

Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species

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Summary

Study of latitudinal variation in seasonality of reproduction and recruitment of benthic marine invertebrates is useful in generating and testing hypotheses about causal factors acting on reproduction such as temperature and larval food supply that might be altered by changes in world climate. Analysis of latitudinal variation in reproductive patterns might be made with comparisons (a) among species with a common phylogenetic history from different latitudes and habitats and (b) among phylogenetically different taxa from the same location. Hypotheses on variation of reproductive seasonality with latitude are tested here with results of a study on nine species of caridean and two species of sicyoniid shrimp sampled from a tropical seagrass meadow in Puerto Rico. Breeding condition was determined by the presence or absence of incubated embryos (carideans) and the state of ovarian development in both carideans and sicyoniids. Recruitment was estimated from the percentage of individuals of monthly population samples in the juvenile size classes. Comparison of reproductive patterns among tropical, subtropical, and cool temperate *Sicyonia* spp. supports the paradigm of continuous reproduction in the tropics with increased restriction of breeding season with an increase in latitude. A greater intensity of breeding effort appears to accompany the shorter breeding period associated with an increase in latitude. At the tropical site most females of all caridean species carried embryos during all months of the year. With the onset of sexual maturity, caridean females produced consecutive broods for the rest of their relatively short (< 6 month) life span. In both sicyoniid and caridean species, recruitment occurred throughout the year but was highly variable, i.e., episodic rather than truly continuous or seasonal. Patterns of recruitment were highly concordant among but not between sicyoniid and caridean species, indicating that different sets of environmental factors controlled recruitment in the two groups. It is suggested that simultaneous study of adult reproduction and larval ecology is necessary to understand patterns of reproduction and recruitment. Coordinated effort on a global scale in studying latitudinal variation in reproduction and recruitment is suggested in order to predict the consequences of climate change on commercially and ecologically important marine invertebrate species.

Introduction

Making generalizations about biological phenomena from empirical studies is a useful and necessary tool for summarizing information on those phenomena. More importantly, such generalizations or general principles serve a heuristic function by acting as a model or paradigm for making and testing hypotheses on causal factors or selective pressures that may be responsible for the patterns observed. Quite often generalizations are oversimplifications that do not hold up as more studies are conducted on the biological phenomenon of interest and contradictory results are encountered. The paradigm is then either discarded or modified, but in the process new, often important information is discovered, and our understanding of the biological world increases.

Generalizations about latitudinal variation in annual patterns of reproduction in near-shore, benthic marine invertebrates have been useful in suggesting the underlying environmental factors that might account for the patterns observed. Orton (1920) hypothesized that relatively constant temperature conditions in tropical seas with high water temperatures year-round was the cause of continuous reproduction in populations of a variety of tropical marine invertebrates. Seasonal variation in water temperature, the pattern of which is strongly tied to latitude, has always been considered an important proximate factor or environmental stimulus in triggering and maintaining gametogenesis and thus defining the breeding season of marine invertebrates as well as other marine and terrestrial animals. Thorson (1950) suggested that the important selective pressure acting on timing of reproduction in marine invertebrates with planktotrophic larvae might be the temporal variation of larval food supply, that is, the seasonal pattern of primary and secondary productivity. Thus, the temporal availability of larval food supply was supposed to be the "real" reason ("ultimate factor"; Baker, 1938) for the observed seasonality (or lack thereof) in reproduction and larval output in benthic invertebrates. Temperature (and/or other environmental variables) act as environmental cues ("proximate factors") on the physiological systems of these benthic invertebrates. By means of these cues, spawning of eggs or release of planktotrophic larvae is timed to coincide with periods of favorable food supplies in the plankton.

Thorson's (1950) classic paper presented evidence for several invertebrate groups that the breeding season became more restricted or seasonal with an increase in latitude. As noted above, he attributed this

to temporal patterns of plankton productivity in which the duration of high productivity is negatively correlated with latitude. Thus, reasoning from Thorson's ideas, at low latitudes there is relatively little variation in primary and secondary productivity (larval food supply) throughout the year in coastal areas, and there is little selection for seasonality in reproductive cycles. At higher latitudes (temperate, boreal), breeding seasons and peak larval output should roughly coincide with the seasonal pulses of productivity. The situation is more complex in polar regions where temperature variation is again slight. Although primary and secondary productivity in the plankton is highly seasonal, restricted to intense bursts in the polar summer, current information shows that reproduction of invertebrates with planktotrophic larvae is not necessarily highly seasonal and correlated with the summer pulse of planktonic productivity (Pearse et al., 1991; Thorson, 1950).

