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THE UNIVERSITY OF ALBERTA

DIFFERENTIAL PREDATION UPON EMBRYOS AND LARVAE OF TEMPERATE PACIFIC ECHINODERMS

by

STEVEN SEWARD RUMRILL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

Fall 1987

ISBN 0-315-41029-9

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17 Sept. 87

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DATED 17 September 1987

"Just inside the deep fjord called Barclay Sound (sic). Quiet waters but with plenty pelagic larvae of surfswept animals, to be sorted out by the environment and by the physiological needs of the beasts themselves, and by eating and being eaten. That sorting out is a curious process."

Ed Ricketts (1945)
The Outer Shores. Part 1. Ed Ricketts
and John Steinbeck Explore the Pacific
Coast. J. W. Hedgpeth, ed. Mad River
Press. Inc. (1978)

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled DIFFERENTIAL PREDATION UPON EMBRYOS AND LARVAE OF TEMPERATE PACIFIC ECHINODERMS submitted by STEVEN SEWARD RUMRILL in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Supervisor

External Examiner

Date 18 September 1987

ABSTRACT

A fundamental premise of benthic marine invertebrate life history theory asserts that energetic costs associated with lecithotropic and brooding modes of development are offset by decreased rates of mortality during periods of embryo and larval development. These energetic tradeoffs are presumably the basis for the evolution of dichotomous modes of development among several invertebrate taxa, and they provide the foundation for an inverse correlation between fecundity and offspring survivorship.

In this thesis, I describe a series of experimental observations to test the hypothesis that rates of embryo and larval mortality are inversely correlated with initial egg size and mode of development. Tests of hypotheses rely primarily upon comparisons made in the laboratory among echinoderm larvae from the Pacific Northwest. The life history patterns and differential susceptibility of planktotrophic and lecithotrophic larvae to predation by carnivorous zooplankton support the size-mortality hypothesis, although stage-specific differences in embryo and larval susceptibility were found to vary substantially among species with planktotrophic and lecithotrophic modes of development. Microcosm feeding experiments demonstrate stage-specific differences in the susceptibility of echinoderm embryos and larvae to predation by carnivorous zooplankton. The occurrence of similar stage-specific

susceptibility curves among phyletically divergent types of echinoderm larvae, and among different types of predatory zooplankton, allow predator-prey interactions to be assessed at a functional-group level that recognizes five distinct patterns of larval susceptibility. The fixed shapes of stage-specific susceptibility curves at various temperatures suggests that cumulative losses of embryos and larvae to predation are directly related to rates of larval development in nearshore waters.

Ontogenetic changes in the behavior of echinopluteus larvae can be an effective deterrent to predation by brachyuran zoeae. In contrast, the swimming behavior of asteroid larvae increased their probability of capture by two species of benthic suspension feeders. These investigations highlight the importance of larval behavior at low Reynolds numbers. Differences in the field distribution of juvenile asteroids, coupled with information from zooplankton tows and laboratory feeding and substratum selection experiments, support the hypothesis that communities of benthic suspension-feeders can influence the survivorship of echinoderm larvae during settlement.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the assistance and support of my supervisor, Fu-Shiang Chia, for providing an atmosphere of scholarship and camaraderie during my tenure as a graduate student. Fu-Shiang's expertise with echinoderms and his sense of curiosity about marine invertebrate larvae have been a steady source of motivation; I also appreciate his subtle insistance that I maintain a tenacious grip on the more tractable aspects of the research.

I thank the members of my supervisory and examination committees, H. F. Clifford, D. A. Craig, J. C. Holmes, A. R. Palmer, T. E. Reimchen, R. S. Scheltema, and the late D. M. Ross for advice and criticism during the formulative and final stages of this dissertation, and for freedom to conduct the research unencumbered at Bamfield Marine Station. Their contributions to the design of experiments and editorial comments improved the dissertation considerably.

Appreciation is extended to the Academic and Management Councils of the Western Canadian Universities Marine Biological Society for maintaining research facilities at Bamfield Marine Station that are conducive to studies of this nature. I have been fortunate to conduct this investigation in a location that is at the same time remote and at the heart of things (in a biological sense). These attributes will continue to make Bamfield an attractive site for future studies of invertebrate embryology and larval ecology. I am also grateful to D. Boag, R. Peter, and A. Spencer (University of Alberta, Department of Zoology), G. Kaplan, (Vice President of Reseach), and the Faculty of Graduate Studies and Research for the provision of funds that allowed me to travel to international meetings in Ireland and England; conversations with colleagues at these times provided a much needed break from field work and served ultimately to shape some of the ideas presented in the dissertation.

The thesis benefitted from the generosity and contributions of several individuals. Numerous colleagues discussed chapters with me, read versions of manuscripts, or gave access to unpublished data. Others donated time as diving companions, loaned equipment, offered technical assistance to overcome hurdles, or facilitated the final preparation of the thesis. These include: W. Austin, C. Baron, J. Buckland-Nicks, S. Carson, C. Chaffee, J. Cunningham, J. Dalby, T. Daniel, P. Dunn, J. Elliott, R. Emlet, G. Gibson, M. Koehl, R. Koss, L. McEdward, F. McEuen, R. Mandryk, P. Marino, A. Martel, D. Padilla, P. Quian, R. Shimek, G. Shinn, K. Smiley, S. Smiley, R. Sproule, M. Strathmann, R. Strathmann, C. Walker, and C. Young. Special thanks are due to Tim Pennington. Tim shared in the initial excitement and discovery of stage-dependent differences in larval susceptibility; for his enthusiasm, skepticism, and friendship I am truly grateful. I also thank L. Druehl and R. Hopkins for allowing me to coordinate parts of the research from the solitude of their cabin on Grappler Inlet.

I have been privilaged to make use of excellent laboratory facilities at Bamfield Marine Station and Friday Harbor Laboratories. I thank the directors of these institutions, R. E. Foreman and A. O. D. Willows for the use of seawater systems and research space. This research has been generously funded by grants from the Natural Science and Engineering Research Council of Canada to F. S. Chia, and by research and teaching assistantships at the Department of Zoology, University of Alberta.

My deepest appreciation is reserved for Jeanne Cureton. Jeanne's contributions are evident throughout the thesis; she skippered small boats during rainstorms, collected animals from frigid tidepools, maintained larval cultures, prepared figures, and was a critical editor, all with a dedication and enjoyment of the rigors of conducting laboratory and field work at a remote site. Jeanne's keen observations as a natural historian and constant good humor bring back fond memories of our time spent in the Pacific Northwest. "Este disertacion es como se dijera tu logro como mio. Tu ardiente buena voluntad como ayudante, y encanto como querer amiga tiene hecho estos ultimos anos a recuerdo grato. Gracias a su ayuda, tuvimos exito."

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CHAPTER I

GENERAL INTRODUCTION

Planktonic larval stages are an integral component of the complex life cycles exhibited by many species of benthic marine invertebrates (Wilbur, 1980). Recent theoretical and empirical studies have sought to clarify the role played by marine invertebrate larvae in determining the tempo and mode of evolutionary changes among benthic populations. For example, larval dispersion has been shown to affect the biogeographical distribution of species and reputedly to influence the maintenence of genetic heterogeneity (Scheltema, 1968, 1971, 1975, 1978, 1986; Gooch, 1975; Marcus, 1977; Levinton, 1980; Slatkin, 1981; Jablonski and Lutz, 1980, 1983; Hedgecock, 1982, 1986; Burton, 1983, 1986; Prince et al., 1987). In addition, patterns of larval availability and recruitment contribute to variation in the abundance and age structure of benthic populations (Yoshioka, 1982; Caffey, 1985; Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1985; Levin, 1986). The conspicuous role played by larvae in these studies provides an indication that parameters associated with larval survivorship are central to our understanding of the local abundance patterns and persistance of benthic populations.

Comparative information about rates of larval mortality are also critical to analyses of the evolution of marine invertebrate life history traits. Since the sizes of invertebrate embryos are thought to be representive of their probablity of survival to metamorphosis (Vance, 1973a,b; Chia, 1974; Strathmann, 1977; Turner and Lawrence, 1979; Caswell, 1981; Lawrence et al., 1984), rates of larval mortality can be considered as a measure of adult reproductive investment (Christiansen and Fenchel, 1979). Furthermore, the body form and trophic mode of larvae have important implications concerning the duration of the planktonic period (Chia, 1974; Strathmann, 1980). Finally, larval body size and swimming behavior are paramount in determining encounter rates with predatory zooplankton (Gerritsen and Strickler, 1977; Greene, 1985). As a consequence, ontogenetic changes in larval body size and behavior are inherently linked with the probability of larval survival and with the relative risk of predator-induced mortality in nearshore marine habitats.

A. LIFE HISTORY TRAITS OF BENTHIC MARINE INVERTEBRATES

The conceptual basis for understanding the life history evolution of benthic marine invertebrates has developed along two primary avenues over the past several decades (see reviews by Stearns, 1976, 1977; Hines, 1986). Foremost among these has been the classification of reproductive patterns into a series of developmental modes that recognize planktotrophy, lecithotrophy, direct development, and viviparity as fundamentally different adaptations for the production of offspring (Thorson, 1946, 1950; Mileikovski, 1971; Chia, 1974; Jablonski and Lutz, 1983). A second perspective views contrasting life history adaptations in light of their evolutionary implications, energetic considerations, and demographic consequences (Cohen, 1968; Murphy 1968; Schaffer, 1974; Stearns, 1976, 1977; Caswell, 1981, 1982; Lawrence _et al_., 1984; Roughgarden _et al_., 1985). Although these conceptual avenues offer different vantage points to survey the findings of past and recent research, both approaches can be improved by a critical examination of several intrinsic assumptions.

Energetic considerations and mortality rates of planktonic invertebrate larvae are both fundamental components of contemporary life history models (Vance 1973a,b; Christiansen and Fenchel, 1979; Pechenik, 1979; Strathmann, 1977; Jackson and Strathmann, 1981; Grant, 1983). Mathematical expressions of invertebrate life history traits generally pivot upon 1) differences in parental energetic investment per offspring, and 2) rates of planktonic mortality. The assumption that variability in the sizes of ova reflect differences in parental investment has recently been scrutinized by Turner and Lawrence (1979), Lawrence _et al_. (1984), McEdward and Coulter (1987), and McEdward and Carson (1987). Their findings indicate that intraspecific differences in ova diameter can be a poor indicator of energetic content in echinoderms with variable ova sizes. As a consequence, attempts to infer differences in reproductive investment from estimates of ova size alone may be seriously misleading.

B. ESTIMATION OF LARVAL MORTALITY RATES

Current theoretical arguements typically incorporate a larval mortality function that is based on little or no empirical data. Planktonic mortality rates are generally considered to be high in species with long-lived, planktotrophic larval stages. Conversely, mortality rates are generally assumed to be lower in species with shorter-lived lecithotrophic larvae or benthic development. In general, there have been three approaches to estimating characteristics of the larval mortality function. Simplistic models such as those of Vance (1973), Strathmann (1977) and Grant (1983) estimated larval mortality rates to be constant and high for all developmental stages of feeding and non-feeding planktonic larvae. In contrast, Christiansen and Fenchel (1979) and Ayal and Safriel (1982) proposed that planktonic mortality rates may be greater for younger larvae than older larvae, and they incorporated decreasing mortality functions into their models of returns on reproductive effort. A more recent approach (Emlet et al., 1986) estimates the ratio of planktonic mortality rates necessary to balance the high fecundity of planktotrophic species with the lower fecundity of lecithotrophic species. However, like Menge (1975), Emlet *et al.* (1986) make the assumption that larval populations exist at equilibrium densities and that the risk due to predation is distributed equally among various developmental stages.

Non-empirical assessments of instantaneous larval mortality rates are of limited value in the analysis of field data because most field situations are too complex to allow for meaningful predictions. For example, non-empirical estimates of larval mortality cannot take into account important local conditions including temporal and spatial differences in larval production, advective and diffusive transport, larval growth rates, qualitative and quantitative differences in food availability, and the distribution and abundance of predatory zooplankton.

Attempts to monitor natural populations of planktonic larvae are beset by serious methodological problems that challenge the creativity of field-oriented ecologists. Consequently, many investigators have sought alternative methods to obtain estimates larval survivorsh[illegible] parsimonious approach has been to avoid the difficulty of estimating planktonic mortality by conducting periodic examinations of egg masses in species with benthic development (Spight, 1975; Menge, 1975; Shimek, 1981; Race, 1982; Wilson, 1986). Rates of larval mortality have also been estimated from time-series collections of zooplankton samples (Jørgensen, 1981; Rothlisbeg and Miller, 1982) and from differences between apparent larval production and recruitment (Thorson, 1950; Connell, 1970; Menge, 1975; Hines, 1979; Brousseau et al., 1982; Powell et al., 1984). Although they provide a first approximation of mortality rates, these indirect methods rely upon unreasonable assumptions concerning the density and age-stability of larval and adult populations, stage-specific differences in mortality, and rates of advective and diffusive larval transport. Despite the widespread ecological and evolutionary implications that derive from differential rates of larval mortality, few investigators have adequately addressed the fundamental assumptions that form the basis for comparative assessments.

Are marine invertebrate larvae exposed to a high risk of mortality due to the effects of predators? This question has been at the focal point of a controversy that laboratory experiments and non-empirical estimates of instantaneous larval mortality rates have failed to resolve. The prevalent view was first advanced by Thorson (1946, 1950) whose anecdotal observations suggest that predation upon larvae may be a paramount factor leading to large-scale losses of larvae from the plankton (Thorson, 1966). The hypothesis that marine invertebrate larvae are highly susceptible to predation has recently been substantiated in a series of laboratory experiments by Pennington and Chia (1984), Rumrill and Chia (1985), Rumrill et al. (1985), and Pennington et al. (1986). These studies document stage-specific differences in the susceptibility of larvae to predation, and they indicate that field mortality rates can be dependent upon the expression of larval traits and the feeding behavior of predatory zooplankton.

In contrast, alternative arguements express the opposing view that marine invertebrate larvae migrate into the plankton during early development to obtain food and to seek refuge from benthic predators (Jagersten, 1972; Strathmann, 1985). Implicit in the "safety-and-feeding" hypothesis is the assumption that feeding larvae are less vulnerable to predators than non-feeding larvae (Highsmith, 1985). However, planktotrophic larvae typically differ from lecithotrophic larvae in several fundamental traits including initial body size and morphology, patterns of ciliation, and swimming behavior. All of these characteristics are potentially significant in determining the relative susceptibility of larvae to capture by predatory zooplankton.

The "high-susceptibility" and "safety-and-feeding" hypotheses are not mutually exclusive. For example, it is possible that marine invertebrate larvae are exposed to a high risk of predator-induced mortality during the planktonic period, and that risk increases as larvae approach the bottom prior to settlement. Detailed studies of predator-prey interactions must be completed to determine the relative significance of planktonic and benthic rates of larval mortality.

In order to obtain accurate estimates of the mortality rates of marine invertebrate larvae, it is necessary to simultaneously evaluate several potentially synergistic parameters that contribute to larval losses. Accurate estimates of larval mortality must consider: 1) advective immigration and emigration of larval populations, 2) input of new individuals by spawning, 3) rates of larval feeding and growth, 4) stage-specific differences in the susceptibility of embryos and larvae, 5) density-dependent predation by zooplankton, and 6) rates of larval settlement. To my knowledge, studies are not available that adequately examine this suite of factors for any population of marine invertebrate larvae. Consequently, little convincing evidence exists to either support or refute the hypothesis that larval mortality is a selective agent in the evolution of invertebrate life history traits.

C. SOURCES OF LARVAL MORTALITY

Larvae of benthic marine invertebrates risk mortality from several different sources during the planktonic period. In his pioneering studies of invertebrate larval ecology, Thorson (1946, 1950, 1966) considered the major sources of loss to be: 1) failure of fertilization, 2) poor food supplies, 3) inadequate thermal conditions, 4) the absence of a proper substratum for metamorphosis, 5) offshore transport by currents, and 6) predation upon embryos and larvae.

The effects of genetic abnormalities and larval diseases are two potentially important and yet virtually unexplored sources of embryo and larval death. Large numbers of embryos and early larval stages often fail to develop in synchrony with their siblings in laboratory cultures, and these individuals are typically discarded by researchers. It is possible that a substantial proportion of siblings possess genetic abnormalities that result in aborted development and death. Similarly, although long-lived marine invertebrate larvae may be exposed to a variety of pathogens during their planktonic period, the toll taken by larval diseases and the role of larval immune responses have not been investigated. Since little information exists concerning the frequency of aborted development and susceptibility of larvae to disease, the relative importance of these factors cannot be compared with other sources of larval mortality.

Recent information concerning the reproductive biology and larval ecology of benthic marine invertebrates has made it possible to elucidate the relative importance of several factors that influence larval survival. For example, seasonal gametogenesis and synchronization of spawning have been suggested as adaptations to ensure fertilization in several temperate and tropical invertebrates (Pearse, 1975, 1981). Seasonal maturation of gonadal tissues appears to be mediated through the activities of nervous and endocrine systems (Pearse, 1965, 1981; Pearse and Eernisse, 1982;

Pearse and Walker, 1986; Pearse and Beauchamp, 1986; Iliffe and Pearse, 1982). These systems are responsive to proximate factors such as seasonally oscillating temperature, photoperiod, salinity, lunar cycles or the abundance of food (see Giese and Pearse, 1974; Kennedy and Pearse, 1975; Olive, 1980, 1981; Olive and Garwood, 1983). Synchronization of spawning and the chemotactic attraction of spermatozoa to recently spawned ova (Miller, 1973, 1977, 1981, 1982) both serve to increase the probability of fertilization in freely spawning invertebrates with dispersive larvae. However, Pennington (1985) gathered field evidence to suggest that sperm dilution may decrease the frequency of encounters between ova and sperm in the sea urchin, Strongylocentrotus droebachiensis. Nevertheless, aggregation of adults, spawning synchrony and the evolution of elaborate electrical and microstructural blocks against polyspermy (see Austin, 1965) are evidence that the ova of benthic marine invertebrates probably experience a high degree of fertilization success.

Rates of larval feeding and diet can also affect larval survivorship, but the direct effects of food supply have proven difficult to analyze in the field. Laboratory studies have shown that differences in larval survivorship are related to both the quality and quantity of food (Davis and Guillard, 1958; Paulson and Scheltema, 1968; Anger et al., 1981; Fenaux, 1982; Lucas, 1982; Paulay et al., 1985; and numerous others). However, it is difficult to ascertain the relative importance of larval feeding and starvation, particularly in light of recent discoveries concerning the uptake of dissolved organics as a source of larval nutrition (Manahan, 1983; Manahan and Crisp, 1982: Manahan et al., 1983; de Burgh and Burke, 1983; Davis and Stephens, 1984).

The effects of ambient thermal conditions on embryological development and survival have received widespread attention (Kinne, 1970; Pechenik, 1981; Clarke, 1982; Bosch et al., 1984). The thermal conditions under which successful reproduction can occur are typically narrower than the range of adverse temperatures normally tolerated by adults (Mileikovsky, 1960; Scheltema and Williams, 1982). However, temperatures that are detrimental to early embryological stages are generally similar to the ambient extremes encountered by embryos and larvae during the pelagic period (Lonning, 1959; Moore, 1959; Davis and Calabrese, 1964; Calabrese, 1969). Furthermore, Andronikov (1975) demonstrated that thermal tolerance increases substantially in later embryos and larvae from several molluscs and echinoderms. In most cases, natural changes in sea temperature were a limiting factor only during critical early stages of development. The detrimental effects of pollutants and other adverse environmental conditions have also been studied with respect to their influence on the survival of marine invertebrate larvae (Bookhout and Costlow, 1974; Bigford, 1979; Crisp, 1984; Marsh et al., 1986), although the negative effects of sub-optimal habitats are generally thought to be restricted to bodies of water characterized by slow replacement rates such as lagoons, partially enclosed bays, and fjords.

Substratum selection is also an important process influencing the survivorship of marine invertebrate larvae. Obrebski (1979) proposed a simple model to account for differences in adaptations for colonization by settling larvae, and he made the intuitive prediction that traits that reduce larval mortality, such as larval defenses and discriminatory substratum selection, should be favored when conditions for larval survival in the plankton are poor. Nearly all species with dispersive larvae exhibit some degree of substratum selectivity (see reviews by Meadows and Campbell, 1972; Crisp, 1974; Scheltema, 1974; Chia *et al*., 1984). However, studies that examine the relative importance of substratum selection to the survivorship of settling larvae and post-settlement stages are still in their infancy (Connell, 1985; Gaines and Roughgarden, 1985; Young and Chia, in press). Presumably, recognition of specific cues associated with suitable habitats should serve to decrease the loss of larvae due to settlement in a hostile site. Meaningful assessments of the relative importance of pre-settlement and post-settlement events in determining temporal and spatial patterns of larval survivorship and juvenile recruitment constitute a challenge worthy of considerable attention.

Large-scale losses of planktonic larval stages have also been attributed to offshore transport of larval populations into areas that are unsuitable for settlement. Jackson and Strathmann (1981) examined the synergistic interactions between eddy mixing, rates of larval mortality, and the lengths of the precompetent and competent periods of development as factors in their model of larval survivorship. Jackson and Strathmann (1981) concluded that offshore mixing could potentially be as detrimental to larval populations as high rates of predation or the inability of a larva to locate a suitable settlement site. However, Jackson and Strathmann's (1981) predictions are based on the assumption that predators kill larvae at equivalent rates during the precompetent and competent periods. Although some empirical data have been gathered to support this assumption (Rumrill, 1987), in most cases the susceptibility of early larval stages differs substantially from that of later stages (Rumrill et al., 1985; Rumrill, 1987). Offshore transport can indirectly influence larval survivorship by: 1) increasing the risk of predation as larvae prolong their planktonic period in the absence of a suitable settlement site, or 2) by the establishment of pseudopopulations composed of non-reproductive individuals (Mileikovsky, 1968; Gage and Tyler, 1981). By comparison, the direct detrimental effects of offshore mixing may be minimal along continental shelf regions where the net advective transport of larvae is along the shore rather than prependicular to the coast.

Although several factors contribute to the mortality of marine invertebrate larvae, it is likely that adverse hydrographic conditions, failure to locate an adequate substratum for settlement, and predation upon larvae are the most significant sources of larval death. Since little empirical data exist to critically examine rates of invertebrate larval mortality, it is premature to estimate whether larval losses due to predation exceed or are surpassed by losses due to offshore transport or the inability of a larva to locate a suitable site for settlement and metamorphosis. These processes have important implications concerning the dynamics of benthic invertebrate populations because the availability of metamorphically competent larvae dictates the intensity and spatial pattern of recruitment events.

D. PRIMARY OBJECTIVES OF THE RESEARCH

In the present study, I develop the thesis that larval mortality is a fundamental component of the contrasting life history traits exhibited by benthic marine invertebrates. In particular, I address the following questions: (1) Are the life history traits of marine invertebrate faunal assemblages influenced by environmental variability on small as well as large geographic scales? (2) Do characteristic patterns of age and stage-specific larval mortality exist in nearshore waters, or are the life tables for planktonic larval populations essentially chaotic? (3) How is the risk of predation during the planktonic period related to initial ova size and the intrinsic rate of development? (4) Can marine invertebrate larvae be considered as "sitting ducks" in predator-prey equations? If not, what types of ontogenetic features function effectively in the defense of larvae against predatory zooplankton? (5) How does mortality during the planktonic period compare with mortality during settlement?

Given the thesis that predation upon larvae is a primary cause of death during the planktonic period, and provided that laboratory studies of predator-prey interactions are appropriate to describe stage-specific differences in survivorship, it should be possible to discover a series of general patterns of larval susceptibility.

E. APPLICABILITY OF ECHINODERM EMBRYOS AND LARVAE

The extant Echinodermata are representative of an ancient phylum of deuterostomate metazoans that first appeared in the fossil record during the lower Cambrian (Sepkoski, 1981). The phanerozoic history of the echinoderms, like that of several other groups of benthic marine invertebrates, has been one of diversification followed by periods of decline and rediversification (Valentine, 1973; Valentine and Jablonski, 1983; Raup, 1979; Sepkoski, 1981). Early echinoderms underwent an initial period of diversification during the Ordovician, and during their apex in the Silurian the phylum was represented by over 25 classes. The diversity of echinoderms declined drastically during the Permian-Triassic extinctions, followed by a second period of diversification in the middle Jurassic. These periods of Paleozoic and post-Paleozoic diversification provided a historical testing ground for the success of novel body plans. Comparisons of modern and fossil assemblages indicate that the Recent echinoderm fauna is largely representative of species that inhabited shallow continental seas during the late Jurassic and Cretaceous periods (Fell, 1966; Blake, 1982; Smith, 1984).

Interest in the origins and evolution of echinoderms has led to the inference that the ancestral larval form was pelagic and planktotrophic (Jagersten, 1972; Strathmann, 1978). The ancestral planktotrophic larval form has presumably been lost from the Crinoidea, and the published literature suggest that the extant crinoids may be entirely lecithotrophic (Mortensen, 1920; Dan and Dan, 1941; Hyman, 1955; Strathmann, 1978; Mladenov and Chia, 1983; Chia et al., 1986). In contrast, the other principal echinoderm clades (Asteroidea, Ophiuroidea, Echinodiea, and Holothuroidea) have retained a greater degree of developmental flexibility. Members of these groups exhibit planktotrophic, lecithotrophic, and vivparous modes of development (Chia, 1966; Hendler, 1975; Rumrill, 1982; McEuen, 1986; Emlet et al., 1986). The larval stages of Recent echinoderms provide an opportunity to study the ecological consequences associated with divergent reproductive traits, and to address questions concerning the evolution of complex life cycles.

The approach of studying intraspecific and interspecific variability of larval susceptibility among echinoderm embryos and larvae has inherent advantages and disadvantages. Advantages offered by this phylum include: 1) widespread ecological interest in the rates of development, feeding biology and survivorship of larval echinoderms, 2) a diversity of larval body forms and trophic modes, 3) considerable published information about the breeding periods and modes of development for local species, 4) convenience of rearing large numbers of sibling larvae under controlled laboratory conditions, and 5) the existance of a body of literature spanning over a century that identifies laboratory techniques for manipulations of larval morphology, size and behavior. Disadvantages associated with conducting the research with echinoderms include: 1) restrictions on the types of swimming behavior exhibited by larvae, 2) seasonal breeding periods that prohibit direct comparisons of the effects of seasonally abundant predators, and 3) relatively long-lived larvae that require considerable laboratory attention.

F. ORGANIZATION OF THE THESIS

The central theme of this research is an examination of patterns and processes that contribute to predator-induced mortality of echinoderm embryos and larvae. The thesis is written in the form of 5 papers, each dealing with different aspects of echinoderm larval mortality. The research topics were selected from Thorson's (1950) plenary catalog of factors that influence rates of larval mortality. As a consequence of their similar theme, the thesis chapters overlap partially in their reference to published literature and in their discussion of the implications of differential larval susceptibility. I have made a conscious effort to keep the redundancy to a minimum. Each paper is written in the format required by the journal to which it has been or will be submitted for publication.

In the first appendix of the thesis, I describe small-scale biogeographic variation in the diversity of life history traits among 37 species of echinoderms from a variety of habitats within Barkley Sound, British Columbia. The survey provides comparative information about the diversity, abundance, and life history traits of echinoderms along an environmental gradient ranging from protected mudflats to exposed rocky intertidal and subtidal habitats. In addition, I compare factors that contribute to small and large-scale biogeographic patterns in the distribution of planktotrophic, lecithotrophic and brooding species among echinoderm faunal assemblages located along the north-east Pacific coast.

Chapter Two documents stage-specific differences in the susceptibility of sand dollar embryos and larvae to predation by a carnivorous microcrustacean. Losses of larvae to predators are examined in a series of laboratory microcosm feeding experiments to allow for the recognition of larval susceptibility patterns in single and mixed-stage feeding experiments. I describe a post-contact predator avoidance response in echinopluteus larvae, and I draw speculative conclusions about the importance of high rates of early mortality in estimating the losses of larvae due to predation in nearshore waters.

In Chapter Three, I examine the effects of development rate on the cumulative risk of predation during the planktonic period for 3 species of sea urchins and 4 species of sea stars. Interspecific differences in ova volume and temperature-dependent changes in development rate are utilized to compare the effects of accelerated and retarded differentiation on predation by carnivorous microcrustaceans.

Hydromechanical aspects of locomotion and prey capture are analyzed for raptorial zoea larvae of a decapod crustacean in Chapter Four. I utilize stroboscopic photography and flow-visualization techniques to describe the mechanics of swimming and prey capture. My results indicate that swimming velocities fluctuate markedly over short periods of time, and that unsteady aspects of locomotion (acceleration and deceleration) can be an important component of predation upon non-motile embryos and ciliated echinoderm larvae.

In the Fifth Chapter, a post-facto approach is developed to assess the relative importance of pre-settlement and post-settlement factors that influence patterns of echinoderm recruitment. A spatially heterogeneous pattern of recruitment between adjacent populations of an asterinid sea star, Asterina miniata (Brandt, 1835) is described, and I present empirical laboratory and field data to address several alternative hypotheses that may be invoked to explain the observed pattern of recruitment. Experimental evidence suggests that larval substratum selectivity and differences in the abundance and spatial distribuion of benthic suspension feeders can be key determinants of success or failure of A. miniata larvae during settlement.

