Ecology of the pterioid bivalves *Pinna bicolor* Gmelin and *Pinna nobilis* L.

Écologie des mollusques bivalves pterioides Pinna bicolor *Gmelin et* Pinna nobilis *L.*

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ABSTRACT

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Pinna nobilis *L. is considered a threatened species in the Mediterranean and there is some local pressure on* Pinna bicolor *Gmelin in South Australia. We examine and compare existing data on the ecology of these species, and suggest topics for future research. It is argued that the life-history pattern of both these species is one of long life and limited reproductive investment, with the result that recruitment is sporadic, population dynamics depend on the "storage effect", and natural populations will not survive heavy exploitation. A hatchery program would be essential for any sustainable exploitation of* Pinna.

RÉSUMÉ

Butler Alan, N. Vicente, B. de Gaulejac, 1993 - [Écologie des mollusques bivalves pterioides Pinna bicolor *Gmelin et* Pinna nobilis *L.] Mar. Life 3 (1-2) : 37 - 45*

Pinna nobilis *L. est considérée comme une espèce menacée en Méditerranée et* Pinna bicolor *Gmelin subit une certaine pression en Australie du Sud. Nous présentons les données actuelles sur l'écologie des deux espèces et nous suggérons des axes de recherche pour l'avenir. Il est envisagé que les stratégies des deux espèces concernent une vie de longue durée et des capacités reproductrices limitées ayant pour conséquence un recrutement sporadique. La dynamique des populations est dépendante de "l'effet d'approvisionnement", et les populations naturelles ne peuvent survivre à une agression et à une exploitation intenses. Un programme d'élevage serait essentiel pour la survie et l'exploitation des populations de* Pinna.

INTRODUCTION

Bivalve molluscs have long featured in studies of physiological ecology (e.g. Bayne, 1976 ; Bayne and Newell, 1983) because of their experimental tractability and commercial interest. They continue to attract interest in the context of more recent developments in functional ecology, and its interactions with evolution and with practical environmental problems. Thus for example they are prominent in the volume on environmental stress edited by Calow and Berry (1989).

Members of the family Pinnidae have not been the subject of major ecological or physiological research programmes, although some such work has been done on *Pinna nobilis* in the Mediterranean (Combelles, 1984 ; Combelles *et al.*, 1986 ; de Gaulejac, 1989, 1993 ; de Gaulejac and Vicente, 1990 ; Moreteau and Vicente, 1980, 1982 ; Vicente *et al.*, 1980, 1989 ; Vicente, 1990 ; Vicente and Moreteau, 1991) and some on *Pinna bicolor* (Butler, 1987 ; Butler and Brewster, 1979 ; Butler and Keough, 1981 ; Rosewater, 1961 ; Scheltema, 1983 ; Scheltema and Williams, 1983). They are anatomically extreme bivalves (Yonge, 1953), large in size and having a great posterior extension of the mantle, shell and gills which protrudes above the sediment in the animal's normal habit. This invites speculation about their life-history patterns, the kind of environment to which they are adapted and the effects of environmental changes upon them.

Possible environmental changes include increased fishing pressure (including collection for bait or as souvenirs), entry of toxins into the habitat, sedimentation due to dredging and shore works, changes in seawater temperature, and alterations to current patterns and to the environment of the larvae which may change recruitment patterns. Other, more subtle changes are also possible.

In this paper we summarise existing data about the ecology of two species of *Pinna*, namely *Pinna bicolor* Gmelin in South Australia and *Pinna nobilis* L. in the Mediterranean. We make some suggestions about the kinds of "tradeoffs" likely in the evolution of the life-history pattern of this particular form of bivalve, and indicate the data needed for testing these ideas.

We conclude tentatively that *Pinna* may be a relatively stress-tolerant form of bivalve mollusc, adapted to a nutrient-poor environment, and committed to a strategy of long adult life and relatively small investment in reproduction. If so, it is especially vulnerable to over-exploitation.