Although reviews and summaries of the literature on marine invertebrate reproduction certainly do seem to indicate a tendency for extended reproductive seasons at lower latitudes, with more restricted ones at higher latitudes, there are certainly many exceptions reported [see reviews for invertebrates in general in Giese and Pearse (1974); for crustaceans in Sastry (1983)]. Thus, there are tropical taxa in which different species may either have seasonal or continuous breeding (Cameron, 1986; Hendler, 1979). Tropical reef corals often have restricted breeding periods (Harrison et al., 1984; Schlesinger and Loya, 1985). Some tropical species have semiannual breeding seasons in areas subject to major semi-annual environmental perturbations, i.e., monsoons (Giese and Pearse, 1974).

Thus, general or simplistic models about the relationship between length of breeding pattern and latitude may not be applicable to all or most near-shore benthic invertebrates. There probably is no one generalization about reproduction or recruitment that can be made about all or most taxa. The term "near-shore benthic invertebrate" refers to a variety of taxonomic groups with very different phylogenetic histories, each taxa with its own reproductive capabilities and constraints imposed by its particular body plan, physiology, and ecology. At similar latitudes there may be much variation from one benthic habitat to another in a variety of abiotic and biotic factors that influence reproductive patterns.

A corollary to the hypothesis of a latitudinal gradient in breeding and larval production of near-shore invertebrates is that recruitment patterns should mir-

ror (with a suitable lag period) reproductive patterns, i.e., continuous recruitment in tropical latitudes with increasing seasonality of recruitment with an increase in latitude in temperate and boreal latitudes (Bauer, 1989). The caveat expressed above about comparisons of reproductive patterns among different taxa also applies to recruitment. Different taxa may have planktotrophic larvae that are affected by very different pressures in the plankton (e.g., disparate food supplies, predators) that may influence larval success and recruitment in a variety of ways. As larvae arrive at the juvenile and adult habitat, benthic predators may be acting differentially on the larvae and post-larvae as they settle and metamorphose during recruitment into the benthic population of the species.

Perhaps the most constructive approach to an analysis of the relationship between seasonality in reproduction and recruitment with change in latitude would be to make comparisons that factor out, as much as possible, variation due to differences in (a) phylogenetic history and (b) habitat. Thus, one might study and compare temporal patterns in reproduction and recruitment (1) among (relatively) unrelated taxa from similar latitudes and habitats, i.e., species that experience similar environmental pressures but which have separate phylogenetic histories and/or (2) among (relatively) closely related taxa from different latitudes and/or habitats, i.e., species with a common phylogenetic history exposed to dissimilar environmental pressures. Thus, differences in breeding and recruitment patterns among unrelated taxa from the same sampling site might be attributable to taxon-specific reproductive and recruitment capabilities and constraints. Among closely related species from different latitudes or habitats, variations in reproduction and recruitment might be ascribed to major environmental factors that vary among sampling sites.

In this report I use the approach outlined above to compare and contrast reproduction and recruitment between two relatively unrelated groups of decapod crustacean shrimps, sampled at the same location, with distinct modes of reproduction. Caridean shrimps, like all pleocyemate decapods (crayfish, lobsters, crabs), incubate their embryos to advanced zoeal larvae. In contrast, penaeoid shrimps (Decapoda, Dendrobranchiata) spawn eggs that are immediately fertilized and released into the plankton where embryonic development takes place, after which they hatch as relatively undeveloped nauplius larvae. I will make comparisons of reproductive and recruitment patterns among and between nine species of carideans and two penaeoids (*Sicyonia*) from the same habitat

(seagrass meadows) in a tropical locale, Puerto Rico, West Indies, based on data reported in Bauer (1989) and Bauer and Rivera Vega (1992). In addition, comparisons will be made among *Sicyonia* species from this tropical locale (Bauer and Rivera Vega, 1992) and *Sicyonia* spp. from other latitudes using data taken from other studies (Anderson et al., 1985; Kennedy et al., 1977). These comparisons are made possible because the intensity of sampling and the methods of estimating reproductive activity were similar among the three studies cited.

Data Base

Populations of shrimps were sampled monthly for one year in seagrass meadows, composed of turtle grass (*Thalassia testudinum*) and manatee grass (*Syringodium filiforme*), located at Dorado (18°N, 66°W), on the north coast of Puerto Rico, West Indies. Samples were taken with pushnets both during the day and night, but the vast majority of individuals for all species were captured at night when the shrimps and other macroinvertebrates are most active. Nearly 75,000 caridean shrimps were collected belonging to 18 species (Bauer, 1985a). Nine species accounted for 99.9% of this abundance (Table 1), and the reproductive and recruitment patterns of these species were analyzed (Bauer, 1989). Approximately 7,500 penaeoid shrimps were collected, and 85.9% of these individuals belonged to two species, *Sicyonia parri* and *S. laevigata* (Bauer, 1985b) whose breeding and recruitment patterns were reported in Bauer and Rivera Vega (1992).