The Sixth Chapter describes the results of a broad survey of echinoderm embryo and larval susceptibility patterns. Results from the survey allow for the recognition of predator functional groups. In addition, I describe five different patterns of differential susceptibility. The Type A pattern (high susceptibility of embryos and early larvae) appears frequently within the matrix and may be typical of mortality patterns in the field.

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CHAPTER II.

DIFFERENTIAL SUSCEPTIBILITY OF MARINE INVERTEBRATE LARVAE: PREDATION UPON Dendraster excentricus (ECHINOIDEA: CLYPEASTEROIDA) EMBRYOS AND LARVAE BY ZOEAE OF THE RED ROCK CRAB Cancer productus (CRUSTACEA: DECAPODA) [1]

A. INTRODUCTION

Recent life history models consider rates of larval mortality as pivotal points in the evolution of reproductive traits in benthic marine invertebrates. In general, the energetic costs and reproductive benefits associated with planktotrophic, lecithotrophic and brooding modes of development are compared intuitively, and mathematical solutions are derived that minimize the cost and benefit ratio (Vance, 1973; Chia, 1974; Strathmann, 1977; Grant, 1983). Although this approach provides valuable insight for contrasting life history patterns among benthic invertebrates, it is not entirely satisfying because estimates of relative cost must take into account energetic expenditure and larval survivorship.

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1. **A version of this chapter has been published. Rumrill, S. S., Pennington, and F. S. Chia. 1985. Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, Dendraster excentricus (Eschscholtz) embryos and larvae by zoeae of the red crab, Cancer productus Randall. J. exp. mar. biol. Ecol. 90: 193-208.**

Planktonic embryos and larvae are preyed upon by a variety of predators including carnivorous zooplankton, planktivorous fish, benthic invertebrates and protozoans (Lebour, 1922, 1923; Korringa, 1941; Thorson, 1946; Barnes, 1959; Yamaguchi, 1973; Mileikovsky, 1974; Sebens and Koehl, 1984; Young and Chia, in press). Despite the potential importance of predation to larval survival, little is known of the interactions that occur between predators and their invertebrate larval prey. The susceptibility of embryos and larvae to capture may change during ontogeny due to: 1) predator size-selection (Landry, 1978), 2) stage-dependent differences in prey distribution (Omori and Hamner, 1982; Yen, 1982), and 3) developmental changes in prey morphology and behavior (Pennington and Chia, 1984). As a consequence, discriminatory prey selection and differential larval susceptibility may apply selective pressures on the larval phase of invertebrate life histories favoring traits that reduce predator-induced mortality.

The sand dollar, Dendraster excentricus, is a common member of sandy intertidal and subtidal communities along the Pacific coast of North America (Merrill and Hobson, 1970; Birkeland and Chia, 1971). Individuals of D. excentricus spawn from March-June (Mortensen, 1921; Niesen, 1977) and the embryos develop into feeding larvae that have a planktonic period lasting from 5-6 wk (Highsmith, 1982). Throughout the planktonic period embryos and larvae of D. excentricus are exposed to risk from a variety of potential predators that include the mussel, Mytilus edulis and the solitary ascidian, Styela gibbsii (Cowden et al., 1984) as well as several species of carnivorous zooplankton (Pennington et al., 1986). Timko (1979) reported that adult sand dollars from southern California preyed upon conspecific larvae in laboratory cultures; larviphagy, however, could not be demonstrated in D. excentricus from Puget Sound (Chia and Atwood, 1982). Benthic tanaid crustaceans (Leptochelia dubia) prey upon recently metamorphosed D. excentricus (Highsmith, 1982), and L. dubia and epibenthic amphipods also capture settling D. excentricus plutei (Rumrill, personal observations).

In this study I describe predator-prey interactions between various developmental stages of Dendraster excentricus (Eschscholtz) and zoea larvae of the red rock crab, Cancer productus Randall. Decapod zoeae were chosen as predators because they often occur in dense aggregations in nearshore waters and are suspected to be important predators of larvae and other small zooplankton (Sulkin, 1974, 1978, 1984; Sulkin and Van Heukelem, 1980; Incze and Paul, 1983). Although C. productus zoeae and D. excentricus larvae may not always interact in temperate nearshore waters, C. productus are representative of carnivorous microcrustaceans that co-occur with planktonic larvae of D. excentricus. Laboratory observations demonstrate stage-dependent susceptibility of D. excentricus embryos and larvae to capture by C. productus zoeae. The ability of

D. excentricus plutei to reverse the direction of swimming is identified as a post-contact encounter response that reduces rates of larval mortality.

B. MATERIALS AND METHODS

The research was carried out from April-June 1983 at the Friday Harbor Laboratories, Washington (48° 32'N, 123° 05'W), and from June-August, 1983, at Bamfield Marine Station, British Columbia (48° 50'N, 125° 08'W).

1. Larval Abundance

Distribution patterns of echinoid larvae and brachyuran zoeae were determined in Barkley Sound, British Columbia, from a series of vertically stratified zooplankton tows taken at three depth strata with 125 µm mesh, 0.5 m diameter standard and closing nets. Three replicate samples were taken between depths of 0-30 m, 30-60 m, and 60-90 m. All plankton tows were taken on 15 July 1983, between 0930 and 1015 hrs. Each tow was preserved in 10% buffered formalin immediately after collection and sorted under a Wild M5A stereomicroscope. Dendraster excentricus larvae were examined with cross-polarized light and identified on the basis of skeletal characteristics (Strathmann, 1979). Cancer productus zoeae were identified using keys provided by Trask (1970) and Hart (1971).

2. Functional Response of Cancer predation

Fifth zoea stage Cancer productus were selected as predators for the feeding experiments because they were the most abundant zoea instar in the surface waters. Individuals of C. productus were collected in hand-held jars and maintained in the laboratory in running unfiltered seawater aquaria for 3-5 days before they were used in experiments. Carapace diameters of zoeae averaged 1.7 mm and the mean rostrum-dorsal spine length was 4.6 mm. Prey stages of Dendraster excentricus were obtained by inducing adults to spawn with intracoelomic injections of 0.52 M KCl. Echinopluteus larvae of D. excentricus were cultured at 12°C in 3.7 liter glass bottles containing 1 μm filtered seawater. Echinoplutei were fed a 2:1 mixture of Dunaliella tertiolecta Butch. (Chlorophyta) and Pavlova lutheri Droop (Chrysophyta) every 2-3 days when the seawater was replaced.

The effects of prey density on Cancer productus predation rates were determined in laboratory feeding experiments. In each trial, Dendraster excentricus embryos were counted into 1 liter glass jars filled with 1 μm filtered seawater. At the initiation of each experiment five C. productus zoeae were added to each jar. No zoeae were added to control jars. Each trial consisted of three replicate predator treatments and two controls. Separate experiments were conducted with D. excentricus embryos at concentrations of 25, 50, 100, 250, and 500 prey l^{-1}. The jars were strapped horizontally around the long axis of a cylindrical mixing device (see Yen, 1982) that rotated at 1.7 rpm to keep the predators and prey suspended. All feeding experiments were conducted in a cold room or incubator at 12°C with 12L:12D photoperiod. After 24 hrs the remaining larvae were counted and C. productus clearance rates were calculated as:

$$C = (V / t) (\ln D_1 - \ln D_2)$$

where C is the clearance rate in liters zoea^{-1} day^{-1}, V is the volume of seawater available per zoea, t is the duration of the experiment, and D_1 and D_2 are the initial and final densities of prey (Vanderploeg and Scavia, 1979).

3. Differential Susceptibility of Embryos and Larvae.

The relative susceptibility of Dendraster excentricus embryos and larvae to predation was determined by conducting feeding experiments with seven different ontogenetic stages of prey (see Table 1). The prey categories were : 1)ova surrounded by intact jelly coatings and pigment cells, 2) ova without jelly coatings and pigment cells, 3) embryos through gastrula stages, 4) prism larvae, 5) 4-armed plutei, 6) 6-armed plutei, and 7) 8-armed plutei. Prey items for category no. 2 were prepared by passing fully hydrated D. excentricus ova through 125 um mesh. Prey stages in category # 3 were non-motile embryos at the beginning of the experiment but had developed into swimming gastrulae when the experiments were terminated.

Differential prey susceptibility was examined

Table 1

Categories of *Dendraster excentricus* prey used in feeding experiments and their characteristic shapes, sizes and motility: Table entries are means; n = 25 measurements per category; (a) diameter; (b) greatest length; (c) greatest width X greatest length.

PREY CATEGORY	SHAPE	SIZE (µm)	MOTILITY
1. Ova with jelly coats	Spherical	155 (a)	Non-motile
2. Ova without jelly coats	Spherical	121 (b)	Non-motile
3. Embryos - Gastrulae	Prolate Sphere	121 - 142 (b)	Forward Swimming
4. Prism Larvae	Pyramidal	115 X 132 (c)	Forward Swimming
5. 4-armed Pluteus	Elongate Pyramid	328 X 284 (c)	Forward + Reverse Swimming
6. 6-armed Pluteus	Elongate Pyramid	479 X 654 (c)	Forward + Reverse Swimming
7. 8-armed Pluteus	Elongate Pyramid	504 X 716 (c)	Forward + Reverse Swimming

independently by simultaneously offering several different stages of Dendraster excentricus to Cancer productus zoeae. Two series of mixed stage feeding experiments were conducted. In the first set, 20 embryos, 20 prism larvae and 20 6-armed plutei were placed into a 2 liter separating funnel containing 5 zoeae. In the second set 20 gastrulae, 20 4-armed plutei and 20 8-armed plutei were added to the funnel along with 5 zoeae. The initial density of prey in both sets of experiments was 30 D. excentricus liter^{-1}. Each set of experiments consisted of three replicate treatments with C. productus zoeae and two controls without zoeae. Filtered seawater in the funnel was maintained at 12-13°C by a jacket of circulating seawater, and a stream of small air bubbles (5-8 min^{-1}) kept the predators and prey suspended. After 24 hrs the number of D. excentricus remaining was determined for each prey category.

The effectiveness of several potential prey defenses was investigated by conducting feeding experiments with variously treated prey. First, increasing prey size was evaluated by comparing rates of predation upon normal and dwarf-sized 4-armed plutei. Dwarf plutei were obtained by culturing blastomeres that had been physically separated following the second cell division. Dwarf plutei were similar in form and behavior to normal plutei, and nearly equivalent in size to gastrulae and prism larvae cultured from non-dissociated blastomeres. Second, the effects of prey visibility were examined by conducting feeding experiments under conditions of constant illumination and darkness. Predation experiments were also conducted with dyed prey under constant illumination. Four-armed plutei were dyed crimson by immersing them for 10 min in seawater containing 0.01% Neutral Red. Dyed plutei remained active and swam normally for up to 72 hrs following the dye treatment. Third, the effects of prey motility were assessed by comparing rates of predation upon swimming and non-swimming plutei. Four-armed plutei were immobilized by heating them to 40°C for 60 s. Finally, the importance of periodic reversals in the direction of swimming was evaluated by comparing rates of predation upon normal plutei and plutei whose capability for ciliary reversal had been blocked by 0.01% $MgCl_2$ (Mackie _et al_., 1969; Strathmann, 1971). The $MgCl_2$ appeared to have a negligible effect on the swimming and feeding of _Cancer productus_ zoeae but inhibited ciliary reversal and backwards swimming in _Dendraster excentricus_ plutei. All experiments with treated prey were conducted for 24 hrs at initial densities of 50 prey liter^{-1} and consisted of three replicate predator treatments and two controls without predators.

4. _Post-Contact Encounter Response_

To analyze the swimming behavior of different prey stages of _Dendraster excentricus_ during encounters with _Cancer productus_ zoeae, I placed _D. excentricus_ gastrulae and 4-armed plutei together with zoeae in a glass observation chamber (6 X 2 cm) containing 1 µm filtered seawater. The observation chamber was illuminated with transmitted diffuse light and cooled to ambient sea temperature with a circulating bath. Swimming movements of the zoeae were restricted by tethering their dorsal spines to glass capillary tubes filled with plasticene. The tethered zoeae continued to beat their maxillipeds and create ventrally-directed feeding currents in the observation chamber for periods lasting up to 8 days. The direction and velocity of feeding currents near the carapace of the tethered zoeae ranged from 5.9 to 8.6 mm s^{-1} and were nearly identical to the direction and velocity of currents generated during normal swimming (see Rumrill, 1987). An outline of a tethered zoea was traced with a camera lucida to provide a reference for plotting predator-prey encounters. The slow swimming speeds of larval D. excentricus (0.94 mm s^{-1}) made it possible to visually record encounters between prey and the stationary C. productus zoeae. Stage-specific capture frequencies were calculated as the proportion of attacks resulting in capture and ingestion.

C. RESULTS

1. Larval Abundance Patterns

Echinoid larvae and brachyuran zoeae were both concentrated in surface waters and showed distribution patterns that were significantly different from uniform

(Table 2, Kruskal-Wallis ANOVA, $p < 0.05$). Cancer productus zoeae were more abundant than Dendraster excentricus in plankton tows collected from 0-30 m, but low numbers of both C. productus and D. excentricus occurred in water deeper than 30 m. Total numbers of larvae were highly variable between successive tows and provide an indication that predator and prey populations had patchy spatial distributions. Dense aggregations of C. productus zoeae and megalopae commonly occur in the upper surface waters where they have been observed by submersible and SCUBA divers (Rumrill, pers. observations).

2. Functional Response of Cancer Predation

The ingestion rate by Cancer productus zoeae increased in a curvilinear manner with increasing initial prey abundance (Figure 1a, $t = 6.35$, $p < 0.001$). The mean (± s.d.) ingestion rate was 11.05 ± 8.52 embryos zoea^{-1} day-1 for initial Dendraster excentricus densities between 25 and 500 prey l^{-1}. In contrast, clearance rates by C. productus zoeae generally declined with increasing initial prey density and showed a Holling (1966) Type II functional response curve (Figure 1b). The increase in C. productus foraging effort in response to low prey availability indicates that the rate of embryo capture is directly related to the frequency of encounters between zoeae and D. excentricus embryos in feeding vessels.

3. Differential Susceptibility of Embryos and Larvae

Clearance rates by Cancer productus zoeae upon various

Table 2

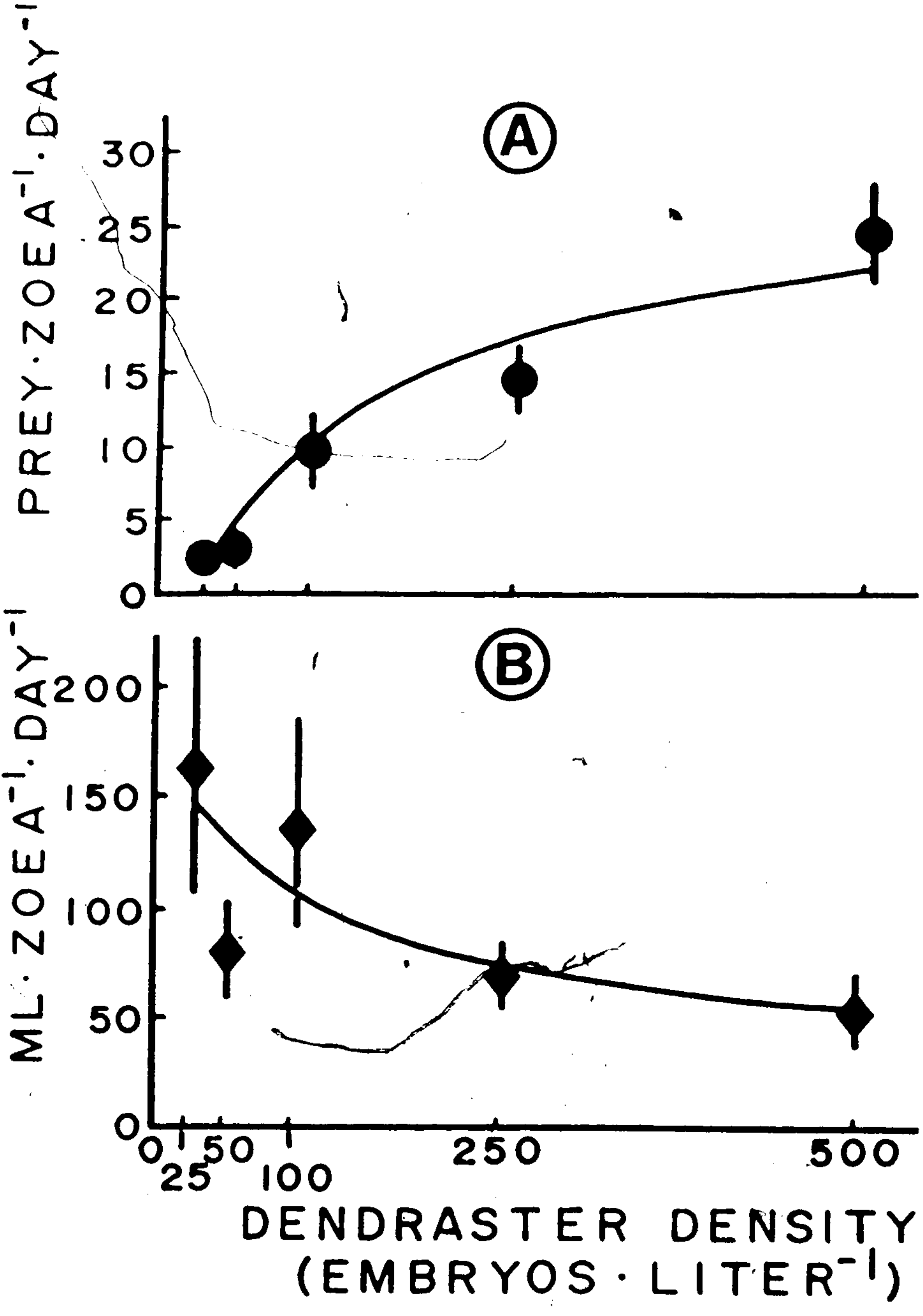
Vertical abundance of echinoid larvae and brachyuran crab zoeae by depth stratum in Barkley Sound, British Columbia: Values shown are mean ± s.d.; values in parentheses indicate numbers of _Dendraster excentricus_ and _Cancer productus_ larvae. The results of Kruskal-Wallis ANOVA tests of the depth stratification of larvae are also shown along with their associated probability values.

DEPTH STRATUM m	NUMBER TOWS	SAMPLE VOLUME m^3	PLUTEI # m^{-3}	ZOEAE # m^{-3}
0 - 30	3	11.8 ± 2.9	136 ± 62 (12 ± 6)	515 ± 292 (47 ± 30)
30 - 60	3	11.7 ± 2.0	44 ± 46 (3 ± 3)	37 ± 14 (3 ± 1)
60 - 90	3	12.3 ± 3.1	0	10 ± 8 (1 ± 1)

Kruskal-Wallis ANOVA (stratification by depth)

All echinoplutei	H = 7.2099	p = 0.0272
Dendraster excentricus	H = 7.7968	p = 0.0203
All brachyuran zoeae	H = 7.2000	p = 0.0273
Cancer productus	H = 7.1813	p = 0.0275

Figure 1. Functional response of _Cancer productus_ predation to abundance of _Dendraster excentricus_ embryos. Values shown are means ± s.d. A. Ingestion Rate. Regression curve has the equation $Y = -23.04 + 7.6 \ln X$; $r^2 = 0.90$. B. Clearance Rate. Regression curve has the equation $Y = 242.61 - 29.93 \ln X$; $r^2 = 0.41$.


A
PREY·ZOEA⁻¹·DAY⁻¹
30
25
20
15
10
5
0
B
ML·ZOEA⁻¹·DAY⁻¹
200
150
100
50
0
0
25
50
100
250
500
DENDRASTER DENSITY
(EMBRYOS·LITER⁻¹)

developmental stages of Dendraster excentricus are shown in Figure 2. Ova (with and without jelly coatings) were captured at a high rate (pooled mean = 0.55 ± 0.17 liters zoea^{-1} day^{-1}, n = 15) while gastrulae and prism larvae were captured at an intermediate rate (pooled mean = 0.22 ± 0.11 liters zoea^{-1} day^{-1}, n=18). Low clearance rates were observed for pluteus larvae that had 4, 6 or 8 arms (pooled mean = 0.05 ± 0.02 liters zoea^{-1} day^{-1}, n = 25). Clearance rates differed significantly between the high, intermediate and low susceptibility groups (ANOVA, $p<0.001$). In all cases losses of prey in the feeding trials were significantly greater than incidental losses in controls. Differences in clearance rates were consistently low between the various prey categories; there were no significant differences ($p > 0.05$) between ova with and without jelly coatings (two-sample t-test, t = 0.7826, n.s.), between gastrulae and prism larvae (t = 1.4233, n.s.), nor between pluteus larvae having various numbers of arms (4 vs. 6 arms, t = 0.2147, n.s.; 6 vs 8 arms, t = 1.5119, n.s.; 4 vs. 8 arms, t = 1.5729, n.s.).

High clearance rates were also observed for embryos, gastrulae and prism larvae when Cancer productus zoeae were offered mixed stages of prey in 2 liter vessels (Figure 3). Clearance rates of C. productus averaged 0.18 liters zoea^{-1} day^{-1} for pre-pluteus stages and 0.03 liters zoea^{-1} day^{-1} for pluteus larvae. Decreased susceptibility of pluteus larvae to predation (Figures 2

Figure 2. Clearance rates by *Cancer productus* zoeae upon various developmental stages of *Dendraster excentricus* during single-stage feeding experiments. Solid bars = high vulnerability eggs; hatched bars = intermediate vulnerability zygotes, gastrulae and prism larvae; stippled bars = low vulnerability echinoplutei; Open bars = loss of prey in controls. All values shown are means ± s.d.

Predation of Dendraster by Cancer zoea

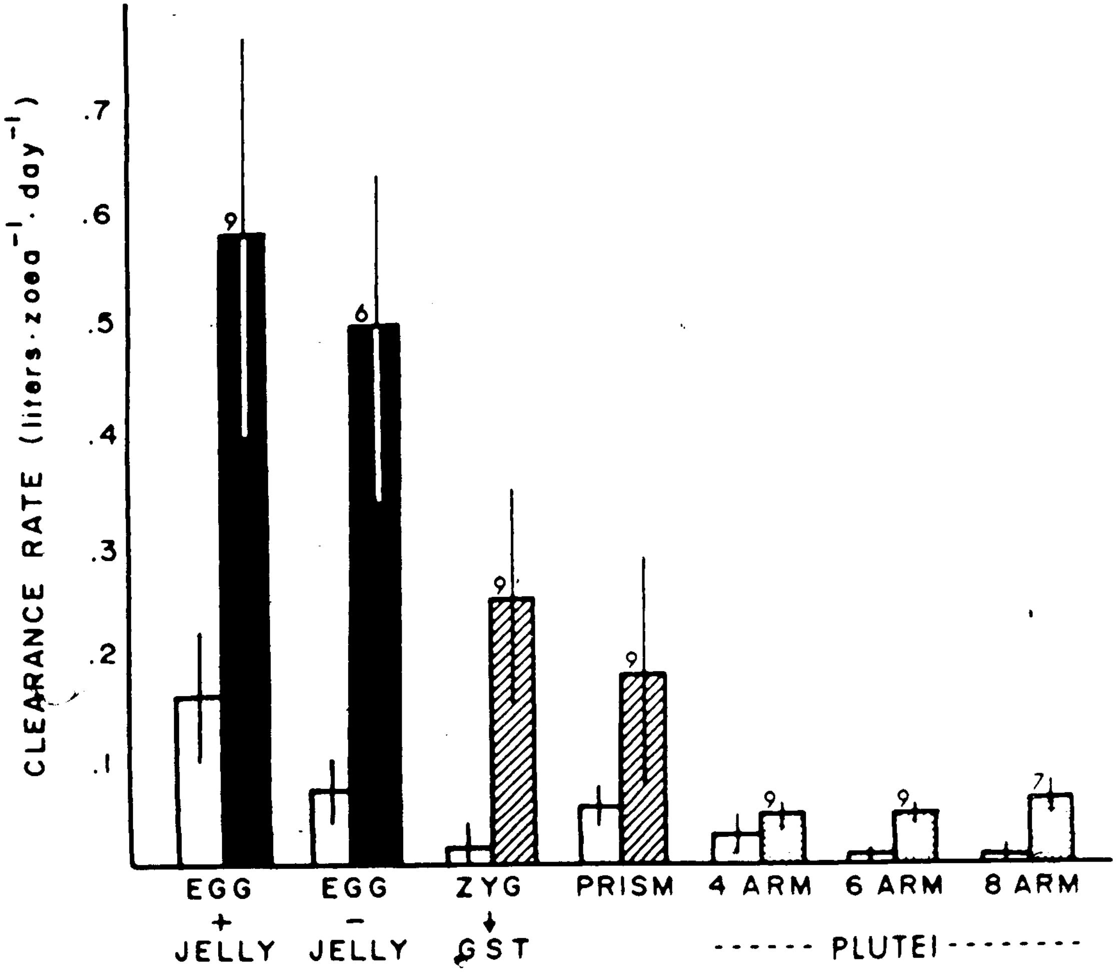
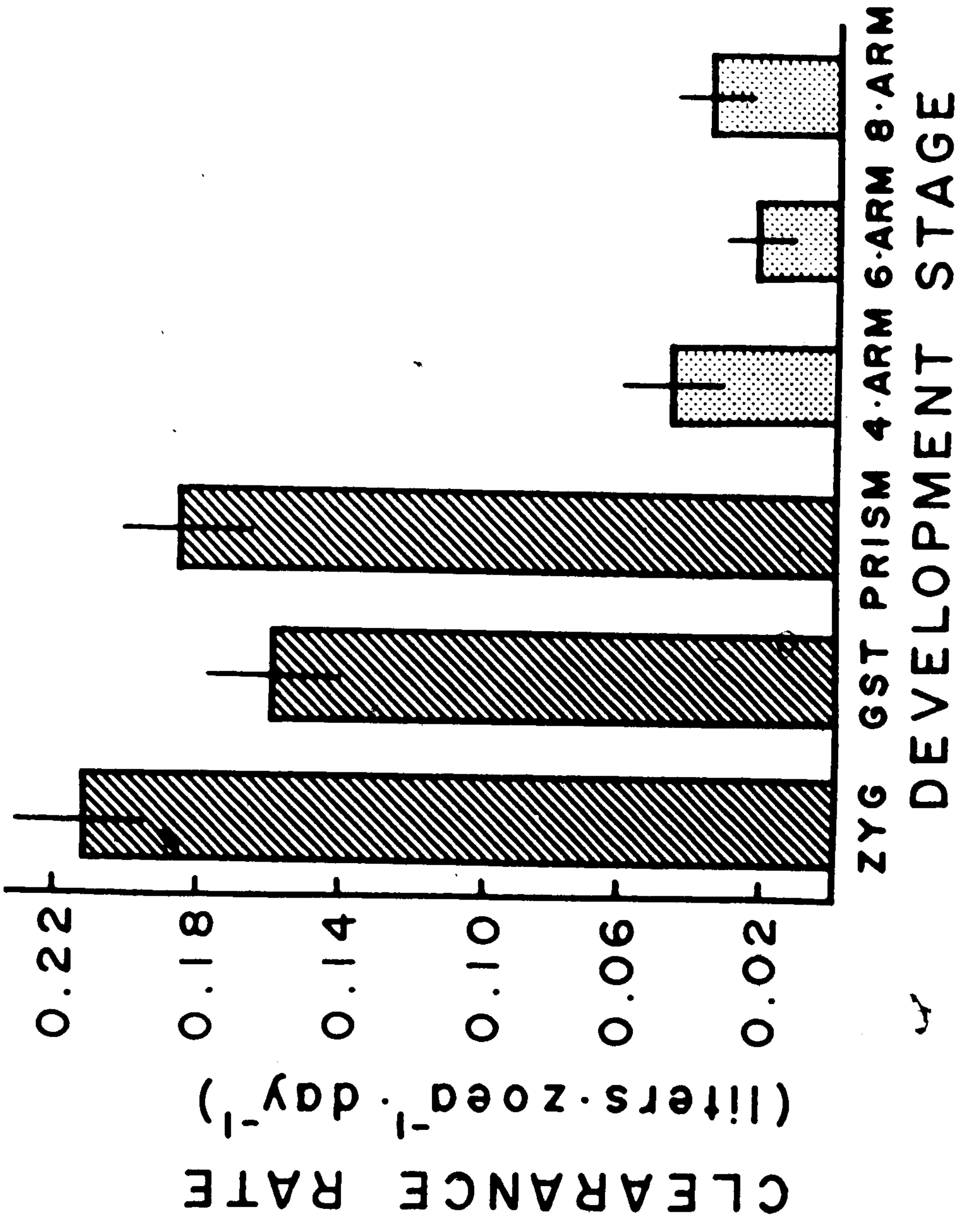


Figure 3. Clearance rates by Cancer productus zoeae upon various developmental stages of Dendraster excentricus during mixed-stage feeding experiments. Hatched bars = intermediate vulnerability zygotes, gastrulae and prism larvae; stippled bars = low vulnerability echinoplutei. All values shown are means ± s.d.


