Copepod reproductive strategies: life-history theory, phylogenetic pattern and invasion of inland waters

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Abstract

Life-history theory predicts that different reproductive strategies should evolve in environments that differ in resource availability, mortality, seasonality, and in spatial or temporal variation. Within a population, the predicted optimal strategy is driven by tradeoffs that are mediated by the environment in which the organisms live. At the same time, phylogenetic history may circumscribe natural selection by dictating the range of phenotypes upon which selection can act, or by limiting the range of environments encountered. Comparisons of life-history patterns in related organisms provide a powerful tool for understanding both the nature of selection on life-history characters and the diversity of life-history patterns observed in nature. Here, we explore reproductive strategies of the Copepoda, a well defined group with many phylogenetically independent transitions from free-living to parasitic life styles, from marine to inland waters, and from active development to diapause. Most species are iteroparous annuals, and most (with the exception of some parasitic taxa) develop through a relatively restricted range of life-history stages (nauplii and copepodids, or some modification thereof). Within these bounds, we suggest that there may be a causal relationship between the success of numerous copepod taxa in inland waters and the prevalence of either diapause or parasitism within these groups. We hypothesize that inland waters are more variable spatially and temporally than marine habitats, and accordingly, we interpret diapause and parasitism as mechanisms for coping with environmental variance. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The evolution of any character under natural selection is mediated through its impact on life-history. Thus, a central challenge of biology is to understand the effect of each trait that an organism possesses (whether molecular, developmental, physiological, morphological, or behavioral) on survival and reproduction in the environment in which it lives. One route to understanding the linkages between traits and environments is through a comparison of the life histories of organisms sharing a common ancestry but living in different habitats. The Copepoda are a particularly good group for such an exploration: they are clearly monophyletic, and inhabit a variety of

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environments including epibenthic and interstitial habitats, the open ocean pelagic zone, estuaries, inland waters, ground water, moist terrestrial soils, and symbiotic associations with a wide variety of animal taxa (Huys and Boxshall, 1991): a single Bauplan challenged in many different ways.

Each major habitat in which copepods are found has experienced repeated independent invasions (Huys and Boxshall, 1991). Ancestral copepods are assumed to have been marine epibenthic animals. The Platycopioida and the Misophrioida have remained in this habitat, as have many of the Harpacticoida and Cyclopoida. The marine pelagic zone has been colonized by five orders (the Calanoida, the Mormonilloida, and a few Harpacticoida, Cyclopoida, and Poecilostomatoida) via at least 10 independent invasions. According to Huys and Boxshall (1991), inland waters have been independently invaded 19 times by six copepod orders (the Calanoida, Cyclopoida, Harpacticoida, Gelyelloida, Poecilostomatoida, and Siphonostomatoida). A number of groups (the Poecilostomatoida, the Siphonostomatoida, and the Monstrilloida, as well as a few species of Cyclopoida and Harpacticoida) have taken on associations with a variety of marine and freshwater animals, often as parasites. These symbiotic relationships have apparently been independently established many times.

These multiple colonizations of distinct ecological habitats provide an opportunity to study the association between life-history traits and environments. Does a particular environment select for a narrow range of survival and reproductive characteristics in all taxa found there? To what extent are closely related species constrained to respond to a particular selection regime in a narrowly defined way, especially in comparison with more distantly related taxa? Do particular lineages possess distinct life-history traits that facilitate the invasion of some habitats? To ask such questions, we need a formal framework that can be used to understand what traits should be favored under any given set of ecological conditions or phylogenetic constraints. That framework is life-history theory.

The theory of life-history adaptations is a formal consideration of the limitations placed by either material resources or time on reproduction and survival. The result of limited material resources such as energy or nutrients is that there are tradeoffs in the allocation of those resources to different functions.

2. Allocation

Two fundamental life-history allocation ''decisions'' faced by organisms are (1) how to apportion the resources invested in reproduction between offspring size and offspring number, and (2) how much resource to invest in current reproduction versus how much to save for future survival and reproduction. The answers to both questions depend upon survival probabilities of either the offspring or the parent and offspring, parameters which will certainly differ for copepods living in different habitats.

