

# Random Mating and Planktotrophic Larval Development in the Brooding Hermaphroditic Clam *Lasaea australis* (Lamarck, 1818)

by

DIARMAID Ó FOIGHIL<sup>1</sup>

Friday Harbor Laboratories, Friday Harbor, Washington 98250, U.S.A.

*Abstract.* *Lasaea australis* differs markedly from congeners in important details of its early ontogeny and reproduction. Adults brood their young to a straight-hinged veliger stage and an obligate planktotrophic larval period precedes settlement and metamorphosis. Several lines of evidence indicate that *L. australis* reproduces primarily by cross-fertilization. These include the maintenance of a Hardy-Weinberg-Castle equilibrium, and an observed heterozygosity level of 0.635, at the highly polymorphic glucose-6-phosphate isomerase locus. In addition, *L. australis* appears to be an alternate sequential hermaphrodite and has a large male allocation (approximately 50% in terms of gonadal volume). These results are the first to provide evidence of amphimixis in *Lasaea*. A profound dichotomy exists within the genus in developmental and reproductive modes, and population genetic structure. *Lasaea australis* probably represents the ancestral condition, and congeners that lack a planktonic larva form a complex assemblage of uncertain taxonomic status.

## INTRODUCTION

The galeommatacean bivalve genus *Lasaea* is known from the Eocene period and has attained a near-cosmopolitan distribution (CHAVAN, 1969). *Lasaea* are small ( $\leq 6$  mm in valve length) crevice dwellers, found in the rocky intertidal within cracks, algal holdfasts, barnacle test interstices, lichen tufts, and under rocks (KEEN, 1938; MORTON, 1954; MORTON *et al.*, 1957; OLDFIELD, 1964; GLYNN, 1965; PONDER 1971; BOOTH, 1979; SEED & O'CONNOR, 1980; CRISP *et al.*, 1983; ROBERTS, 1984; BEAUCHAMP, 1986; McGRATH & Ó FOIGHIL, 1987). Although *Lasaea* is one of the better studied and most readily sampled marine bivalves, its taxonomy and some aspects of its reproduction are subject to conflicting interpretations.

Bivalve systematists have traditionally relied heavily on shell morphology to distinguish between species. There is much individual variation in *Lasaea* shells (DALL, 1900; PONDER, 1971; ROBERTS, 1984; Ó FOIGHIL, 1986a; Ó FOIGHIL & EERNISSE, in press) and this poses a difficult taxonomic dilemma. KEEN (1938) lists >40 species dis-

tinguished from each other on the basis of slight differences in shell morphology and color. A number of more recent workers, however, have been unable to separate many of these nominal *Lasaea* species (SOOT-RYEN, 1960; DELL, 1964; BARNARD, 1964; PONDER, 1971; HADERLIE & ABBOTT, 1980; BEAUCHAMP, 1985). An extreme alternative view is that the genus is monospecific (DALL, 1900; LAMY, 1906; DAUTZENBERG, 1929). PONDER (1971) concluded that many of the nominal *Lasaea* species are merely regional subspecies or ecotypes of the type species *Lasaea rubra* (Montagu, 1803). However, he distinguished two additional species, *L. australis* (Lamarck, 1818) and *L. maoria* (Powell, 1933), on the basis of shell and soft part morphology.

Population genetic studies of *Lasaea* in Europe (CRISP *et al.*, 1983) and the northeastern Pacific (Ó FOIGHIL, 1986a; Ó FOIGHIL & EERNISSE, in press) have revealed the existence of a variety of non-hybridizing, frequently sympatric, genetic strains. These results have important implications for understanding morphological variation and systematic relationships within the genus. CRISP *et al.* (1983) concluded that the populations they examined were composed of female, apomictic clones. They apparently overlooked an earlier detailed study (OLDFIELD, 1961) which

<sup>1</sup> Present address: Biology Department, University of Victoria, P.O. Box 1700, Victoria, British Columbia, Canada V8W 2Y2.

described European *Lasaea* as simultaneous hermaphrodites with greatly reduced male allocation, recently confirmed by McGRATH & Ó FOIGHIL (1986). Ó FOIGHIL & EERNISSE (in press) consider that northeastern Pacific *Lasaea* strains are either products of prolonged autogamy (self-fertilization), or pseudogamy in association with meiotic parthenogenesis.

Galeommatacean species investigated to date brood their young, either to a straight-hinged veliger (CHANLEY & CHANLEY, 1970; Ó FOIGHIL & GIBSON, 1984) or to a crawl-away juvenile stage of development (GAGE, 1979). *Lasaea* developmental modes have been determined in European (OLDFIELD, 1964; SEED & O'CONNOR, 1980; McGRATH & Ó FOIGHIL, 1986), Ascension Island (ROSEWATER, 1975), New Zealand (BOOTH, 1979), Hawaiian (KAY, 1979) and northeastern Pacific (GLYNN, 1965; Ó FOIGHIL, 1986; BEAUCHAMP, 1986) populations. In all of these cases, offspring are released as crawl-away juveniles. There are indications, however, that *L. australis*, which occurs around the Australian continent (DELL, 1964), may differ from its congeners in its developmental mode. PONDER (1971) reports that *L. australis* has a smaller prodissoconch (approximately 200  $\mu\text{m}$  in length) relative to other *Lasaea* (500–600  $\mu\text{m}$ ). Prodissoconch size is directly related to egg size and developmental mode in eulamellibranch bivalves (OCKELMANN, 1965; WALLER, 1981; JABLONSKI & LUTZ, 1983). The smaller *L. australis* prodissoconch is indicative of a shorter brooding period, possibly involving an obligate planktonic larval state. ROBERTS (1984) investigated the reproductive cycle of *L. australis* in Western Australia and described it as being larviparous, without reporting the developmental stage when released from the parent, egg size, or brood number. *Lasaea* that retain their young to a juvenile stage of development have also been frequently described as brooding "larvae" (BOOTH, 1979; KAY, 1979). Confirmation that *L. australis* does indeed differ in its developmental mode from other *Lasaea* is important because developmental modes exert a profound influence on population genetic composition and consequently on the evolution of reproductive patterns (CHARLESWORTH & CHARLESWORTH, 1981; STRATHMANN *et al.*, 1984; LANDE & SCHEMSKE, 1985). Though there is yet no evidence for cross-fertilization in this genus, a reproductive mode involving an obligate larval dispersal is likely to result in high population genetic diversity (BERGER, 1983) which would form a potent genetic penalty for self-fertilizers in the form of a pronounced inbreeding depression (MAYNARD SMITH, 1978). Accordingly, an obligate planktonic larval period in *L. australis* should select for a predominantly cross-fertilizing reproductive mode.

