

LARVAL PROBLEMS AND PERSPECTIVES IN LIFE HISTORIES OF MARINE INVERTEBRATES

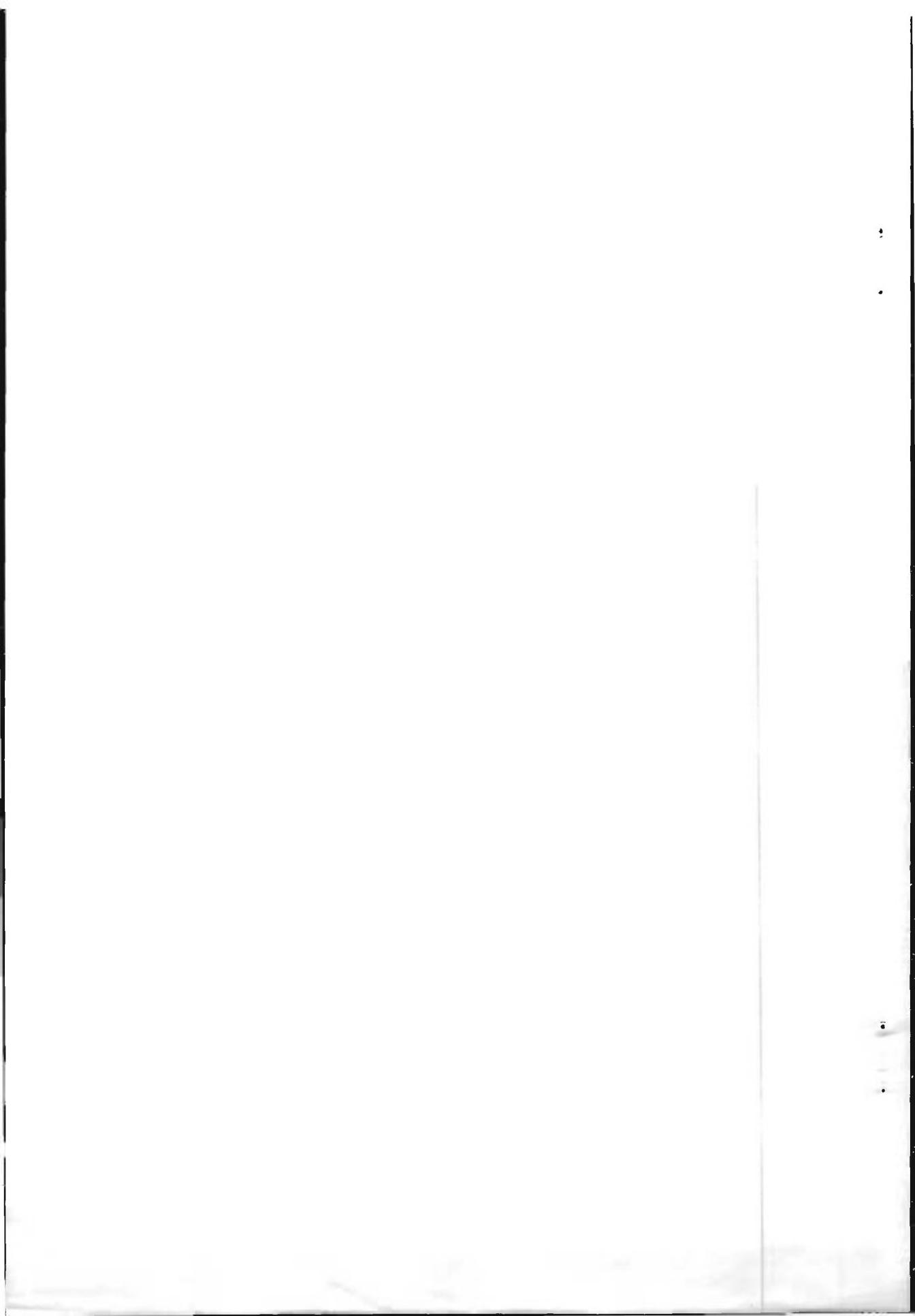
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ABSTRACT

Research on larval biology and life history strategies of marine invertebrates has been influenced by the perspectives of Thorson's (1946; 1950) categorization of developmental modes and of theoretical models (e.g., r- and K-selection, bet hedging, and energetic trade-offs) which explain demographic patterns. Using these two perspectives, recent developments in five main problems are reviewed: (1) validations and challenges to the perspective that developmental/larval mode primarily determines life history strategies; (2) the significance of variability and flexibility in the larval phase and other aspects of life history strategies; (3) the need for studies of heritability of life history traits; (4) the importance and difficulty of measuring larval mortality; and (5) the need to measure covariation and evolutionary constraints of larval and other life history variables. This review indicates that the analysis of life history strategies of marine invertebrates is in a transition period without a clear new perspective. However, eight recommendations for new research are presented.

Two recent perspectives have shaped research approaches to larval problems in life history strategies of marine invertebrates. One of these originates from Thorson's (1946; 1950) classification of reproductive patterns into four developmental modes (planktotrophic, lecithotrophic, and direct development, plus viviparity) and his quantification of the relative abundance and latitudinal distribution of these modes. Thorson's ideas have been refined and amplified in subsequent reviews (Mileikovsky, 1971; Chia, 1974; Day and McEdward, 1984) to distinguish attributes of dispersal (planktonic versus non-planktonic), trophic mode (planktotrophic versus lecithotrophic), and parental care (brooding versus broadcast spawning). Planktotrophic larvae cost relatively little parental investment and, by virtue of their large numbers, improve dispersal, but they incur high mortality due to presumably intense predation and dilute sources of food in the plankton. The main advantage conferred upon a larva by a larger, lecithotrophic egg is presumed to be trophic independence from fluctuating food supplies in the plankton (Chia, 1974; Vance, 1973a; 1973b). The correlates of increased egg size in lecithotrophy are increases in energy allocation per unit of reproductive output and concomitant decreases in fecundity. The prevalence of large, lecithotrophic eggs and brooding at high latitudes is viewed as an adaptation to the short reproductive season at the poles (Thorson, 1950), and as a necessary constraint of species with small body size which could not produce enough eggs (even of the minimal size to develop into a multicelled larva) to withstand the high mortality in the plankton (Chia, 1974). Apart from the constraints of small adult body size, however, egg size is not considered a variable adaptive to post-settlement phases of the life cycle, and the larval and post-settlement phases of life histories are usually viewed as being subject to separate evolutionary pressures (Istock, 1967; Jagersten, 1972). Thus, egg size as the energetic measure of adult reproductive investment is viewed as the primary parameter which predicts discrete categories of developmental pattern, fecundity, dispersibility, and general larval ecology (Vance, 1973a; 1973b; Christiansen and Fenchel, 1979).

