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Inter- and Intraspecific Patterns of Reproductive Effort in Four Species of Cone Shells (*Conus* spp.)

F. E. Perron *

Pacific Biomedical Research Center; 41 Ahui Street, Honolulu, Hawaii 96813, USA

Abstract

Patterns of reproductive effort were examined both within and between 4 species of the tropical marine gastropod genus *Conus* from Hawaii in 1979. Caloric content was measured for the somatic tissues of female cone shells and for their egg capsule masses. These data were used to calculate (1) current reproductive effort, which was the ratio of annual energy produced as spawn to the sum of the annual energy produced as spawn plus the annual energy produced as somatic tissue; and (2) weight-specific reproductive effort, which was the ratio of annual energy produced as spawn to the total energy content of the female body just before spawning. For *C. pennaceus*, during the approximately 10 yr of life of a female, current reproductive effort rose from about 0.35 at 2 yr to about 0.85 at 10 yr. In contrast, weight-specific reproductive effort remained relatively constant throughout life for *C. pennaceus* (about 0.2 to 0.5), *C. abbreviatus* (about 0.2 to 0.3), *C. flavidus* (about 0.2 to 0.3) and *C. quercinus* (about 0.1 to 0.2). It is suggested that weight-specific reproductive effort may be useful as an index of the selective importance of the survival cost of present reproduction, while current reproductive effort more closely reflects the selective importance of energy allocation tradeoffs. Data on the 4 species of *Conus* examined support the hypothesis that reproductive effort should be positively correlated with extrinsic adult mortality and negatively correlated with the variability of juvenile survivorship. The data also suggest a possible relationship between reproductive effort and the cost of parental care.

Introduction

The costs and profits of such life history characteristics as growth and fecundity have frequently been evaluated in terms of the common currency of energy (Vance, 1973; Todd, 1979). The proportion of an organism's energy budget that is devoted to reproduction is termed the reproductive effort (Fisher, 1930). Reproductive effort may vary markedly from one species to the next and, within a given iteroparous species, may depend on an individual's age.

Comparative studies on reproductive effort within groups of closely related species can be instructive. For marine prosobranch gastropods, such comparisons have been made for muricids (Spight and Emlen, 1976) and for littorinids (Grahame, 1977; Hughes and Roberts, 1980). The genus *Conus* contains over 500 living species, and is thus especially favorable for interspecific comparisons of reproductive effort.

The present study includes an examination of age-specific reproductive effort in the marine gastropod *Conus pennaceus*, and a comparative analysis of reproductive effort in *C. pennaceus, C. quercinus, C. abbreviatus* and *C. flavidus*. The latter three species are ecologically similar in that they all have small diameter eggs (170 to 190 μm) and long-term planktotrophic larvae (Perron, 1981 a). *C. pennaceus*, on the other hand, produces large eggs (500 μm) which develop into non-pelagic lecithotrophic larvae (Perron, 1981 a). Other differences between these species will be discussed in relation to differences in levels of reproductive effort. All species of *Conus* are dioecous and probably reproduce annually during relatively long lifetimes.

The present study not only contributes to our knowledge of the important genus *Conus*, but also provides a basis for testing current ideas on the evolution of life history patterns (as reviewed by Stearns, 1976, 1980). If natural selection moulds life histories so as to maximize for each age the expected fecundity at that age plus the sum of all future expected fecundities (Schaffer, 1974), then the "cost" of reproduction at each age must be critical to the shape of the age-fecundity function. Williams (1966 a, b) recognized that high levels of present reproduc-

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* Present address: F. E. Perron, Micronesian Mariculture Demonstration Center, P.O. Box 359, Koror, Palau 96940

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tive effort, and therefore fecundity, may jeopardize prospects for future reproductive success. Since the potential magnitude of this risk decreases as an animal approaches the end of its reproductive life, Williams theorized that reproductive effort should increase with age within a species. Using similar logic, Williams (1966 a, b) predicted that semelparous species should make greater reproductive efforts than do iteroparous species. Finally, Hirshfield and Tinkle (1975) have proposed that among long-lived iteroparous species, reproductive effort should be positively correlated with extrinsic adult mortality and negatively correlated with the variability of juvenile survivorship.