CLEARANCE RATE
(liters · zoea^{-1} · day^{-1})
0.22
0.18
0.14
0.10
0.06
0.02
ZYG
GST
PRISM
4·ARM
6·ARM
8·ARM
DEVELOPMENT STAGE

and 3) suggests that stage selective feeding by *C. productus* or the developmental features associated with the transition of prism larvae into plutei may function to reduce rates of *C. productus* predation.

Table 3 shows the results of feeding experiments conducted to distinguish among factors that may have contributed to the decreased susceptibility of 4-armed *Dendraster excentricus* plutei. Differences in prey visibility did not alter the susceptibility of *D. excentricus* to capture by *Cancer productus*; clearance rates in experiments carried out in complete darkness and in illuminated conditions with dyed prey were not significantly different from experiments conducted with untreated plutei in the light (Table 3). Feeding experiments conducted with dwarf-sized plutei indicate that susceptibility was independent of absolute body size. Clearance rates during feeding upon dwarf-sized and normal *D. excentricus* plutei were nearly identical (Table 3) despite the significantly smaller postoral arm lengths of dwarf plutei ($\bar{X}$ = 183.11 ± 41.19 µm) compared with normal plutei ($\bar{X}$ = 388.90 ± 48.46 µm, $t = 22.8806$, $p<0.001$). Additional feeding experiments indicated that the motility of *D. excentricus* had a substantial effect on clearance rates by *C. productus*. Non-motile heat-killed plutei were captured at significantly greater rates than swimming plutei (Table 3, $p = 0.0012$). Predation rates upon non-motile plutei were comparable with the intermediate

Table 3

Summary of clearance rates during predation upon variously treated *Dendraster excentricus* plutei by *Cancer productus* zoeae. Table entries indicate mean ± s.d. The results of t-test comparisons with feeding experiments conducted with normal-sized plutei in constant light are indicated under the Comparison column. Probability values greater than 0.05 are considered as not significant (n.s.) in the text.

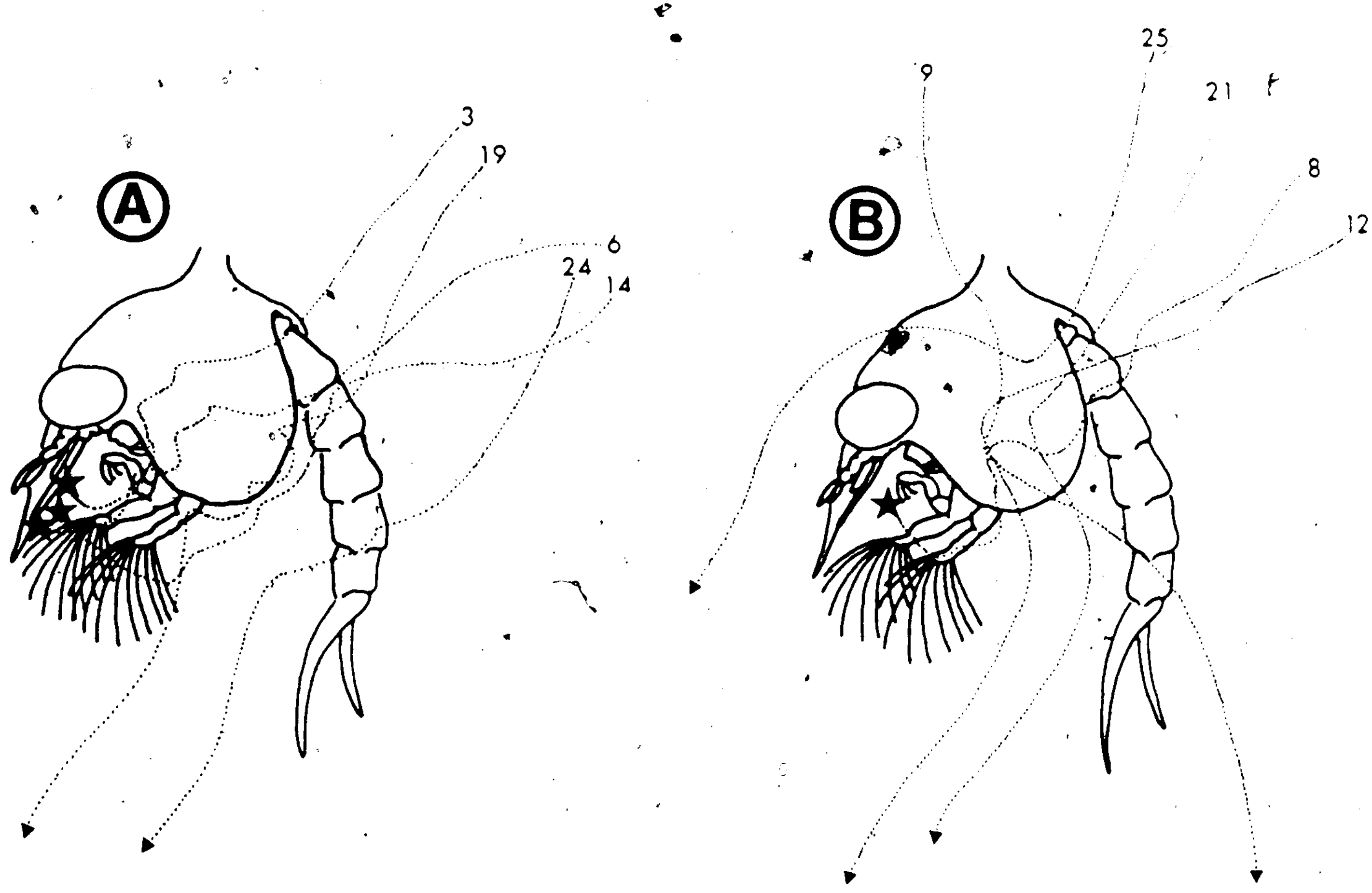
TREATMENT	N	CLEARANCE RATE (ml zoea^{-1}day^{-1})	COMPARISON t	p
Constant Light	5	41.9 ± 18.2	---	---
Constant Dark	6	39.3 ± 12.4	0.6658	0.5206
Dyed Plutei	6	47.9 ± 18.8	0.3631	0.7241
Dwarf-Size Plutei	5	41.5 ± 15.8	0.0291	0.9775
Heat-Killed Plutei	6	109.7 ± 24.4	4.6265	0.0012
Anaesthetized Plutei	8	87.5 ± 32.9	2.6865	0.0212

clearance rates observed for earlier stage D. excentricus prism larvae (Figure 2). Increased clearance rates were also observed for plutei whose ability to reverse the direction of ciliary beating was blocked with 0.01% $MgCl_2$ (Table 3, p = 0.0212). Plutei of D. excentricus develop the ability to reverse the direction of swimming during the transition from prism to pluteus. Since $MgCl_2$-treated plutei were incapable of reversed swimming, the high predation rates observed in treatments in which reversal was inhibited indicate that the ability of plutei to reverse the direction of swimming can have a direct effect on the probability of capture by C. productus zoeae.

4. Post-Contact Encounter Response

Interactions between Dendraster excentricus and Cancer productus are shown graphically in Figure 4. Gastrulae and pluteus larvae of D. excentricus made initial contact with the zoea near the postero-dorsal region of the zoea carapace and abdomen due to the flow of ventrally-directed swimming currents generated by the 1st and 2nd maxillipeds. Following the initial contact, D. excentricus gastrulae continued to swim forward and made repeated contact with the zoea carapace, maxillipeds and maxillary setae (Figure 4a). In most cases, gastrulae made repeated contact with the zoea prior to capture. Plutei of D. excentricus also

Figure 4. Camera lucida tracings of encounters between _Dendraster excentricus_ gastrulae and echinoplutei and tethered _Cancer productus_ zoeae. A. Gastrulae. B. Echinoplutei. Each drawing was prepared by selecting five tracings at random from a set of 25 encounter tracings. Values indicate tracing number; arrows show the direction of prey movement; stars indicate capture and ingestion.


A
3
19
6
24
14
B
9
25
21
8
12

direction of swimming and moved away from the tethered zoea. Plutei resumed forward swimming when they were 2-3 mm away from the zoea. Plutei of *D. excentricus* were captured in 12% of the encounters compared with a 56% capture frequency for gastrulae. These observations provide direct evidence that the development of reversed swimming reduces the susceptibility of pluteus larvae to capture by *C. productus* zoeae in the laboratory.

D. DISCUSSION

Results from this study demonstrate that *Cancer productus* zoeae are able to capture embryos and early larval stages of *Dendraster excentricus* at a high rate compared with capture rates for older pluteus larvae. Clearance rates by *C. productus* zoeae were consistently lower in single and mixed-stage feeding experiments after *D. excentricus* had developed skeletal elements and the ability to reverse the direction of swimming. The high susceptibility of non-motile stages such as ova and pre-hatched embryos suggests that *D. excentricus* may be at the greatest risk to planktonic predators immediately after spawning. Factors that may influence the decreased susceptibility of *D. excentricus* plutei to predation include: 1) size-selectivity, 2) larval morphology, 3) motility, and 4) behavioral responses.

1. Size-Selective Predation

[illegible]e explanation for the observed pattern of differential susceptibility to predation is that Cancer productus zoeae may prefer small ova and embryos over larger plutei. Size-selective feeding has been reported for several freshwater and marine zooplanktonic crustaceans (Dodson, 1974; Kerfoot, 1977; Landry, 1978; Mullin, 1979; Zaret, 1980; Murtaugh, 1981; Pastorok, 1981; Yen, 1982; Landry et al., 1985) in which the predators typically have a greater selective impact on small and intermediate-sized prey. Similarly, early stage decapod zoeae are generally limited in the sizes of prey they can consume (Costlow and Bookhout, 1959; Rust and Carlson, 1960; Sulkin, 1975). Prey selection, however, appears to be related both to the size and stage of the zoea as well as the size and nutritional content of the prey (Sulkin, 1978; Levine and Sulkin, 1984). Later stage zoea from several species of crabs including C. productus have been reared on diets composed of rotifers, polychaete trochophores, sea urchin gastrulae, and brine shrimp nauplii (Costlow and Bookhout, 1959; Rust and Carlson, 1960; Costlow et al., 1966; Poole, 1966; Herrnkind, 1968; Reed, 1969; Trask, 1970; Rice and Williamson, 1971; Sulkin, 1975; Christiansen and Yang, 1976). All of these prey items have body lengths ranging from 70 to 350 µm. I observed predation by C. productus upon barnacle nauplii (Pollicipes polymerus) and Dendraster excentricus plutei that had body lengths greater than 500 µm (Rumrill, personal observations). The 5th instar C. productus zoeae were able to capture and ingest all sizes of prey offered in the feeding experiments. Low clearance rates observed during predation upon dwarf-sized *D. excentricus* plutei suggest that the reduced susceptibility of pluteus larvae is not solely due to increasing prey size. Consequently, explanations other than size-selection must be considered.

2. *Larval Morphology*

A second possibility for differential prey susceptibility is that later developmental stages of *Dendraster excentricus* may require longer handling times than earlier stages prior to ingestion by *Cancer productus*. Growth of post-prism *D. excentricus* larvae is accompanied by the development of a rigid internal skeleton and a band of cilia that extends around the periphery of the larval arms (Burke, 1983). Handling times of *D. excentricus* may increase following the development of the skeleton, and could result in a decreased average ingestion ra[illegible] fo[illegible] later prey stages. However, significantly higher capture rates were observed for heat-killed plutei compared with normal plutei, despite the presence of skeletal ossicles and long postero-lateral and postoral arms in live and heat-killed prey. Emlet (1982) noted that echinoplutei of *D. excentricus* have fenestrated skeletal spicules and are capable of flaring the postero-lateral arms when disturbed. Arm flaring temporarily increases the width of the pluteus, and Emlet (1983) suggested that fenestrated arms and flaring behavior may deter predation. Although experiments have not been conducted that specifically address arm-flaring, results from this study indicate that the development of a rigid skeleton is not entirely effective in eliminating predation. Analysis of C. productus gut contents with cross-polarized light immediately following feeding experiments revealed crushed sections of fenestrated spicules along with other tissues from ingested D. excentricus plutei. No differences in prey susceptibility could be detected between D. excentricus and other echinoplutei (Strongylocentrotus franciscanus and S. purpuratus) that have non-fenestrated skeletons and are incapable of flaring behavior (Rumrill and Chia, 1985). However, the possibility that arm flaring and skeletal morphology may reduce predation rates by increasing the handling times of plutei prior to ingestion cannot be excluded.

3. Dendraster Motility

The encounter model developed by Gerritsen and Strickler (1977) predicts that increasing prey swimming speed will increase the probability of encounters between predators and prey. The slow swimming speed of Dendraster excentricus and low densities of Cancer productus zoeae in Barkley Sound indicate that ontogenetic differences in the swimming speed of D. excentricus will have a negligible effect on encounter rates with C. productus in nature. For example, the maximum density of C. productus observed in Barkley Sound was 73 zoeae m^{-3}. Assuming random distributions of predators and prey, non-motile D. excentricus embryos should encounter C. productus zoeae once every 29 hrs compared with an encounter interval of 28 hrs for swimming D. excentricus plutei. Encounter rates with C. productus zoeae were also similar between non-motile (2.31 zoeae embryo^{-1} hr^{-1}) and motile prey stages (2.32 zoeae pluteus^{-1} hr^{-1}) at the elevated predator and prey densities in laboratory experiments. Despite these small differences in encounter frequencies, the results from feeding experiments showed that clearance rates by C. productus during feeding upon non-motile ova were 60% greater than clearance rates during feeding upon swimming gastrulae and prism larvae. Similarly, non-motile heat-killed plutei were captured at significantly greater rates than swimming plutei with identical body sizes and morphology (Table 3). These observations indicate that the development of swimming cilia in D. excentricus contributes to the decreased susceptibility of motile prey stages in a manner that is independent of their encounter rate with C. productus.

4. Dendraster Swimming Behavior

The low susceptibility of Dendraster excentricus plutei in single and mixed-stage feeding experiments appears to depend upon the ability of the plutei to actively avoid capture after they have entered the low Reynolds number hydrodynamic environment immediately surrounding the Cancer productus zoeae. During the transition from prism to pluteus, echinoid larvae develop the ability to reverse the direction of ciliary beating (Mackie et al., 1969; Strathmann et al., 1972). Episodes of ciliary reversal appear to be mediated by contact with objects such as suspended algal cells (Mackie et al., 1969), other larvae, walls of culture containers, or the layer of seawater surface tension (Rumrill, personal observations). Tracings of encounters between D. excentricus plutei and C. productus zoeae indicate that plutei approach the zoeae while swimming in the forward direction. After making contact with the zoea carapace, the plutei reversed the direction of ciliary beating and swam backwards until they were swept away in currents generated by the zoea maxillipeds. High rates of predation upon $MgCl_2$ anesthetized plutei that were inhibited from swimming backwards (Table 3) are consistent with the observations that reversed swimming behavior functions as a post-contact encounter response that reduces the susceptibility of plutei to capture.

Localized episodes of ciliary reversal are utilized by echinoid plutei to capture algal cells (Strathmann, 1971). These small-scale reversals typically involve groups of 18 to 20 cilia. Presumably, larger-scale ciliary reversals that involve major regions of the ciliated band and the locomotory epaulettes are responsible for changes in swimming direction. A network of nerve cells is located along the inner margin of the ciliated band in Dendraster excentricus plutei (Burke, 1983). In plutei of Strongylocentrotus purpuratus the nerve cells are integrated via non-synaptic connections to a series of axonal tracts located beneath the ciliated band (Burke, 1978). Branched microvilli adjacent to the ciliated band and epaulettes make connections with the subciliary nerve cells. The sensory microvilli may detect changes in fluid pressure or deformation rate and induce ciliary reversals as the pluteus approaches an object such as a predatory microcrustacean. Mechanoreceptor microvilli and subciliary nerve cells are absent in gastrula larvae of D. excentricus (Burke, 1983). In the present study, encounter tracings showed that D. excentricus gastrulae typically made repeated contact with the Cancer productus zoeae as they were swept past the carapace and maxillipeds. Repeated contact with C. productus apparently increases the probability of capture by increasing the liklihood that prey will enter the immediate capture sphere of the zoea.

During the planktonic period, stage-specific differences in predation intensity are influenced by stage-specific encounter frequencies and by the probability of capture and escape at each embryonic and larval stage. Estimates of encounter rates between species pairs such as Dendraster excentricus and Cancer productus substantially underestimate the risk due to predation because D. excentricus embryos and larvae are preyed upon by several different types of zooplankton predators

(Pennington et al., 1986). Since the pattern of differential susceptibility to predation observed between D. excentricus and C. productus is applicable to interactions with other microcrustacean predators, D. excentricus appear to be most vulnerable to predation during the early embryonic period because non-motile zygotes and embryos occur in higher densities than later larvae and do not have the behavioral response and handling difficulties of pluteus larvae. Dendraster excentricus plutei are less vulnerable to predation than zygotes and embryos due to their lower densities and post-contact encounter response. These findings suggest that although the planktonic distribution patterns of D. excentricus larvae in nearshore waters appear to be dictated primarily by passive circulation and advective processes (Cameron and Rumrill, 1982; Emlet, 1986), the success or failure of predation attempts is dependent on active larval processes that occur on a much smaller spatial scale.

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CHAPTER III.

EFFECTS OF OVA SIZE, DEVELOPMENT RATE, AND AMBIENT TEMPERATURE ON THE EARLY MORTALITY OF PLANKTOTROPHIC ECHINODERM LARVAE

A. INTRODUCTION

One of the most striking dichotomies recognized by larval biologists is the distinction between exogenous (= planktotrophic) and endogenous (= lecithotrophic) sources of nutrition for developing larvae of benthic marine invertebrates. These contrasting larval trophic modes are typically associated with differences in ova sizes and with subsequent differences in the shape and form of the larval body. Current theoretical concepts of marine invertebrate life history tactics assume that mortality during the larval period is inversely correlated with egg size (Vance 1973; Chia, 1974; Strathmann, 1977; Palmer and Strathmann, 1981). In general, these heuristic models assert that the rate at which zooplankton predators capture and consume invertebrate larvae is inversely proportional to the energy invested in each offspring. Subsequently, it is generally assumed that the high mortality of planktotrophic larvae is offset by a relatively low parental investment per larva (Ayal and Safriel, 1982). Accordingly, life history models predict that planktotrophic invertebrate larvae will be highly susceptible to predation whereas lecithotrophic larvae will be less susceptible. Although indirect comparisons of larval susceptibility between planktotrophic and lecithotrophic species indicate that the assumption of an inverse relationship between ova size and mortality may be valid, the comparisons are indirect because planktotrophic and lecithotrophic larvae are not preyed upon by the same types of carnivorous zooplanktivores (Rumrill, 1987). Comparisons between planktotrophic and lecithotrophic species are also weak because the selective forces that shape invertebrate life histories operate on subtle intraspecific variation in energetic investment and mortality rather than on interspecific differences in these parameters. More direct comparisons can be made of the relationships between ova size and mortality among groups of species that are entirely planktotrophic or lecithotrophic.

Since the susceptibility of marine invertebrate larvae to predation typically changes during ontogeny (Pennington and Chia, 1984; Pennington <u>et</u> <u>al</u>., 1986; Rumrill and Chia, 1985; Rumrill <u>et</u> <u>al</u>., 1985), variation in the rate of morphogenesis has important consequences concerning the loss of pelagic larval stages to predatory zooplankton. The application of differences in ova size and development rate as indices of mortality depends strongly upon the magnitude and shape of the stage-specific susceptibility curve obtained by investigating predator-prey interactions for particular groups of species (Rumrill <u>et</u> <u>al</u>., 1985;

Pennington et al., 1986). A corollary to the development rate-mortality concept is that since ambient sea temperature affects rates of larval development, then variability in temperature should also directly affect the duration of the high and low susceptibility periods. Consequently, losses of invertebrate larvae to predatory zooplankton should vary predictably with changes in temperature, particularly during the critical high susceptibility period. As with differences in ova size and development rate, the application of temperature as an index of mortality is also dependent upon the shape of the stage-specific susceptibility curve (Rumrill and Chia, 1985; Rumrill et al., 1985).

In this chapter, I report a series of experiments to test the generalizations that losses of planktotrophic echinoderm larvae to predation are related to ova size, temperature and rate of development. Results from this study directly address the assumption of an inverse relationship between development rate and risk, and they lend empirical support to the prevalent view that rapid morphogenesis through the early pre-feeding stages of development should be favored in invertebrate life histories that include a long-lived planktotrophic larval phase.

B. MATERIALS AND METHODS

This research was carried out at Bamfield Marine

Station, on the west coast of Vancouver Island, British Columbia (48°50'N; 125°08'W). Adult echinoderms were collected from intertidal and subtidal habitats near the vicinity of Bamfield Marine Station.

1. Study Organisms

Three species of echinoids, Strongylocentrotus franciscanus, S. purpuratus, Dendraster excentricus, and four species of asteroids, Pisaster ochraceus, Orthasterias koehleri, Patiria miniata, and Dermasterias imbricata were used in this study. The species were selected on the basis of availability and because of their range in ova sizes (Table 4). Gametes were obtained either from natural spawning in the laboratory, or by inducing gravid adults to spawn by intracoelomic injections of 0.52 M KCl (echinoids) or 10^{-5} M 1-methyl adenine (asteroids). Larvae were fed *ad libitum* with a 2:1 mixture of Dunaliella tertiolecta (Chlorophyta) and Pavlova leutheri (Chrysophyta).

Predatory zooplankton used in feeding experiments were all carnivorous crustaceans and included zoea larvae of the brachyuran crab, Pugettia producta, the hyperiid amphipod, Parathemisto pacifica, and the mysid, Neomysis rayii. These particular species of planktonic crustaceans were selected for several reasons. First, all three species co-occur along with planktotrophic echinoderm larvae in surface waters in Barkley Sound (Littlepage, 1971; S. Rumrill, pers. obs.). Second, the species were readily available during the early spring and summer months; P. producta zoeae were reared in the laboratory from egg masses obtained from ovigerous female crabs (see Rumrill 1987; Chapter 4). *P. pacifica* were captured from surface water in oblique zooplankton tows taken with a 125 µm mesh, 0.5 m diameter standard net. *N. rayii* were captured from schooling swarms with a slurp gun and plastic bags operated [illegible] SCUBA divers. Finally, the species were selected because they were known to exhibit a variety of stage-specific predation responses during feeding experiments upon embryos and larvae of planktotrophic echinoderms (Rumrill, personal observations; Pennington *et al.*, 1986).

2. Measurements of Ova Size

The diameters of ova were measured to obtain estimates of interspecific and intraspecific variation in ova size. For each species, naturally spawned ova were placed into a Sedgewick-Rafter chamber and the diameters of 100 ova were measured with a calibrated ocular micrometer at a magnification of 40 X. Ova were assumed to be spherical and ova volumes were calculated as Volume = 1/6 Π Diameter[illegible]

3. Effects of Temperature on Development Rates

Ova of each echinoderm species were fertilized with a dilute sperm suspension, and the zygotes were raised in 1000 ml glass beakers. Cultures of embryos and larvae were maintained at 3 temperatures in laboratory incubators under a 16L:8D photoperiod regime. A maximum-minimum thermometer indicated that temperatures in the incubators fluctuated by about ± 3°C, so the cultures experienced thermal regimes of 8 ± 2, 12 ± 2, and 15 ± 2°C. Embryo and larval cultures were agitated with a slow stream of small air bubbles supplied through intramedic surgical tubing. Cultures were examined every 2 hrs during the first 20 hrs following fertilization and every 8 hrs after hatching.

4. Predation by Zooplanktonic Crustaceans

Susceptibility of echinoderm embryos and larvae to predation was examined in the laboratory in a series of microcosm feeding experiments. The methods used in the feeding experiments were similar to those reported by Rumrill _et_ _al_. (1985; Chapter 3), although a mixing apparatus was used that could simultaneously process up to 36 replicate predator-prey microcosms.

Functional response feeding experiments were carried out to determine the effects of changes in prey density on rates of predation. Feeding experiments were conducted at 6 different prey concentrations (10, 25, 50, 100, 150, and 250 prey liter^{-1}). Ova were obtained from each species of echinoderm, inseminated with a dilute sperm suspension, and washed several times to remove excess sperm. The zygotes were placed into 1 liter glass jars filled with 1 µm filtered seawater, a single predatory crustacean was added, and the jars were sealed and attached to the mixing apparatus. All functional response experiments were conducted at 12 ± 2°C in an incubator with 16L:8D photoperiod. Each feeding experiment consisted of 8 replicate predator treatments and 4 controls without predators. The duration of each experiment was 12 hours, so the echinoderm zygotes developed through the early cleavage stages to late un-hatched morulae during the course of each experiment. The entire series of functional response experiments required over 9 weeks to complete, although predation experiments at increasing prey densities were always conducted on successive days for any particular species of prey. All functional response experiments with Neomysis rayii were conducted over a period of 19 days.

Stage-specific differences in larval susceptibility were examined for each species of echinoderm in microcosm feeding experiments conducted at an initial prey density of 50 prey liter^{-1}. The 6 categories of prey used in the majority of experiments of feeding upon echinoids were: 1) unfertilized ova, 2) non-motile embryos, 3) motile blastulae and gastrulae, 4) prism larvae, 5) 4-armed plutei, and 6) 6-armed plutei. Trials with eight armed plutei were also conducted in feeding experiments with Pugettia producta. In the asteroids, feeding experiments were carried out with 6 categories of prey: 1) unfertilized ova, 2) non-motile embryos, 3) motile blastulae and early gastrulae, 4) late gastrulae, 5) early bipinnaria larvae, and 6) brachiolaria larvae. Feeding experiments were conducted with a homogeneous group of single prey stages for all 7 species of echinoderms. Feeding experiments were also carried out with heterogeneous mixtures of Strongylocentrotus franciscanus developmental stages. All stage-specific susceptibility experiments were were carried out in an incubator at 12 ± 2°C. Each series of experiments was terminated after a period of 12 hrs.

Because the development rates of all 7 species of echinoderms were responsive to differences in ambient temperature, a series of feeding experiments were conducted under different thermal conditions to determine how variation in development rates affects the susceptibility of embryos and larvae to predation during the planktonic period. A series of long-term feeding experiments were conducted to analyse the effects of predation by <u>Pugettia producta</u> at different temperatures. One hundred and fifty zygotes from each of the seven species of echinoderms were placed into 1 liter glass jars filled with 1 µm filtered seawater. At the beginning of each experiment a single stage I zoea larva of <u>P. producta</u> was placed into the jar. The jars were sealed and attached to the rotating mixing device. Each set of trials consisted of 5 replicate predator treatments and 3 controls without predators. The experiments were terminated after a period of 120 hrs. Separate sets of feeding experiments were conducted at 8 ± 2, 12 ± 2 and 15 ± 2°C. Although seawater in the jars was not replenished during the course of the experiments, the zoeae and remaining echinoderm larvae appeared in good health when they were examined at the end of the experiments.

Additional feeding experiments were conducted at 5 temperatures (8, 10, 12, 14, 16°C) to assess the effects of temperature on rates of Pugettia producta predation upon embryos of Strongylocentrotus franciscanus and Pisaster ochraceus. These experiments were composed of between 6 and 10 replicate predator treatments and 3 to 5 controls without predators. The initial density of prey items was 100 embryos liter^{-1}, and each feeding trial lasted 12 hrs.

C. RESULTS

1. Variation in Ova Size

Interspecific and intraspecific variation in the sizes of echinoderm ova are summarized in Table 4. Ova sizes among the 7 planktotrophic echinoderm species ranged from 85 μm to 172 μm in diameter and from 0.32 X 10^6 to 2.7 X 10^6 μm^3 in volume. Thus, ova diameters varied by a factor of 2 between Strongylocentrotus purpuratus and Dermasterias imbricata, and the volume of individual ova varied by a factor of 8 between these two species (Table 4). Size-frequency analysis of ova diameters indicated that all populations of ova were unimodal. However, coefficients of variation were generally greatest for species with small ova (S. purpuratus, Dendraster excentricus) and suggest that greater variability in ova sizes occurred among samples of ova collected from species with small eggs.

Table 4

Comparison of the diameters and volumes of naturally spawned ova from seven species of echinoderms. Sample size is 100 ova for each species. Table entries show means; standard deviations are indicated in parentheses. CV columns indicate coefficients of variation. Scaling column shows scale relationships for diameter and volume in comparisons with ova from *Strongylocentrotus purpuratus*.

SPECIES	DIAMETER (μm)	C.V. (%)	VOLUME ($10^6 \mu m^3$)	C.V. (%)	SCALING dia / vol
Strongylocentrotus purpuratus	84.6 (4.7)	5.6	0.32 (0.06)	17.4	1 / 1
Strongylocentrotus franciscanus	152.1 (4.3)	2.8	1.84 (0.15)	8.1	1.8 / 5.7
Dendraster excentricus	120.1 (6.4)	5.3	0.91 (0.14)	15.9	1.4 / 2.8
Pisaster ochraceus	160.1 (5.5)	3.4	2.16 (0.22)	10.4	1.9 / 6.7
Orthasterias koehleri	139.1 (5.2)	3.7	1.40 (0.21)	14.8	1.6 / 4.4
Patiria miniata	136.7 (5.6)	4.1	1.34 (0.17)	12.46	1.6 / 4.2
Dermasterias imbricata	171.6 (6.5)	3.8	2.66 (0.29)	11.05	2.0 / 8.3

2. Effects of Temperature on Development Rates

Measurements of embryo and larval development rates in laboratory cultures showed that there was substantial interspecific and intraspecific variability in the time needed for planktotrophic echinoderm larvae to reach particular stages of development. The majority of embryos and larvae developed at nearly identical rates, but a portion of the population exhibited retarded rates of morphogenesis compared with others in the same culture vessel.