The aim of this study is to assess the systematic status of *Lasaea australis* within this unusual genus by characterizing its developmental and reproductive modes. A live sample was obtained (courtesy of W. F. Ponder, Australian Museum), from which the hinge structure, duration of brood care, sex allocation, and population genetic structure at a polymorphic isozyme locus were determined.

## MATERIALS AND METHODS

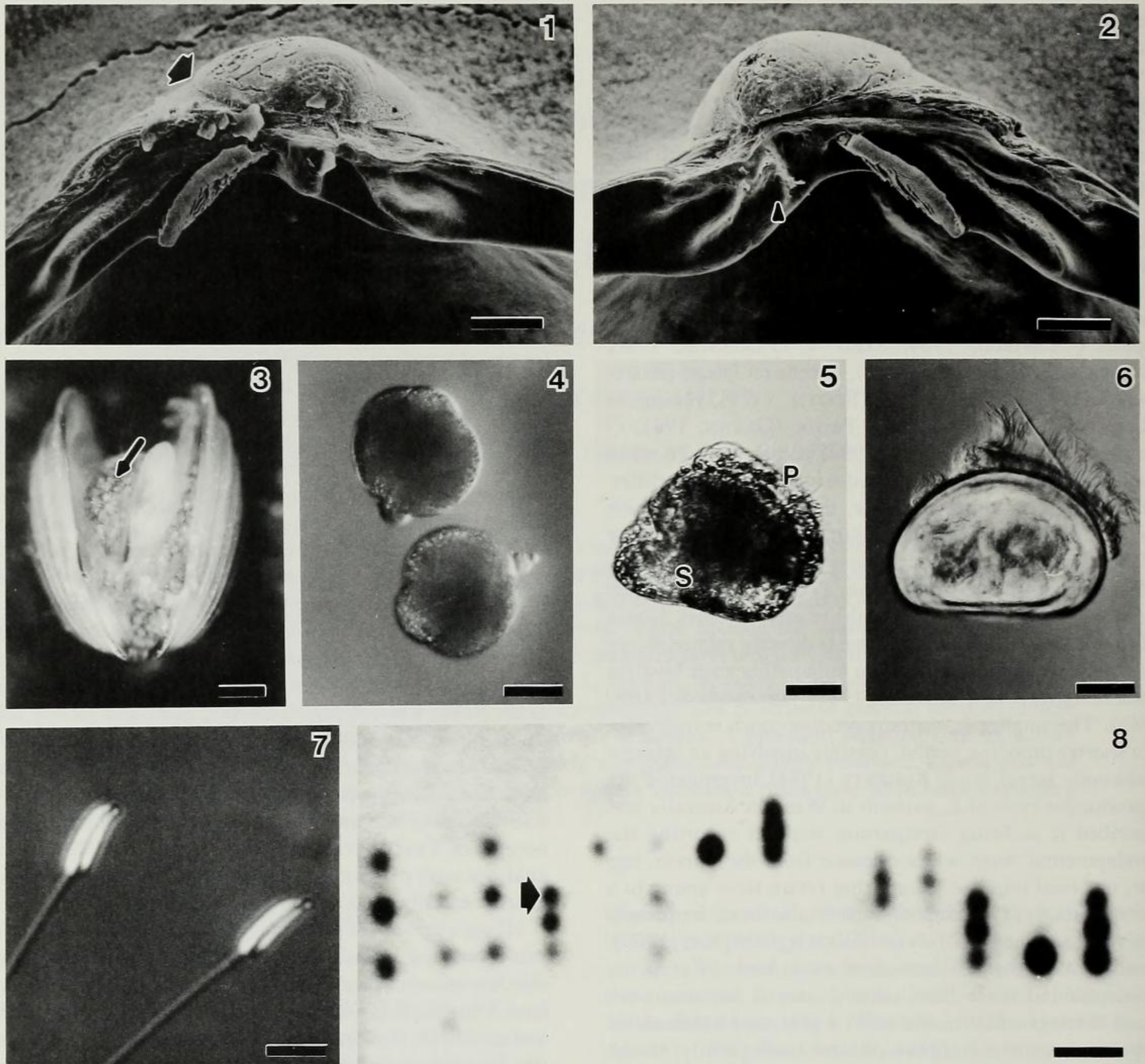
One hundred and five specimens of *Lasaea australis* were sampled in August 1987 from the intertidal zone at Long Reef, New South Wales, Australia (33°44'S, 151°18'E) by P. H. Colman. They were heat-sealed in a plastic bag containing approximately 50 mL of seawater, were air mailed, and arrived at the Friday Harbor Laboratories 10 days later. All specimens survived the trip; indeed, many had spawned en route and were brooding developing embryos upon arrival. They were maintained in seawater tanks at room temperature (18–20°C) and fed cultured *Thalassosira pseudonana* (strain 3H) for a week, then starved for one day before electrophoretic analysis.