Materials and Methods

Data on reproductive effort in species of *Conus* were obtained by collecting females along with their own egg masses. Only egg masses collected with a single ovipositing female were used in this study. Females of *C. pennaceus* probably lay only one egg capsule mass per year (Perron, 1981 c), and the seasonal spawning behavior of the other species examined suggests that they also reproduce only once annually in Hawaii. Therefore, the egg capsule mass found with an individual female was assumed to represent the entire annual reproductive production of that individual. Weights and caloric contents of ova were determined by analysis of uncleaved eggs only.

For *Conus pennaceus*, 140 females, with their egg masses, were collected in 0.1 to 0.5 m of water on a subtidal reef platform at Hauula, Oahu, Hawaii. Eight *C. abbreviatus* and 5 *C. flavidus* females with their own egg masses were also collected from the same reef habitat at Hauula, and an additional 17 female specimens of *C. quercinus* were collected from a depth of 15 m in Maalaea Bay off the island of Maui. Egg capsule production of *C. quercinus* was monitored by maintaining the gastropods in sea-water tanks at the Kewalo Marine Laboratory of the Pacific Biomedical Research Center in Honolulu, Hawaii during the short (February–April) spawning season of this species in 1979. Egg masses of *C. pennaceus, C. abbreviatus* and *C. flavidus* were collected during the months of April through June, 1979. For all species, the shell of each individual was measured to the nearest 0.1 mm in length before being crushed in a vise for ease of soft-body removal. After the body had been extracted, both this and the shell were dried for 24 h at 80 °C and weighed separately on a Mettler balance.

The caloric content of *Conus pennaceus* somatic tissue was measured in a Phillipson microbomb calorimeter (Gentry Instruments Inc.). The body tissues of 15 spawned-out females were dried, pulverized, pelletized and burned in the calorimeter. The percentage of ash in somatic tissue was determined from 50 incinerations carried out in a muffle furnace at 500 °C for 3 h. The organic content of the shell was estimated as the amount of weight lost after ashing for 3 h at 500 °C. Percentage of organic content was based on 46 incinerations of pulverized shells.

Neogastropod spawn is composed of proteinaceous capsules within which the ova are suspended in a mucous intracapsular fluid. In studies of gastropod reproductive energetics, the caloric content of spawn has sometimes been determined by drying and combusting entire capsules or egg masses (Hughes, 1972; Todd, 1979). For the following reasons, this method was not adopted in the present study. First, calorimetric analysis of whole capsules would obscure differences in energy content between ova, capsule wall material and intracapsular fluid (Perron, 1981 b). Second, preliminary studies revealed that intracapsular fluid has an extremely high ash content (approximately 75% by weight), and contributes up to 50% of the total weight per capsule. If whole capsules were pulverized and burned without first removing the intracapsular fluid, total ash content would exceed the 25% level considered by Paine (1971) to be maximal for reliable caloric analysis. Caloric and ash content of ova, capsule wall material and intracapsular fluid were therefore determined separately (by techniques described by Perron, 1981 b). Total caloric investment per spawn mass was calculated by summing calories in ova, capsule wall material and intracapsular fluid on a per capsule basis and then multiplying by the number of capsules in the cluster.

Reproductive effort was calculated in two ways: (1) Current reproductive effort (Hughes and Roberts, 1980) is most simply expressed as $R\,(R+S)^{-1}$, where R and S are reproductive and somatic production in calories per year, respectively; R was calculated for each female as the total number of calories in her annual egg mass; annual somatic production (S) was estimated from the relationship between postspawn calories (including shell) and age; the relationship between shell length and age in *Conus pennaceus* was determined by fitting a von Bertalanffy growth curve to mark-recapture data obtained at the Hauula study site (Perron, 1981 c). (2) Weight-specific reproductive effort (as defined by Hughes and Roberts, 1980) is the proportion of prespawn energy in body and shell tissues allocated to reproduction each year, or $R\,W^{-1}$, where R is the annual production of energy in spawn and W is the total energy content of the body immediately before spawning. The age-specific distributions of $R\,(R+S)^{-1}$ and $R\,W^{-1}$ were then plotted for the Hauula *C. pennaceus* population. $R\,W^{-1}$ was also plotted as a function of female shell length for *C. pennaceus, C. quercinus, C. abbreviatus* and *C. flavidus.*

Throughout the present paper, all means are presented plus or minus one standard deviation. Regression analyses were carried out using a curve-fitting computer program.