For the carideans the index of breeding activity used was the percentage of *adult* females that were ovigerous, i.e., incubating fertilized embryos. Stage of ovarian maturity on a scale of 1 (no development) to 4 (ovary full of large vitellogenic eggs, female near spawning) was also observed and recorded for females (Bauer, 1989). In the sicyoniid (penaeoid) shrimps in which females do not incubate embryos, the ovarian maturity (immature versus mature, based on visual estimates of relative frequency of postvitellogenic eggs) was recorded for all females examined (Bauer and Rivera Vega, 1992).

In each caridean species females were defined as "adult" (potentially capable of reproducing) if they were as large or larger than the smallest female observed carrying embryos. In *Sicyonia* spp. adult females were those as large or larger than the smallest female observed with a mature ovary.

Table 1. Comparison in caridean and *Sicyonia* (Penaeoidea) shrimp species in monthly values for percentage of adult females with mature ovaries

Species	Percentage of adult females with mature ovaries			
	Median	Min	Max	N
Caridea:				
<i>Alpheus normanni</i>	16	0	35	588
<i>Latreutes fucorum</i>	24	15	56	1147
<i>Leander tenuicornis</i>	24	0	56	184
<i>Processa bermudensis</i>	28	13	55	468
<i>Hippolyte curacaoensis</i>	28	9	46	601
<i>Processa riveroi</i>	30	29	70	198
<i>Latreutes parvulus</i>	38	12	80	502
<i>Periclimenes americanus</i>	40	23	60	486
<i>Thor manningi</i>	43	32	84	466
Penaeoidea:				
<i>Sicyonia parri</i>	13	0	26	848
<i>Sicyonia laevigata</i>	26	0	42	456

min, minimum; max, maximum; N, total number of adult females examined.

Recruitment was defined as the entry of individuals from the plankton into the juvenile and adult shrimp populations in the seagrass beds. Monthly recruitment was estimated by calculating from monthly size frequency distributions the proportion of the population in the "juvenile" size classes, which were defined as the lower 25% of all possible size classes observed in that species. The upper size limit defined in this way for "juveniles" approximately coincided with the size of male and female sexual maturity in both the caridean and sicyoniid species (Bauer, 1989; Bauer and Rivera Vega, 1992).

Comparisons among Caridean and Sicyoniid Species at the Same Tropical Location

Bauer (1989) analyzed reproductive patterns of the nine caridean species listed in Table 1 based on the percentage of adult females incubating embryos. A relatively high percentage of adult females in all species were ovigerous throughout the year. Statistical tests for possible concordance among species in highs and lows of this estimate of breeding showed no common pattern. Thus, on the population level reproduction was continuous throughout the year with-

out a recognizable seasonal component. Furthermore, it was possible to determine if females carrying embryos were developing another batch for spawning after the current brood of incubated embryos hatched. This was done by recording the stage of ovarian development and stage of embryonic development in females from samples and observing the pattern of hatching and spawning in captive females. In all species observed the sequence of events in live ovigerous females was hatching of embryos, a molt within a day or two of hatching, and subsequent spawning of the eggs in the mature ovary within a day or two of the post-hatching molt. In preserved material there was a statistically significant correlation between stage of ovarian maturity and stage of embryonic development in all species. Thus, as a brood of previously spawned embryos was being incubated, the ovary of most females matured so that a new spawn took place soon after hatching of the embryos, female molting, and mating (there is no sperm storage in these carideans). Periods between spawns varied from 1-2 weeks in these species. Reproduction in these small seagrass carideans can be characterized as both continuous and intense, both at the level of the population and the individual. Cohort analysis of some of the species indicated that female life span on the seagrass meadows is a matter of months, certainly much less than a year (Bauer, 1986; Rivera Vega, 1985; Salva, 1984), probably due to the intense fish predation that occurs on small macroinvertebrates in seagrass meadows (Heck and Orth, 1980; Randall, 1967).

The index of breeding intensity or activity differed for the carideans (percent adult females incubating embryos) (Bauer, 1989) from that used for the sicyoniids (percent adult females with mature ovaries), as the latter do not incubate embryos (Bauer and Rivera Vega, 1992). I have calculated values for percentage of adult females with mature ovaries (stages 3 and 4) for the caridean species for comparison with sicyoniid species in which "mature" (dominated by large post-vitellogenic eggs) ovaries were used as the indicator of reproductive activity (Table 1). The median, minimum, and maximum values for the caridean species are generally higher than those of the two sicyoniid species (Table 1).

What might account for the apparently higher level of reproductive intensity in terms of ovarian development of the carideans relative to the sicyoniids? One might first ask if the values are comparable. Is the period for ovarian development, i.e., period between spawns, shorter in carideans? The time interval be-

tween spawns varied from 1–2 weeks in females of the nine caridean species. Although the period of an ovarian cycle in the tropical *Sicyonia* species is unknown, it is doubtful that it could be shorter than that determined for the carideans. Anderson et al. (1985), for instance, reported a mean period of 19 days between spawns in *Sicyonia ingentis*. If the duration of ovarian development is longer in the sicyoniids than that given for the carideans, or if ovarian cycles are not continuous as in the caridean species, then the intensity of reproductive effort, as estimated in Table 1, would appear lower than that of the carideans.