In his paper ''Copepodology for the ornithologist,'' Hutchinson (1951) pointed out that there might be tradeoffs between clutch size and egg size among copepods experiencing differing selection regimes. The theoretical relationship between investment in the fitness of individual offspring and investment in offspring number was formally developed by Smith and Fretwell (1974). They proposed that the fitness of a parent increases as a function of the product of each offspring's fitness times the total number of offspring produced. If, in addition, offspring fitness initially increases as investment per egg increases, but then levels off, there is an intermediate optimal investment per offspring. This relationship was recently explored for the Copepoda by Poulin (1995). In analysis of 71 families representing seven orders, with correction for phylogenetic contrasts (Harvey and Pagel, 1991), he found a significant negative relationship between change in relative clutch size and change in relative egg size. Unfortunately, there is not space here to further evaluate his stimulating findings.

A critical assumption of all reproductive allocation models has been that larger offspring are more fit, which may be correct when provisioning offspring increases their ability to survive between patches of food, to avoid potential predators, or to find a host. Large size, however, may also increase vulnerability to predation when a predator hunts either visually (Brooks and Dodson, 1965; O'Brien, 1979), or selects prey that yield the greatest resource supply per feeding effort (i.e., as predicted by optimal foraging theory, see Stephens and Krebs (1986)).

Certainly, there can be a cost to producing large clutches of eggs in the presence of fish predation (Hairston et al., 1983; Winfield and Townsend, 1983; Svensson, 1995). Furthermore, size-selective predation may be a selection force acting on the size of individual offspring and hence indirectly on egg size, as Kerfoot (1974) proposed for the ''cladoceran'' *Bosmina longirostris*. It would be instructive to modify the juvenile survival function in allocation models that address these tradeoffs (e.g., Smith and Fretwell, 1974; Winkler and Wallin, 1987) to account for the possibility that predation intensifies as both clutch size and offspring body size increase.

The second allocation question above asks when should an organism be semelparous and when iteroparous? For most copepods, which reproduce during only one year, iteroparity in the adult stage means that the animal produces more than one clutch of eggs during the reproductive season, i.e., what Begon et al. (1990) call an ''iteroparous annual.'' We include in this definition the few copepod species that take longer than one year to mature (e.g., Elgmork, 1965; Schminke, 1982), because they, almost certainly, exhibit only a single season of reproduction. The basic theory concerning how often to reproduce was laid out by Charnov and Schaffer (1973) (see also Charlesworth (1980) and Winkler and Wallin (1987)), who conclude that high adult survival relative to juvenile survival, and a low rate of population increase, favor iteroparity. The case of iteroparous annuals will differ mathematically (and it would be useful to work out the details), but the logic would seem to be the same: high relative adult survival and slow population growth should favor multiple bouts of reproduction.

Onychodiaptomus sanguineus, which inhabits lakes and ponds throughout northeastern North America, is typical of many copepods that live less than a single year, but produce multiple clutches when they mature. Braner and Hairston (1989) estimated mortality rates for both naupliar and copepodid stages for two cohorts of a population of this species from population data fitted using a numerical algorithm. The population, living in Bullhead Pond, Rhode Island, has two cohorts per year, one in winter and the other in spring. In both cohorts in 1985, adult survival between clutches far exceeded juvenile survival: by a factor of 2.5 in winter and by a factor of 26.7 in the spring. This suggests that ''annual iteroparity'' should be favored. Now, if we use the daily adult mortality rate to calculate the probability of an adult surviving all the way through to the following year, the value falls well below juvenile survival (adult survival/juvenile survival = 0.56 using winter cohort data, and $\ll 0.001$ using spring cohort data), demonstrating that reproduction in multiple years should not be favored.

Allan (1976) and Allan and Goulden (1980) have pointed out for freshwater zooplankton communities that population growth rate is low for calanoid copepods relative to that for rotifers and cladocerans. In contrast, adult survival is probably generally high for copepods compared with these two other taxa because copepods are better at escaping predation (Drenner and McComas, 1980; Hambright and Hall, 1992) and survive better under low food or poor food conditions (Lampert and Muck, 1984; Richman and Dodson, 1983). Both trends are consistent with annual iteroparity.