THE ECOLOGY OF *PINNA NOBILIS* AND *PINNA BICOLOR*

The family Pinnidae is a tropical and subtropical family, only a few species ocurring in temperate zones. *Pinna bicolor* is widely-distributed in the Indo-Pacific, from the equator to the latitudes of Hawaii and southern Australia. Published work on its ecology comes from the warm temperate zone of southern Australia and the following remarks refer to that area (Rosewater, 1961 ; Shepherd and Sprigg, 1976 ; Butler and Brewster, 1979 ; Butler and Keough, 1981). It occurs from the intertidal to 20 m, but is locally patchy ; typical densities are 2-5m^{-2}. *P. nobilis* is only recorded from the Mediterranean, at depths of 0.5 to 60 m. It too is locally patchy ; a typical density is 0.01m^{-2},

but densities up to 4-6m^{-2} have been recorded (Combelles *et al.*, 1986 ; de Gaulejac, Vicente, 1990 ; de Gaulejac, 1993). The two species occur in similar physical conditions. Where *P. bicolor* has been most studied, water temperature is seasonal, ranging from 10-23°C ; salinity ranges from 35-42‰, the water is generally clear, though turbid after rough weather, and concentrations of nutrients are considered to be generally low (Rochford, 1980). We have little information about conditions in other parts of its range, but temperatures in the tropics are certainly higher. For *P. nobilis*, water temperature ranges from 7-28°C, salinity *ca.* 34-40‰ ; the water is generally clear (Zavodnik, 1967 ; Zavodnik *et al.*, 1991) ; nutrient concentrations are poorly documented. Both species live in sites with only slight water movement.

Both species reach sexual maturity at a young age ; *P. bicolor* by 1+ yr (Butler, 1987) and *P. nobilis* by 1-2 yr (de Gaulejac, 1993). They both display seasonal gonad maturation (spring-summer) and in *P. nobilis* there can be numerous, successive spawnings (Butler and Keough, 1981 ; Butler, 1987 ; Combelles *et al.*, 1986 ; de Gaulejac, 1989 ; de Gaulejac, 1993 ; Roberts, 1984). Reproductive effort is unstudied ; quantitative data on gonad mass or egg number relative to body size are difficult to obtain in these species, but it is obvious visually that the fully-developed gonad makes a smaller proportion of the tissue than in, e.g., oysters or scallops.

Pinna have external fertilization. For a spawning animal the chances of successful fertilization must depend on the proximity of other *Pinna* spawning at the same time, as well as on other factors, especially water movement (Denny, 1988 ; Levitan *et al.*, 1992). We have no data on fertilisation success for *Pinna*, but it seems likely that failure of fertilization would be a significant problem when a population becomes very sparse, as is the case for some of those in the Mediterranean.

Following fertilization, a veliger larva develops. It will presumably be denser than water and will sink unless it swims actively. Many Pinnidae, including *P. bicolor*, have teleplanic larvae, capable of being transported on long distances (Scheltema, 1977 ; Scheltema and Williams, 1983), but this does not imply that they always are. De Gaulejac (1989) suggested from electron microscopic observations of the larval shell that the duration of larval life in *P. nobilis* may be of the order of 5 to 10 days. Even with a longer larval period, larval behaviour could limit the distance travelled by larvae (e.g. Butman, 1987 ; Cronin and Forward, 1986 ; Knowlton and Keller, 1986).

Clearly from our observations on both species, *Pinna* must be understood as existing in metapopulations (i.e., patchy systems with more or less dispersal between patches ; Sinclair, 1988). In such a system the nature of the dispersal between

patches is crucial to understanding the dynamics within any patch as well as that of the whole population system (e.g., Johnson and Black, 1991 ; Mc Shane and Smith, 1991 ; Todd *et al.*, 1988 ; Watts *et al.*, 1990). If the planktonic period is short in *P. nobilis* (de Gaulejac, 1989), then separate stands may be relatively isolated and a depleted bed of *P. nobilis* may not easily be recolonised. In order to understand population dynamics it would be valuable to have further information on effective dispersal distances, not merely as maxima or means, but as frequency distributions. This is not easy to obtain in the tideless Mediterranean where currents are not necessarily consistent through time, but at certain sites a relationship between the locations of adults and recruits might be sought. There is a principal current (the Ligure) running from east to west along the coast of Provence as far as the mouth of the Rhône, where it turns offshore. Although there are local, contrary currents, and variations dependent upon meteorological conditions, it is possible that the distribution of adults and recruits can be assessed relative to this predominant east-west current. The larvae of other Pinnidae, including *P. bicolor*, are teleplanic (Scheltema, 1977 ; Scheltema and Williams, 1983). In South Australia, however, preliminary data on allozyme frequencies in *P. bicolor* (C. Chesson and A. Butler, unpublished data) suggest differences between subpopulations even within the Gulf of St Vincent ; thus, effective dispersal of *P. bicolor* may be more limited than suggested by its long larval period. Further work on population genetics of this species is planned in conjunction with studies of hydrology in the Gulf and studies of larval behaviour (cf. the efforts to understand outbreaks of crown-of-thorns starfish on the Great Barrier Reef ; Johnson, 1992 and other papers in the same issue).