Ninety-eight specimens were characterized electrophoretically using 13% starch gels and standard power supplies. Broods were dissected from reproducing individuals; the adults were then removed from their valves and homogenized with glass rods in an equal volume of gel buffer. A single discontinuous tris-citrate buffer system (electrode: 18.55 g boric acid and 2.4 g sodium hydroxide/L, pH 8.2; gel: 9.21 g tris and 1.05 g monohydrate citric acid/L, pH 8.7) was used. The following enzymes yielded monomorphic protein phenotypes: leucine amino peptidase, peptidase with glycyl-lysine, and peptidase with leucyl-valine and leucyl-tyrosine substrates. Glucose-6-phosphate isomerase (GPI; EC 5.3.1.9), however, produced closely migrating, polymorphic protein phenotypes, which were sufficiently resolved when gels were run at 200 volts until the front had reached a preset "destiny" of 130 mm. The GPI staining assay and method of scoring electromorph phenotypes of TRACEY *et al.* (1975) were employed. Statistical analyses were performed using standard techniques as previously described (Ó FOIGHIL & EERNISSE, 1987).

Hinge structure of air-dried, gold-coated *Lasaea australis* valves was examined using a JOEL JSM-35 scanning electron microscope and compared with that of congeners from Victoria, B.C. (Canada), New Zealand (lots m. 21828 and m. 21011, National Museum of New Zealand), Japan (lot 78-14, Los Angeles County Museum of Natural History), Florida (lot PSM-743, Indian River Coastal Zone Museum), Britain (lot 35873, Museum of Zoology, University of Michigan), South Africa (lot A32355, South African Museum), and the Seychelles (lot 2222, British Museum of Natural History). Brooding individuals were photographed with a Wild Photomicroscope. Straight-hinged veliger larvae released by brooding parents were relaxed in 6.7%  $\text{MgCl}_2$  at 4°C and fixed in 2% formaldehyde. Embryos, larvae, and sperm cells were photographed using Nomarski differential interference contrast optics on a Nikon Optiphot light microscope.

## RESULTS

Figures 1 and 2 respectively show the hinge structure of the left and right valves of a *Lasaea australis* specimen 1.2 mm in valve length. The left hinge contains a single truncated anterior lateral tooth, a short thornlike cardinal (more



## Explanation of Figures 1 to 8

Figure 1. Scanning electron micrograph (SEM) of left hinge of *Lasaea australis* specimen 1.2 mm in valve length. Arrow indicates prodissoconch-dissoconch boundary. Scale bar = 75  $\mu$ m.

Figure 2. SEM of right valve of same *L. australis* specimen as in Figure 1. Arrow indicates small spur on posterior end of ventral anterior lateral tooth. Scale bar = 75  $\mu$ m.

Figure 3. Light micrograph (LM) of a brooding *L. australis*, with opened valves, revealing brood mass (arrow) in the suprabranchial chamber. Scale bar = 0.5 mm.

Figure 4. Nomarski differential interference contrast (DIC) LM of *L. australis* eggs removed from the brood chamber just prior to first cleavage. Each egg bears polar bodies at the animal pole and a polar lobe at the vegetal pole. Scale bar = 40  $\mu$ m.

Figure 5. Nomarski DIC LM of a *L. australis* larva dissected from the brood chamber at a late trochophore stage of development. Note developing shell (S) and faint prototroch (P). Scale bar = 30  $\mu$ m.

Figure 6. Nomarski DIC LM of a *L. australis* straight-hinged veliger just after release from parent. The well-developed velum is partially retracted. Scale bar = 40  $\mu$ m.

Figure 7. Nomarski DIC LM of *L. australis* sperm cells. Scale bar = 5  $\mu$ m.

Figure 8. GPI electromorphs of 13 Long Reef *L. australis* individuals showing all five alleles detected in this study. Arrow indicates the modal allele (100). Scale bar = 10 mm and is placed anodally.

pronounced in larger specimens), an oblique resilium, and a lamellar posterior lateral tooth. In the right hinge, the short anterior lateral is bifurcate, forming a groove that accepts the left anterior lateral. In larger individuals this bifurcation is less evident and the ventral anterior lateral becomes much more pronounced, developing a spur at its posterior end which may represent a fused cardinal tooth (Figure 2). The right hinge also contains a pit which articulates with the left cardinal tooth, an oblique resilium, and two lamellar posterior laterals. The ventral posterior lateral is relatively more pronounced, and the groove separating the two laterals accepts the single posterior lateral of the left hinge. Shell shape, color, and sculpture are variable as previously found by PONDER (1971) and ROBERTS (1984). Individuals could be entirely white or pinkish-red in external valve coloration and many specimens had abruptly changed shell coloration during valve growth. Some individuals had heavy concentric folding on their external valve surfaces.