Copepods appear generally to be iteroparous annuals, including the species previously discussed, as well as other calanoids (e.g., three *Acartia* species studied by Lonsdale (1981) and George (1990) and *Eurytemora herdmani* studied by George (1985)), cyclopoids (e.g., *Oithona colcarva*, Lonsdale, 1981; *Metacyclops minutus*, Maier, 1992), the epibenthic estuarine harpacticoid *Coullana canadensis* (Lonsdale and Levinton, 1985), and several marine parasitic species (e.g., the siphonostomatoids *Lepeophtherius thompsoni* and *L. europaensis*, De Meeüs et al., 1993). It may be that not all copepods have an iteroparous-annual life-history pattern, but we were unable to find clear exceptions reported in the literature. Does the general pattern of annual iteroparity seen in virtually all other members of the Copepoda represent a plesiomorphy of the group? Dussart and Defaye (1995) pointed out that among Crustacea, ''copepods have been cited as possessing the most complete example of metamorphosis.'' Is the conserved reproductive pattern of copepods constrained by a life-cycle which mandates multiple discrete immature stages? That is, does a long period of immature development (dictated by the large number of life-history stages), combined with the relatively brief interclutch interval, mandate the high adult relative to juvenile survival?

3. Timing

With timing questions, we ask when during the life of an organism should a particular life-history character be expressed. The answer depends to varying degrees upon the intrinsic nature of the life cycle of the organism and upon the extrinsic environment.

3.1. Ontogenetic niche shifts

Copepods possess a complex life history composed of many distinct instars. Primitively, they have six naupliar stages followed by six copepodid stages, the last of which is the adult. The most dramatic alteration in body form occurs at the transition from the last naupliar stage (typically NVI) to the first copepodid stage (CI) in which segmentation, size, and appendage structure all change substantially (Dussart and Defaye, 1995). Is there an optimal point in the life of a copepod for this metamorphosis? Does the optimal time vary depending upon the selection imposed by the environment in which the copepod lives? Twombly (1996) recently investigated the appropriateness of models of amphibian metamorphosis for the cyclopoid copepod *Mesocyclops edax* and concluded that, in general, the size at metamorphosis appears to be tightly constrained at least in terms of phenotypic plasticity.

One approach to the question of optimal time at metamorphosis is that developed by Werner and Gilliam (1984) who proposed that niche shifts occur so as to maximize fitness. By assuming that fitness is measured as the potential growth rate of a population possessing a particular set of life-history characteristics, they showed that the optimum size for life-history shift between two distinct environments (which we take here to be the point of metamorphosis) is the one that minimizes the ratio of instantaneous mortality rate (μ) to instantaneous growth rate (g) (Werner and Gilliam, 1984; Werner, 1986). Many cyclopoid copepods switch from herbivory to being omnivorous at the transition from nauplius to copepodid. They also alter their swimming ability (and hence predator escape ability) markedly as they change morphology to a more fusiform body shape and add swimming legs. We can ask if these changes take place at the size that optimizes μ/g. Is there some size, as a copepod grows, at which μ/g is lower for

a copepodid than for a naupliar life style? Is this the size at which the metamorphosis takes place?