Results

The caloric and ash content of *Conus pennaceus* somatic tissues are given in Table 1. When shell material was ashed at 500 °C, the percentage weight loss was 2.39 ± 0.33. This weight loss was the result of combustion of the proteinaceous periostracum and shell matrix. This material was assumed to have the same caloric value as soft-

Table 1. *Conus pennaceus.* Caloric and ash content of somatic tissues and spawn. *N*: number of individuals or egg capsules analyzed

	N	Ash-free calories g^{-1}	% ash
Soft-body tissues	15	5 463 ± 101	17.31 ± 5.02
Shell	46	5 463 ± 101	97.61 ± 0.13
Ova	15	6 221 ± 152	2.52 ± 0.50
Capsule wall material	15	5 551 ± 52	11.93 ± 4.40
Intracapsular fluid	5	4 274 ± 8	74.50 ± 1.00

Table 2. *Conus pennaceus, C. quercinus, C. abbreviatus* and *C. flavidus.* Percentage of total spawn calories allocated to ova, capsule wall material and intracapsular fluid. Numbers in parentheses indicate numbers of egg capsules examined for each species

Spawn component	*C. pennaceus* (1 400)	*C. quercinus* (170)	*C. abbreviatus* (80)	*C. flavidus* (50)
Ova	47.61 ± 7.63	65.96 ± 1.79	71.74 ± 3.47	69.45 ± 2.59
Capsule	38.54 ± 3.37	26.89 ± 0.75	23.72 ± 2.31	21.46 ± 2.36
Fluid	13.55 ± 4.32	7.19 ± 2.46	4.54 ± 2.43	9.08 ± 1.62

body tissue. The caloric content of shell material was therefore calculated as 5 463 × 0.0239 or 130.56 calories per gram (Table 1). The caloric content per gram of somatic tissue was assumed to be the same for all 4 species examined.

Although *Conus pennaceus* is a relatively thin-shelled species (Kohn, 1959), its shell contributes 93.96 ± 0.88% of total dry weight per animal, the percentage of shell being the same for all age classes. *C. quercinus, C. abbreviatus* and *C. flavidus* have thicker shells, which contribute 95.10 ± 1.13, 96.24 ± 0.40 and 96.48 ± 0.83% of total dry weight, respectively.

In energetic terms, the shell accounts for 33.09 ± 6.04% of the total prespawn calories of *Conus pennaceus* females. Since the correlation between the percentage of calories in shell and shell length is non-significant ($r = 0.145$, $DF = 48$), the ratio of shell calories to soft-body calories probably does not vary with age. The total postspawn caloric content ranged from 700 calories for 2 yr old females to 8 400 calories for 10 yr olds (Fig. 1). The relationship between postspawn body calories (soft tissues plus shell protein) and shell length is best described by the cubic power function $Y = 0.052\ X^{3.083}$ ($r = 0.986$, $P < 0.001$). When body calories are plotted against age, the relationship becomes approximately linear (Figs. 1 and 2). Similar relationships were observed in *C. quercinus, C. abbreviatus* and *C. flavidus.*

Caloric and ash content of ova, capsule wall material and intracapsular fluid of *Conus pennaceus* are given in Table 1. Since there are no major differences in caloric content for spawn of several species of Hawaiian *Conus* (Perron, 1981 b), the values determined for *C. pennaceus* were used for all 4 species examined in the present study.