As in other *Lasaea*, developing young are retained in the suprabranchial chamber (Figure 3). The brood is held in both inner and outer demibranchs; the latter is reduced to one-third the size of the inner demibranch. Brood sizes of 440 and 2870 were produced by two individuals, 2.16 and 4.25 mm in respective valve lengths. *Lasaea australis* eggs are 90–95  $\mu\text{m}$  in diameter and undergo two maturation divisions before first cleavage (Figure 4). Early development is similar to that found in other galeommatacean bivalves that retain their offspring to a straight-hinged veliger stage of development (Ó FOIGHIL & GIBSON, 1984). A shell is formed at the late trochophore stage and it gradually extends to cover a poorly developed prototroch (Figure 5). When released from the parent, the larvae are planktotrophic veligers (Figure 6) and have a mean length of  $144 \pm 3.9 \mu\text{m}$  SE ( $n = 15$ ). *Lasaea australis* prodissoconch morphology is typical of bivalves with planktotrophic development (OCKELMANN, 1965; CARRIKER & PALMER, 1979; WALLER, 1981; JABLONSKI & LUTZ, 1983; Ó FOIGHIL, 1986b). Newly metamorphosed juveniles possess an umbonate hinge line, a small prodissoconch-I (130–150  $\mu\text{m}$  in length) and have a mean length of  $249 \pm 19.6 \mu\text{m}$  SE ( $n = 10$ ), based on prodissoconch-II measurements.

Specimens brooding early embryos did not retain any residual vitellogenic oocytes in the gonad and had obviously just spawned as females. However, the testes of these individuals were usually full of mature sperm (7 out of 9 cases). These data imply that *Lasaea subviridis* is a sequential alternate hermaphrodite, although observations of actual spawnings are necessary to confirm this. Male allocation in *L. australis* is considerable, being roughly equal to female allocation in terms of gonadal volume. *Lasaea australis* sperm morphology at the light microscope level conforms to the "primitive" sperm type found in most externally fertilizing aquatic organisms (FRANZÉN, 1956; AFZELIUS, 1972). The sperm heads contain a fully condensed nucleus and are uniform in shape and size (Figure 7).

Table 1

Allelic frequencies of Long Reef *Lasaea australis* at the GPI locus.

Allele	Frequency $\pm$ 1 SE
82	0.0306 $\pm$ 0.0123
92	0.3367 $\pm$ 0.0337
100	0.3673 $\pm$ 0.0344
108	0.2449 $\pm$ 0.0307
114	0.0306 $\pm$ 0.0123

$N_e$  (effective number of alleles) = 3.225. Number of alleles screened = 196. Observed proportion of heterozygotes ( $H_o$ ) = 0.653. Expected proportion of heterozygotes ( $H_e$ ) = 0.690.  $D = -0.053$  when  $D = (H_o - H_e)/H_e$  (SELANDER, 1970).

GPI electromorphs from the 98 individuals analyzed for this enzyme consisted of either one or three bands (Figure 8), indicating that this enzyme has a dimer subunit structure in *Lasaea australis*. The protein phenotype combinations observed are consistent with the hypothesis that five distinct alleles segregating through a single locus were distinguished. Therefore, single-banded individuals were assumed to be homozygous and three-banded animals heterozygous at the GPI locus. Allele frequencies and genotype distributions are presented in Tables 1 and 2 respectively. The calculated  $D$  value (SELANDER, 1970) of  $-0.053$  is marginally less than the expected value of 0 and indicates that there is a slight deficiency of heterozygotes at the GPI locus. However, the observed allele combination frequencies do not differ significantly from random mating expectations ( $0.75 < P < 0.9$ ).

## DISCUSSION

*Lasaea australis* differs from all congeners studied to date in important features of its reproductive and developmental biology. The maintenance of a Hardy-Weinberg-Castle equilibrium at the GPI locus ( $0.75 < P < 0.9$ ) indicates that random mating occurs in the Long Reef population and provides the first evidence for cross-fertilization in this genus. Occasional self-fertilization by *L. australis* cannot be excluded; however, the observed GPI locus heterozygosity level of 0.653 suggests that, if it occurs, it is a rare event. Frequent self-fertilization would lead to a rapid drop in heterozygosity at all loci in the genome (SELANDER & KAUFMAN, 1973; BELL, 1982; BUCKLIN *et al.*, 1984).

Additional evidence for an amphimictic reproductive mode is provided by the large male allocation, approximately 50% of gonad volume, which is theoretically consistent with an outcrossing reproductive mode (HEATH, 1979; FISCHER, 1981; CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982). European (OLDFIELD, 1964; McGRATH & Ó FOIGHIL, 1986) and northeastern Pacific (Ó FOIGHIL, 1985a; BEAUCHAMP, 1986) *Lasaea* populations are composed of simultaneous hermaphrodites, the male allocation of which is approximately an

Table 2

Genotype distributions of the three most common GPI alleles of Long Reef *Lasaea australis*.

Genotype	Observed frequency	H-W-C expected frequency
92/92	11	11.110
92/100	26	24.239
92/108	13	16.162
100/100	14	13.221
100/108	13	17.631
108/108	9	5.878

$G = 0.88387$ ,  $df = 3$ ,  $0.75 < P < 0.9$  when  $G$  is the Log Likelihood Ratio.

order of magnitude smaller than that of *L. australis*. Sperm morphology is also different in *L. australis* in that sperm nuclei are fully condensed, resulting in a sperm head that is uniform in size and form. In European and northeastern Pacific *Lasaea* populations the degree of sperm nuclear condensation and the sperm head size and shape are variable (Ó FOIGHIL 1985a; McGRATH & Ó FOIGHIL, 1986).