An application of the broad predictions of the Werner and Gilliam (1984) theory and its extensions (e.g., Werner, 1986, 1988; Rowe and Ludwig, 1991) is a comparison of the patterns of metamorphosis across copepod taxa with different life styles. For example, the theory predicts that the life-history stage living in the environment with the highest available resources (hence highest g) and the lowest mortality should dominate the life cycle. For caligid copepods that are parasitic on fish, the chalimus, preadult and adult stages living attached to the host are undoubtedly both better fed and better protected from mortality than are the free-swimming, dispersing naupliar stages. Theory (and common sense) predicts that the transition from the free-swimming to the parasitic stages should occur early in the life of the copepod, at a relatively small size. This is in fact the case: the 13 caligid species reviewed by Lin and Ho (1993) have only two naupliar instars followed by a single copepodid instar (that finds and attaches to the host) and then six to eight parasitic instars including four to six chalimus stages, one or two preadult stages and the adult. The non-feeding, lecithotrophic nauplii are apparently retained purely as dispersal stages. Some parasitic taxa have completely eliminated the naupliar stages and develop directly to the first or second copepodid stage (e.g., members of the Siphonostomatoida, Kabata and Cousens, 1973; members of the Cyclopoida, Goudey-Perrière, 1979). In contrast, there are a number of parasitic copepod taxa that are less closely associated with their hosts and so presumably provide a range of mortality and growth functions that would be interesting to compare. The Ergasilidae, for example, are only parasitic as adult females and have retained all six naupliar (planktotrophic) and all five copepodid stages (G. Boxshall, personal communication). The Monstrilloida are parasitic in the larval stage and free-living as non-feeding adults. Does the transition to adult in this taxon take place at a larger relative size than in taxa with free-living nauplii and parasitic later stages?

3.2. Diapause timing

All environments vary temporally and many can become limiting to growth, reproduction, or survival.

One way that copepods can avoid harsh periods is to enter diapause. This neurohormonally mediated state of arrested development (Tauber et al., 1986) leads to a substantial reduction in potential population growth rate due to lengthened generation time. As a result, diapause must have substantial fitness consequences, and there should be natural selection to optimize its timing and duration.

Theory for optimal diapause timing was initially developed by Cohen (1970). The intuitive result of his model is that an environment becomes critically harsh when the expected rate of population change in the active state falls below that in the diapausing state. Hairston and Munns (1984) extended this model for the situation in which the timing of the catastrophe date varies stochastically between years. Using numerical simulation, they showed that the ESS timing of diapause moves progressively earlier in the season, and further from the mean catastrophe date, as environmental unpredictability increases. Field data on the spring transition from production of immediately hatching eggs to diapausing eggs for two populations of *Onychodiaptomus sanguineus* fit theoretical predictions well (Hairston and Munns, 1984; Hairston, 1987). In these two populations, catastrophe dates were driven by the seasonal onset of predation. For a near-shore marine copepod species, Marcus (1979, 1982) proposed that the August to September onset of diapausing–egg production by *Labidocera aestiva* is an adaptation to the approach of winter conditions.

3.3. Duration of diapause

Once a copepod enters diapause, how long should it remain in that state? This question has both short-term and long-term components. The short-term question of when during the season diapause should terminate has been explored for *O. sanguineus* by De Stasio and Hairston (1992), and will not be discussed further here. In the long term, the question concerning when to emerge from diapause is: what fraction of the dormant individuals should terminate diapause in any given year? Cohen's theory for plant seed germination (Cohen, 1966) can be applied equally to copepods making diapausing eggs: all eggs should hatch the year after they are produced if the variance in reproductive success is small. If this

variance is high, the fraction of eggs remaining in diapause annually should be roughly equivalent to the probability that per capita reproduction is zero or nearly zero. Ellner (1985) went on to demonstrate that the acquisition of an evolutionarily stable hatching fraction will result in a reduction in fluctuations in population size: the population's harmonic mean growth rate should correlate strongly with the survivorship of its diapausing eggs.

The numbers of diapausing eggs in buried aquatic sediments (i.e., ''egg banks'') of centropagoid copepods are impressive. Typical egg densities in both marine and inland aquatic environments range between 10^4 and 10^6 m^{-2} (reviewed by Hairston (1996)). However, the egg ages where sedimentation rates have been obtained can vary widely. Maximum ages range between 2 and 300 years, and mean ages can be as low as one year and as high as 50–70 years (Marcus et al., 1994; Hairston et al., 1995; Hairston, 1996). Thus, depending upon the species or the habitat, or both, some variable fraction of copepod diapausing eggs delays hatching. One question is: do these eggs contribute to future populations, or are they just ''the living dead'' —viable eggs that will never have the opportunity to hatch? For *O. sanguineus*, data from emergence traps placed over the sediment surface at Bullhead Pond, RI, showed that eggs continue to hatch for at least 3 years without new input from the water column (De Stasio, 1989), and similar results have been obtained for diaptomid copepods from a large lake in New York (Hairston and van Brunt, 1994; Hairston, personal observation). However, much more research needs to be carried out on this topic before we have sufficient data to begin to explore the ways that copepod egg banks contribute to the population dynamics of different species.