In addition to dispersal itself, the feeding and mortality of larvae is of importance, and virtually unknown in Pinnidae. Food supply may be crucial for a planktotrophic larva and, in the habitats of both *P. nobilis* and *P. bicolor*, the waters are noted for being clear ; nutrients are limited and plankton generally not dense (Rochford, 1980 ; GESAMP, 1990). There are, however, variations in plankton density, and these may be important in determining the survival of larvae.

Thus, a combination of limited, irregular dispersal and variable larval survival may explain what we do clearly know for both species, namely that recruitment to local populations is highly variable (Butler and Keough, 1981 ; Combelles *et al.*, 1986 ; Vicente *et al.*, 1980 ; de Gaulejac, 1993). Further studies of the planktonic stages of *Pinna* will be rewarding. These studies will not be easy (Levin, 1990) and may require indirect approaches, such as (1) estimating the correlations of physical conditions and plankton blooms with recruitment of *Pinna* and (2) estimating the gene flow between populations using allozymes or DNA techniques.

Small juveniles of both species are found in sand (the adult habitat), commonly in or near seagrass beds. The competent *Pinna* larva presumably settles in sand ; we have never found any evidence of a two-stage recruitment like that reported for *Mytilus*, with primary settlement to one type of substratum and subsequent movement to another. Vicente *et al.* (1980) did argue for movement of juvenile *P. nobilis* from shallow into deeper water as they grow, but these were benthic, byssally-attached animals large enough to be tagged by investigators. Some capacity for movement is evident at this age ; Vicente (unpublished observations between 1975 and 1986) has seen adult animals lying on the sand and later discovered them re-established in the normal position as far as 1-3 m from their original location. Most juvenile and adult *Pinna* are, however, quite sessile.

Soon after settlement, the new benthic *Pinna* is extremely small and fragile. At settlement the postlarva is a little over 1 mm in length ; even at 1-2 cm the shell is very fragile and the attachment weak. At this stage the animals are vulnerable to a range of risks, including those of being ingested by deposit feeders such as holothurians, of being eaten by predators such as naticid gastropods, octopods, asteroids and fish (e.g. *Sparus auratus* in France), and of being unable to feed effectively because of movement of the sediment or (as for the planktonic larvae) because the supply of suspended food is too dilute. Water movement in the boundary layer close to the sediment is slight even in a high-current area. The nutrition of very small benthic *Pinna* is unknown. It may involve elements of deposit feeding (cf. Thiesen, 1972 for *Mytilus edulis*). The ability to absorb dissolved organic matter (DOM) may also be important, but is unstudied in this genus, and needs much further investigation for suspension-feeders generally (Okamura, 1990).

We know most about the animal from juvenile through adult stages, and it is these stages that will mainly be discussed below. Survivors of the early benthic stages, beyond a shell length of about 2 cm in *P. bicolor* and 5 cm in *P. nobilis*, grow rapidly (Butler and Brewster, 1979 ; Butler, 1987 ; Moreteau and Vicente, 1982 ; de Gaulejac, 1993), but they are typically about 10 cm in shell length before the posterior gape of the shell is significantly elevated above the surface of the sediment. After this stage, they can begin to adopt the adult "strategy" which we discuss below. The shell increases rapidly in length and thickens. Growth of *P. bicolor* is indeterminate, rapid when small and slow after 2 yr, and can be approximated by a seasonally-adjusted von Bertalanffy growth curve (Butler and Brewster, 1979 ; Butler, 1987 ; Roberts, 1984). Maximum length (*ca.* 45 cm) is approached after 4-7 yr. Growth of *P. nobilis* has similar properties, but with a greater maximum length (85 cm), approached after 12-15 yr

(Moreteau and Vicente, 1980, 1982 ; de Gaulejac, 1993).