In Table 2, the percentages of total spawn energy allocated to ova, capsule wall material and intracapsular fluid are given for *C. pennaceus, C. quercinus, C. abbreviatus* and *C. flavidus.* Calories in each capsule mass, the product of calories in each capsule and the number of capsules in the capsule mass, ranged from 460 to 3 800 for *C. pennaceus,* 1 031 to 2 016 for *C. abbreviatus,* 1 725 to 3 368 for *C. flavidus* and 5 157 to 27 195 for *C. quercinus.*

In *Conus pennaceus,* current reproductive effort $[R\ (R+S)^{-1}]$ rises steeply in early life and approaches an asymptote with increasing age (Fig. 3). However, when weight-specific reproductive effort ($R\ W^{-1}$) is plotted as a function of age in *C. pennaceus* (Fig. 4), or shell length in all 4 species (Fig. 5), no dramatic age- (or size-) specific changes are seen. Therefore, females of all 4 species allocate a relatively constant proportion of their body calories to reproduction each year regardless of age or body size.

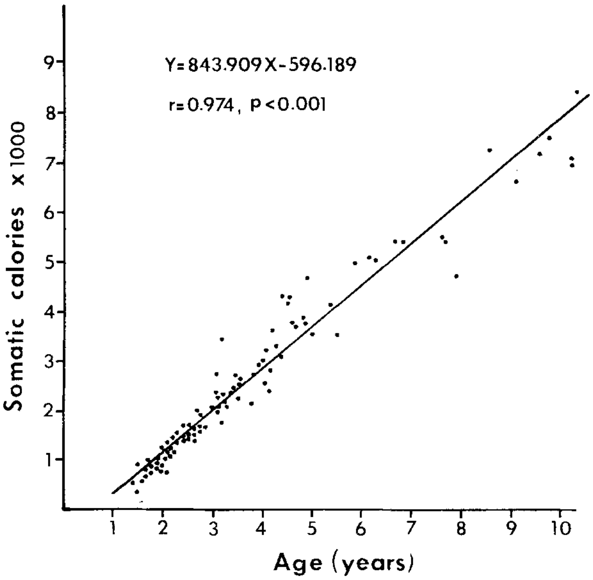

Fig. 1. *Conus pennaceus.* Relationship between age and postspawn somatic calories (body + shell) immediately after spawning

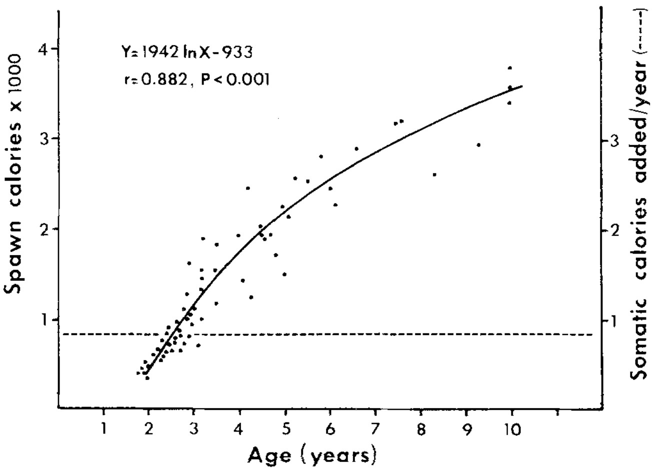

Fig. 2. *Conus pennaceus.* Age-specific pattern of energy allocation to spawn. Dashed line shows age-specific allocation of energy to somatic growth (calculated from Fig. 1)

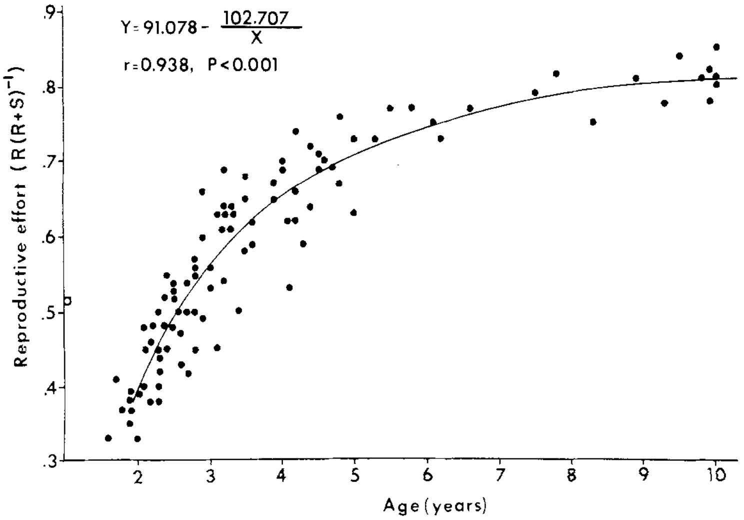

Fig. 3. *Conus pennaceus.* Age-specific reproductive effort as measured by $R\,(R+S)^{-1}$, where R is annual reproductive production and S is annual somatic production. Both R and S are measured in calories