Prolonged diapause (as opposed to seasonal diapause) is fundamentally a mechanism to reduce variance in annual population growth rate. Production of a long-lived diapausing stage slows the rate of population increase in years that are favorable for survival and reproduction, but the emergence of these stages also prevents the elimination of the population in bad years. Other life-history characters can also serve as variance reducing mechanisms. Both long adult life span (multi-year iteroparity) and dispersal are commonly hypothesized to be a mechanisms to over-

come years of local recruitment failures (Levin et al., 1984; Cohen and Levin, 1985; Rees, 1993, 1994), although long adult life span is virtually absent in the Copepoda.

Within the context of exploring the linkages between habitat and the phylogenetic distribution of life-histories, the Copepoda present an interesting picture. Four distinct clades have independently evolved diapause (Table 1, top). Of these, three clades (three families of the calanoid superfamily Centropagoidea, and one family each in the harpacticoids and the cyclopoids) have successfully invaded inland waters. Of the species that diapause, only the calanoid Calanidae, which have a non-encysting diapause of less than one year, have failed to invade inland waters. Within the Centropagoidea, diapausing eggs are found in six of seven families, and Bayly (1992) and Lindley (1992) have suggested that this trait ''pre-adapted'' the group for invading inland waters. Lindley (1992) proposed that their tough chorion facilitated the invasion of inland waters by members of this taxon by protecting the embryos from osmotic stress. The link between diapause and invasion of inland water is consistent with the same

Table 1

Evolution of diapause, invertebrate parasitism, and fish parasitism in the Copepoda, and whether acquisition of the trait was associated with invasion of inland water habitats

Order	Clade: diapausing stage	Invade inland waters?
Acquisition of diapause		
Calanoida	Calanidae: copepodid	No
	Centropagoidea: egg	Three times: Acartiidae, Centropagidae, Diaptomidae
Cyclopoida	Cyclopidae: copepodid	Yes
Harpacticoida	Canthocamptidae: copepodid	Yes
Acquisition of invertebrate parasitism		
Calanoida	Aetideidae	No
Cyclopoida	Archinotodelphyidae/Notodelphyidae/Mantridae	No
	Ascidicolidae/Ozmanidae	Yes: Ozmanidae
Harpacticoida	Cancrincolidae	(Terrestrial invasion)
	Canuellidae	No
	Diosaccidae	No
	Laophontidae	No
	Paramesochridae	No
	Peltidiidae	No
	Porcellidiidae	No
	Tegastidae	No
	Thalestridae	No
	Tisbidae	No
Monstrilloida	Monstrillidae	No
Poecilostomatoida/Siphonostomatoida	Ancestor to these orders	Yes: Sabelliphilidae
Acquisition of fish parasitism		
Cyclopoida	Lernaeidae	Yes
Siphonostomatoida	Siphonostomatoida	Twice: Caligidae, Lernaeopodidae
Poecilostomatoida	Bomolochidae/Telsidae	No
	Chondracanthidae/Lernaeosoleidae	No
	Ergasilidae	Yes
	Pharodidae	No
	Philichthyidae	No
	Shiinoidae	No
	Taeniacanthidae	No
	Valgamidae	Yes

broader association between these traits documented by Hairston and Cáceres (1996) for all crustaceans. However, the prevalence of diapause in inland-water populations can also be interpreted as a variance-reducing mechanism. Copepods uniformly lack inter-annual iteroparity (see above), and dispersal between inland-water habitats is likely to be completely unreliable as a means of surviving short-term catastrophes. Hairston and Cáceres (1996) proposed that an alternative explanation to Lindley's (1992) is that taxa with the ability to produce a diapausing stage may be better suited to long-term persistence in inherently variable inland-water habitats than taxa without this trait. The fact that both harpacticoid and cyclopoid families which possess diapause in the chorionless copepodid stage have also successfully invaded inland waters supports this interpretation.