Longevity is up to 18 yr in *P. bicolor*, with the rate of mortality approximately constant after 2 yr (Butler, 1987). It is possibly about the same (20 yr) in *P. nobilis* but the evidence is less detailed ; mortality in this species probably decreases with age (Combelles *et al.*, 1986 ; Vicente *et al.* 1980 ; de Gaulejac, 1993). Over a period of two or more years the animal becomes much less vulnerable to many of its enemies than the tiny juvenile, although once again we have only limited data. For instance, Butler (1987) recorded no attacks by naticid gastropods on *P. bicolor* above 29.3 cm in length and Vicente (unpublished observations), no attacks by octopus on *P. nobilis* above 20 cm. Adults do harbour macroscopic commensals or parasites, the effect of which is unknown. None have been definitely recorded from South Australia but they are known in *P. bicolor* in the tropics (Butler, 1987 ; Hipeau-Jacquotte, 1974). *P. nobilis* harbours Pinnotheridae (Zavodnik *et al.*, 1991). An unidentified microscopic parasite has been recorded as causing castration of *P. nobilis* (de Gaulejac, 1993).

Other aspects that have been studied include the following. There is a tendency to be oriented with the currents at some sites (Butler, unpublished data ; Combelles *et al.*, 1986 ; Vicente *et al.*, 1989). Shell morphology varies with age and perhaps between populations ; the spines are variable, more pronounced in the young and, in *P. nobilis*, less in seagrass than open habitats (Butler and Brewster, 1979 ; Butler, unpublished data ; Vicente *et al.*, 1980 ; Combelles *et al.*, 1986). The epibiota of the shell has been recorded by Butler and Brewster (1979), Keough and Butler (1983), Escoubet (unpublished observations), Zavodnik (1967), Corriero and Pronzato (1985) and especially by Keough (1984a, b ; Kay and Keough, 1981 ; Keough and Butler 1983), who used the epibiota of *P. bicolor* as a model system to study the ecology of patchy habitats. The depauperation of the epifauna of *P. bicolor* associated with heavy metals was studied by Ward and Young (1983). Harmelin (1977) examined the cryptofauna of dead shells of *P. nobilis*. In the same species, renal concretions were studied by Hignette (1978) and Lucas and Hignette (1983), and shell ultrastructure by Cuif *et al.* (1980, 1983, 1985) and Cuif and Raguideau (1982).

TRADEOFFS IN THE LIFE-HISTORY OF *PINNA*

Amongst bivalves, *Pinna* are large and long-lived, though not exceptionally so (Heller, 1990). Long life necessitates maintenance and defence. There are no data on the costs of this but little doubt (Sibly and Calow, 1989) that there must be costs associated with the outstanding ability of *Pinna* to clean the inside of the mantle cavity, and to repair the shell after damage (Stenta, 1927 ; Yonge, 1953 ; Butler unpublished observations). For feeding, access to the water column is necessary ; feeding must be much less efficient whilst the animal is small and confined to the boundary layer. It is thus advantageous that *Pinna* grows very rapidly when young. Both points suggest a tradeoff - the cost of rapid growth when young and rapid repair at any age might be a reduction in the number of gametes produced. This, coupled with the considerable difficulties of life for a larva and a newly-settled juvenile, may account for the sporadic recruitment in both species.

It is, however, difficult to estimate the costs involved, especially since their realistic assessment must consider the extreme variability in the environment ; occasionally, conditions may be good for both the feeding of the adults and the survival of the young, and those events may lead to a good recruitment which supports the population for a long time by the "storage effect" (Chesson, 1986 ; Butler, 1987). Finally, variations in physical conditions could be very important because of their effect on the metabolism of the animals, and on key processes such as calcification in the shell. A program of assessment of the energetic tradeoffs of *Pinna* in a proper ecological context must therefore be a long-term one, or a shorter-term physiological study linked to long-term data on productivity, meteorological conditions and hydrological processes.

The scarcity of nutrients in these waters is not uniform. Nutrient enrichment, localized in space and/or time (Shepherd *et al.*, 1989 ; Vicente, 1983 ; GESAMP, 1990) is of particular interest in the present context but its effects unstudied. In addition, if the nutrition of the animals depends partly on detritus, either *via* particulate matter or *via* dissolved organic matter, then weather conditions that suspend that detritus may be important in their population dynamics (e.g. Cranford and Grant, 1990 ; Frechette and Grant, 1991).

It has been postulated that animals that have to survive periods of stress, such as periods of poor nutrition, may be characterised by a low metabolic rate (Hoffman and Parsons, 1989, 1991), and we have begun to investigate this in *Pinna* (Vicente *et al.*, 1991 and unpublished data). Rates of oxygen consumption appear to be similar in the two species after correction for size and temperature, and *Pinna* appears not to be exceptional amongst bivalves. This cannot, however, be concluded with confidence because of the great variability in the measurements. We are now seeking greater precision, especially by improving field measurements of oxygen consumption.