However, reproductive effort per spawn in terms of numbers of fertilized eggs produced is probably greater in the sicyoniids than in the carideans. The incubatory caridean females produce larger eggs and fewer embryos than do the free-spawning sicyoniids. Egg size at spawning was 240–440 μ in the nine caridean species (Bauer, 1991) compared with approximately 200 μ in the two *Sicyonia* spp. The median number of embryos per brood (spawn) in the nine caridean species varied from 56–600 and was less than 100 in five species (Bauer, 1991). The number of eggs spawned by the *Sicyonia* spp. has not been measured, but in the much larger *S. ingentis* the mean number of eggs per spawn was 86,000 (Anderson et al., 1985). Even scaled down for the differences in size of adult sicyoniid females (Table 2), it is likely that the number of eggs spawned in the tropical *Sicyonia* is at least an order of magnitude larger than that for the comparably sized carideans.

Table 2. Relationship between size (carapace length) and longevity of females in *Sicyonia* species from three different latitudes (biogeographical areas)

Species	Size range of adult female (mm CL)	Longevity (months)
<i>S. parri</i>	3–9	6–8
<i>S. laevigata</i> (tropical)		
<i>S. brevirostris</i> (subtropical)	17–35	20–22
<i>S. ingentis</i> (cool temperature)	24–45	≥22 ?

Sicyonia spp. may thus be putting out many more fertilized eggs per spawn than carideans from the

same habitat, with the duration of periods between spawns similar or perhaps somewhat longer than that for the carideans. However, the survivorship of an individual fertilized egg put immediately into the plankton by a *Sicyonia* female is probably less than that for any individual caridean embryo. The sicyoniid embryo, starting out at the zygote stage, must develop completely in the plankton to hatching as a nauplius larva, which then must develop through all the larval stages to the postlarva which will settle out of the plankton as a recruit into the benthic population of the seagrass meadows. The caridean embryo, on the other hand, is cared for by the female throughout its embryonic development and hatches as an advanced zoal larva that will spend much less time subject to the vagaries and dangers of the planktonic environment before settlement into the seagrass meadows. Thus, given the trade-offs among number of embryos produced per spawn, number of spawns per reproductive lifetime, presence or absence of parental care, and duration of time spent by larvae in the plankton, it is probable that the sicyoniids and carideans from the tropical seagrass habitat have similar reproductive effort.

The evidence thus indicates that, once sexual maturity is reached, females of both groups go through continuous cycles of ovarian maturity and spawning until they die, probably through predation, after a life span of a few to several months (less than one year) after arriving at the seagrass meadows. Settlement can occur during anytime of the year (see "Recruitment Patterns..." below). Thus, an individual female cannot "track" any particular season that might be more favorable to breeding, and there can be no selection for seasonality in breeding patterns. Additionally, it may be that there is little or no predictable variation in mortality in the larval (planktonic) environment so that there would be no selection for breeding during any particular time of the year. Although the caridean and sicyoniid shrimps have very different phylogenetic histories and reproductive physiologies, the common selective pressures of the tropical environment in which they co-occur, perhaps together with their short life spans, appear to have produced a similar pattern of continuous, non-seasonal reproduction.

Latitudinal Comparisons in Reproductive Patterns of Sicyoniid Shrimps

In this section I compare temporal patterns in reproduction among *Sicyonia* spp. from different

latitudes. The intensity of sampling and methods for estimating breeding activity (percentage of females with mature ovaries) are comparable among the tropical species *Sicyonia parri* and *S. laevigata* from seagrass meadows in Puerto Rico (18°N; Bauer and Rivera Vega, 1992), *S. brevirostris* from the Atlantic coast of Florida, USA (28°N; Kennedy et al., 1977), and *S. ingentis* from the west coast of California, USA (34°N; Anderson et al., 1985). The east coast of Florida is bathed by the warm, north-flowing Gulf Stream while the sampling site in California is influenced by the cool, south-flowing California current. Thus, comparisons are being made among species from environments that are essentially tropical, subtropical, and temperate.