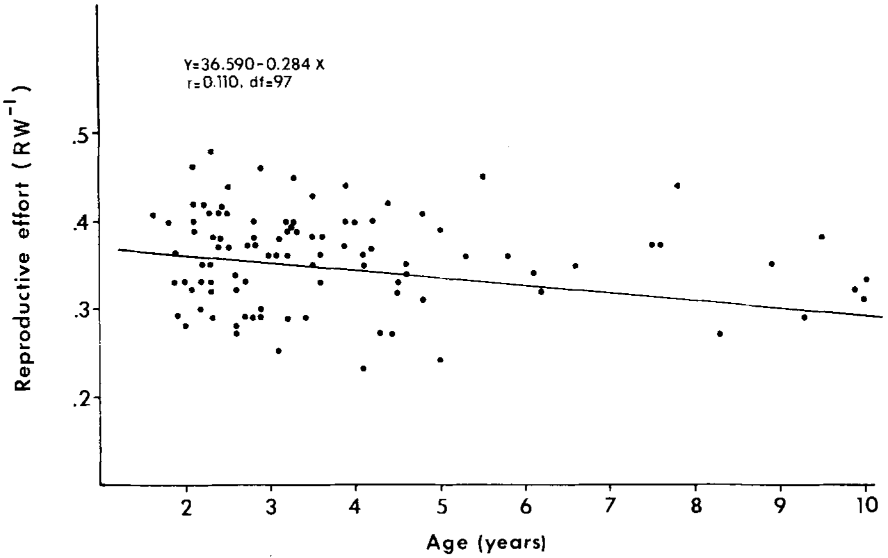

Fig. 4. *Conus pennaceus.* Age-specific reproductive effort as measured by $R\,W^{-1}$, or the ratio of calories in spawn to calories in the body immediately before spawning

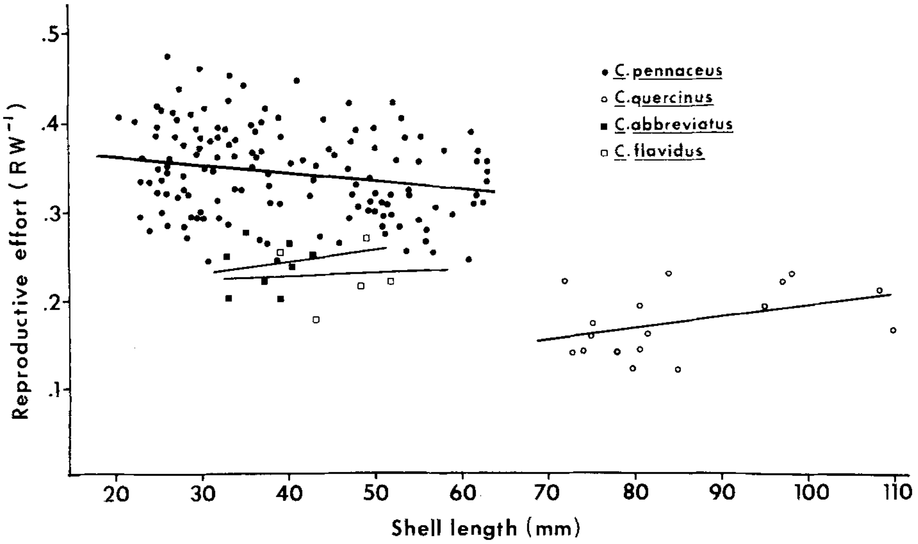

Fig. 5. *Conus pennaceus, C. quercinus, C. abbreviatus* and *C. flavidus.* Relationship between reproductive effort ($R\,W^{-1}$) and shell length

