hermata*, and non-planktotrophic development does not occur in the family Hermaeidae. In this connection it should be noticed that the albumen gland in this family is less branched than in other families, and does not enter the cerata (JENSEN, 1997b). Thus absence of non-planktotrophic larvae may be due to inability to produce sufficient nutritional material.

As the albumen gland in most sacoglossans branches extensively in close association with the digestive gland, it may be speculated

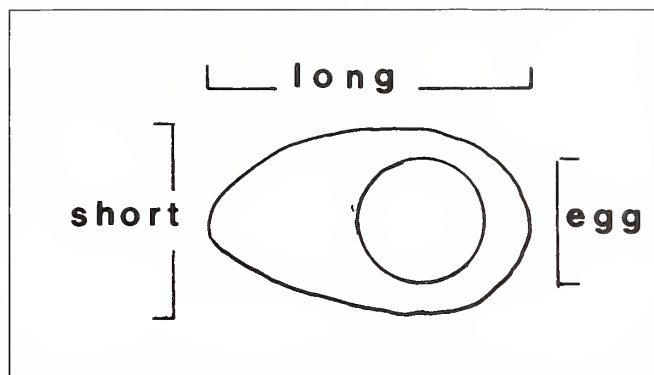


Fig. 1. Measurements used on sacoglossan eggs and egg capsules.

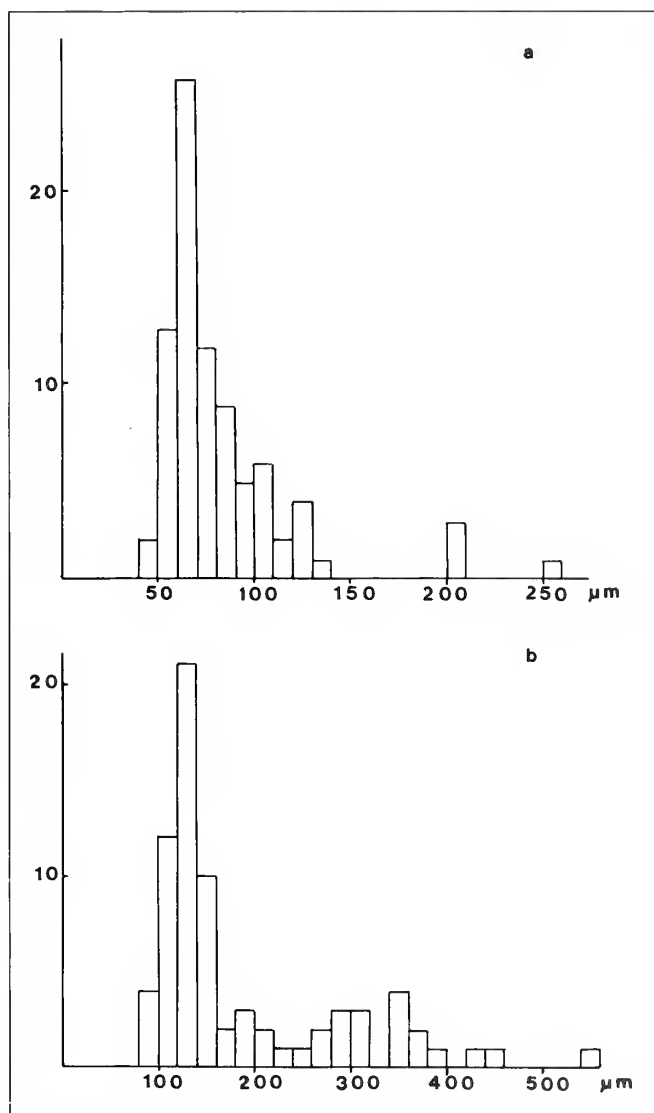


Fig. 2. Size-frequency distribution of (a) egg diameters and (b) capsule diameters in the Sacoglossa. Long diameters have been used where available. Data used is listed in Table 7.

that production of albumen is correlated with food intake and/or production by functional kleptoplastids. Plasticity of the size of egg capsules would be a prerequisite for allocating larger amounts



Table 7. Correlation of egg diameter, capsule size and development type in the Sacoglossa

Taxon	Egg diameter	Capsule size	Dev. type
Volvatellidae			
<i>Ascobulla</i>			
<i>fischeri</i>	?	200µm	P
<i>A. ulla</i>	60 & 84µm	190x250µm	ED
<i>Volvatella</i>			
<i>australis</i>	100.8±6.2µm	236x272µm	L?
<i>V. bermudae</i>	66µm	98x106µm	P
<i>V. ventricosa</i>	97.2±10.5µm	150x204µm	P?
Juliidae			
<i>Julia japonica</i>	65µm	100x150µm	P
<i>Bertbelinia</i>			
<i>australis</i>	54µm	?	P?
<i>B. caribbea</i>	100µm	250x310µm	L
<i>B. darwini</i>	102.8±5.9µm	240x346µm	L?
<i>B. ganapati</i>	50µm	90µm	P
<i>B. limax</i>	250µm	270x380µm	L
<i>B. rotnesti</i>	?	203x274µm	L?
Oxynoidea			
<i>Oxynoe</i>			
<i>antillarum</i>	63µm	97x114µm	P
<i>O. azuropunctata</i>	120 & 113µm	280x370µm	L
<i>O. olivacea</i>	62-69µm	91-109x121-125µm	P
Same	250µm	500µm	?
<i>O. viridis</i>	56-72µm	100x147 & 113x137µm	P
<i>Lobiger</i>			
<i>sagamiensis</i>	?	108x142µm	P?
<i>L. souverbiei</i>	56µm	88x99µm	P
Plakobranchidae			
<i>Elysia</i>			
<i>atroviridis</i>	54±6µm	143x173µm	P?
<i>E. australis</i>	64µm	88x104µm	P
<i>E. bangtawaeensis</i>	?	127x106µm	P
<i>E. catulus</i>	75.3±3.1µm	?	P
<i>E. chlorotica</i>	96±8µm	309±8 & 349±24µm	ED
2nd population	79±3µm	164±12 & 192±36µm	P
<i>E. cornigera</i>	105µm	268x291µm	L?/ED?
<i>E. evelinae</i>	104µm	273x294µm	L/ED
<i>E. expansa</i>	?	129x144µm	P
<i>E. hamatanii</i>	68µm	115-140µm	P
<i>E. hedgpethi</i>	?	95x120µm	P?
<i>E. japonica</i>	91±4µm	166x196µm	P?
<i>E. maoria</i>	70µm	?	P?
<i>E. papillosa</i>	92µm	242x286µm	L
<i>E. patagonica</i>	?	250-300µm	P?
<i>E. patina</i>	63µm	0.00072mm ³	P
<i>E. serca</i>	61µm	109x133µm	P
<i>E. subornata</i>	120µm	400x456µm	ED
<i>E. thompsoni</i>	62µm	115x132µm	P?
<i>E. timida</i>	120µm	200x300µm	ED
Same	70µm	100-125µm	L
<i>E. trisinuata</i>	46µm	77-85µm	P?
<i>E. tuca</i>	111µm	319x361µm	L?
<i>E. viridis</i>	60-76µm	100x180µm	P
<i>Thuidilla</i>			
<i>bayeri</i>	80µm	120-140µm	?
<i>T. hopei</i>	200µm	?	L
<i>Tridachia</i>			
<i>crispata</i>	205µm	276x341µm	L/ED