Populations of the tropical species *Sicyonia parri* and *S. laevigata* exhibited continuous reproduction without any obvious seasonal peak (Bauer and Rivera Vega, 1992). When compared with the subtropical *S. brevirostris* and the temperate zone *S. ingentis*, a pattern of increasing seasonality with at higher latitudes emerges (Fig. 1). Anderson et al. (1985) made the observation that reproductive effort was less intense but annual breeding period was longer in *S. brevirostris* than in *S. ingentis*. The inclusion of a tropical species, *S. parri*, completes the picture and reveals greater intensity of reproduction (percentage of females with mature ovaries) within a shorter time span with an increase in latitude. Thus, populations of *S. parri* show a relatively low percentage of ripe females throughout the year. Breeding also occurs throughout the year in *S. brevirostris*, but there is a strong seasonal peak from December through March (Fig. 1). Breeding and spawning are highly seasonal in *S. ingentis*, in which the percentage of females with ripe ovaries is quite high in the summer and early fall while breeding apparently ceases during the rest of the year (Fig. 1).

It is instructive to interpret these reproductive patterns in terms of some life history characteristics of these species. Table 2 gives a summary of the relationship between size of the adult female and longevity. The estimates of longevity come from cohort analyses from Rivera Vega (1985) for the tropical species and from Kennedy et al. (1977) while that for *S. ingentis* is an approximation based on female size compared with that of *S. brevirostris*. Females of the larger *Sicyonia* spp. live at least two years, so that individual females have the opportunity to breed during a period of the year which might be most favorable for larval development and settlement.

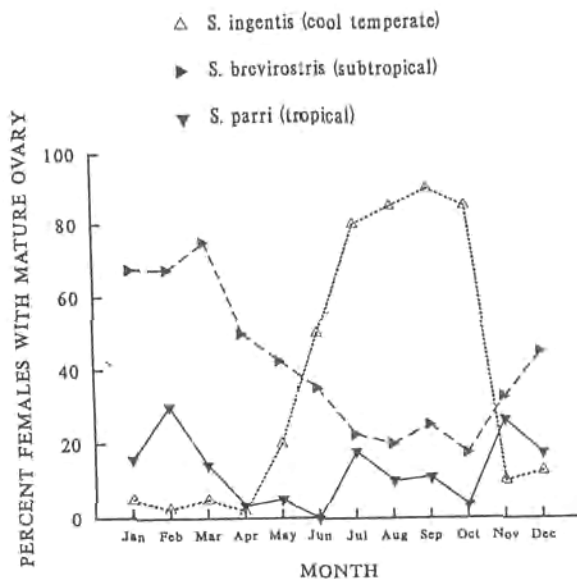


Fig. 1. Temporal pattern of ovarian maturity in three *Sicyonia* spp. from different latitudes. Data for *S. parri* are from Bauer and Rivera Vega (1982), for *S. brevirostris* from Kennedy et al. (1977) (average of data for 1973–1974), and for *S. ingentis* from Anderson et al. (1985).

Thus, there has been selection for seasonality in breeding patterns in these species. The small tropical sicyoniids live less than one year and may settle and grow to sexual maturity at any time during the year (see below). Females cannot afford to delay reproduction for any particular period of the year. The result of the interaction of short life span, settlement at any time of the year, and a physically benign environment favorable to year round gametogenesis and spawning have resulted in continuous reproduction at the level of the population and (probably) at the level of the individual female in the tropical *Sicyonia* spp.

Recruitment Patterns of Tropical Caridean and Sicyoniid Species

Temporal patterns of recruitment estimated by the percentage of the population in juvenile size classes were described for the nine caridean species (Bauer, 1989) and the two *Sicyonia* spp. (Bauer and Rivera Vega, 1992) at the tropical seagrass meadow location. Observations during sampling had indicated that although small juvenile shrimps were taken in all months, intense recruitment had occurred only during certain months of the year, i.e., there were months in which large influxes of juveniles of several species were observed. These observations were confirmed

by statistical analysis of possible concordance among the seagrass species in the estimates of recruitment. For the nine caridean species, tests of concordance in the highs and lows of recruitment were highly significant. The months of high recruitment of carideans did not group into any apparent seasonal pattern; recruitment in these species is best described as "episodic" (Bauer, 1989). Recruitment values for *Sicyonia* species were analyzed later (Bauer and Rivera Vega, 1992). Estimates of recruitment were highly correlated between the two *Sicyonia* species, and again the pattern is best described as episodic. However, when composite values for caridean and sicyoniid recruitment estimates were compared, there was no correlation. The environmental factors controlling caridean and sicyoniid recruitment appear to have been quite different.

Discussion and Conclusions

The classical paradigm of continuous reproduction in the tropics and seasonal reproduction at higher latitudes, increasingly restricted in time with an increase in latitude, receives support from results of the studies on caridean and sicyoniid shrimps addressed in this report. Although caridean shrimps and *Sicyonia* (penaeoid) shrimps are both decapod crustaceans, they have distinct phylogenetic histories (Burkenroad, 1962). Their reproductive capacities and constraints, as well as their larval life histories, are quite different, as discussed above. Yet in the same tropical environment, near-shore seagrass meadows, reproduction in species of both groups was similar (i.e., continuous), both on the level of the population and the individual (certainly so in carideans, probably so in sicyoniids). Common environmental factors (selective pressures) such as a relatively stable, physically benign habitat favorable to reproduction, a (assumed) relatively stable temporal pattern of larval food (plankton productivity), as well as specific life history constraints (life span much less than one year) have selected for continuous reproduction in these tropical species.