Discussion

Somatic Energy Content

Although most somatic energy in *Conus pennaceus* is tied up in soft-body tissues, the present study demonstrates that the gastropod shell may contain a non-trivial portion of total somatic calories. The organic component of the molluscan shell, believed to be primarily proteinaceous, includes an internal matrix within which $CaCo_3$ is deposited (Wilbur, 1964), and an outer periostracal layer. In *C. pennaceus*, the organic component of shell was more than twice the 1.1% by weight determined by Vinogradov (1953) for a gastropod, *Turbo* sp. Even higher shell protein contents than those of *C. pennaceus* have been found in the gastropod *Trochus niloticus* (G. Heslinga, personal communication). Since shell protein accounted for over 33% of the total postspawn somatic calories in *C. pennaceus*, it seems clear that serious errors may result from ignoring the energy content of shell material.

The somatic energy content of *Conus pennaceus* increases as a cubic power function of shell length. However, when body energy is plotted against age (Fig. 1), the relationship is best described by a straight line. This relationship indicates that females of *C. pennaceus* add approximately 844 calories to their somatic tissues during each year of life (Figs. 1 and 2). Of these calories, 279 are accounted for by shell growth alone.

Reproductive Effort in *Conus pennaceus*

Recent formulations of life history theory have emphasized the importance of age-specific variation in reproductive effort (Schaffer, 1974; Pianka and Parker, 1975; Stearns, 1976). The probable tradeoff between present levels of reproductive effort and future fecundity and survival led Williams (1966a, b) and Gadgil and Bossert (1970) to propose that reproductive effort in iteroparous organisms should increase with age as the potential future costs of reproduction decline. However, in *Conus pennaceus*, $R\,W^{-1}$ shows no increase and may even decrease with age (Fig. 4). In contrast, $R(R+S)^{-1}$ nearly doubles during the lifetime of a typical female (Fig. 3). The curves in Figs. 3 and 4 are similar to those obtained for several marine gastropods by Hughes (1971a, b; 1972) and Hughes and Roberts (1980), and for freshwater molluscs by Aldridge and McMahon (1978) and Browne (1978).

The shapes of the $R\,(R+S)^{-1}$ and $R\,W^{-1}$ curves for *Conus pennaceus* are determined by the interaction between the age-specific somatic and spawn production curves of this species (Figs. 1 and 2). $R\,(R+S)^{-1}$ increases with age because, although annual spawn production increases with female size and age, annual somatic production remains relatively constant throughout life (Fig. 2). $R\,W^{-1}$ does not increase with age because W, a measure of total standing crop, increases at roughly the same rate as does R.

In theory, $R\,(R+S)^{-1}$ and $R\,W^{-1}$ should reflect different aspects of the tradeoff between present levels of reproductive effort and probably future reproductive success. The potential future costs accruing from present reproduction may be viewed as being composed of survival costs and energy allocation costs (Shine, 1980). Present reproduction may affect survival to future reproductive seasons by placing physiological stress on the animal (Pearce and Thorson, 1967; Snell and King, 1978), or by increasing the probability of death by predation (Shine, 1980). On the other hand, in species whose fecundity is related to body size, energy allocated to present reproduction may reduce future fecundity by diverting resources away from somatic growth.

Since $R\,W^{-1}$ is a measure of the proportion of the body which is invested in reproduction, an age-specific increase in this index is likely to impose increasing physiological stress on the organism or impair its ability to function normally and avoid predation. For example, Shine (1980) found that gravid females of scincid lizards were more susceptible to predation than were non-gravid ones. Therefore, $R\,W^{-1}$ should reflect the selective importance of the survival cost of reproduction and may be used as an index of "reproductive recklessness" (Calow and Woolhead, 1977; Hughes and Roberts, 1980).