The development rates of all 7 species of echinoderms were dependent upon temperature. Figures 5 and 6 show the time in hours needed to reach various larval stages in laboratory cultures. The time necessary to develop into the first feeding (4-armed pluteus or bipinnaria) larval stages was greatest at 8°C, intermediate at 12°C and shortest at 15°C. Thermal-induced acceleration and retardation of development rates gave Q_{10} values between 1.7 (Patiria miniata) and 2.5 (Pisaster ochraceus). These results indicate that rates of morphogenesis differ among planktotrophic species, and that further intraspecific variation in development rates can be induced by differences in culture temperature that approximate the range of temperatures found in the field.

One of the consequences of variation in ova sizes is a partial correlation with the rate of development to a feeding larval stage. Two comparisons are valid at the

Figure 5. Development rates of echinoid embryos and larvae. Points show the number of hours necessary for zygotes to develop to a particular developmental stage at temperatures of 8 ± 2, 12 ± 2 and 15 ± 2°C. B = unhatched blastula; H = hatching; G = gastrula; Pr = prism larva; P4 = 4-arm pluteus. Dashed lines and numbers on the right side of the figure provide an example of the increased time needed to reach the 4-arm pluteus stage by zygotes of <u>Strongylocentrotus</u> <u>purpuratus</u> at 8°C compared to 15°C.

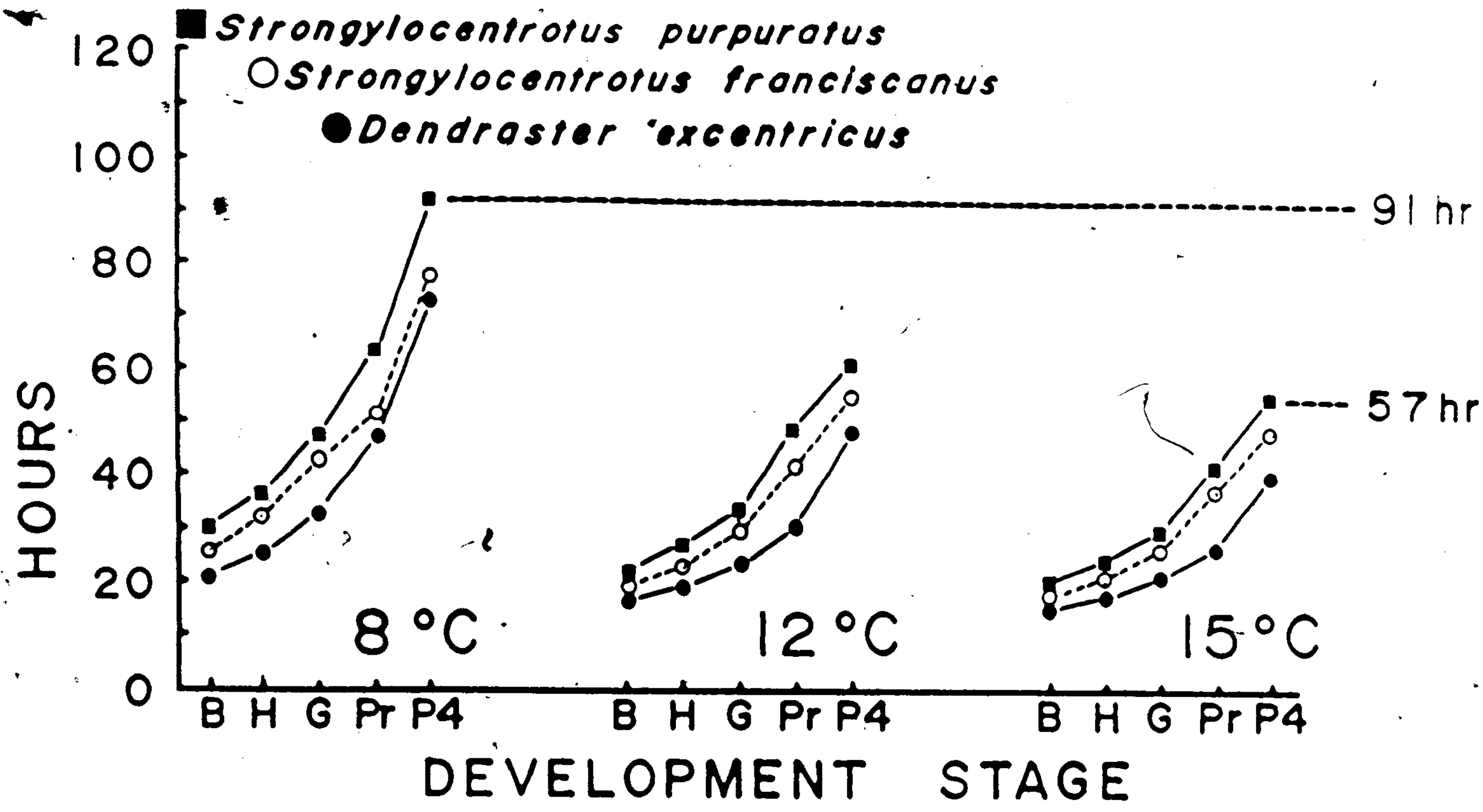
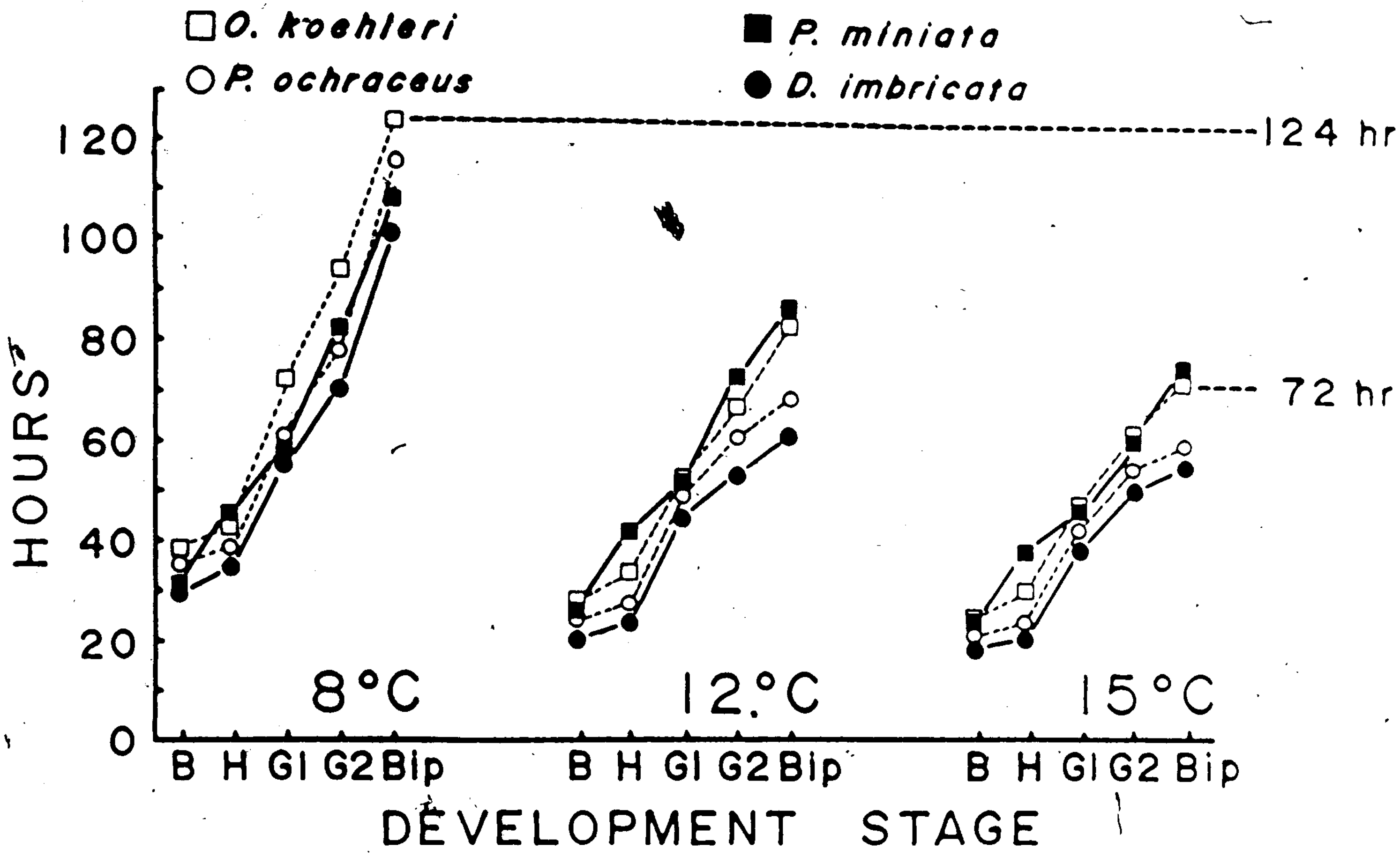

■ Strongylocentrotus purpuratus
○ Strongylocentrotus franciscanus
● Dendraster 'excentricus
HOURS
120
100
80
60
40
20
0
91 hr
57 hr
8 °C
12 °C
15 °C
B H G Pr P4
B H G Pr P4
B H G Pr P4
DEVELOPMENT STAGE

Figure 6. Development rates of asteroid embryos and larvae. Points show the number of hours necessary for zygotes to develop to a particular developmental stage at temperatures of 8 ± 2, 12 ± 2 and 15 ± 2°C. B = unhatched blastula; H = hatching; G1 = early gastrula; G2 = late gastrula; Bip = bipinnaria larva. Dashed lines and numbers on the right side of the figure provide an example of the increased time needed to reach the bipinnaria stage by zygotes of <u>Orthasterias</u> <u>koehleri</u> at 8°C compared to 15°C.


□ O. koehleri
○ P. ochraceus
■ P. miniata
● D. imbricata
HOURS
0
20
40
60
80
100
120
124 hr
72 hr
8°C
12°C
15°C
B H G1 G2 Bip
B H G1 G2 Bip
B H G1 G2 Bip
DEVELOPMENT STAGE

familial level, and three are warranted at the ordinal level. First, within the strongylocentrotid urchins (order echinoida) development rate to a feeding 2-armed pluteus increased with increasing ova diameter (Table 4, Figure 5). The development of Strongylocentrotus purpuratus (ova diam = 84.6 µm) was consistently slower than that of S. franciscanus (ova diam = 152.1 µm) at all three temperatures. Second, the rate of development to a feeding bipinnaria larval stage also increased with ova diameter in the two asterid sea stars, Pisaster ochraceus and Orthasterias koehleri (order forcipulatida). Similarly, the time needed to reach the bipinnaria stage also increased with decreasing ova size in the remaining sea stars (order spinulosida). The rapid development of Dendraster excentricus (ova diam = 120.1 µm, order clypeasteroida) is inconsistent with the prediction from ova diameter, and is comparable to the rapid morphogenesis reported for other clypeasteroids (Kume and Dan, 1968). These comparisons indicate: 1) the echinoids develop to a feeding larval stage at a relatively rapid rate compared with the asteroids, and 2) consideration must be given to the taxonomic position of species in evaluating correlations between ova size and development rate.

3. Predation by Zooplanktonic Crustaceans

Predator-prey interactions between planktotrophic echinoderm larvae and zooplanktonic crustaceans have several components. These include: a) the functional response of predators to increasing prey density, b) differences in the susceptibility of various developmental stages to capture and ingestion, and c) the effects of differences in development rates on the total number of embryos and larvae captured.

a. Functional Response of Predation

The functional responses of crustacean predators to increases in embryo density are shown in Figures 7-9. Predation rates by *Pugettia producta*, *Parathemisto pacifica* and *Neomysis rayii* all increased with increasing embryo density. Although predation rates increased consistently over the range of prey densities offered (ANOVA, $p < 0.001$), the relatively slower rate of increase at high embryo densities suggests that *P. producta*, *P. pacifica* and *N. rayii* all exhibit Holling (1966) Type II functional response curves during feeding upon planktotrophic echinoderm embryos. Most of the plots showed evidence that feeding approached saturation rates at prey densities greater than 150 embryos liter^{-1}. Rates of predation were inversely correlated with ova volume when the results of feeding experiments conducted at initial prey densities of 150 embryos liter^{-1} were compared among all 7 species of echinoderms (*P. producta*: Kendall's tau = -0.4106, n = 56, $p < 0.001$; *P. pacifica*: tau = -0.2628, n = 56, p = 0.0034; *N. rayii*: tau = -0.3991, n = 56, $p < 0.001$).

b. Stage-Specific Susceptibility

Stage-specific differences in the susceptibility of

Figure 7. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon echinoid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Strongylocentrotus franciscanus* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.06X^{0.68}$, $r^2 = 0.83$ (ANOVA, F-ratio = 43.11, $p<0.001$). *Pugettia*: $Y = 0.09X^{0.66}$, $r^2 = 0.91$ ($F = 46.01$, $p<0.001$). *Neomysis*: $Y = 0.08X^{0.81}$, $r^2 = 0.96$ ($F = 73.34$, $p<0.001$). B. Predation upon *Strongylocentrotus purpuratus* embryos. *Parathemisto*: $Y = 0.07X^{0.74}$, $r^2 = 0.88$ ($F = 58.07$, $p<0.001$). *Pugettia*: $Y = 0.07X^{0.83}$, $r^2 =$ [illegible]5 ($F = 109.08$, $p<0.001$). *Neomysis*: $Y = 1.40X^{0}$[illegible], $r^2 = 0.97$ ($F = 144.08$, $p<0.001$). C. Predation upon *Dendraster excentricus* embryos. *Parathemisto*: $Y = 0.09X^{0.66}$, $r^2 = 0.89$ ($F = 61.36$, $p<0.001$). *Pugettia*: $Y = 0.07X^{0.78}$, $r^2 = 0.93$ ($F = 60.34$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.90}$, $r^2 = 0.94$ ($F = 176.19$, $p<0.001$).

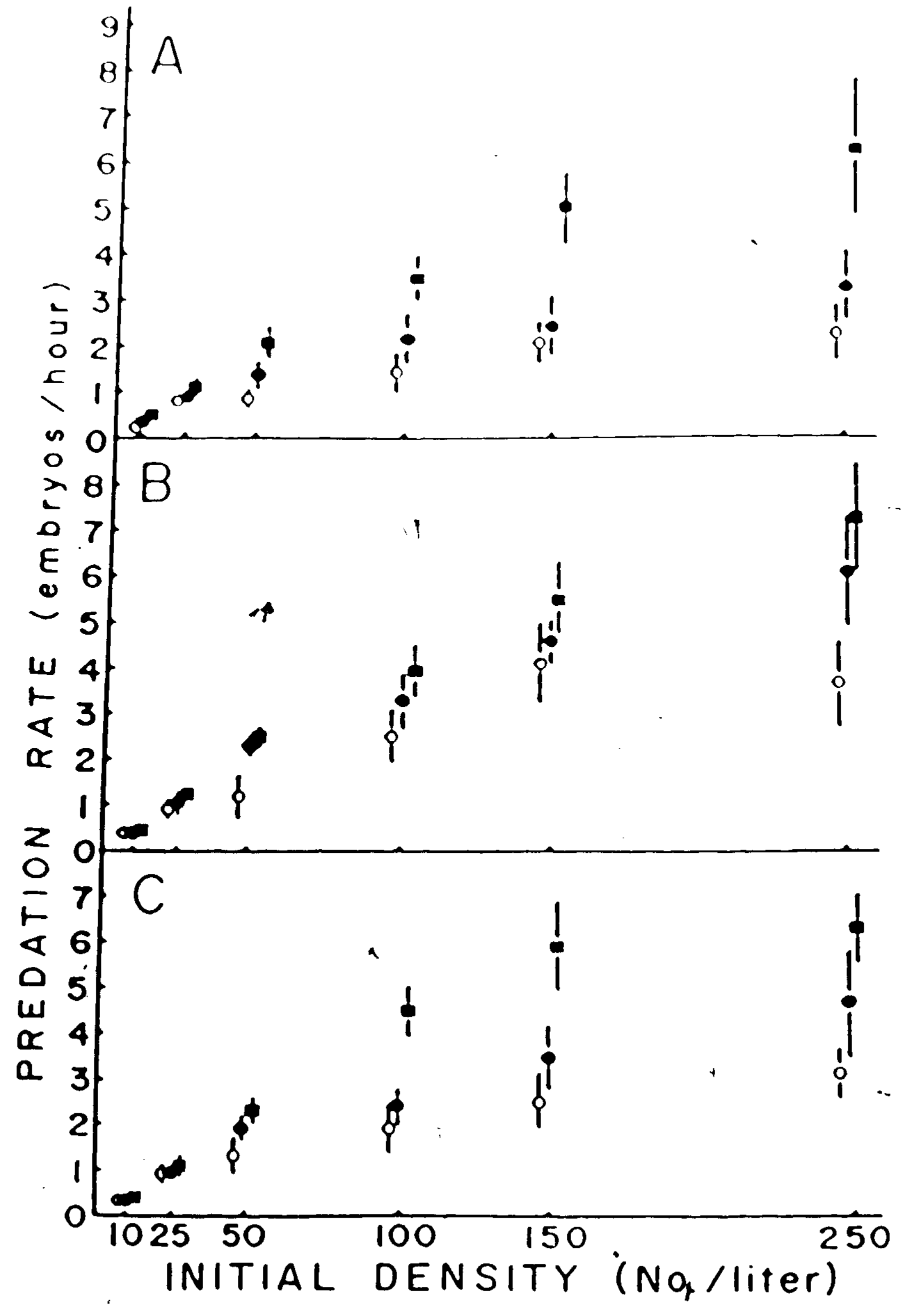

A
B
C
PREDATION RATE (embryos/hour)
0
1
2
3
4
5
6
7
8
9
INITIAL DENSITY (No./liter)
10
25
50
100
150
250

Figure 8. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon asteroid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Pisaster ochraceus* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.08X^{0.72}$, $r^2 = 0.92$ (ANOVA, F-ratio = 96.51 $p<0.001$). *Pugettia*: $Y = 0.08X^{0.73}$, $r^2 = 0.95$ ($F = 101.81$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.86}$, $r^2 = 0.95$ ($F = 107.97$, $p<0.001$). B. Predation upon *Orthasterias koehleri* embryos. *Parathemisto*: $Y = 0.06X^{0.82}$, $r^2 = 0.94$ ($F = 152.53$, $p<0.001$). *Pugettia*: $Y = 0.06X^{0.86}$, $r^2 = 0.97$ ($F = 148.61$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.90}$, $r^2 = 0.97$ ($F = 200.34$, $p<0.001$).

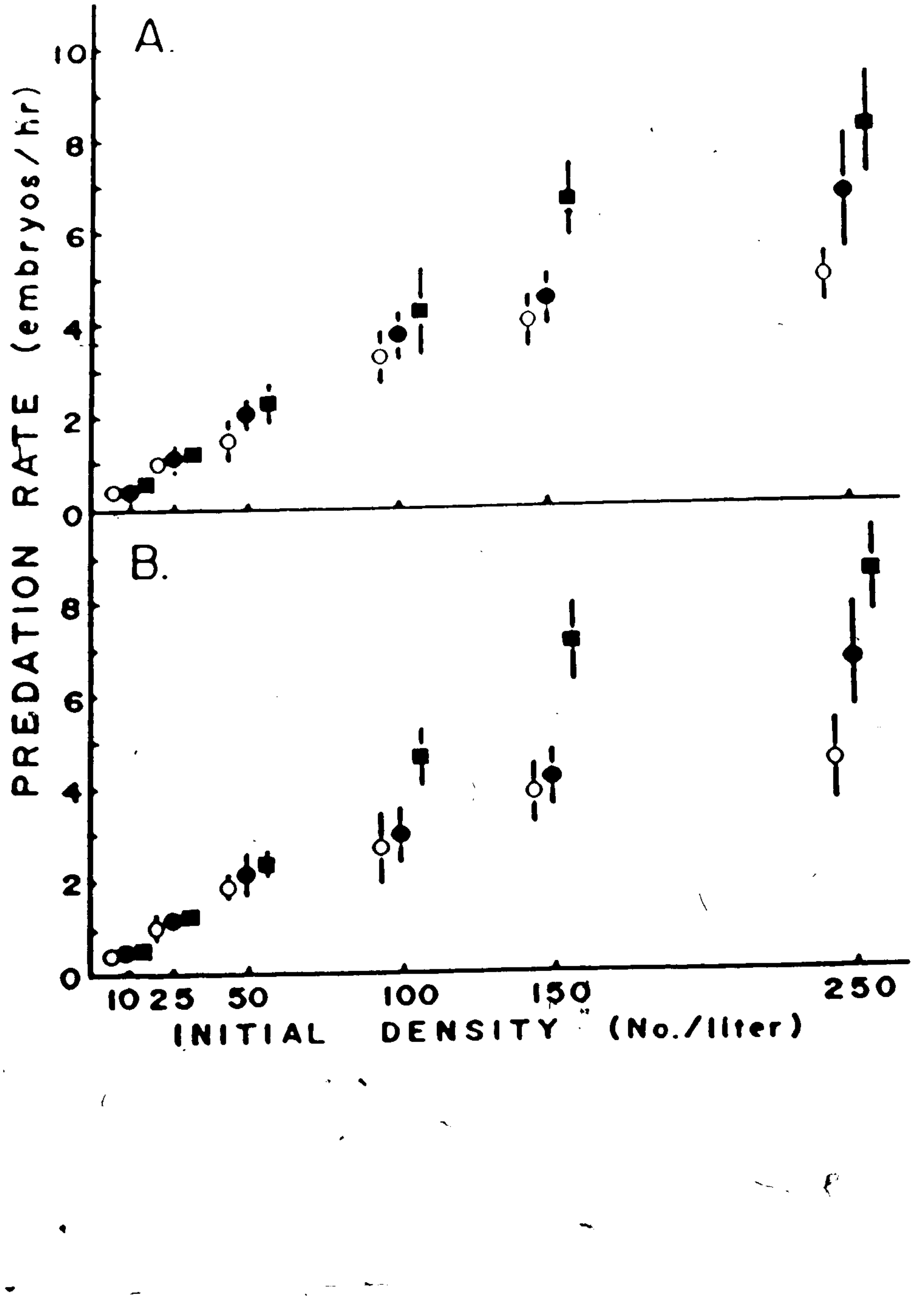
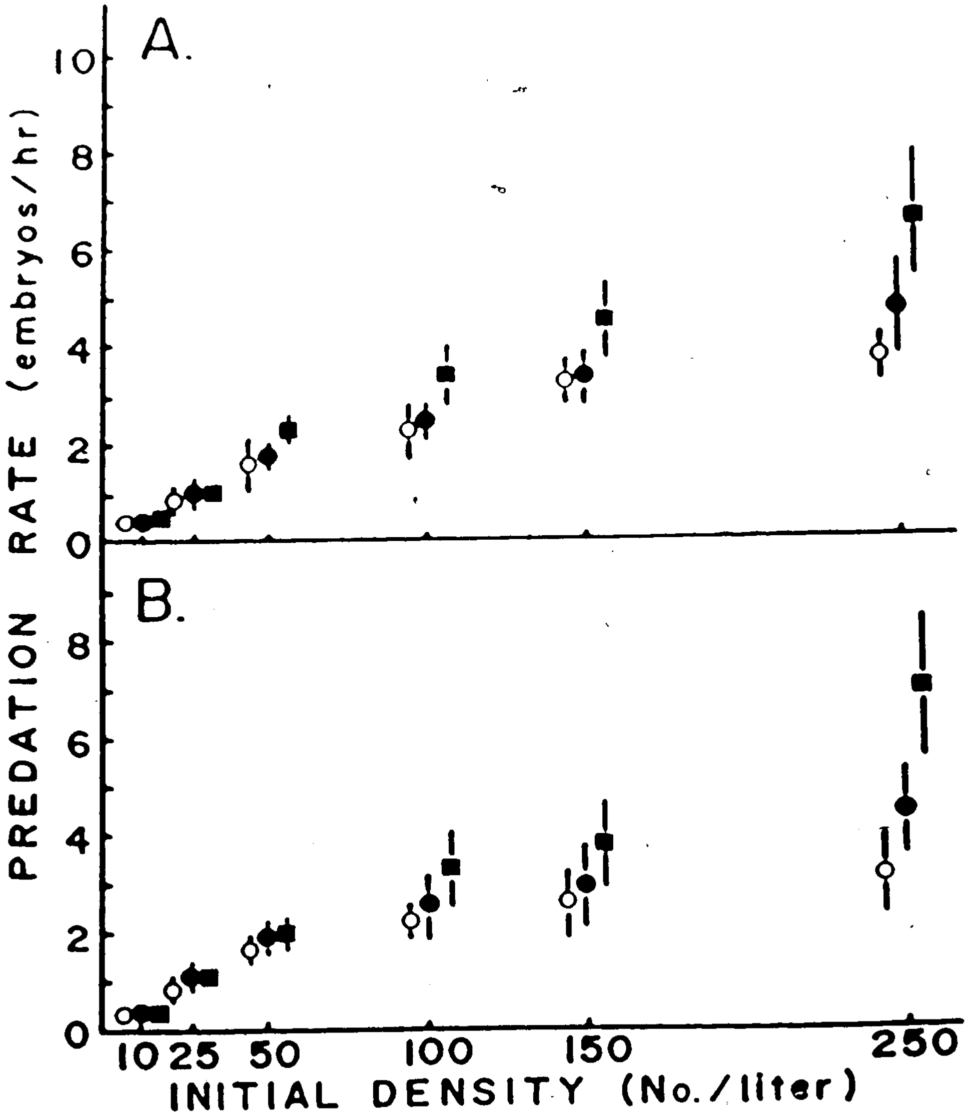

A.
B.
PREDATION RATE (embryos/hr)
0
2
4
6
8
10
10
25
50
100
150
250
INITIAL DENSITY (No./liter)

Figure 9. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon asteroid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Patiria miniata* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.09X^{0.73}$, $r^2 = 0.94$ (ANOVA, F-ratio = 84.29 $p<0.001$). *Pugettia*: $Y = 0.07X^{0.81}$, $r^2 = 0.97$ ($F = 133.39$, $p<0.001$). *Neomysis*: $Y = 0.05X^{0.97}$, $r^2 = 0.98$ ($F = 358.68$, $p<0.001$). B. Predation upon *Dermasterias imbricata* embryos. *Parathemisto*: $Y = 0.09X^{0.67}$, $r^2 = 0.91$ ($F = 57.42$, $p<0.001$). *Pugettia*: $Y = 0.09X^{0.72}$, $r^2 = 0.90$ ($F = 61.85$, $p<0.001$). *Neomysis*: $Y = 0.07X^{0.81}$, $r^2 = 0.95$ ($F = 89.30$, $p<0.001$).


A.
B.
PREDATION RATE (embryos/hr)
0
2
4
6
8
10
INITIAL DENSITY (No./liter)
10
25
50
100
150
250

echinoderm embryos and larvae were evident during the predation experiments. The most complete sets of data were gathered for Strongylocentrotus franciscanus and Pugettia producta. In the feeding experiments with P. producta, rates of predation upon ova, embryos and early larval stages were greater than rates of predation upon later 4, 6, and 8 armed pluteus stages (Figure 10). These stage-specific differences in the susceptibility of S. franciscanus developmental stages to predation were consistent between single-stage and mixed-stage feeding experiments (Figure 10). Stage-specific differences in susceptibility were also observed during the ontogeny of S. franciscanus during predation experiments conducted with Parathemisto pacifica (Figure 11). However, motile blastulae and prism stage larvae were captured at a greater rate than earlier ova and embryos and later pluteus larval stages (Figure 11). As in P. producta, there was no difference in the shape of the stage-specific susceptibility curve during experiments conducted with single and mixed prey stages. Finally, stage-specific differences in the susceptibility of S. franciscanus during single-stage feeding experiments conducted with Neomysis rayii (Figure 12a) were similar to the pattern observed earlier during single and mixed prey experiments with P. producta (Figure 10). However, predation rates upon 4 and 6-armed pluteus larval stages were greater than predation rates upon ova, embryos and early larval stages

Figure 10. Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus* by *Pugettia producta*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae, PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus, PL8 = 8-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.