Data from the present study on early development of *Lasaea australis* confirms ROBERT's (1984) description of this species as being larviparous. *Lasaea australis* differs in its developmental mode from congeners in Europe (OLDFIELD, 1964; SEED & O'CONNOR, 1980; McGRATH & Ó FOIGHIL, 1986), the northeastern Pacific (GLYNN, 1965; Ó FOIGHIL, 1986; BEAUCHAMP, 1986), Ascension Island (ROSEWATER, 1975), New Zealand (BOOTH, 1979), and Hawaii (KAY, 1979) in that it releases its young as straight-hinged planktotrophic veligers rather than as crawl-away juveniles. *Lasaea australis* has a correspondingly smaller egg size, greater fecundity, and assumes a benthic juvenile existence at a smaller size than congeners (McGRATH & Ó FOIGHIL, 1986).

The hinge structure of *Lasaea australis* is very similar to that of congeners from Victoria, B.C. (Canada), New Zealand, Japan, Florida, Britain, South Africa, and the Seychelles. Congeners, however, exhibit great individual variation in the degree of tooth development, especially that of the anterior laterals (Ó Foighil, unpublished data). This variation is much less pronounced in *L. australis*. *Lasaea australis* is readily distinguished from congeners by its larger size (up to 6 mm in valve length), presence of heavy concentric ridges on the external shell surface of some individuals, and smaller prodissoconch (PONDER, 1971).

Electrophoretic characterization of European (CRISP *et al.*, 1983) and northeastern Pacific (Ó FOIGHIL, 1986; Ó FOIGHIL & EERNISSE, unpublished data) populations has revealed a variety of non-hybridizing, sympatric strains to whom species rank cannot yet be assigned with certainty. The profound differences in reproduction, development, and population genetic structure between *Lasaea australis*

and its congeners, in addition to shell characteristics (PONDER, 1971), justify its ranking as a distinct species.

Available data on the population genetic structure, reproduction, and development of *Lasaea* reveal a prominent dichotomy between *L. australis* and European/northeastern Pacific populations (CRISP *et al.*, 1983; Ó FOIGHIL, 1986; Ó FOIGHIL & EERNISSE, in press). *Lasaea australis* is a randomly mating species with an obligate planktotrophic larval development. The other *Lasaea* populations are composed of frequently sympatric, reproductively isolated strains, with no evidence as yet for cross-fertilization, and brood to a crawl-away juvenile stage of development. This population genetic structure can result from a variety of reproductive modes, including prolonged autogamy and apomixis (BELL, 1982).

Northeastern Pacific *Lasaea* are simultaneous hermaphrodites (GLYNN, 1965; BEAUCHAMP, 1986) with minute male allocation, approximately 5% in terms of gonadal volume (Ó FOIGHIL, 1985a), and are capable of reproducing in isolation, apparently by self-fertilization (Ó FOIGHIL, 1987). Reduced male allocation in simultaneous hermaphrodites is a theoretical consequence of high degrees of autogamy (HEATH, 1979; FISCHER, 1981; CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982). Indeed, the population genetic structure of northeastern Pacific *Lasaea*, together with the ability to reproduce in isolation, a minute male allocation, and an apparent absence of specialized sperm transfer mechanisms typically found in cross-fertilizing brooding bivalves (*e.g.*, spermatophores and spermatozogma [COE, 1931; OCKELMANN & MUUS, 1978; Ó FOIGHIL, 1985b], dwarf and complementary males [TURNER & YAKOVLEV, 1983; Ó FOIGHIL, 1985c] and pseudocopulation [TOWNSLEY *et al.*, 1965]) imply that cross-fertilization may be a very rare event in northeastern Pacific *Lasaea* populations (Ó FOIGHIL, 1986a; Ó FOIGHIL & EERNISSE, unpublished data). The conclusion that northeastern Pacific *Lasaea* reproduce predominantly by autogamy (Ó FOIGHIL, 1986a, 1987; Ó FOIGHIL & EERNISSE, in press) is supported by the marked difference in their population genetic structure and male allocation to that of the predominantly amphimictic *L. australis*. An alternative, less parsimonious interpretation is that northeastern Pacific *Lasaea* engage in a combination of pseudogamy and meiotic parthenogenesis (Ó FOIGHIL, 1987). An analysis of the degree of male and female pronuclear interaction is necessary to distinguish between these two possibilities. European *Lasaea* populations are very similar in population genetic structure, male allocation, and presumably reproductive mode to northeastern Pacific *Lasaea* (OLDFIELD, 1961; CRISP *et al.*, 1983; McGRATH & Ó FOIGHIL, 1986).

A strong unidirectional bias exists in the transition between feeding and non-feeding larval development in marine invertebrates because loss of planktotrophy is usually accompanied by an extensive loss of larval feeding structures (STRATHMANN, 1978, 1985). OLDFIELD (1964) in-

terpreted the unciliated "cephalic mass" of *Lasaea rubra* embryos as a velum highly modified for yolk storage. Similar, though less developed, modifications in velar morphology are found in *Thyasira gouldi* and *Cardiomya pectinata* which lack feeding larvae (BLACKNELL & ANSELL, 1974; GUSTAFSON *et al.*, 1986). It is probable that the *Lasaea australis* developmental mode represents the primitive condition in the genus.