One calanoid species that has invaded inland waters, apparently without diapause, is *Scenecella calanoides* in the Aetideidae (Table 2). The population dynamics of this species is little studied, however, and given the prevalence of diapausing eggs among other inland-water calanoids, closer inspection is warranted. Nevertheless, it would not be surprising to find that *Scenecella* truly lacks diapause. It is typically associated with deep, cold lakes of formerly glaciated regions which are inhabited by other glacial relict taxa such members of the Mysida that also lack diapause (Hairston and Cáceres, 1996). Populations of these species would be doomed to extinction if they experienced even one zero-recruitment year; apparently the large lakes in which they live are sufficiently invariant that this has not occurred. Furthermore, each of the other three calanoid families in inland waters is represented by multiple genera and large numbers of species, whereas the Aetideidae only has a single species in this habitat. This further suggests that a lack of diapause may be a factor limiting diversification.

Of the two free-living cyclopoid families that have invaded inland waters, the Cyclopidae diapause as copepodids, whereas the Oithonidae apparently do not (Table 2). In the harpacticoids, eight families have invaded inland waters (Dussart, 1967, modified by H.-U. Dahms personal communication), although many of these invasions are minor or inadequately described (H.-U. Dahms personal communication). Only the Canthocamptidae has been reported to have

Table 2
Invasion of inland waters by Copepoda taxa, and whether the invasion was associated with diapause or parasitism

Order	Family	Diapause?	Parasitic?
Calanoida	Aetideidae	?	No
	Centropagidae	Egg	No
	Diaptomidae	Egg	No
	Temoridae	Egg	No
Cyclopoida	Oithonidae	?	No
	Cyclopidae	Copepodid	No
	Ozmanidae [a]	No?	Invertebrate
	Lernaeidae [a]	No?	Fish
Gelyelloida	Gelyellidae	No?	No
Harpacticoida	Ameiridae	?	No
	Canthocamptidae	Copepodid	No
	Chappuisiidae	?	No
	Cletodidae	?	No
	Harpacticidae	?	No
	Laophontidae	?	No
	Phyllognathopodidae	?	No
	Parastenocarididae	?	No
Poecilostomatoida	Sabelliphillidae	No?	Invertebrate
	Ergasilidae	No?	Fish
	Valgamidae	No?	Fish
Siphonostomatoida	Lernaeopodidae	No?	Fish
	Caligidae	No?	Fish

For diapause, question marks denote that the absence of this trait is difficult to establish for lack of study; ''no'' indicates diapause is probably absent.
[a] The Ozmanidae and Lernaedae probably represent a single freshwater invasion.

diapause (Table 2), however, little is known about the ecology of many species, and it seems highly likely that the many species living in temporary habitats possess diapause even though it has not been observed. Finally, it is significant that the Cyclopidae and the Canthocamptidae are by far the most successful inland-water families in terms of diversity and geographic distribution of their respective orders. There are some 35 genera and 590 known species in the Cyclopidae in inland waters and only a single genus with three species in the Oithonidae (Dussart and Defaye, 1985), and there are some 23 genera and well over 100 known species in the Canthocamptidae, while the other seven harpacticoid families in inland waters contain a total of 13 genera with about 50 known species (Dussart, 1967; Dussart and Defaye, 1995, H.-U. Dahms personal communication). Given the pattern of success and diversification in those families that have some form of dia-

pause, it will be important to look carefully for diapause in all inland-water taxa before concluding that the trait does not exist.