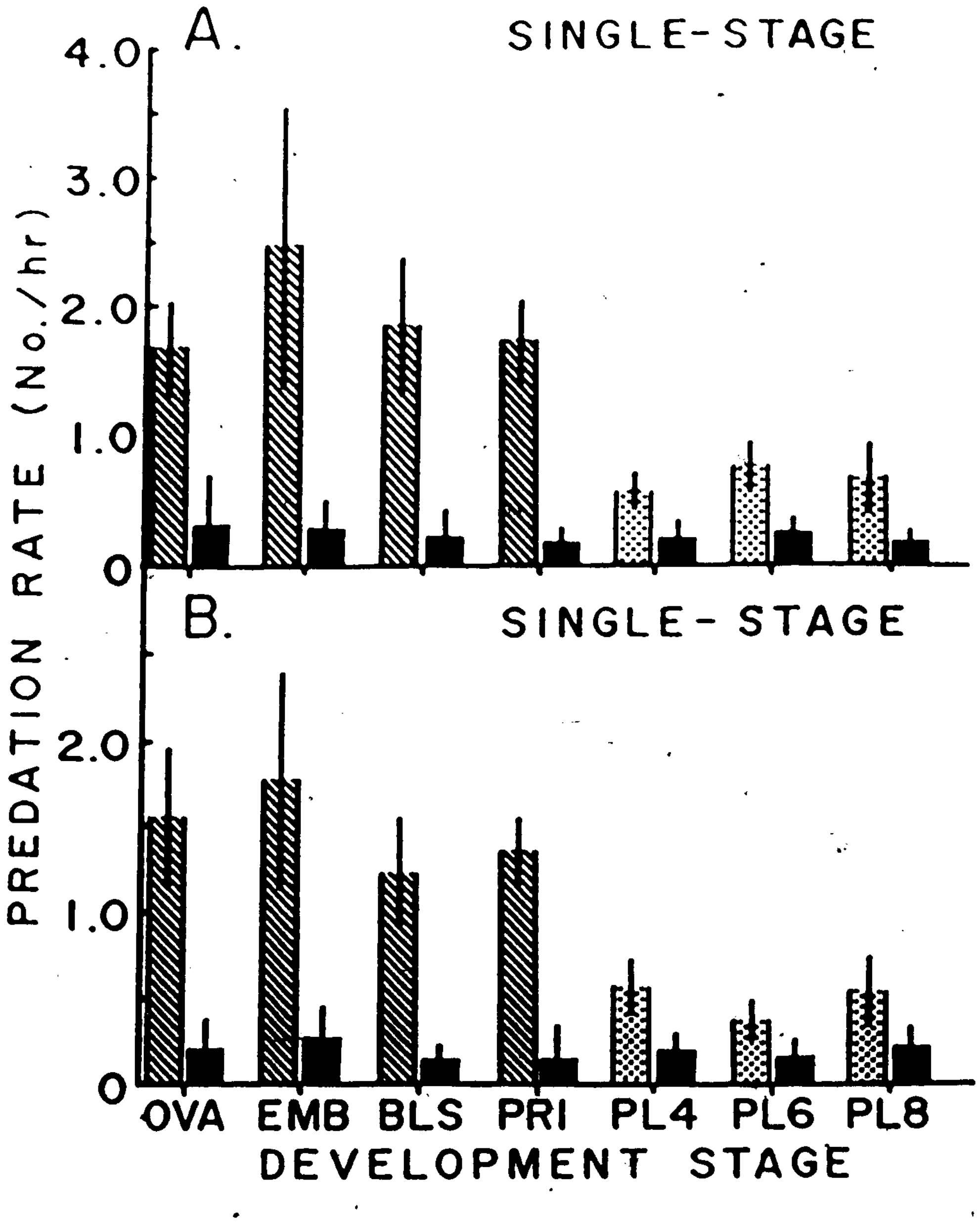

A.
SINGLE-STAGE
B.
SINGLE-STAGE
PREDATION RATE (No./hr)
4.0
3.0
2.0
1.0
0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
PL8
DEVELOPMENT STAGE

Figure 11. Differential rates of predation upon developmental stages of Strongylocentrotus franciscanus by Parathemisto pacifica. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls.
OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae,
PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.

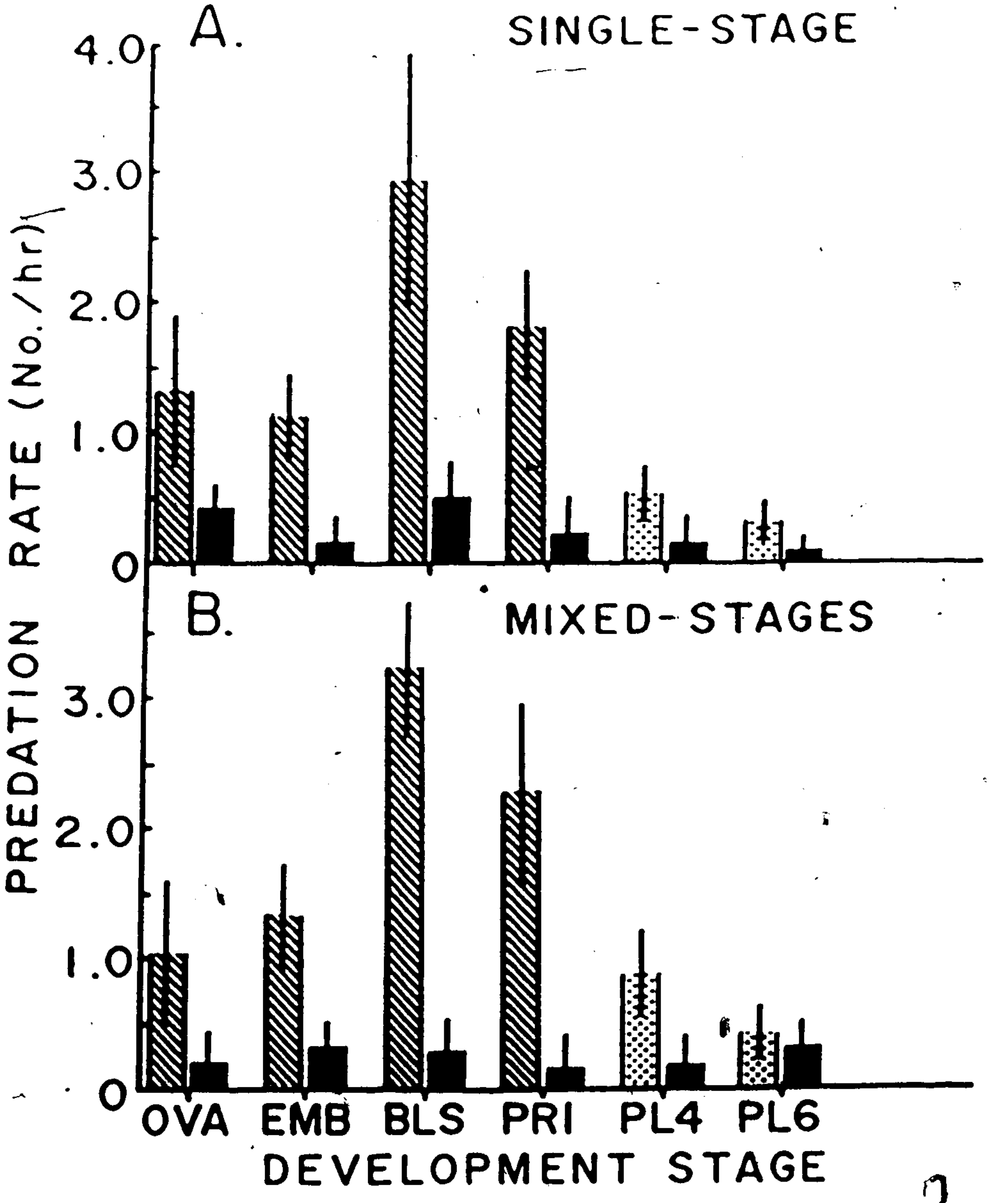
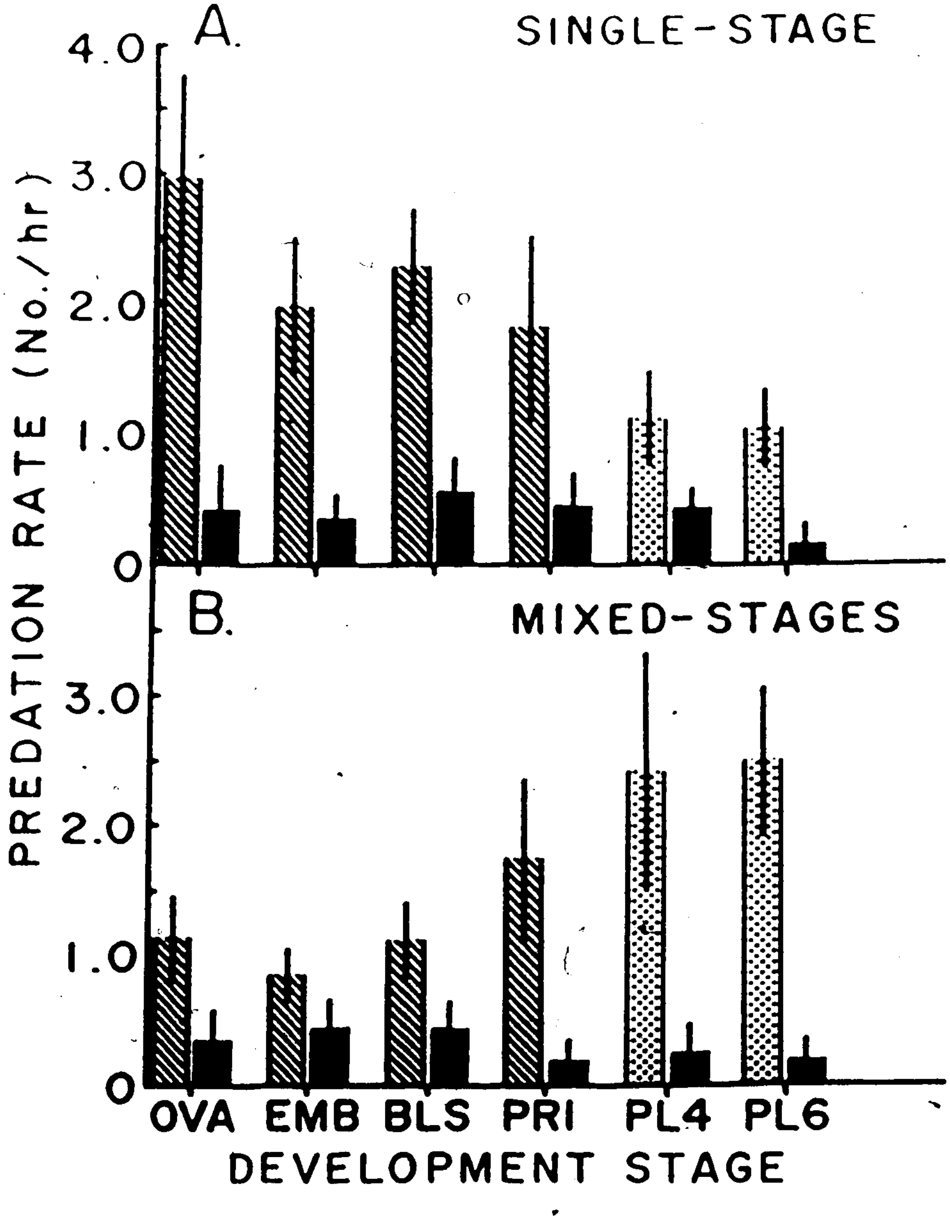

A.
SINGLE-STAGE
B.
MIXED-STAGES
PREDATION RATE (No./hr)
4.0
3.0
2.0
1.0
0
3.0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
DEVELOPMENT STAGE

Figure 12. Differential rates of predation upon developmental stages of Strongylocentrotus franciscanus by Neomysis rayii. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae, PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.


A.
SINGLE-STAGE
B.
MIXED-STAGES
PREDATION RATE (No./hr)
4.0
3.0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
DEVELOPMENT STAGE

when N. rayii were offered a heterogeneous assemblage of mixed S. franciscanus developmental stages (Figure 12b). In this case the proportion of particular S. franciscanus developmental stages offered to N. rayii was experimentally decreased from 100% in the single-stage trials to 33% in the mixed-stage trials. Further experiments with intermediate prey proportions are neccessary to determine the extent of prey switching by N. rayii.

Stage-specific differences in the susceptibility of embryos and larvae were also observed during predation by Pugettia producta upon developmental stages of 4 other species of echinoderms. Ova, embryos and early larval stages of Strongylocentrotus franciscanus and Dendraster excentricus were preyed upon at a greater rate than later pluteus larvae (Figure 13). Similarly, ova, embryos and early gastrula I and gastrula II larval stages of Pisaster ochraceus and Orthasterias koehleri were also more susceptible to predation by P. producta than the later bipinnaria and brachiolaria stages (Figure 14).

c. Long-Term Predation Experiments

The results of the long-term predation experiments with Pugettia producta are shown in Table 5. Predation rates upon echinoderm developmental stages were consistently greatest for all species of echinoderms at 8°C. In the majority of cases predation rates were intermediate at 12°C and lowest at 15°C. Although the relationship between predation rate and temperature may be due in part

Figure 13. Differential rates of predation upon developmental stages of *Strongylocentrotus purpuratus* and *Dendraster excentricus* by *Pugettia producta*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae, PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates upon *Strongylocentrotus purpuratus* during single prey stage feeding experiments. B. Predation rates upon *Dendraster excentricus* during single prey stage feeding experiments.

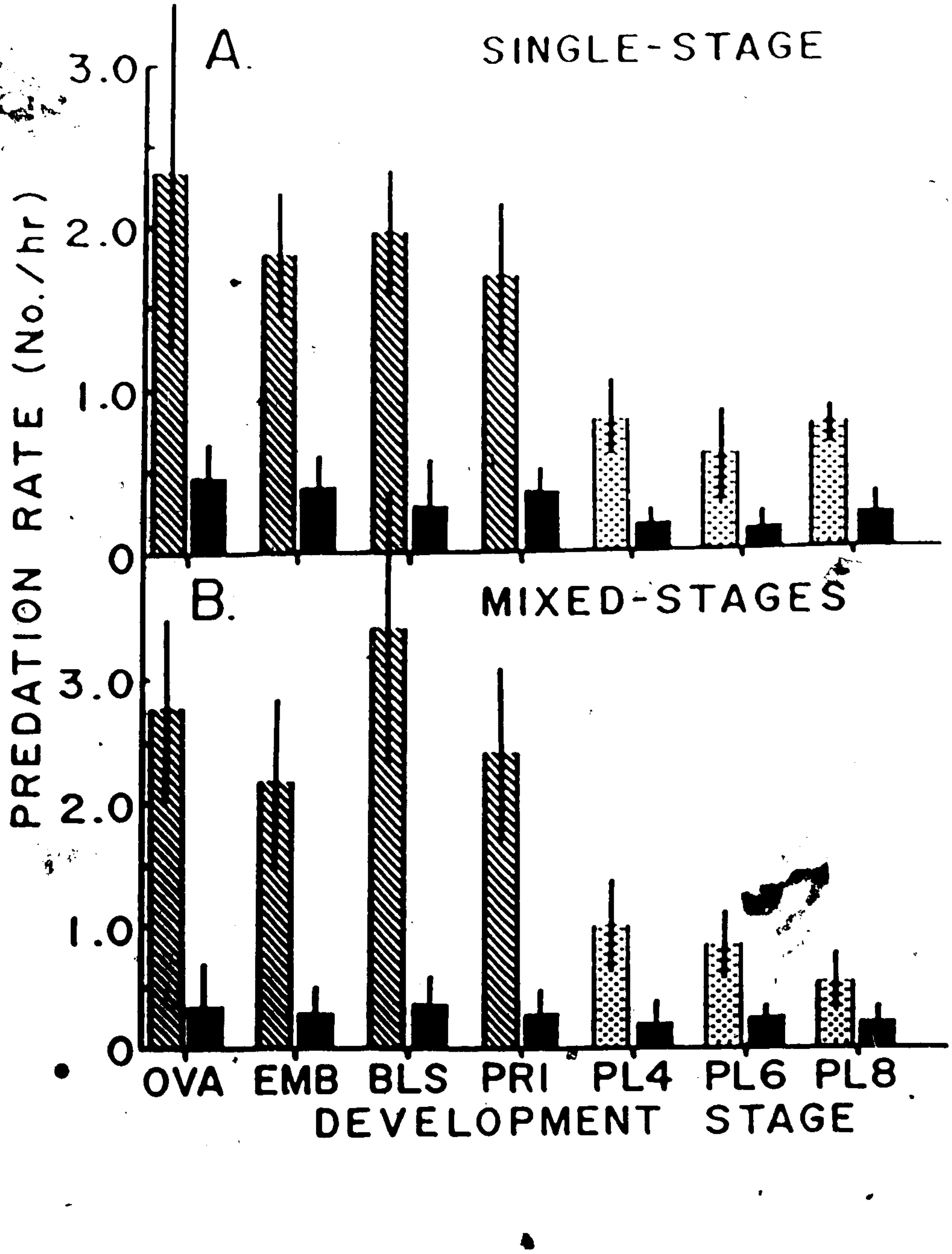

A.
SINGLE-STAGE
B.
MIXED-STAGES
PREDATION RATE (No./hr)
0
1.0
2.0
3.0
OVA
EMB
BLS
PRI
PL4
PL6
PL8
DEVELOPMENT STAGE

Figure 14. Differential rates of predation upon developmental stages of *Pisaster ochraceus* and *Orthasterias koehleri* by *Pugettia producta*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding bipinnaria and brachiolaria larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, GS1 = early gastrula, GS2 = late gastrula larvae, BIP = bipinnaria, BCH = brachiolaria. A. Predation rates upon *Pisaster ochraceus* during single prey stage feeding experiments. B. Predation rates upon *Orthasterias koehleri* during single prey stage feeding experiments.

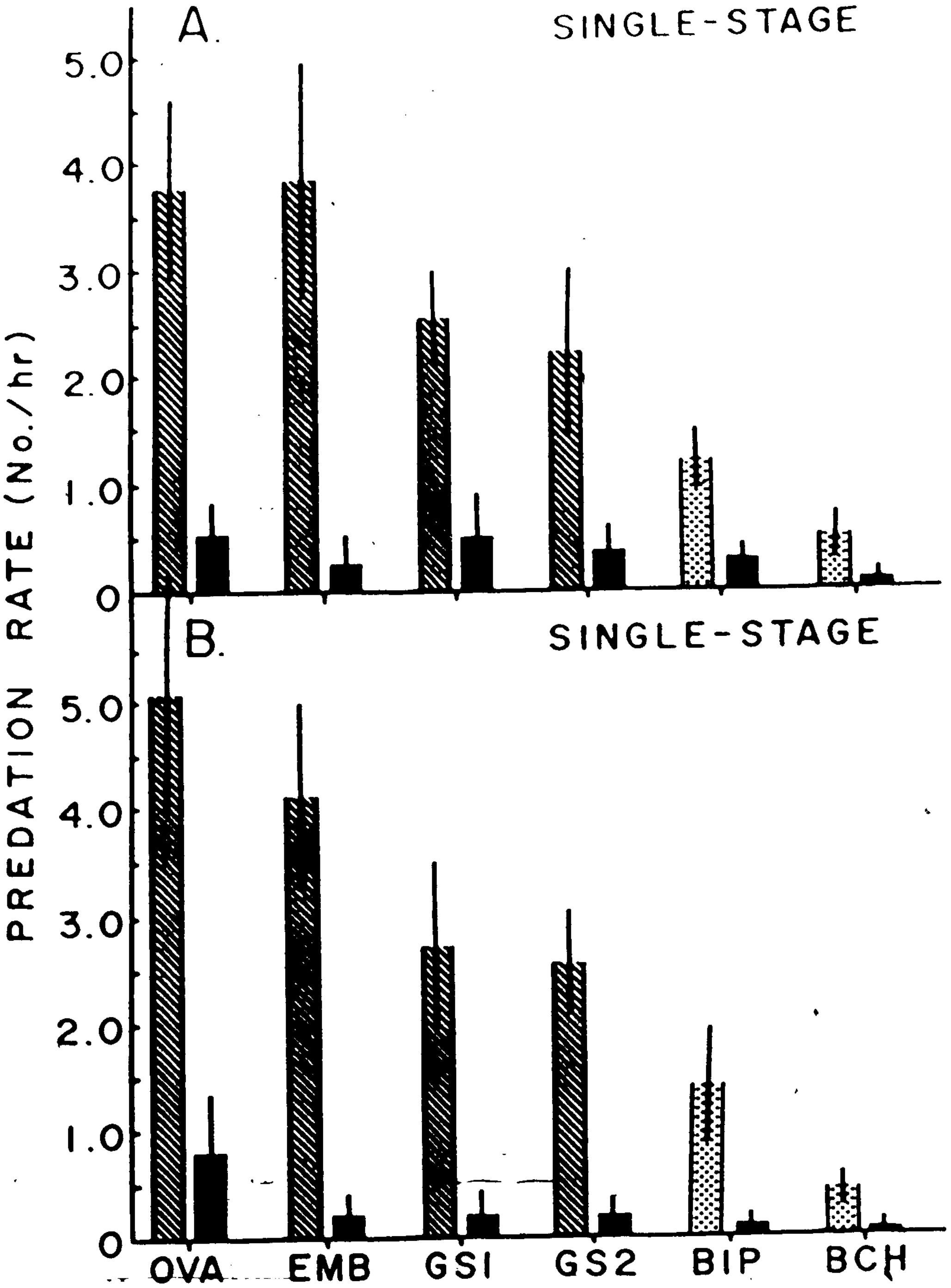

A.
SINGLE-STAGE
B.
SINGLE-STAGE
PREDATION RATE (No./hr)
5.0
4.0
3.0
2.0
1.0
0
OVA
EMB
GS1
GS2
BIP
BCH

Table 5

Predation rates by *Pugettia producta* zoeae upon embryos and larvae of seven planktotrophic echinoderms during long-term feeding experiments. Table entries show mean (± s.d.) from 5 replicate predator treatments in experiments carried out at 8, 12 and 15°C. The initial density of prey was 150 embryos liter^{-1}.

Genus species	TEMPERATURE °C	# HOURS TO FEEDING STAGE	# PREY STAGES CONSUMED / 24 HRS
Strongylocentrotus	8	77	16 ± 3
franciscanus	12	55	11 ± 1
	15	49	10 ± 1
Strongylocentrotus	8	91	19 ± 2
purpuratus	12	60	17 ± 2
	15	54	13 ± 1
Dendraster	8	74	14 ± 2
excentricus	12	49	12 ± 2
	15	41	9 ± 1
Pisaster	8	116	23 ± 2
ochraceus	12	69	16 ± 3
	15	60	14 ± 3
Orthasterias	8	124	23 ± 3
koehleri	12	84	15 ± 2
	15	74	17 ± 2
Patiria	8	109	21 ± 3
miniata	12	88	16 ± 3
	15	76	16 ± 3
Dermasterias	8	103	19 ± 3
imbricata	12	63	15 ± 3
	15	57	12 ± 2

to differences in the metabolic demands upon P. producta zoeae, the clearance rate of zoeae did not change over a range of temperatures from 8 to 16°C (Figure 15). In contrast to the relationship observed previously during functional response experiments (Figures 7-9), predation rates by P. producta were not correlated with the initial size of their prey items during the long-term experiments (Table 6). The difference between these results is not due to differences in initial prey density since both sets of data are drawn from experiments conducted at densities of 150 embryos liter^{-1}. It is likely that the correlation between ova volume and predation rate is significantly negative during the functional response experiments because the zoeae fed rapidly upon abundant prey for a relatively short period of time (12 hrs). In contrast, zoeae may have fed rapidly during the initial hours of the long-term experiment, but in this case the predation rates reflect feeding averaged over a period of 120 hrs. Presumably zoeae were well below saturation feeding rates during the latter part of the long-term feeding experiments.

Predation rates were strongly correlated with the development rates of their respective prey species (Table 6, Figure 16). The correlation between embryo-larval mortality and development rate was highly significant when data from all three temperatures were considered ($p < 0.001$). Furthermore, the relationship was also significant when predation rates from experiments conducted at a single

Figure 15. Clearance rates of *Pugettia producta* zoeae during predation upon *Strongylocentrotus franciscanus* (●) and *Pisaster ochraceus* (○) embryos. Values show means, error bars indicate ± 1 s.d. The numbers above each temperature indicate sample sizes (echinoids / asteroids).

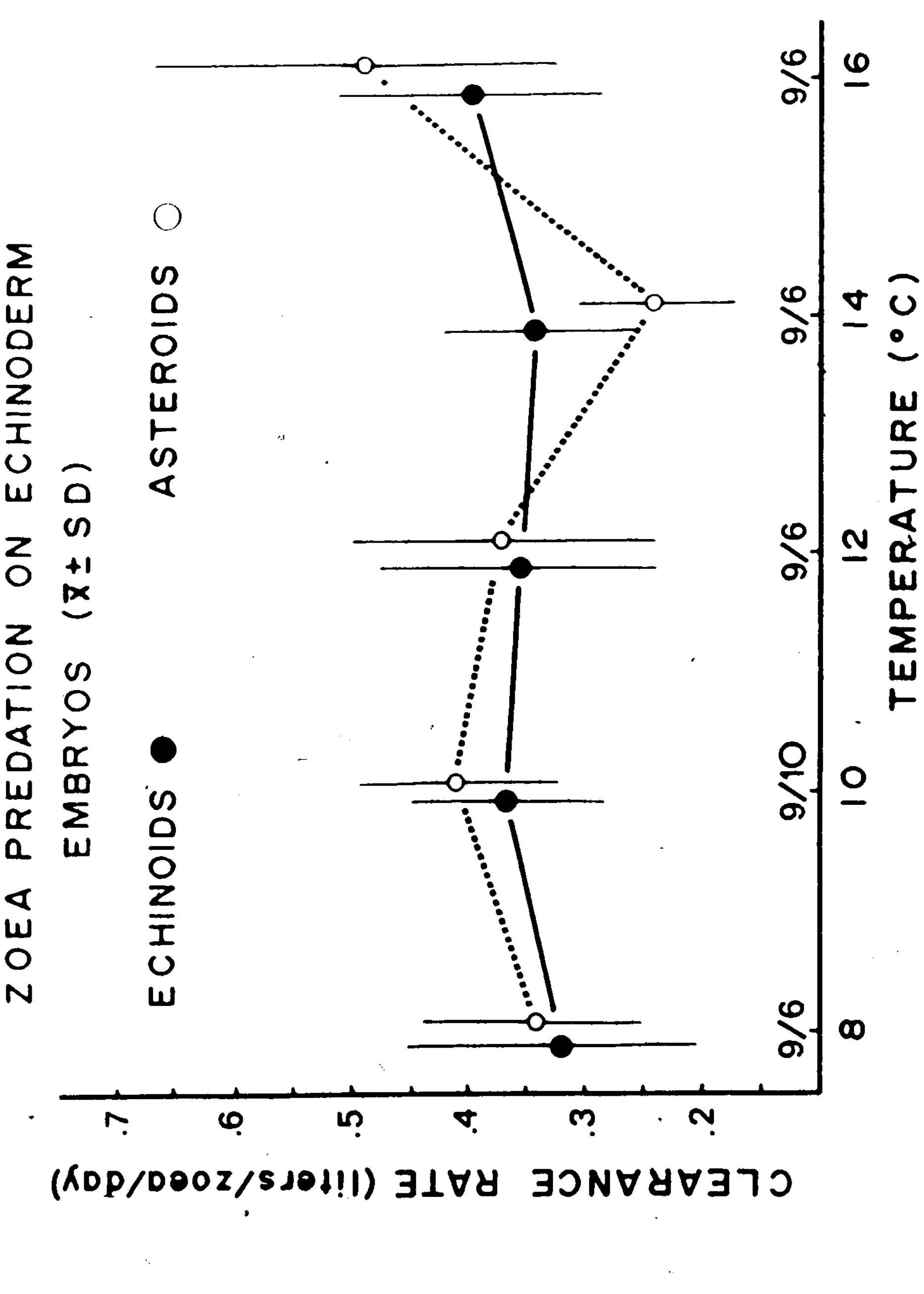
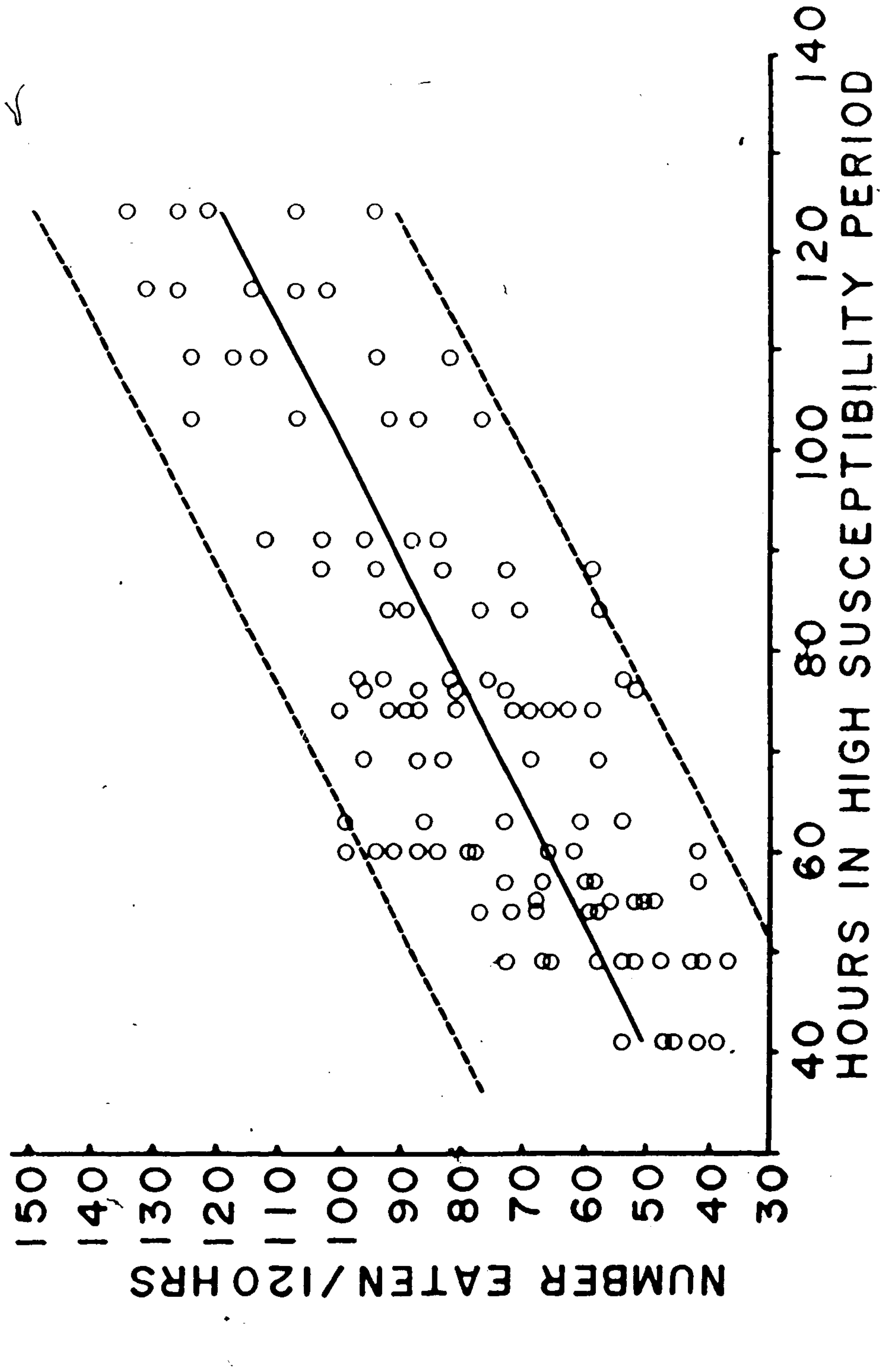

ZOEA PREDATION ON ECHINODERM EMBRYOS ($\bar{X}$ ± SD)
ECHINOIDS ●
ASTEROIDS ○
CLEARANCE RATE (liters/zoea/day)
.7
.6
.5
.4
.3
.2
TEMPERATURE (°C)
8
10
12
14
16
9/6
9/10
9/6
9/6
9/6

Table 6

Comparison of correlation coefficients for relationships between mortality (# prey consumed/120 hrs), ova volume (10^6 μm^3) and development rate to a feeding larval stage (hrs). Correlation statistics are shown for comparisons made at 12°C and for comparisons made from pooled data collected at 8, 12, and 15°C. Values in parentheses indicate probability levels.