The other perspective is largely based on demographic considerations and views life history strategies as integrated suites of coadapted traits encompassing the entire life cycle from egg to age at maturity to longevity. Although this perspective



also has a strong tendency to categorize life histories dichotomously (e.g., r-selected species versus K-selected species; Pianka, 1970), the larval phase is not viewed as evolving separately from post-settlement phases. Age at first reproduction is viewed as the primary parameter predicting life history strategies (Murphy, 1968).

There are at least three hypotheses about the evolution of life history strategies which have been considered in this second perspective. As reviewed by Stearns (1976; 1977) and Giesel (1976), "r- versus K-selection" stems from MacArthur and Wilson's (1967) expansion of earlier work on vertebrate life history strategies (Lack, 1954; Cole, 1954; Williams, 1977) to a more general proposal relating life histories to environmental stability. Subsequent critical analysis (Stearns, 1977) showed that the r- and K-selection hypothesis is seriously flawed because, among other things, there is no adequate way to quantify K-selection as a function of life history traits. Moreover, there have been little or no attempts to measure carrying capacities of specific environments and relate them to the age structures of populations in an explicit quantitative model. As a result of the demise of the deterministic (r-K selection) model, this perspective has placed increasing emphasis on stochastic aspects of survivorship and fecundity (Stearns, 1977). Stearns (1976; 1977) placed a "bet hedging" hypothesis involving ratios of juvenile to adult mortality (Cohen, 1966; 1967; 1968; Murphy, 1968; Schaffer, 1977) in juxtaposition to r- and K-selection as the main alternative explanation for the same dichotomous suites of traits: small vs. large body size; early vs. late production; semelparous vs. iteroparous reproduction; small vs. large parental investment per propagule; etc. However, quantitative tests, and even precise formulation, of the bet hedging hypothesis are also lacking (see below under Larval Mortality). The third category of hypothesis in this perspective invokes a straightforward trade-off in energy allocation between growth and reproduction, so that growth to large size results in delayed maturity. Since many invertebrates are characterized by indeterminate growth, and since many larval biologists tend to have a physiological research orientation, aspects of this hypothesis are implicit in many life history studies of marine invertebrates (Spight et al., 1974). However, the link between growth pattern, population dynamics, and evolution often is not made clearly in studies invoking this trade-off hypothesis.

Although these two perspectives have often reflected differences in the research approach and emphasis of developmental, population and evolutionary biologists, the historical separation is currently being rectified by adjusting the initial assumptions (Perron and Carrier, 1981) and by exploring alternative hypotheses (Strathmann and Strathmann, 1982; Stearns, 1980). Thus, analysis of life histories of marine invertebrates is in a transition period, without a clear new perspective, but with a broad array of current challenges. The purpose of this paper is to consider the current status of research on larval biology in this transition period of life history research. I focus on five major problems which serve both to illustrate the transition and to indicate some of the major directions of new research: (1) recent validations and challenges to the perspective that developmental/larval mode primarily determines life history strategies of marine invertebrates; (2) the significance of variability and flexibility in the larval phase as well as all aspects of life history strategies; (3) the need for studies of heritability of life history traits; (4) the importance and difficulty of measuring larval mortality; and (5) the need to measure covariation and evolutionary constraints of larval and other life history variables. Problems one and two are primarily considered from the perspective of developmental modes, whereas problems four and five are usually considered from the demographic perspective. Problem three concerns all evolutionary perspectives of life history strategies.

DEVELOPMENTAL MODE

Thorson's (1950) basic categorization of developmental modes continues to receive validation (Christiansen and Fenchel, 1979). Major new categories of developmental modes have not been proposed, but two new types of larvae have been discovered as variations on the original categories: demersal larvae, which may be able to exploit the rich detrital and dissolved organic resources near the bottom while avoiding some problems of dispersal away from parental habitats (Pearse, 1969); and teleplanic larvae, which are planktotrophic larvae transported very long distances by transoceanic currents (Scheltema, 1971a; 1971b). Relatively few species appear to have demersal larvae (Gerrodette, 1981; Fadlallah and Pearse, 1982); but the accuracy of the original description of the larva is in question, and there appears to be no evidence indicating demersal larvae are an abundant larval type in Antarctica (Pearse and Bosch, 1986). On the other hand, the prevalence of species with teleplanic larvae has become increasingly well-known in the Atlantic (Scheltema, 1971a; 1971b) and now the Pacific (Scheltema and Williams, 1983; Scheltema, 1986). While Thorson's work stimulated extensive documentation of the range of larval types in the temperate zone, the larval biology of many tropical faunas and whole groups, such as corals (Fadlallah, 1983), are poorly known.