3.4. Diapause, dispersal and parasitism

Prolonged diapause reduces fitness variance by providing a mechanism for averaging the environment over time. Dispersal, in contrast, reduces fitness variance by averaging the environment spatially. Theoretical treatments suggest that when dispersal probability is high, prolonged diapause is less likely to evolve (Levin et al., 1984; Cohen and Levin, 1985). Among the pelagic freshwater Copepoda, members of the Calanoida have diapausing eggs that apparently have a greater capacity for survival over multiple years and decades than do the late-instar diapausing Cyclopoida. Consistent with theory, the Cyclopoida appear to be more effective dispersers than Calanoida; e.g. appearing much earlier in the time-course of colonization of newly dug ponds (Hairston and Cáceres, 1996). At broader ecological and taxonomic scales, we can propose that if diapause is more prevalent among inland-water copepods than it is among marine copepods, we might expect this to be associated with an opposing trend in dispersal. It seems logical to propose that effective dispersal distance must be greater for marine copepods than it is for inland-water taxa, if for no other reason than that inland habitats are interrupted by uninhabitable stretches of dry land. The challenge here is to find an independent measure of effective dispersal. One possibility is to use selectively neutral molecular genetic markers to quantify the geographic structure of copepod species. All else being equal, larger genetic differences between populations reflect lower dispersal rates. To test this hypothesis, we surveyed the modest literature on copepod genetic structure. Although studies are often conducted on different spatial scales or using genetic markers evolving at different rates, we were able to obtain comparable estimates of genetic distance for allozymes in five species of marine (includes estuarine) copepods and six species of inland-water copepods (Table 3). Plots of genetic distance by geographic distance for all pairwise populations within each study revealed no obvious effect of the differing spatial scales examined in each species. Thus, summarizing genetic structure by a single number in each species is unlikely to be biased.

Table 3
Genetic differentiation within species of calanoid copepods

Habitat	Family	Species	Average D	Number of populations	Reference
Marine	Acartidae	*Acartia californiensis*	0.111	2	Trujillo-Ortiz et al., 1995
		Pseudodiaptomus inopinus	0.020	3	Carol Eunmi Lee, pers. commun.
	Calanidae	*Calanus australis*	0.191	8	Afanas'ev et al., 1989 (2 polym. loci)
		Undinula darwini	0.147	11	Afanas'ev et al., 1989 (2 polym. loci)
	Metridiidae	*Metridia pacifica*	0.060	13, 16	Bucklin, 1989, 1991
	Pontellidae	*Labidocera aestiva*	0.165	4	Bucklin and Marcus, 1985
	Pseudocalanidae	*Pseudocalanus acuspes*	0.0003	8	Sévigny et al., 1989 (1 locus)
		Pseudocalanus minutus	0.0003	6	Sévigny et al., 1989 (1 locus)
		Pseudocalanus moultoni	0.003	3	Sévigny et al., 1989 (1 locus)
		Pseudocalanus newmanii	0.009	8	Sévigny et al., 1989 (1 locus)
		Average:	0.071		
Inland water	Temoridae	*Eurytemora affinis*	0.460	7	Carol Eunmi Lee, pers. commun.
	Diaptomidae	*Hesperodiaptomus arcticus*	0.385	3 regions	Boileau, 1991
		Hesperodiaptomus victoriaensis	0.192	2 regions	Boileau and Hebert, 1988
	Temoridae	*Heterocope septentrionalis*	0.124	27	Boileau and Hebert, 1991
		Average:	0.290		

For each species, the average for all values of Nei's D between population pairs is given. Plots of genetic distance (D) by geographic distance between populations did not reveal marked isolation by distance in any species. Studies with low numbers of polymorphic loci are noted. *Hesperodiaptomus arcticus* is hypothesized to contain three separate species by Boileau (1991) based on the high genetic differentiation among populations.

Table 3 shows that marine copepods have significantly less genetic differentiation (as measured by Nei's (Nei, 1975), genetic distance, *D*) between populations than inland-water species ($F = 13.03$; $p < 0.004$). Although there are not enough data to control for phylogeny in any systematic way, this result is consistent with the hypothesis that marine species disperse more frequently than those from inland populations. We conclude that elevated spatial dispersal among marine populations does, in general, decrease genetic differences among populations, and that these species should experience less selective pressure to reduce environmental variance via the temporal-dispersal mechanism of diapause.