Table 7. Correlation of egg diameter, capsule size and development type in the Sacoglossa

Taxon	Egg diameter	Capsule size	Dev. type
Boselliidae			
<i>Bosellia</i>			
<i>mimetica</i>	59-75µm	75-97x90-114µm	P
Platyhedylidae			
<i>Gascoignella</i>			
<i>aprica</i>	?	88x103µm	P?
Polybranchiidae			
<i>Caliphylla</i>			
<i>mediterranea</i>	89µm	117x142µm	P?
Same	50-70µm	70x100 & 110x120µm	P?
<i>Cyerce</i>			
<i>antillensis</i>	112µm	334x422µm	L
<i>Mourgona</i>			
<i>germaineae</i>	62µm	104x130µm	P
Hermæidae			
<i>Hermaea bifida</i>	48µm	104x128µm	P?
<i>H. cruciata</i>	77µm	165x230µm	P?
<i>Aplysiopsis</i>			
<i>maculosa</i>	50µm	?	P?
<i>A. smithi</i>	?	85x125µm	P
<i>A. zebra</i>	71µm	92x138µm	P
Limapontiidae			
<i>Alderia</i>			
<i>modesta</i>	62-87µm	?	P
<i>Calliopaea</i>			
<i>oophaga</i>	61.7µm	96x85µm	P
<i>Costasiella</i>			
<i>ocellifera</i>	98µm	307x340µm	ED
<i>C. nonatoi</i>	69µm	107x127µm	L
<i>C. pallida</i>	84.6±7.7µm	107x133 & 103.1x128.4µm	P?
<i>Ercolania</i>			
<i>boodleeae</i>	65-100µm	100-150µm	P?
<i>E. coerulea</i>	60-70µm	80-123x110-137µm	P
<i>E. emarginata</i>	58-65µm	104-122x124-142µm	P?
<i>E. endophytobaga</i>	77±1.4µm	109-133x128-148µm	P?
<i>E. funerea</i>	59-90µm	90-110x110-146µm	P
<i>E. fuscata</i>	60-65µm	85x115µm	P
<i>E. gopalai</i>	70µm	175µm	P?
<i>E. nigra</i>	70µm	100µm	P
<i>E. nigrovittata</i>	70µm	120x145µm	P?
<i>E. translucens</i>	?	110x123µm	P?
<i>Ercolania</i> n.sp.	58.5±2.6µm	89x114µm	P?
<i>Limapontia</i>			
<i>capitata</i>	82µm	100µm	P
<i>L. depressa</i>	80µm	120µm	P
<i>L. senestra</i>	200µm	350x550µm	AD
<i>Placida</i>			
<i>cremoniana</i>	50-60µm	110x140µm	P?
<i>P. daguilarensis</i>	56µm	117x136µm	P
<i>P. dendritica</i>	47-77µm	90x105µm	P?
<i>P. kingstoni</i>	60µm	123x125µm	P
<i>P. viridis</i>	40-60µm	130x140µm	P?
<i>Stiliger</i>			
<i>aureomarginatus</i>	56±1.6µm	96x122 & 99x127µm	P?
<i>S. bergbi</i>	65µm	100-130µm	P?
<i>S. fuscovittatus</i>	66.5µm	?	P?



Table 8. Development times related to development type in the Sacoglossa.