Despite their pervasiveness, many of the assumptions underlying "Thorsonian" generalizations have come under scrutiny and question. Variability and flexibility in developmental mode and life history patterns defy simple categorization, and these stochastic and versatile aspects merit discussion in a separate section below. Even within Thorson's categorical framework, the energetic correlates of egg size are considerably more variable, and their adaptive significance arguably different, than originally construed. Larger eggs do not necessarily contain more energy than small eggs, because organic matter may be more concentrated in small eggs (Strathmann and Vedder, 1977), because of variations in hydration in large eggs (Turner and Lawrence, 1979), and because of increased inorganic matter in large eggs (Lawrence et al., 1984). Strathmann and Vedder (1977) found that the allometry of organic matter is about a $\frac{3}{4}$ power of egg volume in echinoderms with feeding larvae, whereas Turner and Lawrence (1979) found a nearly isometric relationship. The diversity of biochemical pathways which have evolved to produce energetic resources for the embryo are far more complex and varied than previously assumed, even in closely related species (Ecklebarger and Grassle, 1983). More detailed comparative analyses of the variation in these gametogenic pathways will provide much needed insight into the adaptive radiation of developmental modes within closely related species (Ecklebarger, 1983; 1986). In many groups of invertebrates, including gastropods, cephalopods, and polychaetes, parental investment in reproduction goes beyond the cell membrane of the egg to include nurse cells, gelatinous coating, protective capsules, and capsular fluid. These provide extra-embryonic nutrition and protection from predators and physical stress, and the energetic costs of these structures must be accounted for in analyses of developmental mode (Spight, 1975; 1976; Rivest, 1983; 1986; Pechenik, 1979; Perron and Carrier, 1981; Perron and Corpuz, 1982). In some groups (e.g., opisthobranchs; DeFreese and Clark, 1983) absolute and relative reproductive output are independent of developmental type; and total caloric content per egg (including associated albumen and capsular components) does not differ between planktotrophic and lecithotrophic development, nor between lecithotrophic and direct development, although it did differ significantly between planktotrophic and direct development. Moreover, advanced techniques of organic chemistry

and axenic culture show that planktotrophic larvae may not be dependent upon elusive particulate food, but can take up dissolved organic compounds at extraordinarily dilute concentrations for much of their maintenance metabolism and possibly extensive proportions of their growth (Manahan et al., 1982; Manahan, 1983; Manahan et al., 1983).

This capability for uptake of dissolved organic compounds may minimize the chance that many larvae starve to death in the plankton. Thorson (1950) noted that larvae in poor nutritional condition are rarely if ever seen (Vance, 1973a, pp. 340–341), either nearshore or in the open ocean (Scheltema, personal communication). However, high densities of larvae may significantly deplete their food resources, although the larvae may still grow at near the maximal rates observed in the laboratory (Jorgensen, 1981). Detailed laboratory studies of larval polychaete and crab energy requirements indicate that, while some species are quite resistant to starvation, others have specific, potentially limiting nutritional requirements at critical times during development (Day, 1977; Sulkin, 1978; Anger and Dawirs, 1981; 1982; Anger et al., 1981). Additional details of larval nutritional requirements and energetics have been reviewed recently by Day and McEdward (1984).

In addition to questioning the accuracy of egg size as a predictor of parental investment and trophic independence during larval development, other generalities of developmental mode are being scrutinized. The postulate of bimodality in egg size indicating only two evolutionarily stable extremes in reproductive strategies (Vance, 1973a; 1973b) has been refuted empirically in many groups, including bivalves, gastropods, chitons, barnacles, and stomatopods (Perron and Carrier, 1981). However, there appear to be no known chiton species with feeding larvae or, conversely, no known stomatopod and thoracian barnacle species without feeding larvae. Thus, the frequency distribution in egg size in these groups is not a refutation of the bimodality concept. For many other groups, quantification of statistically useful samples of egg size is not available, suggesting that descriptive patterns not be generalized beyond groups without supporting data. Nevertheless, the evolutionary stability of bimodal distributions in egg size continue to be supported by mathematical models (Grant, 1983) and by good empirical data for a few groups (e.g., asteroids and echinoids; Emler et al., in press). Although Underwood (1974) questioned its validity, developmental time has been positively correlated with egg size in many groups of invertebrates, including amphipods, copepods, decapods, crustaceans in general, tunicates, and bivalves (Steele and Steele, 1975; Steele, 1977; Strathmann, 1980). However, for many groups this relationship has not been quantified adequately and analyzed statistically. Reproductive effort is not related to reproductive mode in at least some common groups where it has been quantified adequately (e.g., *Littorina* spp., Hughes and Roberts, 1980; *Lacuna* spp., Grahame, 1977; 1982). The latitudinal distribution of larval modes appears to be much more complex than originally postulated by Thorson (1950). While the incidence of brooding and lecithotrophy does increase toward the poles in some groups, planktotrophy does not appear to decline at high latitudes (Spight, 1981; Pearse and Bosch, 1986) and the pattern does not hold for all groups (e.g., brachyuran crabs, Hines, 1986). Moreover, the cause of latitudinal changes in developmental mode appears to be much more complex than simple gradients reflecting life history trade-offs. At least in gastropods, high latitude faunas are composed of families that exhibit the range of developmental types, while families characterized by only direct development are found primarily in the tropics (Spight, 1981). These exceptions and objections to the correlates of the broad patterns of developmental mode indicate that "Thorsonian" generaliza-

tions are not adequate to explain the evolutionary causes and mechanisms regulating life histories in marine invertebrates.

Several alternate hypotheses to Thorson's correlates of developmental mode in life history patterns have been proposed. First, dispersal, not parental energy investment or larval trophic independence, is often regarded as the primary consequence of planktonic development. Molluscan species with planktotrophic larvae have the greater capacity for dispersal across habitats, greater genetic mixing, larger geographic ranges, and longer geologic lives than species with lecithotrophic or direct development (Sheltema, 1971a; Shuto, 1974; Hansen, 1980; Palmer and Strathmann, 1981; Jablonski and Lutz, 1983; Strathmann, 1986). However, this may not necessarily be true for all groups, such as corals (Heck and McCoy, 1978) and brachyuran crabs (Hines, 1986), and there have been several objections to the assumption of greater genetic homogeneity in species with greater dispersal abilities (Gooch et al., 1972; Koehn, 1975). Nevertheless, many reproductive strategies selecting evolutionary alternatives between, for example, semelparity and iteroparity or several small spawning episodes and one synchronous spawning per season have major consequences for dispersal of siblings (Strathmann, 1974). Second, the adaptive significance of producing larger eggs may not lie primarily in the energetic reserves provided larvae, but, rather, may lie in producing larger juveniles at settlement (Calow, 1977; Strathmann, 1977). Larger juveniles may have advantages in minimizing predation and maximizing food selection, and, other things being equal, they attain sexual maturity more quickly than small juveniles (Hines¹). Third, Strathmann and Strathmann (1982) analyzed a wide range of hypotheses about the selection for brooding in marine invertebrates. They concluded that no single explanation concerning allometry of egg production and brood capacity, longevity with repeated reproduction and variable recruitment, and dispersal is adequate across the diversity of taxa and habitats exhibiting gradients in the incidence of brooding. Thus, while many of the correlates of Thorson's categorizations of developmental modes have been undermined, there has been no single alternative hypothesis explaining larval patterns in the life histories of marine invertebrates.