Specific comparisons in reproduction could be made among *Sicyonia* spp., i.e., species with a common phylogenetic history from tropical, subtropical, and cool temperate environments. The comparisons showed that with an increase in latitude, reproductive periods become more restricted in time. Within those increasingly seasonal periods of breeding, reproductive effort appears to be greater at higher latitudes. It

is hypothesized that the seasonality is due to increased seasonality of larval food supply in the plankton as suggested by Thorson (1950). The breeding patterns of these sicyoniids are qualitatively concordant with annual patterns of phyto- and zooplankton (larval food) abundances reported in studies carried out at or near areas where the adults were sampled [the south coast of Puerto Rico (Yoshioka et al., 1985); east coast of Florida (Tester and Steidinger, 1979; Walker et al., 1979); southern California coastal waters (Chelton et al., 1982)]. In addition, the life history constraint of female life span must be taken into account. The *Sicyonia* spp. studied outside of the tropics live much longer than the tropical species, long enough for selection for larval output at the most favorable period of the year to have been possible.

Comparisons were not made in the body of this paper between the tropical caridean species (Bauer, 1989) and carideans from other latitudes, as among *Sicyonia* spp., because comparable specific data were not available in the literature. However, Kikuchi (1962) reported that females of seagrass caridean species from Tomioka Bay, Japan, (32°N) were ovigerous seasonally, either during the spring and summer (most species) or during the winter (*Heptacarpus* spp.). Allen (1966), studying caridean shrimp populations off the northeast coast of England, a boreal locale (55°), found that most species were carrying embryos in the winter, although some species were ovigerous in the summer months. Reproduction was thus quite seasonal, and Allen reported that hatching of larvae and their entry into the plankton occurred in synchrony with either the spring (winter breeders) or fall (summer breeders) plankton blooms in that area. Considerable literature exists on breeding patterns in boreal pandalids (see Butler, 1980; Williams, 1984). Ovigerous and hatching periods are certainly highly seasonal in these high-latitude carideans. Extensive research on *Pandalus borealis* (Haynes and Wigley, 1969; Horsted and Smidt, 1956; Rasmussen, 1953) demonstrates an increase in adult life span and incubation period of embryos, as well as hatching of embryos later in spring and summer, with an increase in latitude. These studies show the utility of comparing populations of the *same* widely distributed species among latitudes when looking for causal factors of seasonality of reproduction.

Although the comparisons among tropical, temperate, and boreal groups of caridean species are not as firm as those reported above for *Sicyonia* spp., the conclusion of increased seasonality of breeding sea-

son with increase in latitude is strongly suggested. Thorson's (1950) hypothesis that the selective pressure resulting in seasonality in reproduction (for species with planktotrophic larvae) is seasonality in plankton production is supported by these studies.

Although all tropical shrimp species studied in Bauer (1989) and Bauer and Rivera (1992) were putting larvae or fertilized eggs into the plankton throughout the year, recruitment back from the plankton cannot be truly described as continuous. Recruitment was not seasonal but rather highly variable throughout the year (i.e., episodic). Pulses of recruitment were concordant among caridean species and among the two *Sicyonia* species, but episodes of caridean and sicyoniid recruitment did not occur at the same time. This clearly indicates that different sets of factors were acting on larvae or postlarvae to account for this pattern. However, this tells us nothing about which environmental variables produced these differential patterns in recruitment. As with most such studies on reproduction of adults and settlement of juveniles back from the plankton into the benthic environment, the larvae and the larval (planktonic) environments were not sampled simultaneously with those of the adults. Usually, this level of sampling effort is beyond the scope of individual investigators or small groups of collaborators. But only a study of reproduction and recruitment in the benthic (juvenile and adult) habitat, concurrent with a study on larval mortality in the plankton, together with measurement of environmental variables likely to influence these processes, will yield an understanding of the relationship between breeding and subsequent settlement in marine benthic invertebrates.

Climatic change, whether from natural or anthropogenic causes, will have an effect on patterns of reproduction and recruitment of marine invertebrates. Certainly there is much evidence that global warming and cooling has occurred in the past and that species have been affected by it in various ways, including shifts in distribution and, perhaps of greater concern, extinction. Various climatic models predict global warming due to an increase in "greenhouse" gases in the atmosphere that would be as large as any natural fluctuation the earth has experienced, and more importantly, that might occur at a rate several times faster than that which has ever occurred in the past (Peters, 1991; U.S. Congressional Hearings on Global Warming, 1989). What will be the consequences of predicted rises in sea temperature on coastal invertebrates important in fisheries and aquaculture such as

shrimps, crabs, lobsters, oysters, clams, and cephalopods? Will it be beneficial at a particular site, stimulating reproduction and favorably influencing recruitment and population sizes of commercially and ecologically important species? Or will temperature rise (and its complex effects on and with other variables, such as planktonic productivity) cause population declines and/or unfavorable shifts in distribution? The consequence of doing nothing until the effects of global sea warming (or changes in other climatic variables) are upon us will be that any transformations in coastal fisheries and habitats will not have been anticipated, making it impossible to adjust for them. The economic and social impacts of such changes could be considerable and therefore must be predicted, if possible.