Taxon	Developm. time	Temp.	Developm. type
Oxynoacea			
<i>Ascobulla fischeri</i>	8-9d	25C	P?
<i>Volvatella ventricosa</i>	17d	?	P
<i>Julia japonica</i>	10-11d	?	P
<i>Berthelinia australis</i>	13d	21C	P?
Oxynoe			
<i>azuropunctata</i>	28d	18-21C	L/ED
<i>O. olivacea</i>	7-8d	22C	P
<i>O. panamensis</i>	13d	21C	P
<i>O. viridis</i>	6-7d	22-23C	P
Plakobranchoidea			
Bosellia			
<i>mimetica</i>	13d	16C	P?
Plakobrancheus			
<i>iantbobapsus</i>	8d	?	P?
<i>Thuridilla bopei</i>	20d	21C	L
<i>T. vatae</i>	5d	?	P
<i>Elysia australis</i>	6-7d	22-23C	P
<i>E. bangtawaeensis</i>	7-8d	20-27C	P
<i>E. chlorotica</i>	14d	?	ED
same, 2nd pop.	7-8d	?	P
<i>E. elsiae</i>	5d	?	P
<i>E. evelinae</i>	11-14d	18-21C	L/ED
<i>E. hamatanii</i>	6d	15-25C	P
<i>E. hedgpetbi</i>	14d	?	P?
<i>E. maoria</i>	6d	22-23C	P
<i>E. timida</i>	16-21d	?	L/ED
<i>E. trisinuata</i>	4d	23-27.5C	P
<i>E. viridis</i>	6d	16C	P
same	15-16d	10-12C	P
Limapontioidea			
Cyerce			
<i>crystallina</i>	22d	16C	?
Caliphyllo			
<i>mediterranea</i>	9-14d	16C	P?
<i>Hermaea bifida</i>	10d	?	P?
<i>H. cruciata</i>	5d	19.5C	P
Aplysiopsis			
<i>smithi</i>	5-6d	?	P
<i>Alderia modesta</i>	5-6d	14C	P
Calliopa			
<i>oophaga</i>	4d	20C	P
Ercolania			
<i>boodleae</i>	7d	17-20C	P
<i>E. coerulea</i>	11-13d	16C	P?
<i>E. emarginata</i>	7d	18C	P
<i>E. felina</i>	7-9d	13.2C	P?
<i>E. gopalai</i>	5d	?	P
<i>E. nigra</i>	5d	19-22.5C	P
<i>E. nigrovittata</i>	4d	25.5-27C	P
Limapontia			
<i>capitata</i>	12d	10-14C	P
same	8d	19-21C	P
<i>L. depressa</i>	10d	10-14C	P
same	7d	19-21C	P
<i>L. senestra</i>	24-25d	10-14C	AD
Olea			
<i>bansimeensis</i>	6d	?	P
Placida			
<i>cremoniana</i>	12d	16C	P?
<i>P. dendritica</i>	9d	13-15C	P
<i>P. viridis</i>	8d	16C	P?
<i>Stiliger bergbi</i>	9d	10-20C	P



Table 9. Fecundity expressed as number of eggs in one egg mass related to adult size.

Taxon	No. eggs/mass	Adult size	Taxon	No. eggs/mass	Adult size
Oxynoacea			<i>T. ratna</i>	2250	14-15 mm
<i>Ascobulla ulla</i>	84-1900	?	<i>Tridachia crispata</i>	1020	?
<i>Volvatella australis</i>	210-420	12 mm	Limapontioidea		
<i>V. ventricosa</i>	570-1060	ca. 10 mm	<i>Mourgona germaineae</i>	1960	10-20 mm
<i>Berthelinia australis</i>	50	1 mm	<i>Polybranchia pallens</i>	12-35	?
<i>B. caribbea</i>	14-80	?	<i>Hermæa cruciata</i>	340	?
<i>B. darwini</i>	45-96	4-8 mm	<i>Costasiella mandorabae</i>	70	4-5 mm
<i>B. ganapati</i>	500-3520	3.7-7 mm	<i>Costasiella ocellifera</i>	88	?
<i>B. limax</i>	11-470	2.7-7.2 mm	<i>C. pallida</i>	500	?
<i>Julia japonica</i>	<100->2000	?	<i>Aplysiopsis zebra</i>	5740	?
<i>Oxynoe antillarum</i>	1940	ca. 20 mm	<i>Placida daguilarensis</i>	63-540	5-20 mm
<i>O. azuropunctata</i>	53-2755	10-40 mm	<i>P. kingstoni</i>	1590	?
<i>O. olivacea</i>	1000-5000	20-40 mm	<i>Stiliger fuscovittatus</i>	70	?
<i>O. viridis</i>	640-1500	20-40 mm	<i>Calliopaëa oophaga</i>	31-1458	3-8 mm
same	30.600	?	<i>Olea hansineensis</i>	250-600	4-9 mm
<i>Lobiger souverbii</i>	1630	?	<i>Ercolania boodleeae</i>	35-7700	4-20 mm
<i>L. sagamiensis</i>	6000	?	<i>E. coerulea</i> HK	1100	?
Plakobranchoidea			same, Fla.	1570	?
<i>Gascoignella aprica</i>	600	5-8 mm	<i>E. emarginata</i>	1350	7-15 mm
<i>Elysia australis</i>	420-3000	ca. 10 mm	<i>E. endophytophaga</i>	77-117	3-5 mm
<i>E. chlorotica</i>	176±113	7.6±2.6 mm	<i>E. funerea</i>	800	?
same, 2nd population	8902±7258	20±8 mm	<i>E. fuscata</i>	70	?
<i>E. cornigera</i>	77-137	?	<i>E. gopalai</i>	700-1500	11-12 mm
<i>E. leucolegnote</i>	1070	ca. 30 mm	<i>E. nigra</i>	3435	7-13 mm
<i>E. maoria</i>	1000-6000	?	<i>Limapontia capitata</i>	31-720	?
<i>E. patina</i>	6230	?	same	10-450	?
<i>E. subornata</i>	52-1065	?	<i>L. depressa</i>	73-950	?
<i>E. timida</i>	70-230	25 mm	same	49-199	?
<i>E. tuca</i>	290	?	<i>Limapontia senestra</i>	3-26(40)	?
<i>Thuridilla bayeri</i>	2500	16 mm			

of albumen to individual embryos. Alternatively a higher number of eggs could be produced.

Extracapsular yolk (ECY) is produced in many species of the Plakobranchoidea. It has been speculated that this supplies additional nutrition for embryos or hatching larvae/ juveniles (CLARK *et al.*, 1979; MARIN & ROS, 1993). However, ECY is found in many species with planktotrophic development (BOUCHER, 1983; JENSEN, 1997a). An extended benthic embryonic phase would seem to require parental investment in protection from predators, and it may be suggested that the function of ECY is defensive, either containing toxins produced by parent animal or providing food for predatory ciliates or bacteria. Unfortunately it is not known which structure in the reproductive system produces this ECY, and hence it is unknown whether the amount produced can be changed with changes in food availability. Its distribution in just one superfamily indicates a monophyletic origin, but arrangement and colouration differ among species.