VARIABILITY AND FLEXIBILITY

One of the main objections to Thorson's (1950) generalizations of larval patterns is that they do not account for variation in life history parameters and tend to ignore flexible life history strategies, which are not easily categorized. With due respect to Thorson and many of the proponents of the developmental mode perspective, examples of variability and flexibility usually have been noted at least anecdotally in discussions of categorical patterns (Thorson, 1946; Mileikovsky, 1971; Chia, 1974). However, intensive consideration needs to be given to the incidence and extent of variability and flexibility, ranging from "mixed" developmental strategies to fluctuations between extremely different life history patterns among individuals in a population to stochastic variation among populations and individuals.

"Mixed" developmental strategies incorporate both an embryonic period in some kind of protective egg capsule, which may be brooded or deposited in the environment, followed by a subsequent planktonic larval period before metamorphosis (Pechenik, 1979; Caswell, 1981). These patterns are common in gastropods (especially opisthobranchs), many polychaetes, most nemertean, many

¹ Hines, A. H. Comparative life history strategies of five species of spider crabs (*Brachyura Majidae*). In review.

turbellarians, and also most crustaceans. Development within the capsule is lecithotrophic and may involve extra-embryonic nutrition as well, while the pelagic phase may be lecithotrophic or planktotrophic. Mixed development provides protection for the earliest, and presumably most sensitive, stages while still retaining the advantages of planktonic dispersal. The benefits of encapsulation have been modeled both to be inversely related to planktonic mortality (Pechenik, 1979) and also to be directly related to planktonic mortality and inversely related to the decrease in fecundity required by encapsulation and to capsule mortality (Caswell, 1981).

Facultative switching between developmental modes occurs at several levels. Some lecithotrophic larvae, which are capable of developing completely without feeding, may feed in the plankton when food is available (Todd, 1979; DeFreese and Clark, 1983), although it is unclear whether feeding promotes larval growth, shortens or lengthens the time to settlement (however, see Kempf and Hadfield, 1985; Highsmith and Emlet, 1986). At another level, flexibility in developmental mode from direct development to planktotrophic larvae can occur among individuals within populations of spionid polychaetes (Rasmussen, 1983; Simon, 1968; Blake, 1969; Blake and Kudenov, 1981), sea stars (Scheibling and Lawrence, 1982), and gastropods (Spight, 1975; Gallardo, 1977; Todd, 1979). However, while several of these examples have been verified, careful cross-breeding experiments need to be done to insure against the possibility that some cases of flexibility do not apply to sibling species (Grassle and Grassle, 1976; Gallardo, 1977; Christie, 1982; Scheibling and Lawrence, 1982). At the extreme, Levin (1984) demonstrated with cross-breeding that the spionid polychaete *Streblospio benedicti* exhibits flexibility in developmental mode from individuals which produce few (9–50) large (100–200 μ m) lecithotrophic eggs to individuals which produce many (100–548) small (70–90 μ m) planktotrophic eggs. She suggests that the same individual may be able to switch modes among successive reproductive episodes. At another level, many species exhibit life histories which are opportunistically flexible in response to fluctuating resources. *Asterias* spp. in New England provides a good example of flexibility in response to patchy food resources (Menge, 1986). Reproductive size of these two species of sea stars varies an order of magnitude, depending on the availability of mussels. When food is in short supply, they mature quickly at small size and have a small reproductive output; whereas in areas where mussels are abundant, individuals grow to much larger size, with greatly increased reproductive output. Large individuals may decline drastically in size when food resources are depleted.

Thus, flexibility can provide long-term advantages over more rigid life history patterns, and generalizations about correlates of any variable, such as body size, need to be viewed cautiously. Moreover, the phenomenon of flexibility in developmental modes and life histories can no longer be viewed anecdotally as rare exceptions to a standard pattern, because: (a) the number of examples of flexibility is growing with increased attention to the phenomenon; (b) many of the species exhibiting flexibility are among the most successful members of major habitats; and (c) the range in degree of flexibility appears to be a continuum.

In addition, all life history variables exhibit stochastic variation, which simple categorization of developmental mode does not measure. Egg size within a single spawning can vary over a wide enough range to produce significant differences in larval survivorship (e.g., bivalves, Kraeuter et al., 1982). Many, if not most, planktotrophic and lecithotrophic larvae have the capability to delay metamorphosis to varying degrees after attaining competency until suitable substrate or other conditions are met (Bayne, 1965; Hadfield, 1984; Scheltema, 1971a; 1971b;

Kempf, 1981; Hadfield, 1986). This delay introduces a large amount of variation into any estimates of duration of the larval period with respect to egg size, dispersal, larval growth, and/or larval mortality. Measures of fecundity and egg size are often size-dependent and require samples spanning broad size-ranges of individuals, so that regression analysis and analysis of covariance can be used to test for significant differences among groups (Hines, 1982; Hart and Begon, 1982; Jones and Simons, 1983). Within many species, there is significant variation in reproductive and life history traits (egg size, reproductive effort, body size, fecundity, developmental and growth rates, and age at maturity and longevity) among populations along gradients of latitude, salinity, intertidal level, depth, levels of disturbance, food availability, and other habitat variables (Barnes and Barnes, 1965; 1968; Faller-Fritsch, 1977; Ament, 1979; Hughes and Roberts, 1981; Alon and Stancyk, 1982; Hart and Begon, 1982; Jones and Simons, 1983). These examples all point to the need to provide measures of larval and life history traits which are statistically appropriate for continuous variables, and to avoid circular a priori categorization of variables. The prevalence of variability in all life history traits is not surprising. However, its significance both as an adaptive necessity for spatial and temporal variation in the environment and as the basis for selection has been overlooked by categorical and deterministic models.