$R\,(R+S)^{-1}$ may increase with age independently of $R\,W^{-1}$. *Conus pennaceus* and many other gastropods (Browne and Russell-Hunter, 1978; Hughes and Roberts, 1980) demonstrate this pattern. Therefore, increases in $R\,(R+S)^{-1}$ do not necessarily imply increasing levels of physiological stress or vulnerability to predation. However, age-specific increases in $R\,(R+S)^{-1}$ are related to decreased growth and consequent reductions in future fecundity. $R\,(R+S)^{-1}$ should therefore reflect the selective importance of energy allocation tradeoffs (Shine, 1980).

Since fecundity generally increases with body size in molluscs (Spight *et al.*, 1974; Spight and Emlen, 1976), $R\,(R+S)^{-1}$ will always increase with age in these species as long as annual somatic production is a constant or decreasing function of age. Although nearly all marine invertebrate species so far examined have increasing age-specific $R\,(R+S)^{-1}$ curves (Hughes and Roberts, 1980), $R\,W^{-1}$ curves may remain constant (Barnes and Barnes, 1968; Glynn, 1970; Green and Hobson, 1970; Sameoto, 1971; Menge, 1974; Hughes and Roberts, 1980), decrease (Gonor, 1972; Creaser, 1973; Wyatt, 1973) or increase (Grahame, 1973; Rutherford, 1973; Spight and Emlen, 1976; Thompson, 1979) with age. These observations suggest that $R\,W^{-1}$, rather than $R\,(R+S)^{-1}$, may be the most useful index of reproductive effort for studies of the ecological factors which determine age-specific patterns of energy allocation to reproduction in these species.

Interspecific Differences in Reproductive Effort

When energy allocation to reproduction is expressed in terms of $R\,W^{-1}$, then the reproductive efforts made by

Conus pennaceus, C. quercinus, C. abbreviatus and *C. flavidus* may be directly compared (Fig. 5). Although $R\,W^{-1}$ values are quite variable and show no clear relation to shell length within species, some interspecific differences are obvious. For example, there is no overlap in $R\,W^{-1}$ between *C. pennaceus* (range = 0.23 to 0.48) and *C. quercinus* (range = 0.12 to 0.23). If *C. quercinus, C. abbreviatus* and *C. flavidus* data are lumped, their total range (0.12 to 0.27) only slightly overlaps that of *C. pennaceus*. Therefore, the 3 species with small eggs and planktonic larvae have lower average $R\,W^{-1}$ values than does the one species with large eggs and non-pelagic larvae. According to Hirshfield and Tinkle (1975), reproductive effort should vary inversely with the variability of juvenile mortality. Among marine invertebrates, the variability of juvenile mortality should be strongly influenced by developmental mode, the highest variability being associated with reliance on a planktonic larval stage and lower variability being associated with production of non-pelagic larvae (Thorson, 1946; Hughes and Roberts, 1980). The contrast between *C. pennaceus* and the other three species supports the prediction of Hirshfield and Tinkle (1975).

Hirshfield and Tinkle (1975) also predicted that levels of reproductive effort will be positively correlated with extrinsic adult mortality. *Conus pennaceus* and *C. quercinus* have annual adult mortality rates of 0.419 and 0.187, respectively (Perron, 1981c), while those of *C. abbreviatus* and *C. flavidus* have been estimated at 0.122 (Leviten, 1974). Again, the data in the present paper support current theory. However, since levels of reproductive effort ($R\,W^{-1}$) in *Conus* spp. are correlated with (1) extrinsic adult mortality and (2) variability of juvenile mortality, it is impossible to determine which factor has the most important influence on reproductive energetics within the genus.

Perron (1981b) found that the energetic cost of protective egg capsules increased with egg size among 10 *Conus* spp., including the 4 studied in the present work (Table 2). It was suggested that species with large eggs might obtain the extra energy required for construction of expensive capsules by diverting energy away from the gonads. However, the data in the present study suggest that, at least for *C. pennaceus*, high energy expenditure on egg capsules may be related to high reproductive effort in this species. In fact, the difference in reproductive effort between *C. pennaceus* and the other three species amounts to more than enough energy to account for interspecific differences in allocation of energy to extraembryonic protective structures. The interrelationships among reproductive mode, costs of parental care and reproductive effort remain poorly understood, and further research in this area may lead to new insights into patterns of life history evolution in marine invertebrates.

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