The most direct way to investigate what effect climatic change, especially global sea warming, might have on reproduction and recruitment in coastal faunas is to study latitudinal variation in these processes in species that are as closely related as possible. As discussed in the introduction, such an approach will be most productive if the effects of environmental factors that vary with latitude are studied in species with a common phylogenetic history. This is a "reductionist" approach in the sense that one would begin with low level taxonomic units, make paradigms about reproduction that apply to those taxa, and then expand comparisons to more and more distantly related taxa until the generalization breaks down. The specific paradigm would then be restricted to a particular group of taxa. Larger scale generalizations about variations in reproduction and recruitment among taxa and among biogeographical areas could then be made on a firm basis. A complementary approach would be to look at the effect of common variables at the same locale on a "phylogenetic variety" of species. Predictions about the effects of possible climatic change such as global sea warming on marine organisms would then be based on a solid scientific basis.

My recommendation is that a large-scale global effort be conducted by marine scientists to determine what the current patterns of reproduction and recruitment are in different taxa from different locales, studies which should include both the benthic and (larval) planktonic habitats of species. Coordination of effort, concordance in methodology, and exchange of information among participants would be crucial to such an effort. Cooperation and collaboration among national governments, academic institutions, and

international agencies will be important in order to supply the personnel, funding, and material support needed for such a major but essential undertaking.

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References

- Allen, J.A., The dynamics and interrelationships of mixed populations of Caridea found off the north-east coast of England. In: Some Contemporary Studies of Marine Science, H.B. Barnes, ed., Allen & Unwin, London, 1966, pp. 45-66.
- Anderson, S.L., Clark, W.S. Jr., and Chang, E.S., Multiple spawning and molt synchrony in a free spawning shrimp (*Sicyonia ingentis*: Penaeoidea), *Biol. Bull.*, 168 (1985) 377-394.
- Baker, J.R., The evolution of breeding seasons. In: Evolution, Essays on Aspects of Evolutionary Biology Presented to Professor E.S. Goodrich on his Seventieth Birthday, G.R. De Beer, ed., Oxford University Press, London and New York, 1938, pp. 161-177.
- Bauer, R.T., Diel and seasonal variation in species composition and abundance of caridean shrimp (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico, *Bull. Mar. Sci.*, 36 (1985a) 150-162.
- Bauer, R.T., Penaeoid shrimp fauna from tropical seagrass meadows: species composition, diurnal, and seasonal variation in abundance, *Proc. Biol. Soc. Wash.*, 98 (1985b) 177-190.
- Bauer, R.T., Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea): a novel case of partial protandric hermaphroditism, *Biol. Bull.*, 170 (1986) 11-31.
- Bauer, R.T., Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow, *J. Exp. Mar. Biol. Ecol.*, 127 (1989) 175-187.
- Bauer, R.T., Analysis of embryo production in a caridean shrimp guild inhabiting tropical seagrass meadows. In: Crustacean Egg Production, A. Wenner and A. Kuris, eds., Balkema Press, Rotterdam, 1991, pp. 181-192.
- Bauer, R.T. and Rivera Vega, L., Pattern of reproduction and recruitment in two sicyoniid shrimp species (Decapoda: Penaeoidea) from a tropical seagrass habitat, *J. Exp. Mar. Biol. Ecol.*, in press.
- Burkenroad, M.D., The evolution of the *Eucarida* (Crustacea, Eumalacostraca) in relation to the fossil record, *Tulane Stud. Geology*, 2 (1963) 3-16.
- Butler, T.H., Shrimps of the Pacific Coast of Canada, *Can. Bull. Fish. Aquat. Sci.*, 202 (1980) 280 pp.
- Cameron, R.A., Reproduction, larval occurrence, and recruitment in Caribbean sea urchins, *Bull. Mar. Sci.*, 39 (1986) 332-346.
- Chelton, D.B., Bernal, P.A. and McGowan, J.A. Large-scale interannual and biological interaction in the California Current, *Jour. Mar. Res.*, 40 (1982) 1095-1125.
- Giese, A.C. and Pearse, J. S., Introduction: general principles. In: Reproduction of marine invertebrates. Acoelomate and pseudocoelomate metazoans, A.C. Giese and J.S. Pearse, eds., Academic Press, New York, 1974, pp. 1-49.
- Harrison, P.L., Babcock, R.C., Bull, G.D., Oliver, J.K., Wallace, C.C. and Willis, B.L., Mass spawning in tropical reef corals, *Science*, 223 (1984) 1186-1189.
- Haynes, E.B. and Wigley, R.L., Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine, *Trans. Am. Fish. Soc.*, 98 (1969) 60-76.
- Heck, K.L. Jr. and Orth, R.J., Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Estuarine Perspectives, V.S. Kennedy, ed., Academic Press, New York, 1980, pp. 449-464.
- Hendler, G., Reproductive periodicity of ophiuroids (Echinodermata: Ophiuroidea) on the Atlantic and Pacific coasts of Panama. In: Reproductive Ecology of Marine Invertebrates, S.E. Stancyk (ed.), University of South Carolina Press, Columbia, 1979, pp. 145-156.
- Horsted, S.A. and Smidt, E., The deep-sea prawn (*Pandalus borealis* Kr.) in Greenland waters, *Medd. Dan. Fisk. Havunders (N.S.)*, 1 (1956) 116 pp.
- Kennedy, F.S., Crane, J.J., Schlieder, R.A. and Barber, D.G., Studies of the rock shrimp *Sicyonia brevirostris*, a new fishery resource on Florida's Atlantic shelf. *Fla. Mar. Res. Publ.*, Fla. Dept. Nat. Res., Mar. Res. Lab., No. 27 (1977) 69 pp.
- Kikuchi, T., An ecological study on animal community in *Zostera* belt, in Tomioka Bay, Amakusa, Kyushu (II) Community composition (2) Decapod crustaceans, *Rec. Ocean. Works Jpn. Spec. Number 6*, pp. 135-146.
- Orton, J.H., Sea temperatures, breeding and distribution of marine animals. *J. Mar. Biol. Assoc. U.K.*, 12 (1920) 339-366.
- Pearse, J.S., McClintock, J.B. and Bosch, I., Reproduction