HERITABILITY

Attempts to understand the evolution of life history strategies must ultimately examine the heritability of their component traits. Our present understanding of the genetic regulation of life history traits is confused, even in a species as well studied as *Drosophila melanogaster* (Rose, 1984). The surprisingly few studies of the genetic basis of marine invertebrate life histories indicate a complex array of genetic mechanisms regulating variation in all key traits. Newkirk et al. (1977) showed that the heritability of larval growth rate in *Crassostrea virginica* was 0.25 to 0.50, with much of the genetic variation being additive. They also showed that larval and spat growth rates were highly correlated, indicating that these traits can be selected. Growth rate in *C. virginica* is positively correlated with individual heterozygosity, because the most heterozygous individuals have lower oxygen consumption rates, and thus more energy available for growth, than the most homozygous individuals (Koehn and Shumway, 1982). Variance in larval survival of *Crassostrea gigas* in the laboratory is comprised of genetic and nongenetic components, but the genotypic variance is nonadditive and depends largely on the stage of gonadal development of the parents (Lannan, 1980a; 1980b; Lannan et al., 1980). In work similar to Levin's (1984) preliminary breeding experiments on variation in developmental mode in *Streblospio benedict*, West et al. (1984) hybridized individuals of the opisthobranch *Elysia chlorotica* from two populations with planktotrophic and direct development. Both F₁ and F₂ generations exhibited planktotrophic development. In another opisthobranch, *Phestilla sibogae*, long-term selective inbreeding experiments over 27 generations failed to show obvious genetic components of the wide variance in the age at metamorphic competence and concentration of natural inducer necessary to elicit metamorphosis (Hadfield, 1984). Significant genetically based differentiation in embryonic duration, egg size, and newborn survival was demonstrated in the harpacticoid copepod, *Scottolana canadensis*, taken from a broad range of latitudes and reared in the laboratory (Lonsdale and Levinton, 1985). In laboratory microcosm experiments over about 26 generations, the amphipod *Gammarus lawrencianus* exhibited significant changes in demography and production (Doyle and Hunte,

1981). In these microcosms, the intrinsic rate of population growth increased 1.7-fold as a result of heritable increases in survivorship and fecundity, and "harvestable yield" increased 2.6-fold as a result of faster growth. Much more extensive and intensive comparative research is needed to understand these complex interrelationships between genetic phenotypic, and developmental variations in life histories of marine invertebrates. Increasing emphasis on development of breeding stock for aquaculture species is likely to provide some of this information.

LARVAL MORTALITY

Because of the obvious technical problems of following larvae in the plankton, larval mortality is the most difficult life history variable to measure. Yet good estimates of larval mortality or, conversely, survivorship to settlement are critical to progress in analyzing the evolution of life histories for three main reasons. First, the selective trade-offs among types of developmental and larval modes assume that differences in larval survivorship rates balance differences in parental investment per larva (Strathmann, 1985). Second, the population dynamics of many species are regulated by fluctuations in recruitment. For example, Ebert (1983) showed that differences in the magnitude and frequency of recruitment among populations of sea urchins (*Strongylocentrotus purpuratus*) along the west coast of North America result in markedly different population structures. Annual fluctuations in spatfall regulate population size of many bivalves, such as the oyster *Crassostrea virginica* (Ulanowicz et al., 1980). The availability of cyprids regulates the density and distribution of barnacles in the intertidal zone of central California (Gaines et al., 1985). Recruitment of cyphonautes larvae accounts for about 75% of the variation in the net reproductive index (a measure of population abundance) of the bryozoan *Membranipora membranacea* in southern California (Yoshioka, 1982; 1986). These studies indicate that although small changes in larval survivorship are exceedingly difficult to measure, they can have major effects on survivorship to settlement. For example, a decrease in larval mortality from 99.99% to 99.98% would result in a 100% increase in newly metamorphosed juveniles. Third, many theoretical considerations of the evolution of life history strategies focus on demographic estimates of survivorship for all phases of the life cycle. The hypothesis of r- and K-selection emphasizes optimization of the Malthusian parameter, net reproductive rate, and age-specific reproductive value; but all of these parameters are dependent to varying degrees on estimates of larval survivorship in most marine invertebrates. Other models of life history evolution emphasize pre-reproductive survivorship as the key regulatory variable. The "bet hedging" hypothesis states that variations in juvenile survivorship relative to adult survivorship are the selective determinants of life history strategies (Stearns, 1976; 1977). In order to test these hypotheses, juvenile survivorship must be measured in species exhibiting a range of larval types.

There have been several approaches to the problem (Table 1). The easiest approach has been to avoid the difficulty of estimating planktonic mortality by studying species with direct development, which allows more direct observation of survivorship (Menge, 1975; Spight, 1975; Race, 1982). Although these species indeed may have developmental mortality which is orders of magnitude lower than those with planktonic larvae (Strathmann, 1985), Table 1 shows a wide, overlapping range of survivorship among planktonic and direct development. Also, catastrophically high estimates of egg mortality have been observed during brooding in some populations of crabs with high incidences of nemertean egg predators (Wickham, 1979). But, obviously, this begs the question of measuring planktonic larval mortality.