A very different way for organisms to reduce recruitment variance (i.e., besides spatial or temporal averaging) is for them to adapt to living in a less variable environment. The Gelyelloida, for example, have invaded inland waters (Table 2) by living in subterranean springs, which are presumably relatively invariant compared with other inland habitats. Other, much more diverse groups of copepods have become parasitic, and it may be that a byproduct of the repeated transitions to this mode of life is a reduction in micro-environmental variance. By using the homeostatic abilities of the host organism, a parasite resides in a habitat that varies less than the outside world in physical stress, food availability, and predation risk. It is revealing, then, that a second major route to the successful invasion of inland waters (i.e., other than diapause) appears to be via parasitism. Using Poulin's analysis (Poulin, 1995), together with additional information, we find that of the 22 copepod families that have representation in inland waters, seven are parasitic (Table 2). Further, parasitism on fish appears to have been a more successful route to invading inland-water habitats than parasitism on invertebrates. Five of the parasitic inland-water families have fish hosts, whereas only two have invertebrate hosts (Table 2). In addition, of ten clades that are parasitic on fish, four have invaded inland waters, one of them twice (Table 1, bottom), whereas of 15 clades that are parasitic on invertebrates, only two have invaded inland waters (Table 1, middle). If this difference between invasion via fish or invertebrates is real (the sample size is too small for a statistical test), the reason may lie in the far lower invertebrate diversity in inland water than

in marine habitats, in the fact that homeostasis is generally more tightly controlled in fish than in invertebrates, or in the higher dispersal rates that come with an association with fish than with invertebrates.

Taken together, copepods that exhibit either diapause or parasitism account for at least 12 of the 22 families present in inland waters, and they account for all of the highly successful invasions. Finally, it is interesting that there are no copepod taxa that exhibit both diapause and parasitism, even though both traits have evolved independently within the calanoids, cyclopoids and harpacticoids. This again suggests that these two traits may be alternative adaptations to a single selective pressure.

4. Conclusions

Despite the fact that copepods have successfully taken up life in a wide variety of habitats, their basic life-history remains relatively conserved: adults that mature to produce multiple clutches of eggs during a single year. Most are iteroparous annuals. Postembryonic development always includes a fairly familiar set of instar types: nauplii and copepodids (including adults). The only exceptions are the elimination of nauplii and the introduction of the chalimus by some parasitic taxa. McKinney and McNamara (1991) propose that much of evolution can be attributed to heterochrony; that ''the vast majority of differences among closely related organisms are due to simple changes that are manifested relatively late in ontogeny.'' For the Copepoda, Huys and Boxshall (1991) discuss several morphological features, such as the separation of the genital and first abdominal somites, the sixth legs, and the geniculate antennules, whose interspecific variation can be interpreted as heterochronic in nature. Certainly, the loss or addition of instars, and the numbers of these stages relative to the major nauplius-to-copepodid metamorphosis are evolutionary changes that must have as an underlying basis alternations in the timing of developmental events. But, why are the differences between copepod orders not more dramatic, especially given the variety of environments to which they are exposed? Is it that the scope of copepod ontogeny is for some reason bounded? Or, is it that

the copepod ontogenetic template is highly successful with broad applicability to a wide variety of conditions?

Not only is more research required on phenotypic and genetic variation within species, but such studies need to be coupled with carefully chosen comparisons between taxa with different levels of relatedness living in different types of environments. For this purpose, phylogenetic hypotheses must be constructed that attract some broad level of consensus, and these must be based on characters that are independent of the adaptively significant life-history traits we hope to understand. Molecular data are ideal for this purpose. In addition, much more information is needed on the basic ecology of taxa living in the unusual habitats in which copepod species sometimes occur (e.g., terrestrial leaf litter, ground water, deep sea, various host organisms). Combining studies of interspecific variation and phylogeny with a thorough knowledge of the selection pressures exerted by different environments will be a powerful route to understanding the origin and maintenance of the diversity of copepod life histories.

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