Protoconchs have been used extensively in the prosobranchs to

indicate development type (JABLONSKI & LUTZ, 1983). In opisthobranchs protoconchs usually have few whorls and no ornamentation. In the Sacoglossa protoconchs always have less than two whorls (JENSEN, 1997b), and thus they cannot be used to indicate development type. Other criteria that have been used to indicate non-planktotrophic development type include appearance of eyes prior to hatching, and development of a propodium enabling pedal crawling (THOMPSON, 1967). Also, a reduced velum size indicates non-feeding.

A comprehensive review of reproduction in the Sacoglossa must encompass morphology of reproductive systems and reproductive behaviour as well as life history traits. The morphological characters showing the greatest interspecific variability are penial armature and arrangement of allosperm receptacles. Penial armature occurs in all major sacoglossan clades; it is absent in the Hermæidae and Oxynoidae (JENSEN, 1997b). Loss of penial armature may be an important process in speciation as it may be a simple mutation and most likely ensures reproductive isolation. Size and shape



APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Suborder Oxynoacea		
Family Volvatellidae		
<i>Ascobulla fischeri</i> (Adams & Angas, 1864)	W Australia	Jensen & Wells 1990
<i>Ascobulla ulla</i> (Marcus & Marcus, 1970)	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
<i>Volvatella australis</i> Jensen, 1997	W Australia	Jensen 1997a
<i>Volvatella bermudae</i> Clark, 1982	Bermuda	Clark & Jensen 1981
<i>Volvatella ventricosa</i> Jensen & Wells, 1990	W Australia	Jensen 1997a
Family Juliidae		
<i>Julia japonica</i> Kuroda & Habe, 1951	Japan	Kawaguti & Yamasu 1966
<i>Berthelinia australis</i> (Burn, 1960)	SE Australia	Wisely 1962
<i>Berthelinia caribbea</i> Edmunds, 1963	Florida	Clark & Jensen 1981
<i>Berthelinia darwini</i> Jensen, 1997	W Australia	Jensen 1997a
<i>Berthelinia ganapati</i> Sarma, 1975	India	Sarma 1975
<i>Berthelinia limax</i> (Kawaguti & Baba, 1959)	Japan	Kawaguti & Yamasu 1960
<i>Berthelinia rotnnesti</i> Jensen, 1993	W Australia	Jensen 1993
Family Oxynoidae		
<i>Oxynoe antillarum</i> Mörch, 1863	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
<i>Oxynoe azuropunctata</i> Jensen, 1980	Florida	Clark & Jensen 1981
<i>Oxynoe olivacea</i> Rafinesque, 1819	Mediterranean	present study
Same	Canary Island	Marin & Ros 1988
<i>Oxynoe panamensis</i> Pilsbry & Olsson, 1943	Gulf of California	Jensen 1980
<i>Oxynoe viridis</i> (Pease, 1861)	W Australia	Jensen 1997a
Same	E Australia	Rose 1985
Same		
<i>Lobiger sagamiensis</i> Baba, 1952	Hong Kong	Jensen 1985
<i>Lobiger souverbiei</i> Fischer, 1856	Florida	Clark & Jensen 1981; DeFreese & Clark 1983



APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Suborder Plakobranthacea		
Superfamily Plakobranthoidea		
Family Plakobranthidae		
<i>Elysia atroviridis</i> Baba, 1955	Hong Kong	Jensen 1985
<i>Elysia australis</i> (Quoy & Gaimard, 1832)	W Australia	Jensen 1997a
Same	E Australia	Rose 1985
<i>Elysia bangtawensis</i> Swennen, 1997	Thailand	Swennen 1997
<i>Elysia canguzua</i> Marcus, 1955	Florida	Jensen & Clark 1983
<i>Elysia catulus</i> (Gould, 1870)	Conn. USA	Clark 1975
<i>Elysia chlorotica</i> Gould, 1870	Mass. USA	West <i>et al.</i> 1984
<i>Elysia cornigera</i> Nuttall, 1989	Florida	Nuttall 1989
<i>Elysia elisiae</i> Ostergaard, 1955	Hawaii	Ostergaard 1950
<i>Elysia evelinae</i> Marcus, 1957	Florida	Clark & Jensen 1981
<i>Elysia expansa</i> (O'Donoghue, 1924)	W Australia	present study
<i>Elysia gordanae</i> Thompson & Jaklin, 1988	Mediterranean	Marin & Ros 1988
<i>Elysia hamatani</i> Baba, 1957	Japan	Hamatani 1960
<i>Elysia hedgpethi</i> Marcus, 1961	S California	Greene 1968
<i>Elysia japonica</i> Eliot, 1913	Hong Kong	Jensen 1985
<i>Elysia leucolegnote</i> Jensen, 1990	Hong Kong	Jensen 1990
<i>Elysia maoria</i> Powell, 1937	E Australia	Rose 1985
<i>Elysia ornata</i> (Swainson, 1840)	Florida	Jensen & Clark 1983
<i>Elysia papillosa</i> Verrill, 1901	Florida	Clark & Jensen 1981
<i>Elysia patagonica</i> Munian & Ortea, 1997	Argentina	Munian & Ortea 1997
<i>Elysia patina</i> Marcus, 1980	Florida	DeFreese & Clark 1983
<i>Elysia serca</i> Marcus, 1955	Florida	Clark & Jensen 1981
<i>Elysia subornata</i> Verrill, 1901	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
<i>Elysia thompsoni</i> Jensen, 1993	W Australia	Jensen 1993



APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
<i>Elysia timida</i> Risso, 1818	Mediterranean	Clark & Jensen 1981; Marin & Ros 1993
<i>Elysia trisinuata</i> Baba, 1949	Japan	Hamatani 1967
<i>Elysia tuca</i> Marcus & Marcus, 1967	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
<i>Elysia viridis</i> Montagu, 1804	Mediterranean	Schmekel & Portmann 1982
Same	UK	Kress 1972
Same		
Same	Norway	Hagerman 1970
Same		
<i>Plakobrancheus iantbobapsus</i> Gould, 1852	Hawaii	Ostergaard 1950
<i>Thuridilla bayeri</i> (Marcus, 1965)	Marshall Island	Johnson & Boucher 1983
<i>Thuridilla hopei</i> (Verany, 1853)	Mediterranean	Thompson & Salghetti-Drioli 1984
<i>Thuridilla ratna</i> (Marcus, 1965)	Marshall Islands	Johnson & Boucher 1983
<i>Thuridilla vatae</i> (Risbec, 1928)	Marshall Islands	Johnson & Boucher 1983
<i>Tridachia crispata</i> Mörch, 1863	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
	Family Boselliidae	
<i>Bosellia leve</i> Fernandez-Ovies & Ortea, 1986	Canary Island	Fernandez-Ovies & Ortea 1986
<i>Bosellia mimetica</i> Trinchese, 1891	Florida	Clark & Jensen 1981
Same	Mediterranean	Schmekel & Portmann 1982
Same		
	Family Platyhedylidae	
<i>Gascoignella aprica</i> Jensen, 1985	Hong Kong	Jensen 1985
	Superfamily Limapontioidea	
	Family Polybranchiidae	
<i>Caliphylla mediterranea</i> Costa, 1867	Florida	Clark & Jensen 1981
Same	Mediterranean	Schmekel & Portmann 1982
Same		
<i>Cyerce antillensis</i> Engel, 1927	Florida	Clark & Jensen 1981
<i>Cyerce cristallina</i> (Trinchese, 1881)	Mediterranean	Schmekel & Portmann 1982
<i>Mourgona germaineae</i> Marcus & Marcus, 1970	Florida	Clark & Jensen 1981
<i>Polybranchia pallens</i> (Burn, 1957)	SE Australia	Burn 1998
<i>Polybranchia viridis</i> (Deshayes, 1857)	Florida	Clark 1994



APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
	Family Hermaeidae	
<i>Hermaea bifida</i> (Montagu, 1815)	Mediterranean	Schmekel & Portmann 1982
<i>Hermaea cruciata</i> Gould, 1870	Florida	Clark & Jensen 1981
Same	Chesapeake (USA)	Vogel 1971
Same		
<i>Hermaea evelinemarkusae</i> Jensen, 1993	W Australia	Jensen 1993
<i>Aplysiopsis maculosa</i> (Trinchese, 1874)	Mediterranean	Kress 1972
<i>Aplysiopsis smithi</i> (Marcus, 1961)	S California	Greene 1968
<i>Aplysiopsis zebra</i> Clark, 1982	Florida	Clark & Jensen 1981
	Family Limapontiidae	
<i>Alderia modesta</i> (Lovén, 1844)	Connecticut (USA)	Clark & Goetzfried 1978
Same	UK	Kress 1972
Same		
Same	Denmark	Rasmussen 1951
Same		
<i>Calliopaea oophaga</i> Lemche, 1974	Denmark	Jensen 1986a
<i>Costasiella ocellifera</i> (Simroth, 1895)	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
<i>Costasiella mandorabae</i> Jensen, 1997	N Australia	Jensen 1997c
<i>Costasiella nonatoi</i> Marcus & Marcus, 1960	Bermuda	Clark & Jensen 1981
<i>Costasiella pallida</i> Jensen, 1985	Hong Kong	Jensen 1990; present study
<i>Ercolania boodlea</i> (Baba, 1938)	Japan Usuki 1977	Hamatani 1960;
<i>Ercolania coerulea</i> Trinchese, 1893	Hong Kong	Jensen 1985
Same	Florida	Clark & Jensen 1981
Same		
Same	Mediterranean	Schmekel & Portmann 1982
Same		
<i>Ercolania emarginata</i> Jensen, 1985	Hong Kong	Jensen 1985; present study
<i>Ercolania</i> <i>endophytophaga</i> Jensen, 1999	W Australia	present study
<i>Ercolania felina</i> (Hutton, 1882)	New Zealand	Trowbridge 1995
<i>Ercolania funerea</i> (Costa, 1867)	Florida	DeFreese & Clark 1983
Same	Mediterranean	Schmekel & Portmann 1982
Same		
<i>Ercolania fuscata</i> (Gould, 1870)	Florida	Clark & Jensen 1981
Same		
Same	Conn. USA	Clark 1975



APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
<i>Ercolania gopalai</i> Rao, 1937	India	Rao 1937
<i>Ercolania nigra</i> Lemche, 1935	Denmark	Rasmussen 1951
<i>Ercolania nigrovittata</i> Rao & Rao, 1963	India	Rao & Rao 1963
<i>Ercolania translucens</i> Jensen, 1993	W Australia	present study
<i>Ercolania</i> n.sp.	W Australia	present study
<i>Limapontia capitata</i> (Müller, 1774)	UK	Chia 1971
<i>Limapontia depressa</i> Alder & Hancock, 1862	UK	Chia 1971
<i>Limapontia senestra</i> (Quatrefages, 1844)	UK	Chia 1971
<i>Olea hansineensis</i> Agersborg, 1823	Vancouver	Chia & Skeel 1973; Crane 1971
<i>Placida cremoniana</i> (Trinchese, 1893)	Mediterranean	Schmekel & Portmann 1982
<i>Placida dagnilarensis</i> Jensen, 1990	Hong Kong	Jensen 1990
<i>Placida dendritica</i> (Alder & Hancock, 1843)	Connecticut USA	Clark 1975
<i>Same</i>	UK	Kress 1971
<i>Same</i>	California	Greene 1968
<i>Same</i>	Florida	Clark & Jensen 1981
<i>Placida kingstoni</i> Thompson, 1977	Florida	Clark & Jensen 1981
<i>Placida viridis</i> Trinchese, 1873	Mediterranean	Schmekel & Portmann 1982
<i>Stiliger</i> <i>aureomarginatus</i> Jensen, 1993	W Australia	Jensen 1993; present study
<i>Stiliger bergbi</i> Baba, 1937	Japan	Hamatani 1963
<i>Stiliger fuscovittatus</i> Lance, 1962	Florida	Clark & Goetzfried 1978
<i>Stiliger llerai</i> Ortea, 1981	Canary Islands	Ortea 1981
<i>Stiliger verticillata</i> (Ortea, 1981)	Canary Islands	Marin & Ros 1988

of penial armature is very important in species identification, and probably also serves in recognition of conspecifics. It should be noted that hypodermic impregnation may occur in sacoglossans without penial armature (JENSEN, 1986b). Whether this involves enzymatic action from one or both copulatory partners is unknown. The highly variable arrangement of allosperm receptacles may also serve to ensure reproductive isolation. However, it may also allow the sperm recipient to select among sperm received from different

partners. It is unknown whether single egg masses may be fertilized by sperm from more than one sperm donor.