Table 1. Estimates of larval survivorship for marine invertebrates

Species	Survivorship	Stage	Source
Gastropoda			
<i>Conus quercinus</i>	5.73×10^{-6}	larvae and early juveniles	Perron, 1986
<i>Conus pennaceus</i>	7.01×10^{-4}	brooded embryos to early juveniles	Perron, 1986
<i>Aplysia juliana</i>	8.40×10^{-7}	larvae and early juveniles	Sarver, 1979
<i>Thais lamellosa</i>	4.17×10^{-3}	encapsulated embryos	Spight, 1975
<i>Cerithidea californica</i>	4.23×10^{-1}	encapsulated embryos	Race, 1982
Bivalvia			
<i>Tapes philippinarum</i>	1.59×10^{-5}	larvae and early juveniles	Yap, 1977
<i>Mytilus edulis</i>	1.00×10^{-2}	larvae	Jørgensen, 1981
<i>Mya arenaria</i>	1.46×10^{-5}	larvae and early juveniles	Brouseau et al., 1982
	(range: 2.18×10^{-5} to 9.86×10^{-6})		
	4.98×10^{-4} to 0.0	larvae and juveniles	Brouseau et al., 1982
<i>Crassostrea gigas</i>	1×10^{-2}	larvae	Quale, 1964
Asteroidea			
<i>Leptasterias hexactis</i>	5.55×10^{-1}	brooded embryos	Menge, 1975
<i>Pisaster ochraceus</i>	2.56×10^{-9}	larvae and early juveniles	Menge, 1975
Bryozoa			
<i>Membranipora membranacea</i>	2.5×10^{-3} to 1.8×10^{-6}	larvae	Yoshioka, 1982
Cirripedia			
<i>Chthamalus fissus</i>	1973 4.87×10^{-4}	larvae	Hines, 1979
	1973 6.71×10^{-5}	larvae and juveniles	Hines, 1979
	1974 9.90×10^{-4}	larvae	Hines, unpublished
<i>Balanus glandula</i>	1959 6.20×10^{-5}	larvae and juveniles	Connell, 1970
	1960 6.40×10^{-5}	larvae and juveniles	Connell, 1970
	1973 1.16×10^{-4}	larvae	Hines, 1979
	1973 2.04×10^{-5}	larvae and juveniles	Hines, 1979
	1974 5.71×10^{-5}	larvae	Hines, unpublished
<i>Tetraclita squamosa</i>	1973 4.75×10^{-5}	larvae	Hines, 1979
	1973 4.07×10^{-6}	larvae and juveniles	Hines, 1979
	1974 3.80×10^{-6}	larvae	Hines, unpublished
Copepoda			
<i>Eurytemora affinis</i>	3.57×10^{-1}	larvae	Allan et al., 1976
<i>Acartia tonsa</i>	1.22×10^{-1}	larvae	Allan et al., 1976
<i>Euterpina acutifrons</i>	3.24×10^{-4}	larvae	D'Apolito and Stancyk, 1979
<i>Centropages typicus</i>	6.50×10^{-3}	larvae	Gaudy, 1976
<i>Euterpina acutifrons</i>	1.80×10^{-2}	larvae	Gaudy, 1976
<i>Acartia clausi</i>	4.00×10^{-2}	larvae	Gaudy, 1976
<i>Oithona helgolandica</i>	8.50×10^{-2}	larvae	Gaudy, 1976
<i>Paracalanus parvus</i>	1.90×10^{-1}	larvae	Gaudy, 1976
<i>Oithona nana</i>	5.50×10^{-1}	larvae	Gaudy, 1976
Decapoda			
<i>Pandalus jordani</i>	1971 1.95×10^{-2}	larvae	Rothlisberg and Miller, 1982
	1972 2.30×10^{-3}	larvae	

The simplest approach for planktonic larvae is to assume an equilibrium population, so that each female is replaced in her life time by two juveniles attaining maturity. Larval survivorship is then calculated as a part of juvenile survivorship from fecundity estimates. Menge (1975) estimated that the sea star, *Pisaster ochraceus*, produces 40 million eggs per female per year, resulting in a larval and early juvenile mortality rate of 0.9999999854 (survivorship = 2.6×10^{-9}). This, of course, does not separate larval and early juvenile mortality, nor does it measure fluctuations in survivorship. It also assumes that a female must produce two individuals per year to maintain a stable population, when in fact the replacement only need occur over a lifetime. With a life span estimated at 34 years (Menge, 1975), juvenile survivorship in *P. ochraceus* would be reduced to 7.64×10^{-11} . By assuming that larvae produced by a population are the ones that actually settle into the same area, fluctuations in larval survivorship can be estimated by differences in settlement densities from egg production calculated by measuring population density and size structure. Connell (1970) and Hines (1979) used this method to produce estimates of larval and juvenile survivorship in intertidal barnacles ranging from 1.2×10^{-4} to 3.8×10^{-6} , depending on the species, and these estimates fluctuated among years of study (Table 1). Brousseau et al. (1982) used a Leslie matrix with similar assumptions to estimate survivorship to settlement for the clam *Mya arenaria* ranging from 4.98×10^{-4} to 2.6×10^{-6} . However, larvae are rapidly dispersed in complex, though often directional nearshore currents, which can transport propagules long distances even in the normal time period of 2–8 weeks of many larvae (Palmer and Strathmann, 1981). Therefore, the assumption that larvae produced by a population become the recruits for the parental location is usually wrong. Estuarine and perhaps insular populations appear to be exceptions which retain larvae (Christy and Stancyk, 1982; Stancyk and Feller, 1986; Sulkin and Van Heukelem, 1982; Strathmann, 1982) and could provide better estimates of larval mortality calculated by difference from production and recruitment. In populations that have markedly synchronous spawning, it is possible to follow survivorship of larvae by sampling the cohort through time. Sampling mussel larvae this way, Jørgensen (1981) estimated a mortality of 13% per day over a 30 day planktonic period (survivorship = 1×10^{-2}), although he did not consider dilution during dispersion as a source of error. In a promising approach with fish larvae, Fortier and Leggett (1985) measured mortality of capelin by using a drogue to track a synchronous cohort of larvae moving through discrete water masses, and a similar approach should be possible with invertebrate larvae. In a rather different approach, Ayal and Safriel (1982) examined the effect of varying larval mortality on the Malthusian parameter (r) in closely related species of gastropods and showed the importance of short development and generation times regardless of the larval survivorship from 1×10^{-4} to 1×10^{-0} . Even with the limited data in Table 1, it is clear that there is enormous interspecific and temporal variability in larval survival in the plankton.