Loss of a dispersive life-history stage gives rise to philopatric dispersal patterns which can result in prolonged inbreeding (JACQUARD, 1975). A history of inbreeding predisposes populations to the development of autogamy by removing recessive deleterious alleles (CHARLESWORTH & CHARLESWORTH, 1981; CHARNOV, 1982; STRATHMANN *et al.*, 1984; UYENOYAMA, 1986). Self-fertile hermaphrodites with reduced male allocation appearing in these populations are then at a reproductive advantage because of their greater reproductive efficiency (MAYNARD SMITH, 1978; CHARNOV, 1982; STRATHMANN *et al.*, 1984). The model of STRATHMANN *et al.* (1984) for the evolution of self-fertile hermaphrodites in marine invertebrate brooders that release crawl-away young may apply to all *Lasaea* populations that brood to this ontogenic stage. Once evolved, a completely self-fertilizing reproductive mode may be irreversible owing to a genetic advantage resulting from the "cost of meiosis" (BULL & CHARNOV, 1985).

Although amphimixis has for a long time been regarded as a preadaptation to variable conditions, comparative evidence shows that alternative reproductive mechanisms, including autogamy and apomixis, predominate in harsh and disturbed environments (BELL, 1982). The small size, physiological toughness, and behavioral adaptations of European (BALLANTINE & MORTON, 1956; MORTON *et al.*, 1957; MORTON, 1960; DAVENPORT & BEARD, 1988) and northeastern Pacific (GLYNN, 1965) *Lasaea* enable them to survive in their upper intertidal habitat. Prominent theories concerning the evolution and persistence of amphimixis, such as the Tangled Bank (BELL, 1982) and the Red Queen (JAENIKE, 1978; BELL, 1982), stress its role in generating the genetic diversity necessary to endure in, and more fully exploit, biologically diverse environments. *Lasaea australis* not only differs from its congeners in reproductive mode, but also in habitat, occurring in the more biologically complex lower intertidal zone (ROBERTS, 1984).

A profound taxonomic dichotomy exists in the genus *Lasaea* that may have evolved as follows. Originally, the genus was composed of amphimictic hermaphrodites with an obligate planktotrophic larval development. To date, the only species known to retain this presumably ancestral condition is *L. australis*. Loss of a planktonic larva in some species led to the successful development of a self-fertilizing reproductive mode. It is not yet certain if self-fertilization has been maintained in northeastern Pacific populations, or if it has been replaced by a form of pseudogamy in which endogenous sperm trigger meiotic parthenogenesis. The absence of amphimixis has resulted in the formation

of a complex of non-hybridizing, often sympatric strains in at least northeastern Pacific (Ó FOIGHIL, 1986, Ó FOIGHIL & EERNISSE, in press) and probably in European (OLDFIELD, 1961; CRISP *et al.*, 1983; MCGRATH & Ó FOIGHIL, 1986) populations. Taxonomic relationships among *Lasaea* that lack a planktonic larva are still poorly understood, but are undoubtedly complex (PONDER, 1971; CRISP *et al.*, 1983; Ó FOIGHIL, 1986; Ó Foighil & Eernisse, unpublished data). Resolution of these relationships will require a multidisciplinary approach, applied to a variety of populations of this near-cosmopolitan genus.

#### ACKNOWLEDGMENTS

This study would not have been possible without the help of W. F. Ponder and P. H. Colman of the Australian Museum, for which I am very grateful. *Lasaea* specimens from New Zealand were kindly loaned by B. A. Marshall (National Museum of New Zealand), from Japan by J. H. McLean (Los Angeles County Museum of Natural History), from Florida by P. M. Mikkelsen (Indian River Coastal Zone Museum), from Britain by D. J. Eernisse (Museum of Zoology, University of Michigan), from South Africa by J. Pether (South African Museum), and from the Seychelles by J. D. Taylor and S. Morris (British Museum of Natural History). Financial support and research facilities were obtained through a Friday Harbor Laboratory Post-Doctoral Fellowship. Miles Paul kindly provided work space for writing, and early drafts were greatly improved by D. J. Eernisse, W. F. Ponder, R. G. B. Reid, P. Reynolds, D. McHugh, and two anonymous reviewers.

#### LITERATURE CITED

- AFZELIUS, B. A. 1972. Sperm morphology and fertilization biology. Pp. 131-143. In: R. A. Beatty & S. Gluecksohn-Waelsch (eds.), Proceedings of the international symposium on the genetics of the spermatozoon. Edinburgh University Genetics Department.
- BALLANTINE, D. & J. E. MORTON. 1956. Filtering, feeding and digestion in the lamellibranch *Lasaea rubra*. Jour. Mar. Biol. Assoc. U.K. 35:241-274.
- BARNARD, K. H. 1964. Contributions to the knowledge of South African marine Mollusca. Pt. 5. Lamellibranchiata. Ann. S. Afr. Mus. 47:361-593.
- BEAUCHAMP, K. A. 1985. The reproductive ecology of a brooding, hermaphroditic clam, *Lasaea subviridis*. M.Sc. Thesis, University of California, Santa Cruz. 59 pp.
- BEAUCHAMP, K. A. 1986. Reproductive ecology of the brooding, hermaphroditic clam, *Lasaea subviridis*. Mar. Biol. 93:225-235.
- BELL, G. 1982. The masterpiece of nature. Croom Helm: London. 635 pp.
- BERGER, E. M. 1983. Population genetics of marine gastropods and bivalves. Pp. 563-598. In: W. D. Russell-Hunter (ed.), The Mollusca. Vol. 6. Academic Press: New York.
- BLACKNELL, W. M. & A. D. ANSELL. 1974. The direct development of the bivalve *Thyasira gouldi* (Philippi). Thalassia Jugosl. 10:23-43.