Copulatory behaviour has recently been reviewed (JENSEN, 1999). Most species have a precopulatory mate identification behaviour. The most common copulatory position is with animals facing in opposite directions and right sides touching. Intromission may be unilateral or reciprocal. In the Limapontioidea copulation is usually brief, less than 30 seconds to a few minutes; in the Plakobran-



choidea and Oxynoacea copulation may last more than one hour. Sperm transfer is usually reciprocal, though not always simultaneously so. Allosperm can be stored for variable lengths of time, but no formal studies exist on this aspect. Also, nothing is known about factors controlling fertilization, i.e. whether sperm from different copulations compete, or whether the sperm recipient selects sperm from a particular copulation. These are important aspects for understanding evolution, and it will be worthwhile to study this in the future.

Reproductive effort, that is the total amount of energy allocated to reproduction, has been examined in Caribbean sacoglossans (DEFRESE & CLARK, 1983). It seems to depend more on the size of the parent than on development type.

ACKNOWLEDGEMENTS

I would like to thank the Istituzione Culturale Federico II, Sezione di Malacologia, for inviting me to give a key-note presentation. I am especially grateful to Ms. Vanna Rotolo for her generous hospitality and support.

REFERENCES

- BOUCHER, L.M. 1983. Extra-capsular yolk bodies in the egg masses of some tropical Opisthobranchia. *Journal of Molluscan Studies*, Oxford, 49: 232-241.
- BOUCHIET, P. 1989. A review of poecilogony in gastropods. *Journal of Molluscan Studies*, Oxford, 55: 67-78.
- BURN, R. 1998. Order Sacoglossa. In Beesley, P.L., Ross, G.J.B. and Wells, A. (Eds.): *Mollusca: The Southern Synthesis. Fauna of Australia*. Vol. 5. CSIRO Publishing: Melbourne, Part B, pp. 961-974.
- CHIA, F.-S. 1971. Oviposition, fecundity and larval development of three sacoglossan opisthobranchs from the Northumberland coasts, England. *The Veliger*, Berkeley, 13: 319-325.
- CHIA, F.-S. & SKEEL, M. 1973. The effect of food consumption on growth, fecundity and mortality in a sacoglossan opisthobranch, *Olea banmsiensis*. *The Veliger*, Berkeley, 16: 153-158.
- CLARK, K.B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, Hamburg, 27: 28-69.
- CLARK, K.B. 1984. New records and synonymies of Bermuda opisthobranchs (Gastropoda). *The Nautilus*, Silver Spring, 98: 85-97.
- CLARK, K.B. 1994. Ascoglossan (=Sacoglossa) molluscs in the Florida Keys: rare marine invertebrates at special risk. *Bulletin of Marine Science*, Miami, 54: 900-916.
- CLARK, K.B. & GOETZFRIED, A. 1978. Zoogeographic influences on development patterns of North Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies*, Oxford, 44: 283-294.
- CLARK, K.B., BUSACCA, M. & STIRTS, H.M. 1979. Nutritional aspects of development of the ascoglossan *Elysia cauzei*. In S.E. Stancyk (Ed.): *Reproductive ecology of marine invertebrates*. University of South Carolina Press: Columbia, South Carolina. Pp. 111-124.
- CLARK, K.B. & JENSEN, K.R. 1981. A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *International Journal of Invertebrate Reproduction*, Rehovot, 3: 57-64.
- CRANE, S. 1971. The feeding and reproductive behavior of the sacoglossan gastropod *Olea banmsiensis* Agersborg, 1923. *The Veliger*, Berkeley, 14: 57-59.
- DEFRESE, D.E. & CLARK, K.B. 1983. Analysis of reproductive energetics of Florida Opisthobranchia (Mollusca: Gastropoda). *International Journal of Invertebrate Reproduction*, Rehovot, 6: 1-10.
- DEFRESE, D.E. & CLARK, K.B. 1991. Transepidermal uptake of dissolved free amino acids from sea water by three ascoglossan opisthobranchs. *Journal of Molluscan Studies*, Oxford, 57 (Supplement): 65-74.
- FERNANDEZ-OVIES, C.L. & ORTEA, J. 1986. Descripción de una nueva especie de *Bosellia* Trinchese, 1890 (Mollusca: Opisthobranchia: Ascoglossa) de las Islas Canarias. *Iberus*, Barcelona, 6: 101-106.
- GASCOIGNE, T. 1974. A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society*, London, 55: 53-59.
- GASCOIGNE, T. 1976. The reproductive systems and classification of the Stiligeridae (Opisthobranchia: Sacoglossa). *Journal of the Malacological Society of Australia*, Sydney, 3(3): 157-172.
- GASCOIGNE, T. 1979. Observations on the anatomy of *Hermaea variopicta* (Opisthobranchia: Ascoglossa). *Journal of Zoology*, London, 187: 223-233.
- GREENE, R.W. 1968. The egg masses and veligers of Southern California sacoglossan opisthobranchs. *The Veliger*, Berkeley, 11: 100-104.
- HADFIELD, M.G. & MILLER, S.E. 1987. On developmental patterns of opisthobranchs. *American Malacological Bulletin*, Austin, 5: 197-214.
- HADFIELD, M.G. & SWITZER-DUNLAP, M. 1984. Opisthobranchs. In A.S. Tompa, N.H. Verdonk & J.A.M. van den Biggelaar (Eds): *The Mollusca*, Vol. 7. *Reproduction*. Academic Press., London, pp. 209-350.
- HAGERMAN, L. 1970. The influence of low salinity on survival and spawning of *Elysia viridis* (Montagu) (Opisthobranchia, Sacoglossa). *Sarsia*, Bergen, 42: 1-6.
- HAMATANI, I. 1960. Notes on veligers of Japanese opisthobranchs (1). *Publications of the Seto Marine Biological Laboratory*, Kyoto, 8: 59-70.
- HAMATANI, I. 1963. Notes on veligers of Japanese opisthobranchs (6). *Publications of the Seto Marine Biological Laboratory*, Kyoto, 11: 125-130.
- HAMATANI, I. 1967. Notes on veligers of Japanese opisthobranchs (7). *Publications of the Seto Marine Biological Laboratory*, Kyoto, 15: 121-131.
- HEALY, J.M. 1993. Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea, Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta*, Oxford, 22: 263-276.
- JABLONSKI, D. & LUTZ, R.A. 1983. Larval ecology of marine benthic invertebrates: Paleobiological implications. *Biological Reviews*, Cambridge, 58: 21-89.
- JENSEN, K.R. 1980. *Oxyno azureopunctata* n.sp., a new sacoglossan from the Florida Keys (Mollusca: Opisthobranchia). *Journal of Molluscan Studies*, Oxford, 46: 282-292.
- JENSEN, K.R. 1985. Annotated checklist of Hong Kong Ascoglossa (Mollusca: Opisthobranchia), with descriptions of four new species. In B. Morton & D. Dudgeon (Eds): *The Malacofauna of Hong Kong and Southern China II. Proceedings of the Second International Workshop on the Malacofauna Hong Kong and Southern China*, Hong Kong 1983. Hong Kong University Press, Hong Kong. pp. 77-107.
- JENSEN, K.R. 1986a. Observations on feeding, copulation, and spawning in *Calliopaea oophaga* Lemche (Opisthobranchia, Ascoglossa). *Opbelia*, Helsingore, 25: 97-106.
- JENSEN, K.R. 1986b. Observations on copulation in two species of *Elysia* (Opisthobranchia, Ascoglossa) from Florida. *Opbelia*, Helsingore, 25: 25-32.
- JENSEN, K.R. 1990. Three new species of Ascoglossa (Mollusca, Opisthobranchia) from Hong Kong, and a description of the internal anatomy of *Costasiella pallida* Jensen, 1985. In B. Morton (Ed.): *The marine flora and fauna of Hong Kong and southern China II Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong, 2-24 April 1986. Hong Kong University Press, Hong Kong. pp. 419-432.
- JENSEN, K.R. 1992. Anatomy of some Indo-Pacific Elysiidae (Opisthobranchia: Sacoglossa (=Ascoglossa)), with a discussion of the generic division and phylogeny. *Journal of Molluscan Studies*, Oxford, 58: 257-296.
- JENSEN, K.R. 1993. Sacoglossa (Mollusca, Opisthobranchia) from Rottneest Island and central Western Australia. In F.E. Wells, D.I. Walker, H. Kirkman