The behaviour of both species of *Pinna* at low oxygen tensions appears similar, and is significant in the present context. Both remain

active at low oxygen concentrations. Although resistance to anoxia is common in bivalves, the nature of their responses varies ; some drop to a low metabolic rate but some can maintain a high, anaerobic activity in such conditions (De Zwaan and Putzer, 1985 ; Doeller *et al.*, 1990 ; Pamatmat, 1980 ; Shumway *et al.*, 1983). To remain active may be part of the strategy of an animal which does not normally experience conditions of very low oxygen tensions in its natural habitat, but on the other hand *is* adapted to conditions of low nutrients, where continuous feeding is necessary. Our preliminary data indicate that oxygen consumption decreases as the ambient oxygen concentration decreases, but this would be expected simply from the change in partial pressure gradient between the water and the haemolymph, unless the animal made special effort to keep its consumption up, e.g. by pumping more blood. The significant point is that neither species appears to stop pumping, nor to respire anaerobically. They open the shell extremely widely at low oxygen concentrations but there is no information on filtration then.

Indeed, the filtration of *Pinna* in general is an open research field. The relatively large (Yonge, 1953 ; Yonge and Thompson, 1976) water transporting and filtering structures of *Pinna* are arguably dimensioned for generally low densities of food in water (Jorgensen, 1966, 1975). Both *P. nobilis* and *P. bicolor* have been observed open and actively pumping both day and night, except when disturbed or when the tide is out. This would again be consistent with the hypothesis that food is not superabundant and continuous filtering is adaptive (the metabolic cost of pumping not being great; Bernard and Noakes, 1990). Not all bivalves filter continuously nor at constant rates and it would be valuable to determine whether *Pinna* vary their feeding currents (Okamura, 1990 ; Wildish and Miyares, 1990). Okamura (1990) raises the question of whether feeding modes or techniques vary in ontogeny ; this could be important in *Pinna*, which grows from a tiny newly-settled juvenile (embedded in sand and certainly within any boundary layer, perhaps necessarily a deposit feeder, and perhaps gaining substantially from absorption of DOM) to a large fan reaching far enough above the seafloor for water movement to aid feeding by induced flow.

Pinna lacks siphons ; it is of "mussel" form, having an open pallial cavity but with the inhalent and exhalent chambers completely separated by eulamellibranch gills. The advantage of siphons, which enable suspension feeding by an infaunal bivalve, is achieved in *Pinna* by the large posterior extension of the shell and mantle cavity ; about half the length of a *Pinna* shell is essentially a pair of wide "siphons", supported and protected by shell and therefore able to protrude above the sediment. In view of the results of Bernard and Noakes (1990),

one might expect *Pinna*, with its open mantle cavity, to be able to maintain a fairly high pumping rate without as high an energetic cost as would be incurred if it had siphons. The price of the open mantle cavity, of course, is vulnerability to the entry of sediment. This disadvantage is met in *Pinna* by growing above the level of the sediment as it gets larger and by having specialized adaptations for cleaning both chambers of the mantle cavity (Yonge, 1953 ; Yonge and Thompson, 1976), but there must be some cost for these adaptations, and indeed *Pinna* is absent from areas of severe disturbance of the sediment where only siphonate, infaunal bivalves occur.

The possible effects of living amongst seagrass beds in *Pinna* will repay investigation. Seagrass may reduce predation on young animals, but on the other hand may baffle water currents, thus reducing their feeding. Peterson *et al.* (1984) found that growth of *Mercenaria* was greater in seagrass beds than in sandy bottom outside the beds, but Coen and Heck (1991) showed that this was due to the reduction of siphon-nipping by predators (which depresses growth) inside the seagrass bed ; the seagrass itself actually had a depressing effect on growth, due to reduced water movement. On the other hand, the baffling effect may be advantageous if *Pinna* should in fact need relatively low ambient currents, as in *Placopecten* (Wildish *et al.*, 1987, 1992 found that its feeding was inhibited at flows greater than 10-20 cm.s^{-1} but that scallops would persist in feeding at higher flow velocities if food concentrations were higher). In *P. nobilis*, recruitment has most often been observed in association with seagrass beds, whereas recruits of *P. bicolor* have been found in both habitats but most commonly in bare sand. Relationships with seagrass should be further studied ; they will be complex and will need multifactorial experimental investigation (Peterson and Beal, 1989).