RELATIONSHIP	SAMPLE SIZE	SPEARMAN'S rho	KENDALL'S tau
<u>12°C</u>			
Ova Volume X Dev. Rate	35	0.2143 (0.2115)	0.0476 (0.6721)
Ova Volume X Mortality	35	-0.1366 (0.4257)	-0.1046 (0.3635)
Mortality X Dev. Rate	35	0.4494 (0.0088)	0.3245 (0.0048)
<u>All Temperatures</u>			
Mortality X Dev. Rate	105	0.7623 (<0.001)	0.5902 (<0.001)

Figure 16. Correlation between larval mortality and the duration of the high susceptibility (pre-feeding) period of development. Solid line shows the best fit least-squares regression: $Y = 18.58 + 0.80X$, $r^2 = 0.6195$, $n = 105$. Dashed lines indicate 95% prediction limits above and below the regression line.


NUMBER EATEN/120 HRS
150
140
130
120
110
100
90
80
70
60
50
40
30
HOURS IN HIGH SUSCEPTIBILITY PERIOD
40
60
80
100
120
140

intermediate temperature were used to calculate correlation coefficients (12°C, $p < 0.01$, Table 6). Although the relationship between embryo-larval mortality and development rate is more robust when data from all species and temperatures are considered (Figure 16), the correlation at a single temperature is perhaps more informative because the potentially confounding effects of temperature on zoea metabolic demands are removed. In each case, the number of echinoderm embryos and larvae consumed over a period of 120 hrs was directly proportional to the number of hours necessary for the embryos to develop to the first feeding stage (Table 6, Figure 16). In all species of echinoderms, the early pre-feeding stages were highly susceptible to predation by P. producta in stage-specific feeding experiments (see Figures 10, 13 and 14). Susceptibility to predation by P. producta was consistently lower after larvae began to feed. These results suggest that rapid morphogenesis through the early pre-feeding stages of development may effectively decrease the amount of time spent in the period of high susceptibility to predation by P. producta zoeae.

D. DISCUSSION

The results of this study show that the survival of early embryonic and larval stages of planktotrophic echinoderms are affected in laboratory feeding experiments by the feeding activities of zooplanktonic crustaceans including brachyuran zoeae, Pugettia producta, hyperiid amphipods, Parathemisto pacifica, and mysids, Neomysis rayii. All three crustaceans exhibited similar density-dependent patterns of predation upon embryos of planktotrophic echinoderms. However, there were marked differences in the shapes of stage-specific susceptibility curves between the three predators. These findings suggest that predator-prey interactions between marine invertebrate larvae and carnivorous zooplankton can be complex, and that caution should be exercised in making generalizations about larval mortality patterns from investigations of a few species.

The mortality rates of embryos and larvae of benthic marine invertebrates are generally presumed to be high, but the sources of mortality and dynamics of loss from larval populations are poorly understood (Strathmann, 1985; Hines, 1986). It is likely that adverse hydrographic conditions, failure of larvae to locate an adequate substratum for settlement, and predation upon larvae are major sources of larval mortality. Although laboratory studies of predation upon marine invertebrate larvae cannot directly address rates of embryo and larval mortality in the field, they provide a starting point for the recognition of principles and patterns that emerge from investigations of predator-prey interactions.

In the present study, zoea larvae from Pugettia producta were used as model representatives of carnivorous microcrustaceans. The feeding behavior of brachyuran zoeae has been investigated experimentally by Herrnkind (1968), Sulkin (1978), Incze and Paul (1983), and several others (see Sulkin, 1984, and Rumrill, 1987, for review). In a series of previous papers, Rumrill and Chia (1985), Rumrill et al. (1985), and Pennington et al. (1986) reported differential rates of predation upon echinoid embryos and larvae by several species of brachyuran zoeae. These previous studies provide evidence that zoeae are raptorial cruising encounter feeders (sensu Greene, 1985) that capture a variety of prey items ranging from phytoplankton to invertebrate embryos and larger zooplankton. The results of the present study are consistent with previous reports of brachyuran feeding behavior and predation rates, and they provide further evidence that brachyuran zoeae may be important predators of marine invertebrate larvae in nearshore waters.

The feeding behavior of hyperiid amphipods has been investigated in the laboratory by Sheader and Evans (1975), von Westernhagen and Rosenthal (1976), and von Westerhagen et al. (1979). Their studies show that predatory hyperiid amphipods exhibit a variety of foraging tactics ranging from visual hunting and raptorial feeding to cruising encounter feeding. The high rates of predation upon recently hatched blastulae and prism larvae of Strongylocentrotus franciscanus reported here suggest that Parathemisto pacifica may have used ambush encounter tactics to capture prey in the laboratory predation experiments. Similarly, the feeding behavior of mysids ranges from herbivorous filter-feeding to raptorial carnivory (Mauchline, 1980; Murtaugh, 1981, 1984; Fulton 1982; Mullin and Roman 1986). Murtaugh (1981) reported a tendency for small individuals of Neomysis mercedis to select the smallest prey available in laboratory feeding experiments (< 500 µm). In contrast, larger mysids captured and consumed prey items as large as 3 mm in length. In the present study, individuals of N. rayii captured small prey items at a high rate compared with capture rates for larger prey in single-stage predation experiments. However, a switch in the feeding response of N. rayii occurred when mysids were offered a heterogeneous assemblage of large and small prey items. Observations of P. pacifica and N. rayii made during feeding in the laboratory suggest that both of these species encounter echinoderm embryos and larvae by chance.

Strongylocentrotid urchins such as S. franciscanus and S. purpuratus must develop for 50 to 60 hrs (12-15°C) before they are capable of feeding. Similarly, clypeasteroid larvae such as Dendraster excentricus develop for 40-45 hrs prior to the onset of feeding. In both types of larvae, the onset of feeding is correlated with a substantial decrease in the susceptibility of larvae to predation by Pugettia producta. Similar results have been reported for sea urchin and sand dollar larvae in response to predation by several species of predatory zooplankton (Rumrill et al., 1985; Rumrill and Chia, 1985; Pennington et al., 1986). Rumrill et al. (1985) showed that the decrease in susceptibility of sand dollar echinopluteus larvae was due in part to the development of a post-contact encounter response and the ontogeny of a larval neural system to facilitate large-scale ciliary reversal and backwards swimming.

The implication from benthic marine invertebrate life history studies is that the amount of time spent in embryonic and early larval stages should be minimized to attain maximal numbers of offspring per unit of reproductive effort (Vance, 1973; Caswell, 1981). As a consequence, brood protection and encapsulation of embryos have been suggested as mechanisms to reduce risk during the critical early stages of development (Pechenik, 1979; Grant, 1983; Chaffee and Strathmann, 1984). Results from the present study extend the predictions of life history theory to species with pelagic planktotrophic development. The strong correlation between rates of predation by *Pugettia producta* and development rates to a feeding larval stage indicate that the time period prior to feeding can be considered as an approximate index of the time spent by the embryo or larvae in a period of high risk.

It must be emphasized, however, that the relationship between mortality and development rate is strongly dependent upon the shape of the stage-specific susceptibility curve determined empirically by investigations of predator-prey interactions. For example, when considering the feeding activities of predatory zooplankton such as brachyuran zoeae, carnivorous copepods, euphausids, and perhaps mysids (Rumrill et al., 1985; Rumrill and Chia, 1985; Pennington et al., 1986), the relatively high susceptibility of embryos and early larval stages yields results similar to those shown in Figure 16. The conclusion from these results would be that a developmental program that includes rapid morphogenesis through the early high susceptibility period should be favored when the frequency of encounters with predatory crustaceans is high. However, opposite results are expected from predatory encounters with planktivorous fish and zooplankton such as hydromedusae and ctenophores that exhibit high rates of predation upon later larval stages (Rumrill, pers. observ.; Pennington et al., 1986). As a consequence, the use of development rate as an index to rank larval susceptibility to predation by carnivorous crustaceans is presently restricted to applications between particular groups of species for which predator-prey interactions have been described empirically. Only limited predictions can be made about the impact of predation for marine invertebrate larvae that have similar morphological traits and comparable rates of development.

It is not yet possible to extrapolate the findings of laboratory investigations of predator-prey interactions between particular species pairs to field situations, although it is likely that predator-prey interactions such as those reported here for Pugettia producta and planktotrophic echinoderms may be similar to interactions with other predatory crustaceans. The importance of predation by zooplanktonic crustaceans in controlling natural populations of echinoderm larvae in nearshore coastal zones is unknown. Mortality rates of larvae due to predation will depend on their rates of encounter with several different types of predators, and with the probability of capture and escape associated with each encounter. Many important aspects of these predator-prey relationships can only be revealed by direct observations of feeding behavior and quantification of stage-specific susceptibilities and the effects of prey density.

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CHAPTER IV.

LOCOMOTION AND PREY CAPTURE BY ZOEA LARVAE OF THE KELP CRAB, Pugettia producta (DECAPODA: BRACHYURA: MAJIDAE)

A. INTRODUCTION

The viscosity of seawater plays an important role during locomotion and feeding in several species of herbivorous and raptorial copepods (Ambler and Frost, 1974; Strickler, 1975, 1977, 1982; Alcaraz et al., 1980; Koehl and Strickler, 1981; Andrews, 1983). In contrast, comparatively little information is available about the mechanisms of locomotion and feeding for raptorial brachyuran zoeae (Foxon, 1934; Herrnkind, 1968; Schembri, 1982). Detailed descriptions of locomotion and feeding are necessary to determine whether recent generalities concerning feeding hydrodynamics and chemoreception are widespread among raptorial microcrustaceans for capturing food at low Reynolds numbers.

Locomotion and feeding behavior are prominent aspects of the larval biology and ecology of brachyuran zoeae (Forward and Costlow, 1974; Sulkin, 1975, 1984; Cronin and Forward, 1979, 1983; Shanks, 1983). The mechanisms utilized by zoea larvae to swim and capture food are influenced by the functional morphology of their various appendages. As a result, ontogenetic changes in body form have important consequences regarding the diet, growth, and metabolism of zoea and megalopa larval stages. Swimming and feeding behavior are related to several larval traits including mechanisms of zoea depth regulation (Sulkin, 1984), and patterns of onshore larval transport and recruitment (Sulkin et al., 1980; Sulkin and Van Heukelem, 1986; Kelly et al., 1982; Shanks, 1983; Epifanio et al., 1984). Despite the importance of swimming and feeding to the larval ecology of brachyuran zoeae in nearshore coastal waters, only cursory descriptions are available concerning the hydromechanical aspects of locomotion and prey capture (Foxon, 1934; Herrnkind, 1968; Gonor and Gonor, 1973; Lochhead, 1977; Schembri, 1982).

Adult kelp crabs, Pugettia producta (Randall, 1839) (Majidae), are herbivorous brachyurans that inhabit canopies of giant kelp (Macrocystis spp.) along the west coast of North America (Hines, 1982). Ovigerous females brood continuously throughout the year, and their larvae pass through 2 zoeal stages before molting to the megalopa (Hines, 1982, 1986). In the present study, I describe the mechanisms of swimming and prey capture by P. producta zoeae. I use stroboscopic photography to estimate average velocity profiles for unrestrained zoeae during periods of swimming in laboratory aquaria. Flow visualization techniques were used to examine the movements of fluid generated by oscillations of the maxillipeds in tethered zoeae. Information presented here facilitate interpretations of the functional anatomy of brachyuran zoea larvae. Results from this study contribute to the understanding of brachyuran larval behavior and also to the mechanisms utilized by raptorial microcrustaceans to capture prey.

B. MATERIALS AND METHODS

1. Rearing of Larvae

Stage I and II zoeae were raised in culture from ovigerous female crabs. Adult Pugettia producta were collected from kelp and wharf-pilings near the vicinity of Bamfield Marine Station, British Columbia (48° 50'N, 125° 08'W) and Friday Harbor Laboratories, Washington (48° 32'N, 122° 59'W). Ovigerous female crabs were held in sea tables until hatching occurred. Stage I zoeae accumulated against a well-lit region of a sea table shortly after release and were placed into 60:L X 30:W X 30:H cm plexiglass aquaria. Seawater in the aquaria was maintained at ambient temperatures (12-13° C) and renewed every second day. Zoeae were exposed to natural photoperiod and were provided with a daily ration of newly hatched brine shrimp nauplii (Artemia salina, San Francisco source population).

2. Hydromechanics of Swimming

The swimming behavior of unrestrained and tethered Stage I and II zoeae was observed in laboratory aquaria. Stroboscopic photographs were taken of 15 unrestrained zoeae as they swam in a 102:L X 28:W X 80:H mm glass observation chamber. The film plane of the photographic system was focused on the center of the chamber so that zoea which were at a minimal distance of 2-3 body lengths from the nearest glass wall would produce sharply focused images. Critical distances within the photographic system were initially established by shadow triangulation (see Appendix II) and subsequent focal distances were set according to a table of standard zoea body lengths away from the wall of the observation chamber. Stroboscopic illumination was provided within the observation chamber through a narrow slit at 200 and 900 pulses min^{-1} (3.3 and 15 Hz) by a Strobex 236 Stroboscope. The illumination beam was focused in the plane of the observation chamber through a reversed 55 mm Micro-Nikkor lens at f5.6. The lens was equipped with a # 25 red filter and a heat-absorbing shield. Swimming sequences lasting 2-4 s were photographed with Kodak Tri-X film developed at ASA 1600 in Acufine. The swimming velocities of <u>P</u>. <u>producta</u> zoeae were determined by measuring the successive displacement distances between images of zoeae (see Appendix II). Zoeae which made obvious turns or looping trajectories were not included in the analysis. Average swimming velocity and acceleration profiles were found for each zoea by computing the derivatives of fifth-order polynomials fit to measurements of cumulative displacement distances (Lehman, 1977; Hazony, 1979). Since the limits of resolution possible by these techniques are 300 ms (200 pulses min^{-1}) and 67 ms (900 pulses min^{-1}), the average velocity profiles necessarily underestimate instantaneous velocities.

Movements of fluid and the oscillation frequency of swimming appendages were examined for tethered Pugettia producta zoeae in moving water. Zoeae were tethered with cyanoacrylate adhesive to glass needles that had tip diameters approximately half the diameter of the zoea dorsal spine (10-15 µm). A glass needle was affixed to each zoea at a point along the posterior margin of the dorsal spine about 50 - 100 µm above the carapace (see Figure 24a). Although placement of a glass needle in this position caused an eddy to form immediately downstream of the tethered zoea in a flow tank (Figure 27a), glass needles placed in other positions resulted in greater disruption of currents around the zoea maxillipeds. Tethered zoeae were positioned about 20-22 body lengths away from the walls of a rectangular plexiglass container (400:L X 50:W X 50:H mm) filled with 0.45 µm filtered seawater. The container was mounted on a set of 16 low-friction wheels and pulled along a 1 m track. Force was applied to the container through nylon strings wound around an electrically powered rotating shaft. The flowtank was capable of moving filtered seawater past the tethered zoeae at velocities between 0.6 and 3.7 mm s^{-1}.

Swimming currents generated by the 1st and 2nd maxillipeds of Pugettia producta were examined by photography of dye streamlines. Seawater dyed with 1% aniline blue was released from a micropipette positioned upstream from the tethered zoea and photographed as it moved past the carapace and swimming appendages. Oscillation frequencies and velocities of the swimming and feeding appendages were determined by observing the movements of tethered zoeae while they were illuminated with stroboscopic light. The frequency of oscillation was determined for 12 zoeae by adjusting the stroboscope to freeze the motion of the maxillipeds. Appendage velocities were determined from measurements of the distance traveled by the appendage during effective strokes.

3. Hydromechanics of Particle Capture

Sequential photographs were taken to form a composite record of the feeding events that occurred while tethered zoeae captured and consumed non-motile and motile prey items. Prey items in these observations were freshly excised oocytes, embryos, and gastrula larvae from the sea star, *Patiria miniata*. Prey items moved past the tethered zoeae at a velocity of 1.2 mm s^{-1} in the flowtank. The concentration of prey items in the flowtank was between 5-12 prey ml^{-1}.

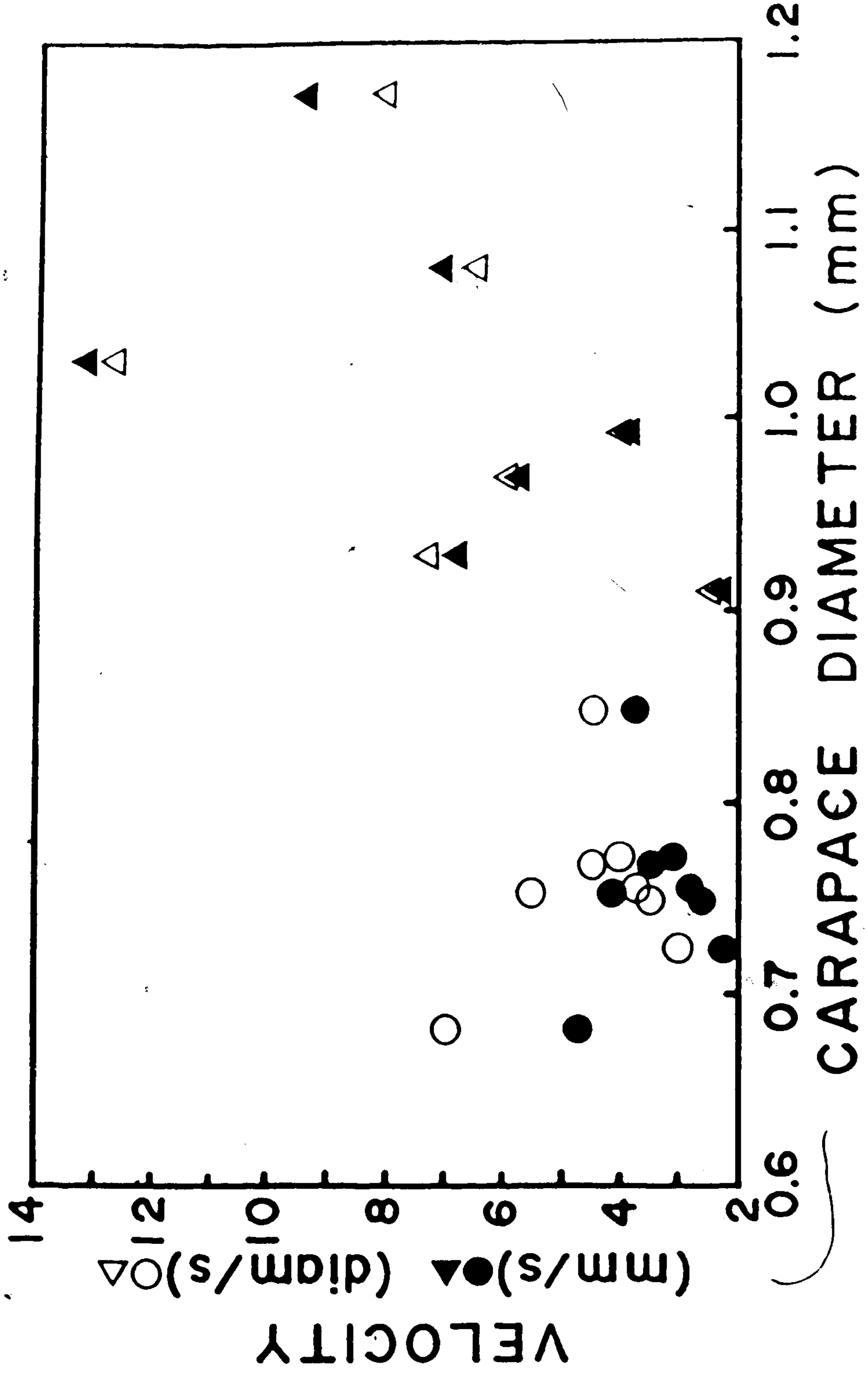
C. RESULTS

1. Swimming Behavior of *Pugettia producta* zoeae

The swimming behavior of *Pugettia producta* zoeae in laboratory aquaria was characterized by jerky or pulsed motion. During periods of oriented swimming, zoeae exhibited frequent periods of acceleration as they propelled themselves in the direction of the dorsal spine. When beating of the maxillipeds ceased, the zoeae rolled anteriorly and sank at 2 to 3 mm s^{-1}. In general, the swimming behavior of P. producta was similar to the gliding motion of calanoid copepods (see Strickler, 1975), although P. producta zoeae often swam with intermittent changes in velocity for 4 to 5 s before changing direction.

Figure 17 shows the relationship between carapace diameter and mean swimming velocity standardized over a period of 3 seconds. Absolute velocities and relative velocities showed similar relationships with increasing zoea carapace diameter. Stage I zoeae of P. producta had an average carapace diameter of 756±47 µm and a mean swimming velocity of 3.3±0.8 mm s^{-1}. By comparison, stage II zoeae had significantly larger carapace diameters (1012±91 µm; $t = 6.99$, $p < 0.001$) and greater swimming velocities (7.4±3.8 mm s^{-1}; $t = 2.92$, $p = 0.012$). The relative velocities reached by stage I zoeae averaged 4.4±1.3 body lengths s^{-1} compared to 6.7±3.3 body lengths s^{-1} for stage II zoeae. The relationship between absolute swimming velocity and carapace diameter was best fit by an exponential least-squares regression equation ($Y = 6.19X^{2.22}$); $r^2 = 0.4899$, $p = 0.004$). The value of the exponent suggests that the faster swimming speeds of stage II zoeae may be directly related to ontogenetic

Figure 17. The relationship between swimming velocity and carapace diameter for stage I and stage II zoea larvae of *Pugettia producta*. Absolute velocities ($mm\ s^{-1}$) of stage I (●) and stage II (▲) zoeae are related to carapace diameter by $Y = 6.19X^{2.22}$, $r^2 = 0.4899$, $p = 0.004$. Relative velocities (carapace diameters s^{-1}) of stage I (○) and stage II (△) zoeae are related to carapace diameter by $Y = -2.37 + 8.98\ X$, $r^2 = 0.2634$, $p = 0.050$.


VELOCITY
(mm/s)●▲ (diam/s)○△
14
12
10
8
6
4
2
0.6
0.7
0.8
0.9
1.0
1.1
1.2
CARAPACE DIAMETER (mm)

changes in the surface area of the maxilliped propulsion system and the distribution of drag forces along the carapace (Table 7, Figure 24).

2. Velocity and Acceleration Profiles

Time-series analysis of stroboscopic photographs showed that each individual *Pugettia producta* zoea exhibited a unique average velocity profile (Figures 18-22). Average velocity profiles obtained from stroboscopic photographs with resolutions of 300 and 67 ms cannot be used to accurately determine instantaneous acceleration values because changes in the velocity of microcrustaceans can occur over much shorter periods of time (see Strickler, 1975; Lehman, 1977). Nevertheless, the average velocities shown in Figures 18-22 provide a first approximation of the locomotory behavior of unrestrained *P. producta* zoeae, and they can serve as minimal estimates of acceleration during changes in zoea swimming velocity.

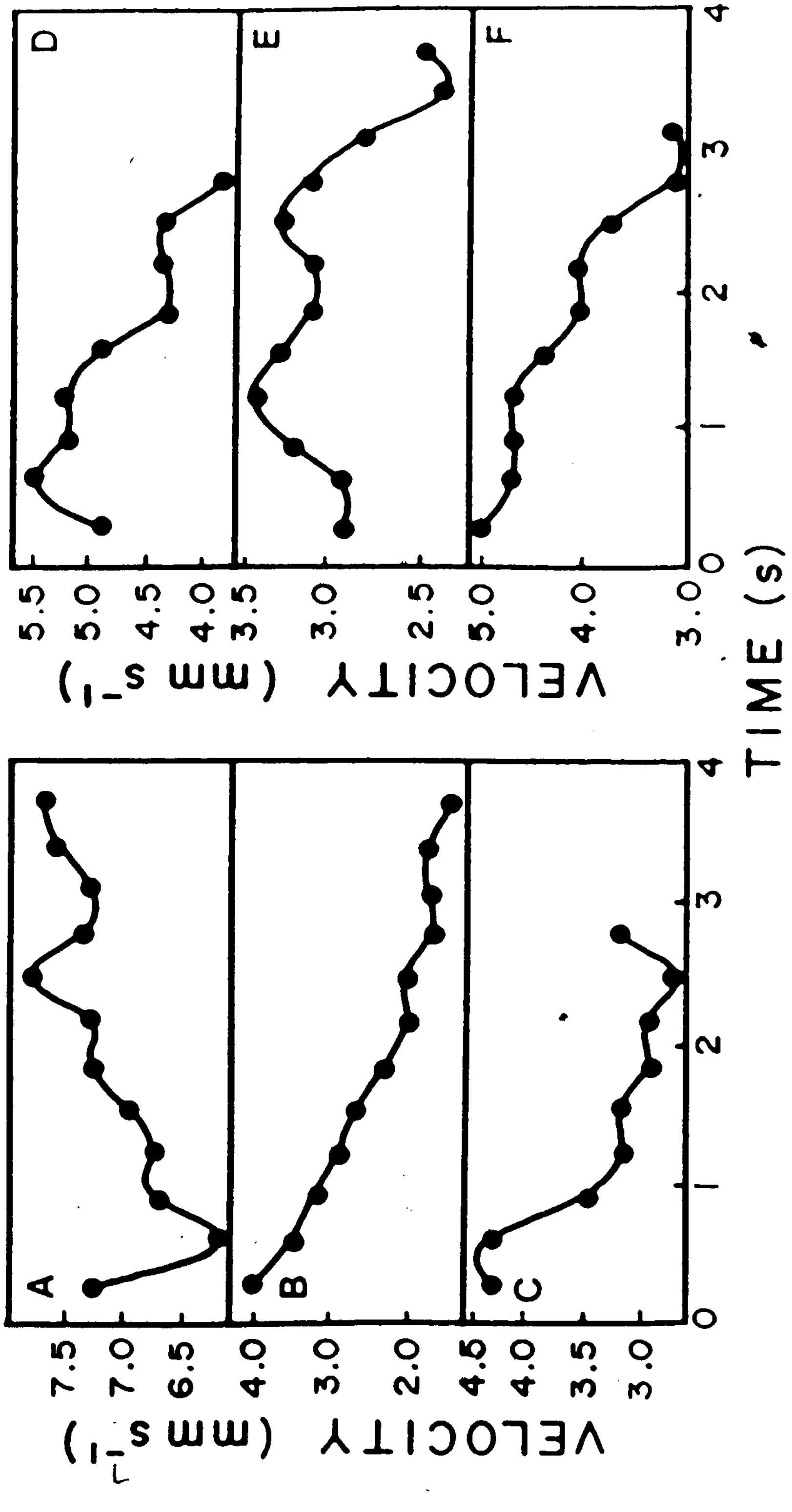
Average swimming velocity profiles are presented graphically for 6 unrestrained *Pugettia producta* stage I zoeae in Figure 18a-f. The first zoea showed a net increase in velocity over the 3.7 s observation period (Figure 18a). The increase in velocity occurred following 4 periods of net acceleration and 2 periods of net deceleration. Similar average velocity profiles were observed for other stage I zoeae. For example, 4 of the zoeae exhibited a net decrease in swimming velocity over the 3 or 4 s observation periods (Figures 18b-d, f). In each case, the overall decrease in

TABLE 7

Comparison of morphological features between stage I and stage II zoea larvae of *Pugettia producta*. Table entries show mean (± s.d.). All units are micrometers unless indicated otherwise.