- and R. Lethbridge Eds): *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*. Western Australian Museum, Perth. pp. 207-253.
- JENSEN, K.R. 1995. Anatomy and biology of *Aplysiopsis formosa* Pruvot-Fol (Mollusca, Opisthobranchia, Sacoglossa) from the Azores. *Agoreana*, Supplement, Ponta Delgada: 217-230.
- JENSEN, K.R. 1996. Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). *Philosophical Transactions of the Royal Society B*, London, 351: 91-122.
- JENSEN, K.R. 1997a. Sacoglossa (Mollusca, Opisthobranchia) from the Houtman Abrolhos Island and central Western Australia. In F.E. Wells (Ed.): *Proceedings of the Seventh International Marine Biological Workshop: The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*. Western Australian Museum, Perth. pp. 307-333.
- JENSEN, K.R. 1997b. *Sacoglossernes systematik, fylogeni og evolution* (Mollusca, Opisthobranchia). *Systematics, phylogeny and evolution of the Sacoglossa* (Mollusca, Opisthobranchia). Vestjysk Forlag, Vinderup, 94 pp.
- JENSEN, K.R. 1997c. Sacoglossa (Mollusca, Opisthobranchia) from the Darwin Harbour area, Northern Territory, Australia. In J.R. Hanley, G. Caswell, D. Megirian and H.K. Larson (Eds): *Proceedings of the Sixth International Marine Biological Workshop: The Marine Flora and Fauna of Darwin, Northern Territory, Australia*. Darwin, Australia; Museums and Art Galleries of the Northern Territory and the Australian Marine Sciences Association. pp. 163-186.
- JENSEN, K.R. In press. Copulatory behaviour in three shelled and five non-shelled sacoglossans (Mollusca, Opisthobranchia), with a discussion of the phylogenetic significance of copulatory behaviour. *Opbelia*, Helsingore.
- JENSEN, K.R. & CLARK, K.B. 1983. Annotated checklist of Florida ascoglossan Opisthobranchia. *Nautilus*, Silver Spring, 97: 1-13.
- JENSEN, K.R. & WELLS, F.E. 1990. Sacoglossa (=Ascoglossa) (Mollusca, Opisthobranchia) from southern Western Australia. In: F.E. Wells, D.I. Walker, H. Kirkman and R. Lethbridge (Eds): *Proceedings of the Third International Marine Biological Workshop: The Marine Flora and Fauna of Albany, Western Australia I*. Western Australian Museum, Perth. pp. 297-331.
- JOHNSON, S. & BOUCHER, L.M. 1983. Notes on some Opisthobranchia (Mollusca: Gastropoda) from the Marshall Islands, including 57 new records. *Pacific Science*, Honolulu, 37: 251-291.
- KAWAGUTI, S. & YAMASU, T. 1960. Spawning habits of a bivalved gastropod, *Tamanovalva limax*. *Biological Journal of Okayama University*, Okayama, 6: 133-149.
- KAWAGUTI, S. & YAMASU, T. 1966. Feeding and spawning habits of a bivalved gastropod, *Julia japonica*. *Biological Journal of Okayama University*, Okayama, 12:1-9.
- KEMPE, S.C. & TODD, C.D. 1989. Feeding potential in the lecithotrophic larvae of *Adalaria proxima* and *Tritonia bombergi*: an evolutionary perspective. *Journal of the Marine Biological Association*, U.K., Plymouth, 69: 659-682.
- KRESS, A. 1971. Über die Entwicklung der Eikapselvolulina bei verschiedenen Opisthobranchier-Atten (Mollusca, Gastropoda). *Helgoländer wissenschaftliche Meeresuntersuchungen*, Hamburg, 22: 326-349.
- KRESS, A. 1972. Veränderungen der Eikapselvolulina während der Entwicklung verschieden Opisthobranchier-Arten (Mollusca, Gastropoda). *Marine Biology*, Berlin, 16: 236-252.
- MARIN, A. & ROS, J. 1988. Los sacoglossos (Mollusca, Opisthobranchia) del sudeste Iberico. *Catálogo de las especies y presencia de cloroplastos algales en las mismas*. *Iberus*, Barcelona, 8: 25-49.
- MARIN, A. & ROS, J.D. 1993. Ultrastructural and ecological aspects of the development of chloroplast retention in the sacoglossan *Elysia timida*. *Journal of Molluscan Studies*, Oxford, 59: 95-104.