Nutrition of benthic stages and/or survival and rate of development of larvae may be influenced both by hydrodynamic resuspension of organic detritus into the water column and by nutrient levels in the water and their effects on plankton populations ; these hypotheses are an exciting area for investigation (e.g. Beukema and Cadee, 1991 ; Jensen, 1990 on bivalves ; Qian and Chia, 1990 on polychaete larvae ; and Brodie, 1992 on crown-of-thorns starfish on the Great Barrier Reef).

The limitation of dispersal, and the variability of recruitment, may possibly be greater in *P. nobilis* than in *P. bicolor* due to differences in their larvae ; it is tempting to speculate that this is compensated for, in the former species, by a greater average longevity, greater maximum size, and thus a greater average lifetime larval production (cf. King and Butler, 1985). This, however, begs the question - what leads to the difference in growth rate and size ? Realised size and longevity certainly vary in

both species (Butler, 1987 ; de Gaulejac, 1993). We need more information as to whether these differences are purely environmental, as a result of differences in food supply, temperature, etc., or whether there is a genetic component. The same question can be asked about the differences between the two species. The variations within each species can be studied by either transplant experiments (cf. Kautsky *et al.*, 1990) or growth under controlled conditions ; for the comparison between the species, the latter is the only method.

MANAGEMENT OF *PINNA* POPULATIONS UNDER EXPLOITATION

We have suggested above that, on present evidence, both species appear to be committed to a life-history in which a relatively great proportion of the animal's resources are devoted to maintaining adult survival and relatively little to reproduction. Recruitment is strong in embayments where, presumably, a high proportion of larvae are entrapped (e.g., *P. nobilis* in l'étang de Diana (Corsica), de Gaulejac, 1993 ; *P. bicolor* in Streaky Bay, South Australia, M.J. Keough and A.J. Butler, pers. obs., and cf. Mc Killup *et al.*, 1993) but otherwise it is weak and variable compared with other bivalves *in the same locations* (e.g. pectinids and other pterioids). An important consequence is that human activities which shorten adult life cannot be compensated for by an immediate response of the population.

Such a response is classically assumed in models used for fisheries management, and is supposed to arise because some kind of pressure on recruitment is lifted by the removal of adults. There is no evidence for that in either species of *Pinna* and it is no surprise that *P. nobilis* has become rare in much of the Mediterranean (Vicente, 1990 ; Vicente and Moreteau, 1991) and *P. bicolor* locally depleted in heavily-collected sites in South Australia (Butler, unpublished obs.). Note also that exploitation will have the effect of removing that part of the adult population that is now relatively invulnerable to predators (the large individuals). Thus, it is plausible that *Pinna* simply cannot adapt to a rise in adult mortality. If so, then any proposal to raise its adult mortality *must* be accompanied by an equally effective means of raising recruitment both locally and globally ; any proposal to exploit *Pinna* must be accompanied by an effective hatchery and reseeding programme.

CONCLUSION

On present evidence the two species are strikingly similar in ecology and physiology, excepting the faster growth and larger maximum size of *Pinna nobilis*. However, the existing data are imprecise, and it remains unclear why even this difference between the species should occur ; better data are needed on metabolism, nutrition and physical conditions in the field.

We have outlined above many lines of future research, especially concerning the life-history strategy of *Pinna*. We have suggested as a working hypothesis that it is "stress-tolerant" - slow-growing, not producing large numbers of offspring, and having population dynamics dependent upon the storage effect, i.e. a highly variable recruitment compensated for by long adult life.

Whilst these ideas are plausible, it will be difficult to test some aspects of them because the conceptual model being proposed is characterised by variability ; it is *a priori* a long-term pattern in which temporal and spatial fluctuations and rare events are crucially important. Some predictions are, however, testable, and there are consequences for management.

There are other successful "strategies" for the bivalve body-plan in the habitats where *Pinna* occurs ; for example, the pterioid *Malleus meridianus* Cotton is abundant in the South Australian Gulfs. It grows to a smaller size than *P. bicolor*, and recruits more densely and regularly (Butler, unpublished data) ; but it is characteristic of hard substrata, not living in sandy bottoms ; thus it may avoid the disadvantages of living as a very small juvenile in the boundary layer. Detailed comparisons of such life-history patterns would be instructive.

ACKNOWLEDGEMENTS

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