- BOOTH, J. D. 1979. Common bivalve larvae from New Zealand: Leptonacea. N.Z. Jour. Mar. Freshwater Res. 13:241-254.
- BUCKLIN, A., D. HEDGECOCK & C. HAND. 1984. Genetic evidence of self-fertilization in the sea anemone *Epiactis prolifera*. Mar. Biol. 84:175-182.
- BULL, J. J. & E. L. CHARNOV. 1985. On irreversible evolution. Evolution 39:1149-1155.
- CARRIKER, M. R. & R. E. PALMER. 1979. Ultrastructural morphogenesis of prodissoconch and early dissoconch valves of the oyster *Crassostrea virginica*. Proc. Natl. Shellfish. Assoc. 69:103-128.
- CHANLEY, P. & M. H. CHANLEY. 1970. Larval development of the commensal clam *Montacuta percompressa* Dall. Proc. Malacol. Soc. Lond. 39:59-67.
- CHARLESWORTH, D. & B. CHARLESWORTH. 1981. Allocation of resources to male and female functions in hermaphrodites. Biol. Jour. Linn. Soc. 15:57-74.
- CHARNOV, E. L. 1982. The theory of sex allocation. Princeton University Press: Princeton. 355 pp.
- CHAVAN, A. 1969. Leptonacea Gray 1847. Pp. 518-537. In: R. C. Moore (ed.), Treatise on invertebrate paleontology. Pt. N. Mollusca (2). Geological Society of America and University of Kansas Press: Lawrence.
- COE, W. R. 1931. Spermatogenesis in the California oyster, *Ostrea lurida*. Biol. Bull. 61:309-315.
- CRISP, D. J., A. BURFITT, K. RODRIGUES & M. D. BUDD. 1983. *Lasaea rubra*: an apomictic bivalve. Mar. Biol. Lett. 4:281-294.
- DALL, W. H. 1900. Trans. Wagner Free Inst. Sci. 3(5):1163.
- DAUTZENBERG, P. 1929. Mollusca II. P. 378. In: A. Gruvel (ed.), Faune des Colonies Francaises. Vol. 3. Société d'Éditions Géographiques, Maritimes et Coloniales.
- DAVENPORT, J. & J. B. BEARD. 1988. Observations on the temperature and salinity relations of *L. rubra*. Jour. Mar. Biol. Assoc. U.K. 68:15-23.
- DELL, R. K. 1964. Antarctic and Subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Discovery Rept. 33:93-250.
- FINLAY, H. J. 1928. The recent Mollusca of the Chatham Islands. Trans. N.Z. Inst. 59:232-286.
- FISCHER, E. A. 1981. Sexual allocation in a simultaneously hermaphroditic coral reef fish. Amer. Natur. 117:64-82.
- GAGE, J. D. 1979. Mode of life and behaviour of *Montacuta phascolionis*, a bivalve commensal with the sipunculan *Phascolion strombi*. Jour. Mar. Biol. Assoc. U.K. 59:635-657.
- GLYNN, P. W. 1965. Community composition, structure and interrelationships in the marine intertidal *Endocladia muricata*-*Balanus glandula* association in Monterey Bay, California. Beaufortia 148:1-198.
- GUSTAFSON, R. G., D. Ó FOIGHIL & R. G. B. REID. 1986. Early ontogeny of the septibranch *Cardiomya pectinata* (Carpenter, 1865). Jour. Mar. Biol. Assoc. U.K. 66:943-950.
- HADERLIE, E. C. & D. P. ABBOTT. 1980. Bivalvia: the clams and their allies. Pp. 355-411. In: R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of California. Stanford University Press, Stanford.
- HEATH, D. J. 1979. Brooding and the evolution of hermaphroditism. Jour. Theor. Biol. 81:151-155.
- JABLONSKI, D. & R. A. LUTZ. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58:21-89.
- JACQUARD, A. 1975. Inbreeding: one word, several meanings. Theoret. Popul. Biol. 7:338-363.
- JAENIKE, J. 1978. An hypothesis to account for the maintenance of sex within populations. Evol. Theory 3:191-194.
- KAY, E. A. 1979. Hawaiian marine shells. Bernice P. Bishop Museum Press: Honolulu. 620 pp.
- KEEN, A. M. 1938. New pelecypod species of the genera *Lasaea* and *Crassinella*. Proc. Malacol. Soc. Lond. 23:18-32.
- LAMY, M. E. 1906. Liste des Lamellibranches recueillis par M. L. G. Seurat aux Iles Tuamotu et Gambier (1902-1905). Bull. Mus. Natl. d'Hist. Natur. 12:214.
- LANDE, R. & D. W. SCHEMSKE. 1985. The evolution of self-fertilization and inbreeding. I. Genetic models. Evolution 39:24-40.
- MAYNARD SMITH, J. 1978. The evolution of sex. Cambridge University Press: Cambridge, U.K. 222 pp.
- MCGRATH, D. & D. Ó FOIGHIL. 1986. Population dynamics and reproduction of hermaphroditic *Lasaea rubra*. Ophelia 25:209-219.
- MORTON, J. E. 1954. The crevice faunas of the upper intertidal zone at Wembury. Jour. Mar. Biol. Assoc. U.K. 39:5-26.
- MORTON, J. E. 1960. The responses and orientation of the bivalve *Lasaea rubra* (Montagu). Jour. Mar. Biol. Assoc. U.K. 36:383-405.
- MORTON, J. E., A. D. BONEY & E. D. S. CORNER. 1957. The adaptations of *Lasaea rubra* (Montagu), a small intertidal lamellibranch. Jour. Mar. Biol. Assoc. U.K., 36:383-405.
- OCKELMANN, K. W. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. Pp. 25-35. In: L. R. Cox & J. F. Peake (eds.), Proceedings of the first European malacological congress. Conchological Society of Great Britain and Ireland, and Malacological Society of London.
- OCKELMANN, K. W. & K. MUUS. 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata*. Ophelia 2:211-221.
- Ó FOIGHIL, D. 1985a. Fine structure of *Lasaea subviridis* and *Mysella tumida* sperm. (Bivalvia: Galeommatacea). Zoomorphology 105:125-135.
- Ó FOIGHIL, D. 1985b. Sperm transfer and storage in the brooding bivalve *Mysella tumida*. Biol. Bull. 169:602-614.
- Ó FOIGHIL, D. 1985c. Form, function, and origin of temporary dwarf males in *Pseudopythina rugifera* (Bivalvia: Galeommatacea). Veliger 27:72-80.
- Ó FOIGHIL, D. 1986a. Reproductive modes and their consequences in three galeommatacean clams: *Mysella tumida*, *Pseudopythina rugifera* and *Lasaea subviridis* (Mollusca: Bivalvia). Ph.D. Thesis, University of Victoria. 256 pp.
- Ó FOIGHIL, D. 1986b. Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis*. Mar. Biol. 92:517-524.
- Ó FOIGHIL, D. 1987. Cytological evidence for self-fertilization in the brooding bivalve *Lasaea subviridis*. Int. Jour. Invert. Reprod. Dev. 12:83-90.
- Ó FOIGHIL, D. & D. J. EERNISSE. 1987. Phosphoglucosylase allozyme evidence for an outcrossing reproductive mode in the hermaphroditic, brooding bivalve *Mysella tumida*. Jour. Moll. Stud. 53:223-228.
- Ó FOIGHIL, D. & D. J. EERNISSE. In press. Geographically widespread, non-hybridizing, sympatric strains of the hermaphroditic, brooding clam *Lasaea* in the northeastern Pacific Ocean. Biol. Bull.
- Ó FOIGHIL, D. & A. GIBSON. 1984. The morphology, reproduction and ecology of the commensal bivalve *Scintillona bellerophon* spec. nov. (Galeommatacea). Veliger 27:72-80.
- OLDFIELD, E. 1961. The functional morphology of *Kellia suborbicularis* (Montagu), *Montacuta ferruginosa* (Montagu) and *M. substriata* (Montagu) (Mollusca; Lamellibranchiata). Proc. Malacol. Soc. Lond. 34:255-295.
- OLDFIELD, E. 1964. The reproduction and development of some