- of Antarctic benthic marine invertebrate: tempos, modes, and timing, *Am. Zool.*, 31 (1991) 65-80.
- Peters, R.L., Consequences of global warming for biological diversity. In: *Global climate change and life on earth*, R.L. Wyman, ed., Routledge, Chapman, and Hall, New York, 1991, pp. 99-118.
- Randall, J.E., *Food habits of reef fishes of the West Indies.*, *Stud. Trop. Oceanogr. Miami*, 5 (1967) 665-847.
- Rasmussen, B., On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.), *Fiskeridir. Skr. Havunders.*, 10 (1953) 160 pp.
- Rivera Vega, L.W., Estudio poblacional sobre los camarones marinos *Sicyonia parri* (Burkenroad) y *Sicyonia laevigata* Stimpson Penaeoidea en praderas de la hierba marina *Thalassia testudinum*, Master's Thesis, University of Puerto Rico, Río Piedras, 1985, 78 pp.
- Salva, Y., Life history patterns of the shrimps *Latreutes fucorum* and *L. parvulus* Stimpson (Caridea: Hippolytidae) in Puerto Rican seagrass (*Thalassia*) meadows, *Master's Thesis, University of Puerto Rico, Río Piedras*, 1984, 69 pp.
- Sastry, A.N., Ecological aspects of reproduction. In: *The Biology of the Crustacea*, Vol. 8, F.J. and W.B. Vernberg, eds., Academic Press, New York, 1983, pp. 179-270.
- Schlesinger, Y. and Loya, Coral community reproductive patterns: Red Sea versus the Great Barrier Reef, *Science*, 228 (1985) 1333-1334.
- Tester, L.A. and Steidinger, K.A., Nearshore marine ecology at Hutchison Island, Florida: 1971-1974. VII. Phytoplankton, 1971-1973, *Florida Mar. Res. Publ.*, 34 (1979) 16-61.
- Thorson, G., Reproductive and larval ecology of marine bottom invertebrates, *Biol. Rev., Cambridge Phil. Soc.*, 25 (1950) 1-45.
- United States Congressional Hearings, Global Warming, Committee on Energy and Commerce, House of Representatives, Serial 101-31, 1989, 177 pp.
- Williams, A.B., *Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida*, Smithsonian Institution Press, Washington, D.C., 1984, 550 pp.
- Walker, L.M., Glass, B.M. and Roberts, B.S., Nearshore marine ecology at Hutchison Island, Florida: 1971-1974. VIII. Zooplankton, 1971-1973, *Florida Mar. Res. Publ.*, 34 (1979) 62-98.
- Yoshioka, P.M., Owen, G.P. and Pesante, D., Spatial and temporal variations in Caribbean zooplankton near Puerto Rico, *Jour. Plank. Res.*, 7 (1985) 733-751.