Mortality leading to variations in recruitment of easily detected juveniles occurs during two phases, the pelagic and the early post-settlement phase (Thorson, 1966; Muus, 1973). One step toward measuring larval mortality is to distinguish between the two, and several recent studies have provided measurements of early post-settlement survivorship both of sessile fauna on hard substrates emphasizing physical causes of mortality (Strathmann et al., 1981; Grosberg, 1981; Keogh and Downes, 1982; Wethey, 1984) and of softbottom fauna emphasizing interactions with adults (Woodin, 1976) as causes of mortality (Fretter and Manly, 1977; Sarver, 1979; Cameron and Schroeter, 1980; Wilson, 1980; Highsmith, 1982; Luchenbach, 1984; Woodin, 1985). Using the death assemblage for assaying newly

settled molluscs in soft sediments, Powell et al. (1984) showed that larval settlement is consistently underestimated and post-settlement survival is overestimated by about 90% compared to estimates from larger live juveniles. These errors would also result in overestimates of planktonic larval mortality when based on recruitment rates of larger individuals. In addition, several recent studies have documented specific sources of larval mortality in the plankton, so that at least the impacts of, for example, specific predators can be measured (Rumrill et al., 1985; Cowden et al., 1984; Pennington and Chia, 1984; Pennington and Chia, in press; Young and Chia, in press). Although these latter studies are largely laboratory-oriented, they provide considerably more information on the possible range of mortality rates in the plankton than general assertions that "mortality must be high to balance fecundity." Extension of this approach into the field holds promise, as exemplified by van der Veer (1985) for coelenterate predation on larval fish.

Nevertheless, proper evaluation of current life history theory requires accurate comparative data on larval mortality. The "bet hedging" hypothesis (Stearns, 1976; 1977) emphasizes variability in juvenile versus adult survivorship as the primary selective pressure shaping life history patterns. However, there remains considerable confusion about which specific aspects of this variation are important: the ratio of juvenile to adult mortality, the magnitude of juvenile mortality, the variability and predictability of juvenile survivorship, and/or the length and predictability of adult life. Perron (1986) provides comparative data on several of these aspects in *Conus* spp. with contrasting developmental modes and emphasizes the importance of juvenile/adult mortality ratio as a reflection of developmental mode. Although he does not provide data on intraspecific, temporal variability of these parameters, Perron's study illustrates the complexity of the problem and the need to provide complete estimates for these parameters in order to test for covariation of traits among closely related species. To my knowledge, however, similar analyses for other species are not available to evaluate the adequacy of the various aspects of larval mortality in predicting life history patterns.

COVARIATION AND EVOLUTIONARY CONSTRAINTS

One of the major shifts in recent analyses of life history strategies has been the move away from simplistic treatments in which traits vary along a unidimensional continuum between two extremes (e.g., an r-K continuum, Pianka, 1970). Instead, increasing emphasis is placed on analyzing combinations of traits, as summarized by Trendall (1982): "If a life history is an integrated assemblage of characters which function as a coadapted unit, then the ability of the life history to respond to the environment will depend upon the nature of the relationships among traits. Fixed relationships, which tie the change of any single trait to the changes of other traits, will limit both the extent and direction of life history change. Variable relationships place fewer restrictions on the change of individual traits and will allow increased flexibility in life history responses to the environment. Defining the extent to which traits are connected by fixed relationships is therefore a means of defining life history variation." Stearns (1980) pointed out that life history traits are often not free to coevolve under the influence of purely demographic forces, as assumed by deterministic (r- and K-selection) and stochastic (bet-hedging) models. Various biological constraints, physiological plasticity, heritabilities of differing complexity, and phylogeny all affect the evolution of life histories and can override demographic selection.

Increasingly, studies of marine invertebrate life histories are considering the importance of biological constraints. Brood weight in brachyuran crabs is limited

to about 10% of female body weight by the space available for yolk accumulation in the cephalothorax (Hines, 1982). Limitations on diffusion rates can restrict the spacing, size, and number of eggs in egg masses and capsules (Perron and Corpuz, 1982; Chaffee and Strathmann, 1984; Strathmann and Chaffee, 1984). Similar surface-to-volume limitations appear to prohibit brooding in larger sea stars, because larger animals can produce more eggs than they have space to brood (Strathmann et al., 1984). Reproductive output in other species such as tubiculous polychaetes which brood may also be limited by space (unpublished observations). However, brood area (maternal gill surface area) does not act as a morphological constraint on reproductive output in the small brooding clam *Transennella tantilla*, because the three-dimensional structure of the brood mass avoids this limitation (Kabat, 1985).

Developmental canalization (*sensu* Waddington, 1939; Gould, 1977) can sharply limit the range of life history variation. The evolutionary derivation of lecithotrophy and direct development from planktotrophy is usually considered to be irreversible (Jagerston, 1972). However, variability, flexibility, and exceptions exist (see above). Moreover, Strathmann (1978a; 1978b) indicates that while many groups (oligomera) do not reacquire a planktotrophic larval phase once it is lost, others (spiralia) have evolved new types of planktotrophic larvae several times. These differences in evolutionary flexibility of developmental mode are associated with functional aspects of the original larval feeding mechanism, degree of reorganization at metamorphosis, adult structure, and perhaps egg capsules with extra-embryonic nutrition. Perron (1986) suggests that developmental mode determines the suite of postlarval life history traits in *Conus* gastropods.