- members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). Proc. Malacol. Soc. Lond. 36:79-120.
- PONDER, W. F. 1971. Some New Zealand and subantarctic bivalves of the Cyamiacea and Leptonacea with descriptions of new taxa. Rec. Dom. Mus. N.Z. 7:119-141.
- ROBERTS, D. 1984. A comparative study of *Lasaea australis*, *Vulsella spongarium*, *Pinna bicolor* and *Donacilla cuneata* (Mollusca: Bivalvia) from Princess Royal Harbor, Western Australia. Jour. Moll. Stud. 59:129-136.
- ROSEWATER, J. 1975. An annotated list of the marine mollusks of Ascension Island, South Atlantic Ocean. Smithsonian Contrib. Zool. 189:41 pp.
- SEED, R. & R. J. O'CONNOR. 1980. Shell shape and seasonal changes in population structure in *Lasaea rubra* (Bivalvia: Erycinidae). Jour. Moll. Stud. 46:66-73.
- SELANDER, R. K. 1970. Behaviour and genetic variation in natural populations. Amer. Zool. 10:53-66.
- SELANDER, R. K. & D. W. KAUFMAN. 1973. Self-fertilization and genetic population structure in a colonizing land snail. Proc. Natl. Acad. Sci. U.S. 70:1186-1190.
- SOOT-RYEN, T. 1960. Pelecypods from Tristan da Cunha. Res. Nor. Sci. Exped. Tristan da Cunha 49:1-47.
- STRATHMANN, R. R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution 32:894-906.
- STRATHMANN, R. R. 1985. Feeding and non-feeding larval development and life history evolution in marine invertebrates. Ann. Rev. Ecol. Syst. 16:339-361.
- STRATHMANN, R. R., M. F. STRATHMANN & R. H. EMPSON. 1984. Does brood capacity link adult size, brooding, and simultaneous hermaphroditism? A test with the starfish *Asterina phylactica*. Amer. Natur. 123:796-818.
- TOWNSLEY, P. M., R. A. RICKEY & P. C. TRUSSEL. 1965. The laboratory rearing of the shipworm *Bankia setacea* (Tyron). Proc. Natl. Shellfish. Assoc. 56:49-52.
- TRACEY, M. L., K. NELSON, D. HEDGECOCK, R. A. SCHLESSER & M. L. PRESSICK. 1975. Biochemical genetics of lobsters: genetic variation and the structure of the American lobster (*Homarus americanus*) populations. Jour. Fish. Res. Bd. Canada 32:2091-2101.
- TURNER, R. D. & Y. M. YAKOVLEV. 1983. Dwarf males in the Teredinidae (Bivalvia: Pholadacea). Science 219:1077-1078.
- UYENOYAMA, M. K. 1986. Inbreeding and the cost of meiosis: the evolution of selfing in populations practicing biparental inbreeding. Evolution 40:388-408.
- WALLER, T. R. 1981. Functional morphology and development of veliger larvae of the European oyster *Ostrea edulis* Linné. Smithsonian Contrib. Zool. 328:70 pp.