	SAMPLE SIZE	STAGE I	STAGE II	COMPARISON	
	Stage I/II	Mean (s.d.)	Mean (s.d.)	t test	p
Carapace	35/24				
Diameter		801.1 (44.1)	1043.4 (71.5)	16.10	<0.001
Projected Surface Area µm²		5.1×10^5 (0.5)	8.6×10^5 (1.2)	15.57	<0.001
1st Maxilliped	19/17				
# of Setae		4	6		
Seta Length		323.3 (10.8)	341.2 (11.0)	4.90	<0.001
2nd Maxilliped	19/17				
# of Setae		4	6		
Seta Length		384.8 (22.8)	364.5 (17.7)	2.94	0.006
Surface Area of Natatory Setal Field µm²	19/17	7.3×10^4 (0.4)	8.2×10^4 (0.4)	6.41	<0.001
Telson	19/17				
Length		758.9 (52.8)	960.9 (49.1)	11.83	<0.001
Width		556.3 (49.7)	805.3 (36.6)	16.94	<0.001
Velocity mm/s	8/7	3.3 (0.8)	7.4 (3.8)	2.92	0.012
Relative Velocity mm/s	8/7	4.4 (1.3)	6.7 (3.3)	1.77	0.099

Figure 18. Velocity profiles for 6 stage I zoea larvae of *Pugettia producta*. Data points show successive swimming velocities calculated from displacement distances on photographs taken with stroboscopic illumination at 200 flashes min^{-1}. Each point shows swimming velocity averaged over a period of 300 ms. Lines show fifth-order polynomials fit to successive velocities.

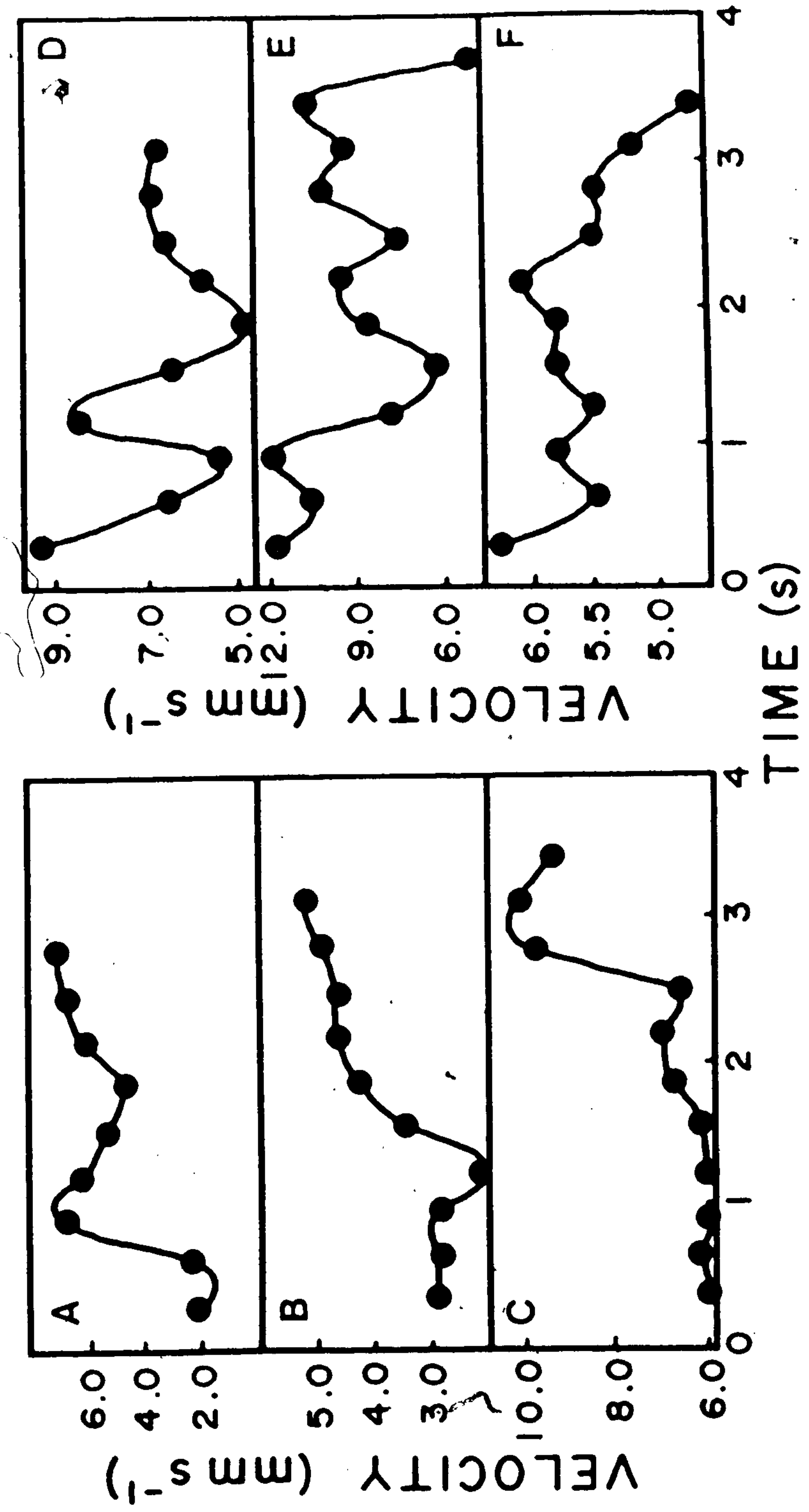

VELOCITY (mm s⁻¹)
7.5
7.0
6.5
4.0
3.0
2.0
4.5
4.0
3.5
3.0
A
B
C
VELOCITY (mm s⁻¹)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
5.0
4.0
3.0
D
E
F
0
1
2
3
4
TIME (s)

swimming velocity occurred after a series of 3 periods of net deceleration. The final stage I zoea showed cyclic changes in swimming velocities between 2.4 and 3.4 mm s^{-1} over a period of 3.1 s, and exhibited 3 periods of net acceleration and 2 periods of net deceleration (Figure 18e). The temporal changes in swimming speed shown by these average velocity profiles provide an indication that the swimming velocity of P. producta zoeae can fluctuate substantially over periods of 3-4 s.

Average velocity profiles for stage II zoeae are shown in Figure 19a-f. Three of the zoeae exhibited net increases in swimming velocity (Figure 19a-c). Each zoea underwent 2 or 3 periods of net acceleration, and their swimming velocities reached 6.9, 5.4, and 9.9 mm s^{-1}, respectively. The average velocity profiles for the remaining stage II zoeae of Pugettia producta exhibited more complex kinematics characterized by several periods of net acceleration and deceleration (Figure 19d-f). During the 4 s observation periods, the swimming velocities changed in a sinusoidal manner with 2-4 periods of net acceleration and 3-5 periods of net deceleration. The greatest speeds reached by these zoeae were 9.2, 12.1 and 6.4 mm s^{-1}, respectively.

Velocity profiles obtained for 3 stage I zoeae from stroboscopic photographs taken at 900 pulses min^{-1} provide a more detailed record of changes in swimming speed (Figures 20-22). Like the previous velocity profiles, the

Figure 19. Velocity profiles for 6 stage II zoea larvae of *Pugettia producta*. Data points show successive swimming velocities calculated from displacement distances on photographs taken with stroboscopic illumination at 200 flashes min^{-1}. Each point shows swimming velocity averaged over a period of 300 ms. Lines show fifth-order polynomials fit to successive velocities.


A
B
C
D
E
F
VELOCITY (mm s⁻¹)
VELOCITY (mm s⁻¹)
6.0
4.0
2.0
5.0
4.0
3.0
10.0
8.0
6.0
9.0
7.0
5.0
12.0
9.0
6.0
6.0
5.5
5.0
0
1
2
3
4
TIME (s)

zoeae shown in Figures 20-22 also exhibited marked fluctuations in their absolute swimming speeds. The first zoea showed a net increase in swimming speed from 1.6 to 3.1 mm s^{-1} over a period of 2.5 s (Figure 20). During the observation period the zoea alternated between positive and negative acceleration values, and changes in velocity occurred at a frequency 4.5 Hz. The remaining zoeae also exhibited sinusoidal changes in velocity and acceleration (Figures 21 and 22) that were typical of the jerky locomotory behavior observed previously for other zoeae (see Figures 18-20). These results indicate that changes in swimming velocity can occur over periods of 67 ms or less, and that zoeae are capable of accelerating at rates approaching 20 mm s^{-2}.

Although the absolute and relative swimming velocities of *Pugettia producta* stage II zoeae were greater than those of stage I zoeae (Figure 17, Table 7), the general pattern of locomotory behavior did not change between molts (Figures 18-19). In all cases, zoeae increased or decreased their swimming velocities over short periods of time. Periods of constant speed were limited to about 140 ms by the resolution of the photographic recording system. Rapid fluctuations in velocity and acceleration indicate that the swimming of *P. producta* zoeae may be incompatible with steady-state hydrodynamics. Furthermore, they suggest that added-mass forces generated during periods of acceleration and deceleration may be an important component of the total

Figure 20. Instantaneous velocity and acceleration profile for a stage I zoea larva of Pugettia producta. Data points show successive swimming velocities and acceleration rates calculated from displacement distances on photographs taken with stroboscopic illumination at 900 flashes min^{-1}. Each point shows swimming velocity and acceleration averaged over a period of 67 ms. Lines show fifth-order polynomials fit to successive velocity and acceleration values.

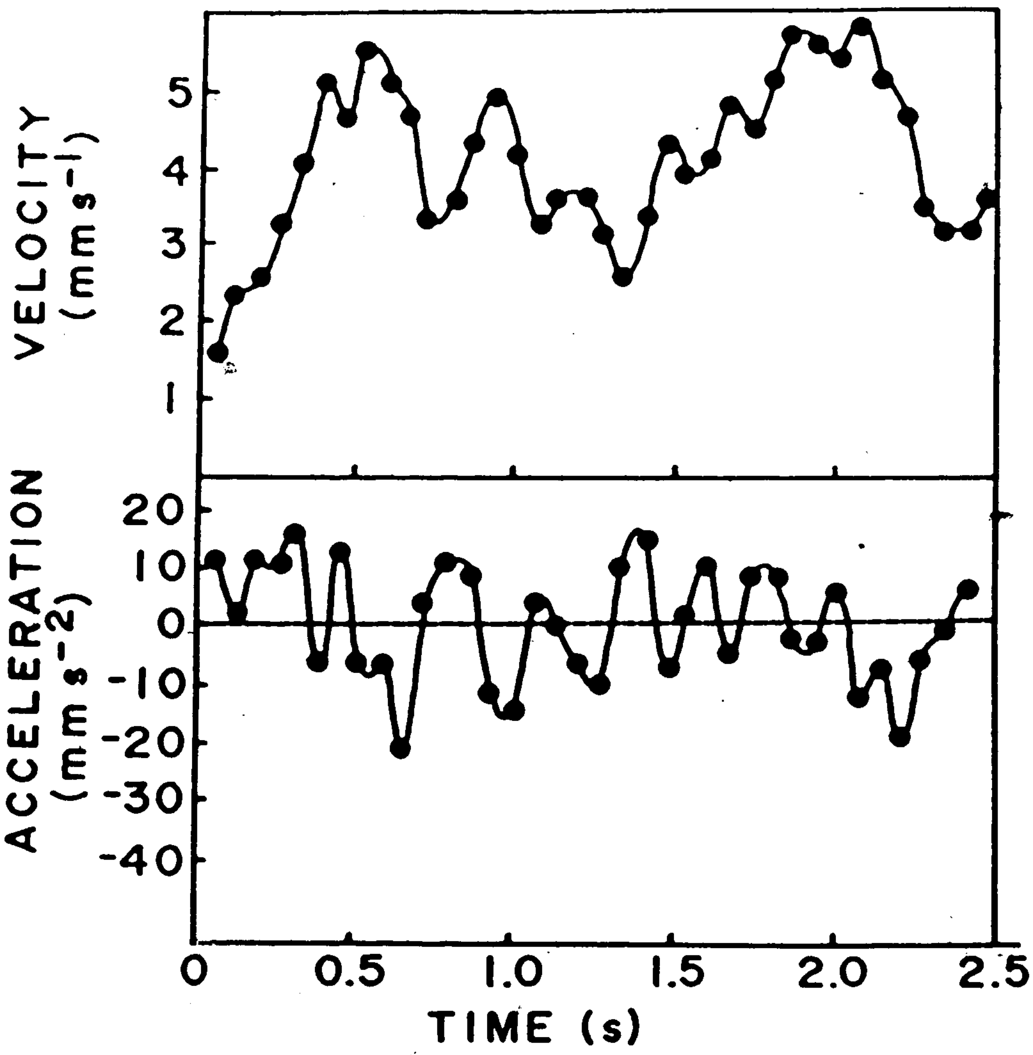

VELOCITY (mm s^{-1})
5
4
3
2
1
ACCELERATION (mm s^{-2})
20
10
0
-10
-20
-30
-40
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

Figure 21. Instantaneous velocity and acceleration profile for a stage I zoea larva of *Pugettia producta*. See Figure 20 for explanation.

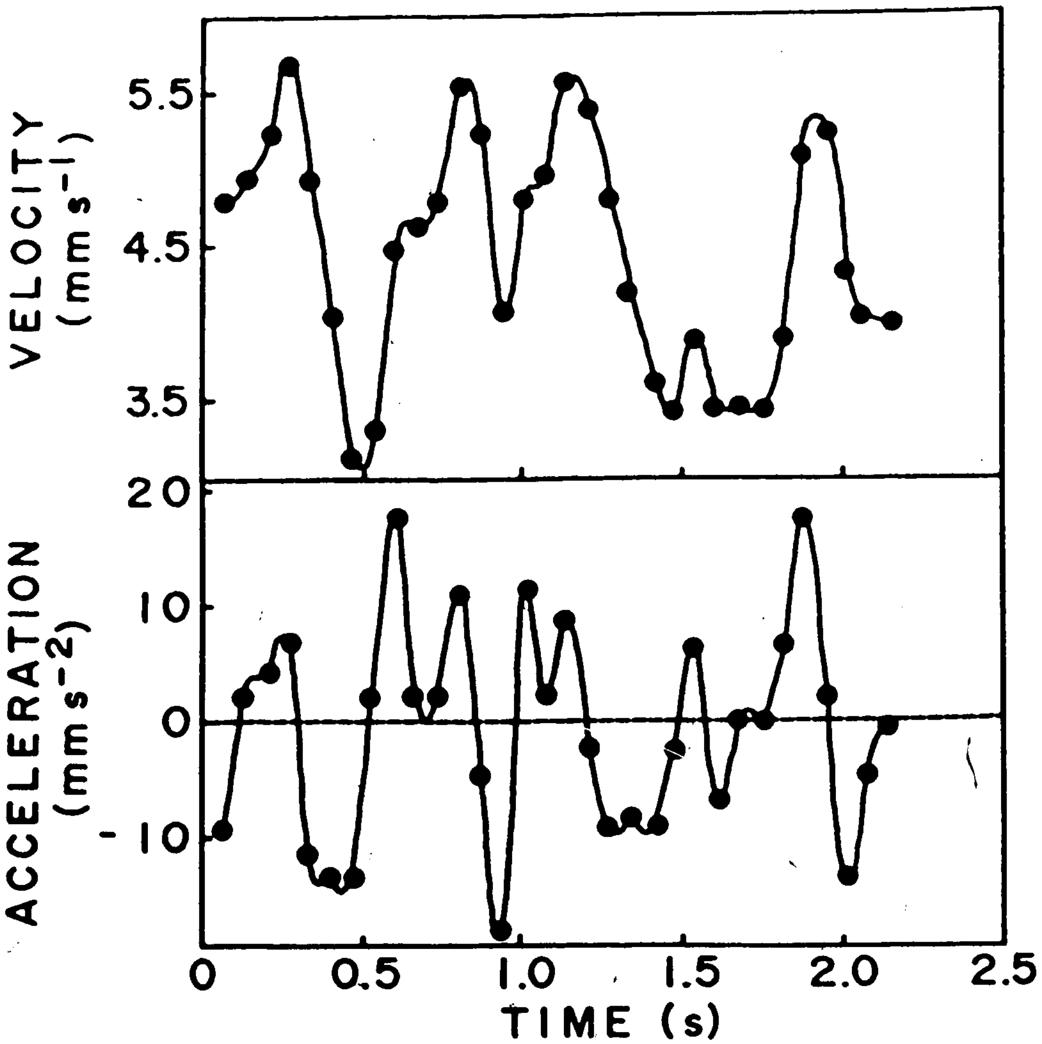
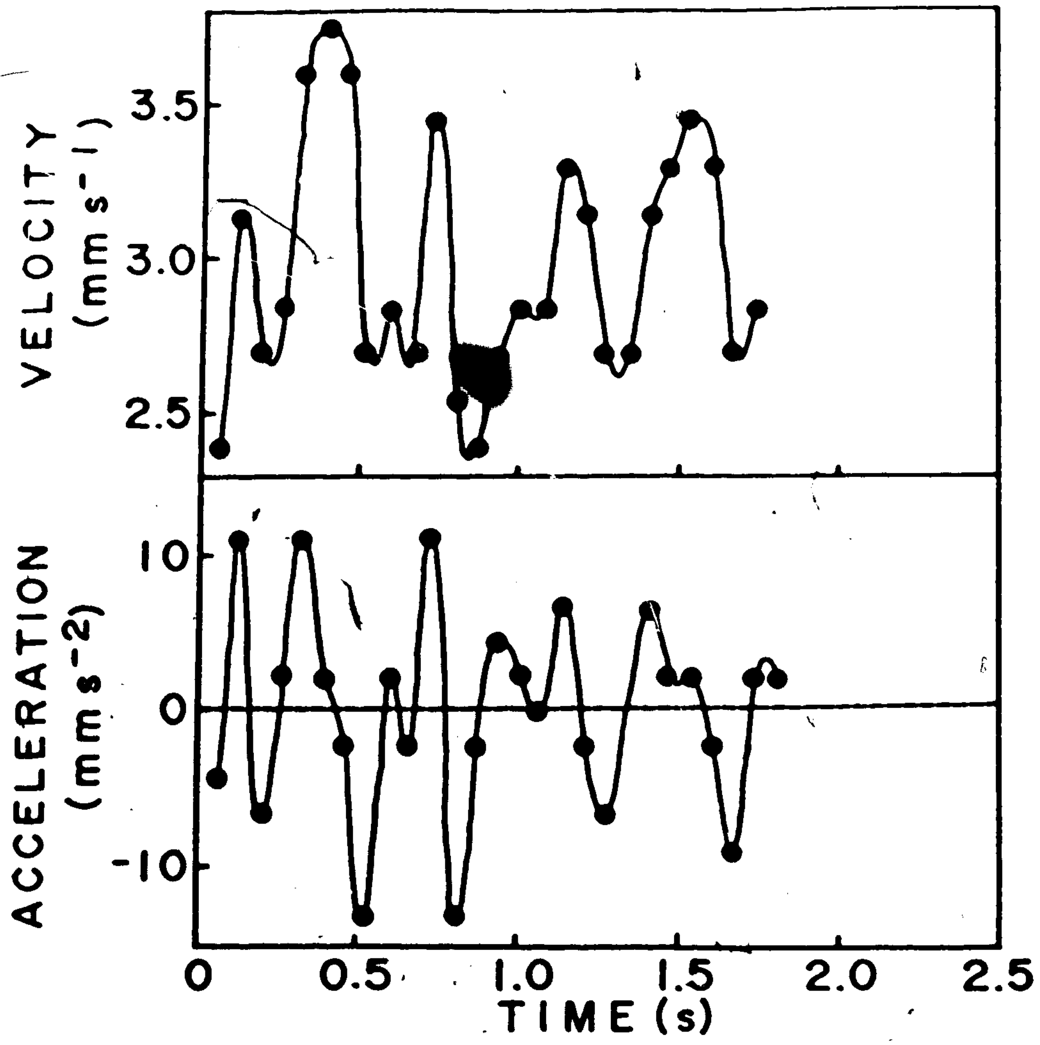

VELOCITY (mm s^{-1})
5.5
4.5
3.5
ACCELERATION (mm s^{-2})
20
10
0
-10
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

Figure 22. Instantaneous velocity and acceleration profile for a stage I zoea larva of *Pugettia producta*. See Figure 20 for explanation.


VELOCITY (mm s⁻¹)
3.5
3.0
2.5
ACCELERATION (mm s⁻²)
10
0
-10
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

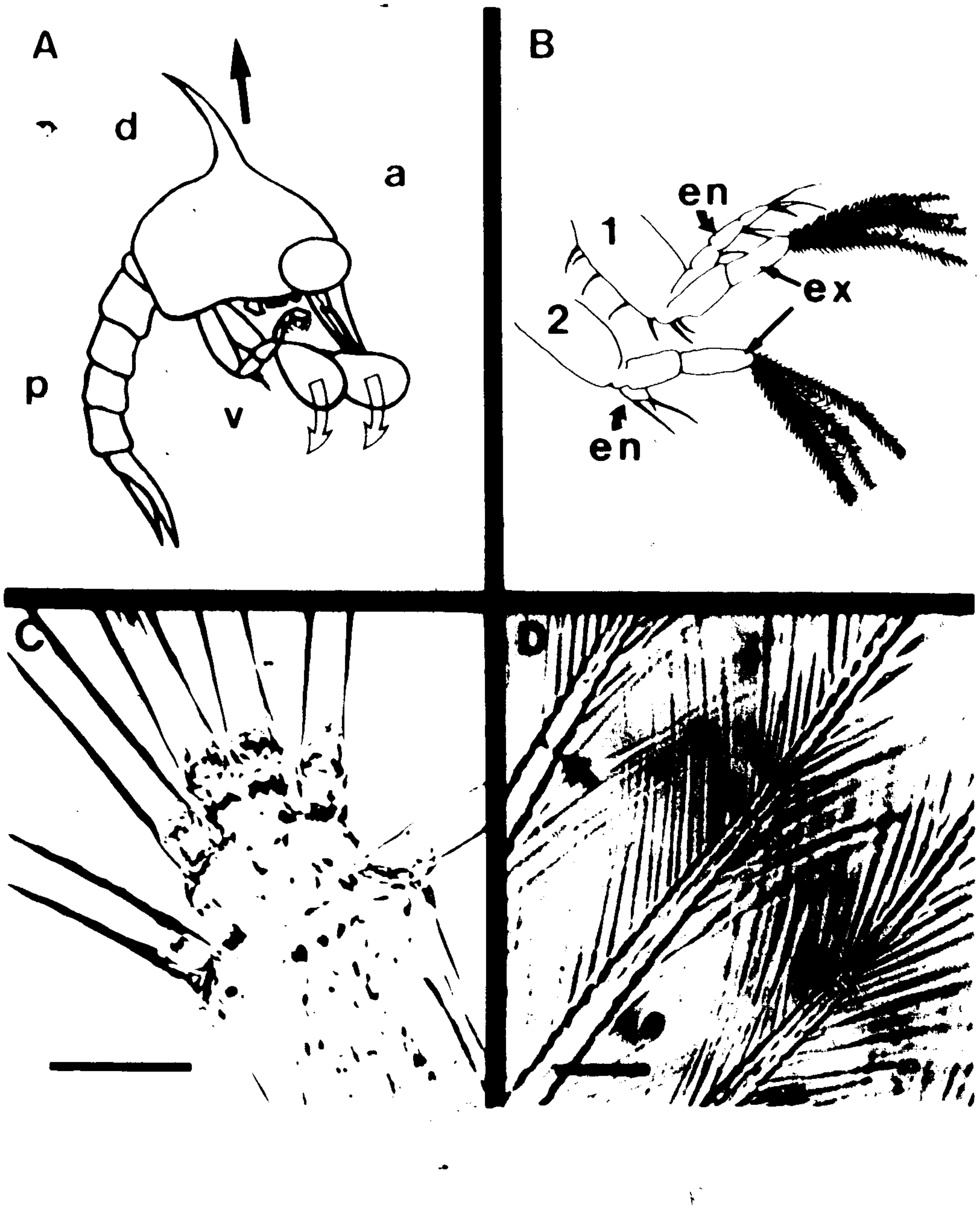
drag forces that resist the motion of a P. producta zoea during locomotion.

3. Morphology of the Swimming and Feeding Appendages

Table 7 shows the ontogenetic changes in body size and other morphological traits that occur during the molt from stage I to stage II in zoea larvae of Pugettia producta. The zoea carapace increases substantially in diameter and projected surface area, and the number of natatory setae on the 1st and 2nd maxillipeds increases from 4 to 6. Although the 1st maxilliped natatory setae increase in length, those of the 2nd maxilliped decrease in length. Nevertheless, the projected surface area of the natatory setal field increases by 12% between molts (Table 7).

Zoea larvae of Pugettia producta generate propulsive forces by rapid oscillations of the 1st and 2nd maxillipeds (Figure 23a). The 1st and 2nd maxillipeds of P. producta are biramous appendages, and each appendage is composed of an endopodite and an exopodite (Figure 23b). Exopodites give rise to 4 natatory setae in the stage I zoea and to 6 natatory setae in the stage II zoea (Table 7, Figure 23c). The natatory setae project distally from the exopodite in the shape of a paddle or fan (Figures 23a, 24c). The natatory setae are plumose and give rise to setules that project laterally to form a lattice throughout the setal field (Figure 23d). Cuticular joints are located 2/3 and 3/4 of the distance along the length of each natatory seta (Figure 23d). In addition, basal joints are located at the

Figure 23. Morphological traits of Pugettia producta zoeae. A. Diagram of general zoea body plan. a=anterior, p=posterior, d=dorsal, v=ventral. Open arrows show direction of 1st and 2nd maxilliped effective strokes. Solid arrow shows direction of locomotion during normal swimming. B. Maxillipeds from stage I zoea. 1=1st maxilliped, 2=2nd maxilliped, en=endopodite, ex=exopodite. C. Basal joints on maxilliped of a stage II zoea. Scale bar = 25 µm. D. Natatory setal field and lattice of setules. Arrows show articulating joints on natatory setae. Scale bar = 25 µm.


A
d
a
p
v
B
en
1
ex
2
en
C
D

point where the natatory setae originate from the exopodite (Figure 23c), and at the base of each setule (Figure 23d).

The Reynolds number, Re, a measure of the relative effects of fluid inertia and viscosity, was computed as

$$Re = p\ U\ L\ /\ u$$

where p and u are the density (1.025×10^3 kg m^{-3}) and dynamic viscosity of seawater (1.1×10^{-3} kg m^{-1} s^{-1}; 15^{o} C, salinity 33 ppt), U is the maximum observed velocity of the zoea or appendage, and L is a linear measurement of the zoea carapace or appendage. Re values were above unity for unrestrained stage I and II zoeae (Table 8) and indicate that non-reversible flows and inertial forces are an important aspect of zoea locomotion when considered at the level of the entire zoea body. Since Re values are scaled to the product of length and velocity, they were inherently correlated with zoea body size and molt ($Y = 6.04X^{4.01}$, $r^2 = 0.75$, $p < 0.001$). Lower Re values (10^{-1} - 10^{-2}) are associated with the telson and various components of the 1st maxilliped (Table 8). These low Re values indicate that fluid motion is governed by the effects of viscosity within boundary layers surrounding the swimming appendages and feeding structures.

4. Hydromechanics of Swimming

Visualization of fluid movements with dye-marked water showed that tethered zoea propel seawater past themselves

TABLE 8

Comparison of linear dimensions, velocities, and Reynolds numbers for zoea larvae and various appendages. Table entries show mean (± s.d.). Linear dimension for Reynolds numbers are indicated by brackets.

	SAMPLE SIZE	LINEAR DIMENSION (µm)	VELOCITY (mm/s)	REYNOLDS NUMBER
Carapace	15	875.64	5.24	4.57
[diameter]		(148.87)	(2.69)	(2.64)
Telson Spine	15	585.67	8.09	0.44
[diameter]		(6.19)	(1.09)	(0.06)
1st Maxilliped				
Exopodite Tip	8	30.85	16.73	0.48
[width]		(2.77)	(3.02)	(0.08)
Natatory Seta	8	6.25	18.14	0.10
[diameter]		(0.71)	(2.67)	(0.02)
Natatory Setule	7	1.92	22.62	0.02
[diameter]		(0.56)	(2.60)	(0.002)
Endopodite Tip	8	30.52	1.36	0.04
[width]		(2.67)	(0.32)	(0.01)

by rapid oscillations of their 1st and 2nd maxillipeds (Figure 24). Observations made with a stroboscope indicate that the maxillipeds oscillate at frequencies between 21 and 34 Hz. Propulsive forces are generated in the ventral direction by effective strokes of the maxillipeds. Drag forces are reduced during recovery strokes by decreasing the projected surface area of the natatory setal field.