Body size and phylogenetic affiliation have significant effects on the covariation of life history traits in many groups of vertebrates, including amphibians (Salthe and Duellman, 1973; Kuramoto, 1978; Kaplan and Salthe, 1979), mammals (Leutenegger, 1979; Robbins and Robbins, 1979; Western, 1979; Western and Ssemakula, 1982; Stearns, 1983), birds (Western and Ssemakula, 1982), reptiles (Stearns, 1984; Dunham and Miles, 1985), and salmonid fish (Hutchings and Morris, 1985). Evolutionary constraints by lineage are also evident in life history strategies of invertebrate groups with sufficiently extensive comparative data. Spight (1975; 1981) showed significant differences among families and orders of prosobranch gastropods in developmental mode and its latitudinal distribution, and he calculated that taxonomic group accounts for more of the variations in developmental time than any other adaptive variable, with higher correlations at the superfamily level than for orders. Several groups of crustaceans exhibit phylogenetic differences in reproductive strategies (Reaka, 1979; 1980; Nelson, 1980; Phillips and Sastry, 1980; Hines, 1982), and larval patterns show constraints by lineage in euphausiids and decapods (Knowlton, 1974), stomatopods (Reaka, 1980; Reaka and Manning, in press), and brachyurans (Rice, 1980; Hines, 1986).

A major part of the shift toward more sophisticated analyses of suites of co-adapted life history traits has been the use of multivariate statistical approaches, including: analysis of covariance both to detect significant covariation and interaction of variables and to remove its effects on other variables (Spight, 1975; Hines, 1982; 1986; Stearns, 1983; 1984; Dunham and Miles, 1985); partial correlation (Hines, 1982) and stepwise multiple linear regression analysis (Buroker, 1985) to partition interactions of life history traits; cluster analysis to visualize groupings of species by suites of life history traits (Stearns, 1983), and principal component analysis to evaluate the relative importance of variables contributing to differences among life histories (Trendall, 1982; Stearns, 1984; Dunham and Miles, 1985). Trendall's (1982) work on mosquito fish showed that covariation

of traits does not follow the pattern expected if the life history were responding as a single, co-adapted unit, and that use of fixed relations between traits to define life history changes is not appropriate because traits vary with different degrees of independence. Stearns' (1984) analysis of the influence of body size and phylogeny in reptiles shows the difficulty and importance of evaluating both covariation of life history traits and evolutionary constraints by lineage. Apart from justified criticism of his data (Vitt and Seigel, 1985; Hedges, 1985), the importance of Stearns' statistical approach has been substantiated (Dunham and Miles, 1985) and indicates the need to assess life history traits at various taxonomic levels in order to partition the allometric variability from the group variation. However, there have been only a few attempts at this analytical approach for marine invertebrates: Spight's (1975; 1981) work on prosobranch gastropods, Hines' (1982; 1986) studies of brachyuran crabs, and a recent paper by Buroker (1985) on oysters. These statistical approaches require substantial comparative data sets with relatively complete estimates for the array of variables, but these data remain scattered and unorganized in the literature for most invertebrate groups.

CONCLUSIONS

Obviously, the five problem areas discussed here are not really distinct, and I have indicated some of their main interrelationships. The willingness of larval biologists to recognize these interrelationships has shifted research on life history strategies of marine invertebrates into the current transition. New research directions are emerging from the transition, as itemized below.

1. Considerations of developmental mode in the life histories of marine invertebrates should analyze continuous variables rather than making a priori categorical assignments to limited sets of patterns.

2. The energetics of larval development needs much more detailed study, with particular attention to: (a) good measurements of reproductive effort as a function of variations in the timing and frequency of reproduction, developmental mode, and the costs of reproduction; (b) variation in the actual caloric contents of eggs rather than size alone; (c) nutritional requirements of larvae, especially under more realistic field conditions of food availability and for the importance of food availability during critical developmental stages; and (d) the effect of delayed metamorphosis on larval energetics and viability.

3. Much more attention needs to be given to measuring variability and flexibility of larval and other life history traits, including reporting measures of stochastic variation and suboptimal developmental rates.

4. The paucity of measures of heritability of developmental, larval and other life history traits must be rectified through controlled breeding experiments.

5. Despite obvious technical difficulties, variation in larval mortality must be measured in the field if theoretical alternatives, such as the range of possible scenarios in the bet-hedging hypothesis, are to be resolved, and if the contribution of fluctuations in the larval phase to population dynamics are to be understood. Promising approaches toward better estimates of larval survivorship include: (a) isolating planktonic from early post-settlement phases of mortality by measuring the latter; (b) measuring predation rates of specific larval predators under controlled but naturalistic conditions; (c) contrasting larval production with larval recruitment, particularly in habitats such as estuaries and islands, where larval retention occurs; and (d) measuring mortality in cohorts of synchronously spawned larvae moving in currents of water tracked with drogues.

6. Physical or "design" constraints (particularly allometric relationships of body

size) and developmental canalization can limit the range of variation in traits, and they must be taken into account in comparisons at all taxonomic levels of life history patterns.

7. Phylogenetic affiliation also can limit variation and covariation among suites of life history traits. Research on marine invertebrates should move away from simplistic, uni-dimensional approaches and should move toward multivariate techniques of analysis in order to measure the effect of lineage and to evaluate the relative contribution and degree of linkage among traits in life history variation.

8. There is a substantial need both for integrating much of the scattered data and for taking more complete, quantitative data on larval and life history variables of marine invertebrates, so that theoretical considerations can be developed with more realistic assumptions and tested statistically. In addition to groups for which there are extensive but scattered data, there are major groups which largely have been ignored, e.g., recent attention to corals. Greater attention also should be given to species of zoogeographic interest, such as those exhibiting endemism and those occurring in provinces and clades of extensive speciation.

ACKNOWLEDGMENTS

Stimulation for this paper came from the Larval Biology Workshop held at Friday Harbor Laboratories, University of Washington, in March 1985. I have attempted to summarize and incorporate the major ideas and problems posed by that group of larval biologists, and I am grateful to them for their input. However, I have also introduced relevant research by others who did not participate in the Workshop, as well as imposing my own selective view of historical and current research trends. I do not suggest that my emphases represent a comprehensive review nor any formal consensus of larval biologists. I am grateful to A. Cameron and R. Strathmann for their support and assistance at the workshop. A. Cameron, P. Haddon, E. Scully, and R. Strathmann gave helpful comments on earlier drafts of the manuscript. This work was supported in part by funds from the Office of Naval Research, Smithsonian Research Opportunities Fund, and the Smithsonian Marine Station at Linkport. Contribution no. 182 of the Smithsonian Marine Station.

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