- MUNIAN, C. & ORTEA, J. 1997. First record of a sacoglossan (= ascoglossan, Opisthobranchia) from Patagonia (Argentina): Description of a new species of genus *Elysia* Risso, 1818. *The Veliger*, Berkeley, 40: 29-37.
- NUTTALL, T.R. 1989. A new *Elysia* (Opisthobranchia: Ascoglossa) from the Florida Keys. *The Veliger*, Berkeley, 32: 302-307.
- ORTEA, J. 1981. Moluscos opisthobranchios de las Islas Canarias. I. Patte: Ascoglossos. *Boletín del Instituto Español de Oceanografía*, Madrid, 6: 180-199.
- OSTERGAARD, J.M. 1950. Spawning and development of some Hawaiian marine gastropods. *Pacific Science*, Honolulu, 4: 75-115.
- RAO, K.V. 1937. Structure, habits and early development of a new species of *Stiliger* Ehtenberg. *Records of the Indian Museum*, Calcutta, 39: 435-464, plates 7-9.
- RAO, K.V. & RAO, K.P. 1963. *Stiliger nigrovittatus* sp. nov., a sacoglossan mollusc from the Gulf of Mannar. *Journal of the Marine Biological Association of India*, Cochin, 5: 232-238.
- RASMUSSEN, E. 1951. Faunistic and biological notes on marine invertebrates, II. The eggs and larvae of some Danish marine gastropods. *Videnskabelige Meddelelser fra dansk naturhistorisk Forening*, Copenhagen, 113: 201-249.
- ROSE, R.A. 1985. The spawn and development of twenty-nine New South Wales opisthobranchs (Mollusca: Gastropoda). *Proceedings of the Linnean Society of New South Wales*, Sydney, 108: 23-36.
- SARMA, A.L.N. 1975. Three new species of the bivalved gastropods *Julia* and *Berthelinia* found in Eastern Indian Ocean. *Venus*, Tokyo, 34: 11-25.
- SCHMEKEL, L. & PORTMANN, A. 1982. *Opisthobranchia des Mittelmeeres*. *Nudibranchia und Sacoglossa*. Springer-Verlag, Berlin, 410 pp.
- STRATHMANN, R.R. 1985. Feeding and nonfeeding larval developments and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics*, Palo Alto, 16: 339-361.
- SWENNEN, C. 1997. Two new gastropods, *Elysia bangtauvaensis* and *E. siamensis* from southern Thailand (Opisthobranchia, Sacoglossa, Elysiidae). *Bulletin Zoologisch Museum*, Universiteit van Amsterdam, Amsterdam, 16(6): 33-39.
- THOMPSON, T.E. 1967. Direct development in a nudibranch, *Cadlina laevis*, with a discussion of developmental processes in Opisthobranchia. *Journal of the Marine Biological Association of the U.K.*, Plymouth, 47: 1-22.
- THOMPSON, T.E. & SALGHETTI-DRIOLI, U. 1984. Unusual features of the development of the sacoglossan *Elysia bopei* in the Mediterranean Sea. *Journal of Molluscan Studies*, Oxford, 50: 61-63.
- TROWBRIDGE, C.D. 1995. Hypodermic insemination, oviposition, and embryonic development of a pool-dwelling ascoglossan (=sacoglossan) opisthobranch: *Ercolania felina* (Hutton, 1882) on New Zealand shores. *The Veliger*, Berkeley, 38: 203-211.
- ŪSUKI I. 1977. Effects of food algae on the nutrition of *Ercolania boodleae* (Baba) (Opisthobranchia, Gastropoda). *Japanese Journal of Ecology*, Kyoto, 27: 103-110.
- VOGEL, R.M. 1971. The biology and a redescription of the opisthobranch mollusk *Hermæa cruciata* Gould, from Chesapeake Bay (Maryland). *The Veliger*, Berkeley, 14: 155-157.
- WEST, H.H., HARRIGAN, J.F. & PIERCE, S.K. 1984. Hybridization of two populations of marine opisthobranch with different development patterns. *The Veliger*, Berkeley, 26: 199-206.
- WISELY, B. 1962. An outline of the development of the bivalve gastropod, *Midori-gai australis* Burn, 1960. *Journal of the Malacological Society of Australia*, Sydney, 6: 37-39.
- WOMERSLEY, H.B.S. 1984. *The Marine Benthic Flora of Southern Australia. Part I*. South Australia, Government Printer, Adelaide.