Laboratory observations of tethered _Pugettia producta_ and other unidentified brachyuran zoeae showed that the following events take place during a typical effective-recovery stroke cycle. Moving fluid first contacts the dorsal surface of the carapace (Figure 24a). Fluid is sheared past the lateral margins of the carapace by sweeping movements of the paired maxillipeds. At the end of the effective stroke, fluid is propelled in the ventro-lateral direction away from the central mass of the zoea body (Figure 23a, 24a). Fluid shed by the tips of the natatory setae gives rise to a pair of toroidal vortices (Figure 24b). The vortex radii increase rapidly as the velocity of the swimming current decreases to ambient levels at a distance 3-4 body lengths away from the tethered zoea.

A diagrammatic summary of the effective and recovery stroke cycle is shown in Figure 25. At the beginning of the effective stroke the maxillipeds and natatory setae extend dorso-laterally at a positive angle of approximately 40-45 degrees (Figures 25 and 26). During the effective stroke,

Figure 24. Movements of fluid and maxillipeds by tethered zoeae. A. Visualization of swimming currents generated by a tethered zoea in a flow tank. The zoea is restrained by a glass needle. Dye released upstream from the zoea was propelled ventrally by rapid beating of the maxillipeds. Solid arrow shows direction of flow tank current (1.2 mm s^{-1}). B. Unidentified brachyuran zoea collected from the plankton. Dye shows toroidal vortex shed by the maxilliped at the end of the effective stroke. C. Natatory setae of the 2nd maxilliped at the end of an effective stroke. Arrows show distance between marginal natatory setae and illustrate large projected surface area of natatory setal field. D. Alignment of the natatory setae at the beginning of the recovery stroke. Arrows show distance between marginal natatory setae and illustrate decrease in projected surface area of the natatory setal field. Scale bars in C and D are 100 µm.

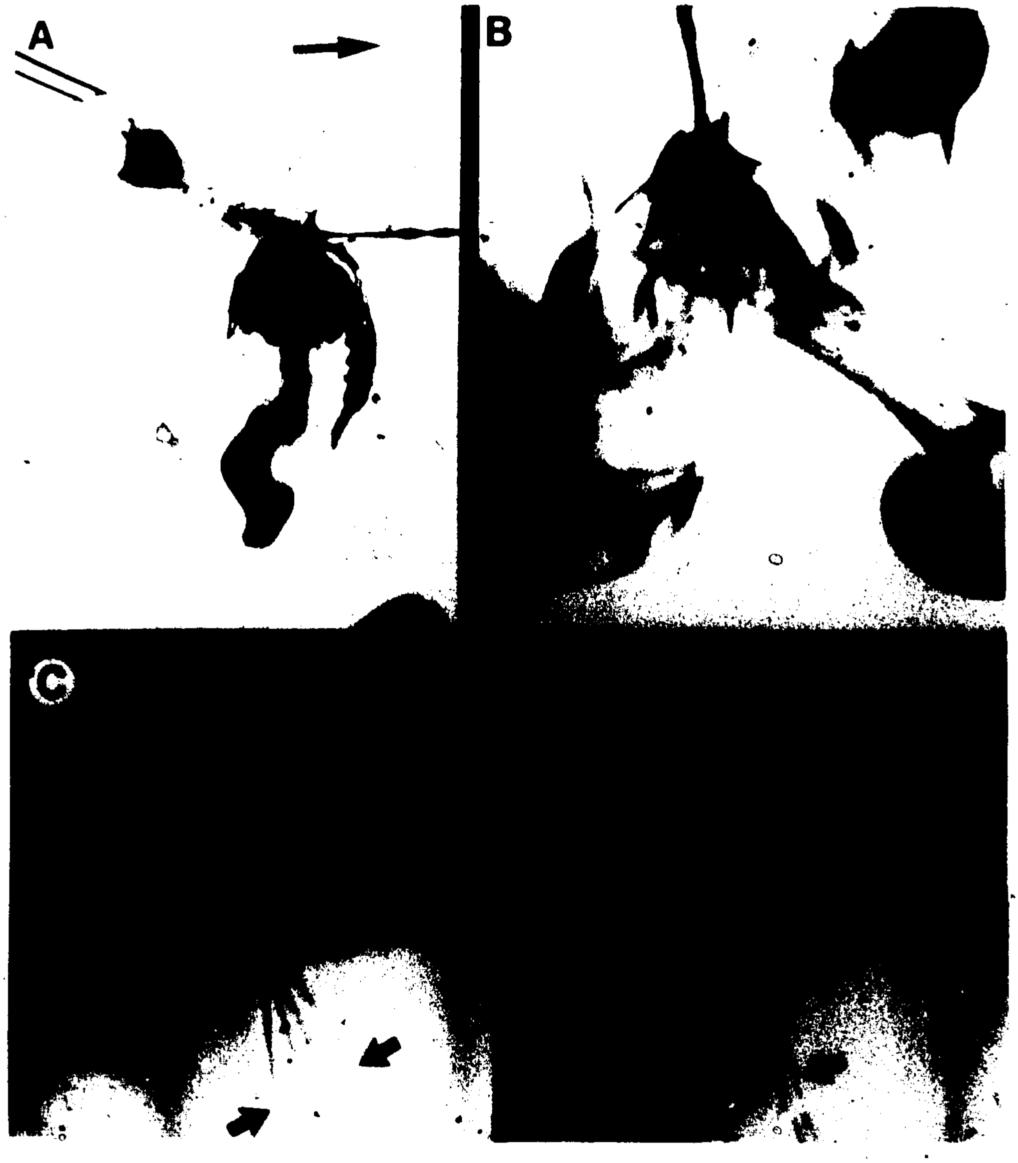

A
B
C

Figure 25. Diagrammatic summary of the oscillation cycle of the 1st and 2nd maxillipeds. Solid appendage and solid arrow indicates 1st maxilliped. Open appendage and open arrow indicates 2nd maxilliped. Oscillation frequencies range from 21 to 34 Hz.

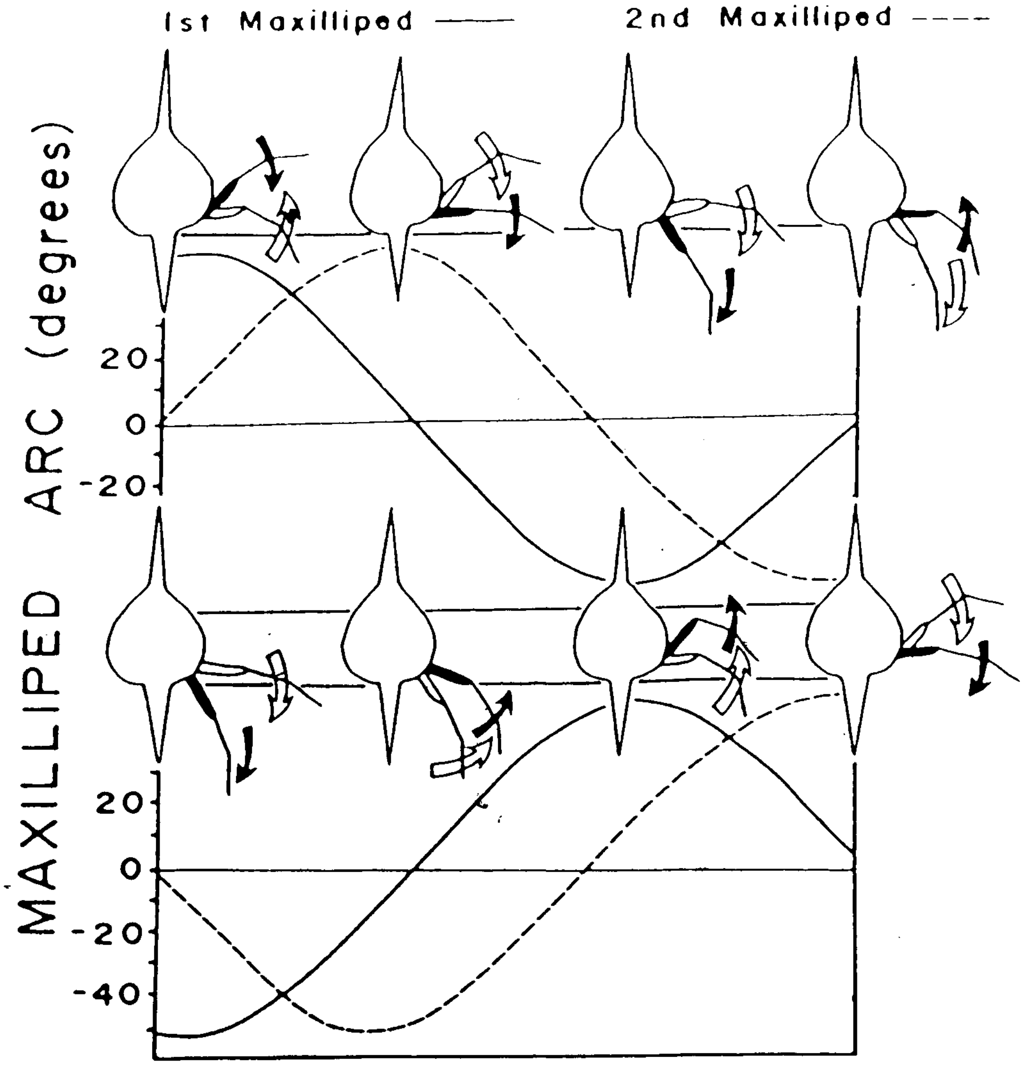
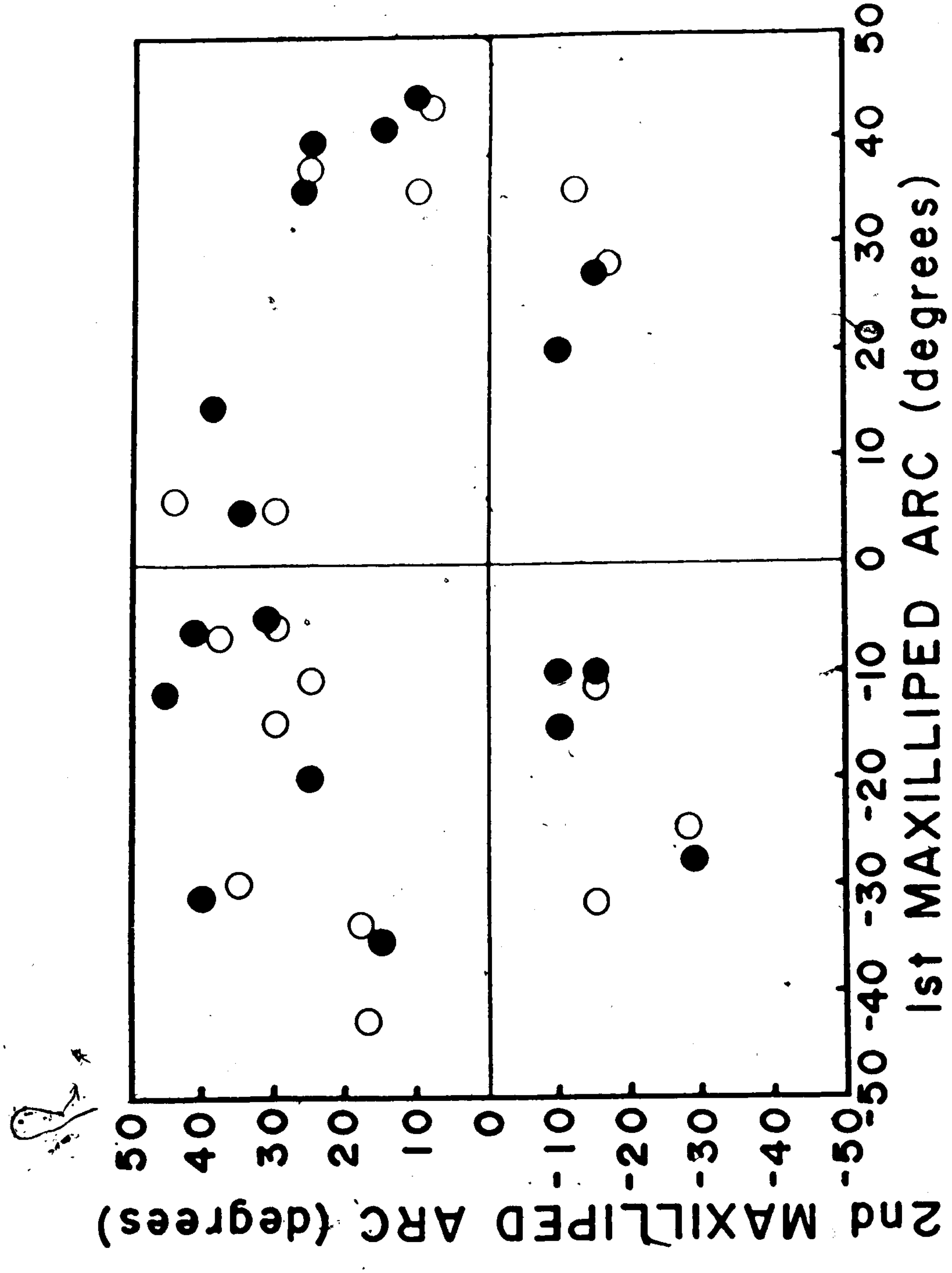

1st Maxilliped ———
2nd Maxilliped - - - -
MAXILLIPED ARC (degrees)
20
0
-20
20
0
-20
-40

Figure 26. Relationship between the effective and recovery stroke cycles of the 1st and 2nd maxillipeds of a *Pugettia producta* stage I zoea. Each point shows the angles of the appendages measured from a series of 18 flash photographs. Solid circles (●) indicate right side of zoea body, open circles (○) indicate left side. Stroke cycle proceeds counter-clockwise with effective stroke across the top of the plot and recovery stroke across the bottom. Positive arc angles indicate dorso-lateral orientation, negative values indicate ventro-lateral orientation.


1st MAXILLIPED ARC (degrees)
-50
-40
-30
-20
-10
0
10
20
30
40
50
2nd MAXILLIPED ARC (degrees)
50
40
30
20
10
0
-10
-20
-30
-40
-50

the natatory setae shear fluid along the dorsal surface of the carapace and sweep it past the body. The natatory setae project laterally from the maxillipeds during the effective stroke with a chord approximately normal to the plane of fluid motion. The tips of the natatory setae describe an arc of 85-95 degrees over the entire effective stroke. At the end of the effective stroke, the maxillipeds and natatory setae project ventro-laterally at a negative angle of 40-50 degrees (Figures 25 and 26).

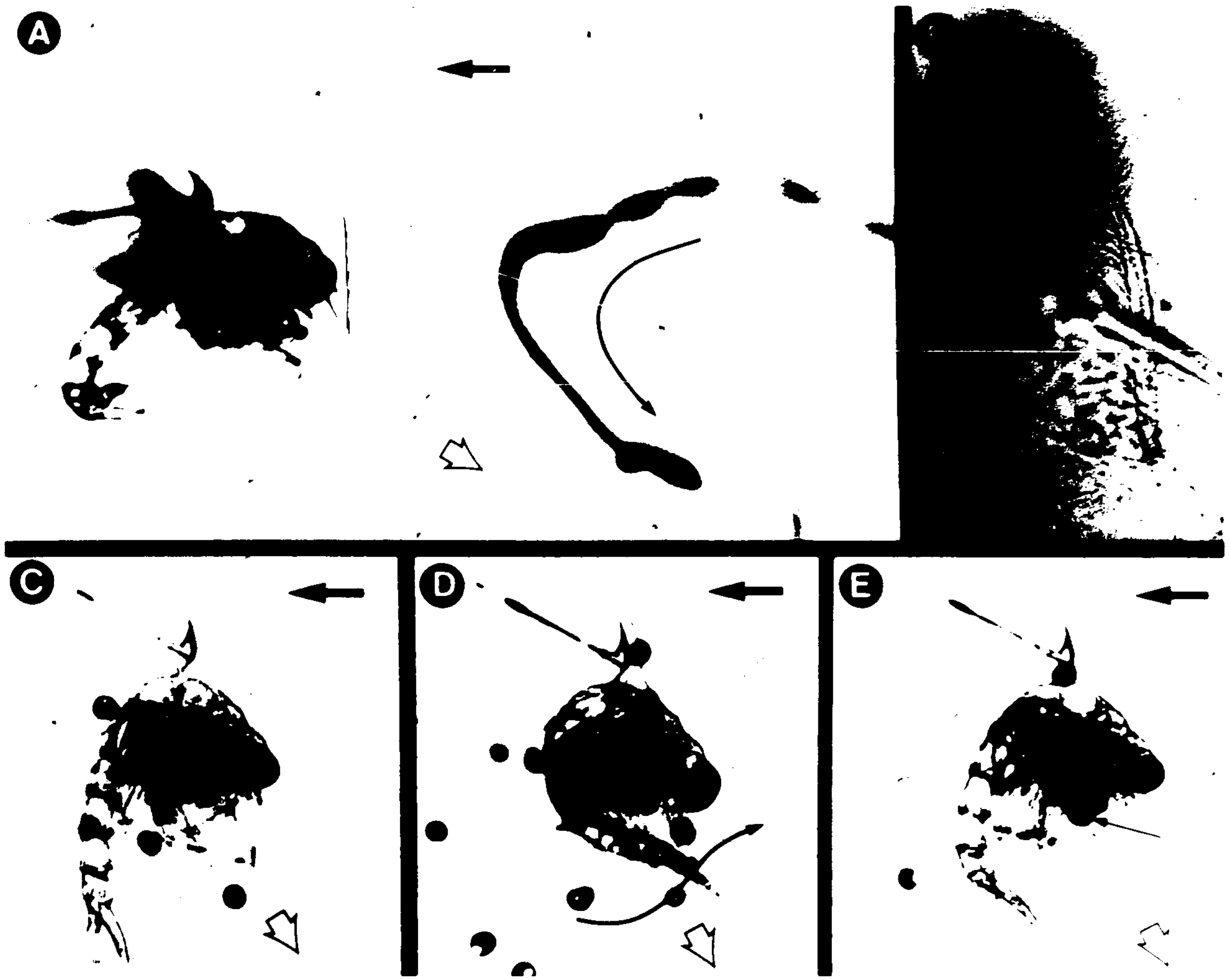
Two different mechanisms are utilized to reduce drag on the natatory setal field during the recovery stroke. First, at the initiation of the recovery stroke the natatory setae are oriented nearly parallel to one another (Figure 24d). Alignment of the natatory setae decreases the basal angle of the setal fan from about 32 to 9 °, thereby reducing the projected surface area of the 2nd maxilliped setal field by 71%. Second, deformation of the natatory setae and setules along the series of cuticular joints results in a further reduction of the projected surface area of the setal field (Figure 23c,d). Rotation of the setal fan out of the plane perpendicular to flow (pronation) does not appear to be utilized to reduce drag during recovery strokes. At the end of the recovery stroke, the maxillipeds and natatory setae return to their starting position and project dorso-laterally at a positive angle of 45-50 degrees (Figures 25 and 26). The stroke cycle of the 1st maxilliped is generally 80-100 degrees out-of-phase with the stroke cycle of the 2nd maxilliped. However, several photographs of tethered zoeae recorded periods when the maxillipeds were beating in-phase at the end of effective strokes.

5. Capture of Prey Items

During normal swimming of Pugettia producta zoeae, dye-marked water does not enter the region immediately surrounding the mouthparts (Figure 27a). During capture of small non-motile prey items, however, seawater is redirected toward the maxillae and mouth by a sweeping effective stroke of the abdomen and telson. Events that occur during the capture of Patiria miniata oocytes by a tethered P. producta zoea are summarized in Figure 27c-e.

Prior to the onset of the feeding response, the abdomen and telson are extended beneath the carapace and fluid movement past the zoea is predominantly in the ventral direction (Figures 24a and 27c). During the effective stroke, the abdomen and telson sweep anteriorly through an arc of 65-70 degrees (Figure 27c,d). Since fluid movements around the telson spines are dominated by viscous forces (Re = 0.4, see Table 8), the ventral surface of the telson pushes fluid anteriorly between the maxillipeds, toward the maxillae and mouth. At the same time, the dorsal surfaces of the abdomen and telson draw fluid in the anterior direction. At the end of the effective stroke, a redirected current moves past the mouthparts toward the antennae and rostrum (Figure 27d). Prey items are captured out of the

Figure 27. Feeding of *Pugettia producta* zoea larvae in moving fluid. A. Prey item approaches zoea from anterior and is propelled away by maxilliped current. Note formation of eddy downstream of the tethered zoea. Solid arrow indicates ambient current in flowtank (1.2 mm s^{-1}), open arrow shows direction of current generated by maxillipeds. Curved arrow shows trace left by dyed *Patiria miniata* oocyte. B. Plumose mechanoreceptor seta located on dorsal margin of the carapace. Scale bar is 25 µm. C-E. Sequence of prey capture events during sweep of the telson and abdomen. Prey items are *P. miniata* oocytes (130 µm dia). Solid arrows show ambient flowtank current (1.2 mm s^{-1}), open arrows show maxilliped current. Curved arrow shows telson effective stroke. C. Time=0 s. D. Time 0.3 s. E. Time 0.9 s. Note *P. miniata* oocyte held by maxillae and mandibles prior to ingestion (thin arrow).


A
C
D
E

current by the endopodites of the 1st maxillipeds (Figure 27e). Small prey items (125-150 µm dia.) are manipulated and held by the maxillae while larger prey (>500 µm) are held by the maxillae, maxilliped endopodites and telson (Herrnkind, 1968; and personal observations).

During the recovery stroke of the abdomen and telson, the abdomen is tucked beneath the carapace and the telson is drawn posteriorly past the maxillae and maxillipeds. Abdominal muscles appear to contract sequentially beginning with the proximal segment during the recovery stroke to allow the abdominal segments to articulate while they return to their original position. The telson spines are extended distally during effective strokes (Figure 27c,d) and pointed anteriorly during recovery strokes. The 1st and 2nd maxillipeds continue to oscillate during capture and ingestion of small prey items.

The mechanism by which *Pugettia producta* zoeae detect prey items passing over the dorsal surface of the carapace remains problematical. Visual cues do not appear to be essential in locating potential prey items since laboratory experiments conducted with *P. producta* and other brachyuran zoeae indicate that they are capable of capturing motile and non-motile prey in complete darkness (Rumrill, 1987; Rumrill *et al.*, 1985). It is possible that zoeae use tactile cues as an alternative to visual cues to detect the presence of prey items. For example, several plumose setae occur along the dorsal and lateral margins of the carapace

(Figure 27b). Each seta extends distally from a junction with the carapace and supports 40-120 setules along its length. These plumose setae are similar in appearance to tactile sensillae found in a variety of crustaceans (see Strickler and Bal, 1973; McIver, 1975). The arrangement and location of the plumose carapace setae suggest that they may function as tactile mechanoreceptors to detect local disruptions of flow along the dorsal and lateral regions of the zoea carapace. Additional putative mechanoreceptor sensillae are located along the dorsal surface of the abdomen and between the spines of the telson. The definitive function of these putative mechanoreceptors remains to be demonstrated by cinematographic, neurophysiological and histological examinations.

D. DISCUSSION

Zoea larvae of brachyuran crabs are an abundant and ubiquitous component of marine zooplankton communities (Lough, 1976; Pennington, 1986). Although several studies have investigated the diets of brachyuran zoeae (Sulkin, 1975, 1978; Sulkin and Epifanio, 1975; Sulkin and Norman, 1976; Christiansen and Yang, 1976; Levine and Sulkin, 1979, 1984; Incze and Paul, 1983; and numerous others), comparatively little attention has been given to their methods of locomotion and prey capture (Herrnkind, 1968; Gonor and Gonor, 1973; Schembri, 1982). Forward (1976, 1977) and Sulkin (1978, 1984) pointed out that locomotion and feeding are of paramount ecological significance in determining patterns of depth regulation and onshore transport in carnivorous brachyuran zoeae. However, there are several fundamental gaps in our knowledge concerning the hydromechanics of locomotion and prey capture in aquatic microcrustaceans (Lochhead, 1977). In particular, the methods employed by brachyuran zoeae to periodically accelerate and to capture and manipulate prey items are outstanding in their absence of detailed studies.

1. Locomotion of *Pugettia* Zoeae

Pugettia producta stage I and II zoeae swam in a characteristically jerky manner in the laboratory aquaria. Brief episodes of steady swimming were interrupted by frequent periods of acceleration and deceleration. In general, the swimming of a *Pugettia producta* zoea can be described as follows: 1) the zoea propels itself in the dorsal direction at an initial velocity, 2) the zoea accelerates and undergoes an increase in velocity, and 3) the zoea either accelerates again or decelerates and resumes swimming at the initial or slower speed.

The limit of temporal resolution available from the recording system used in this study was 67 ms. Consequently, results gathered by these techniques cannot be extended directly to events that occur over shorter periods of time. Strickler (1975) and Kerfoot (1978) recorded changes in swimming velocities of cyclopoid copepods and cladocerans over periods of 5 ms, and Lehman

(1977) found that a resolution of 10 ms was required to accurately determine the instantaneous velocities of a freshwater cladoceran, *Daphnia pulex*, and a calanoid copepod, *Diaptomus franciscanus*. However, the slow relative swimming velocity and large body size of *Pugettia producta* zoeae resulted in the superposition of images when they were illuminated stroboscopically at 900 pulses/min. These results indicate that valuable information about changes in the swimming velocity of a *P. producta* zoea can be obtained from consecutive measurements of displacement distances photographed with a temporal resolution of 67 ms.

Sulkin (1973, 1975, 1984) described the general pattern of swimming behavior exhibited by brachyuran zoeae. Zoeae propel themselves in the direction of the dorsal spine, and propulsive forces are generated primarily by oscillations of the 1st and 2nd maxillipeds. Similar locomotory behavior has been reported for several brachyuran zoeae (Foxon, 1934; Herrnkind, 1968; Bigford, 1979) as well as for anomuran and brachyuran zoeae with markedly dissimilar morphological traits including elongation and reduction of the dorsal and rostral spines and differences in the shape of the telson (Gonor and Gonor, 1973; Schembri, 1982). In all zoeae, propulsive forces are generated primarily by rhythmic beating of the natatory setae located on the 1st and 2nd maxillipeds. In addition, locomotion in the posterior direction can occur following rapid movement of the abdomen and telson (Gonor and Gonor, 1973; Forward, 1977). However, few details have been provided about changes in swimming velocity or rates of acceleration. In addition, there have been no previous reports concerning the movements of fluid around the zoea during locomotory behavior.

In the present study, photographs of dye-marked water indicate that the zoea carapace accelerates dorsally in response to forces generated by the displacement of fluid by the maxilliped natatory setal field. Effective strokes of the maxillipeds generate toroidal vortices that are shed by the tips of the natatory setae. Drag forces appear to arise mainly from viscous shear stresses exerted by fluid along the lateral margins of the carapace, although induced drag due to the shedding of vortices may also resist the motion of zoeae. The abdomen and telson are curved beneath the carapace and do not contribute to the generation of propulsive forces during normal swimming. Weldon (1889) suggested that the telson may aid in steering, and the orientation of the elongated telson spines in P. producta may also function to stabilize the zoea and reduce drag by softening the trailing edge of the rigid carapace during periods of acceleration. Lebour (1928) and Schembri (1982) noted the prevalence of rudimentary telson spines among demersal zoeae, and their observations suggest that rudimentary development of telson spines may be correlated with slow swimming velocities.

Acceleration profiles for Pugettia producta zoeae indicate that changes in swimming velocity occurred at a frequency (3-5 Hz, see Figures 20-22) that was substantially slower than the rapid oscillations of the 1st and 2nd maxillipeds (21-34 Hz). Dissociation of these events suggests that each burst of acceleration is composed of between 4 and 10 oscillations of the maxillipeds.

A plausible explanation for the sinusoidal acceleration of _Pugettia producta_ zoeae is that effective strokes of the 1st and 2nd maxillipeds periodically coincide to generate recurring periods of increased propulsive thrust. Several flash photographs were taken of tethered _P. producta_ zoeae that caught the maxillipeds at a point of alignment along the arc of the effective and recovery stroke cycle (Figure 26). In 5 out of 7 cases, the natatory setae exhibited low deformation angles, indicating that both maxillipeds were near the completion of effective strokes. Asymmetric oscillation cycles would allow the reciprocating appendages to beat in unison for several cycles, and interaction between the 1st and 2nd maxillipeds may result in an increase in the effective surface area of the natatory setal field. Cinefilm analyses with film speeds of 200-500 frames s^{-1} are required to determine with precision the phase relationships of the maxillipeds over several hundred effective and recovery stroke cycles.

Comparisons of average relative velocity and drag forces experienced during locomotion indicate that the performance of _Pugettia producta_ stage I and II zoeae follows the scaling pattern reported for various sizes of aquatic dytiscid beetles (Nachtigall, 1977; Daniel, 1984). The greatest relative velocities reached by stage II zoeae (13 body lengths s^{-1}) are comparable to those of Dytiscus marginalis, although they are substantially lower than the relative velocities attained by smaller water beetles (Nachtigall, 1977). The drag force, D, encountered by a P. producta zoea swimming at an average velocity, U, is found by

$$D = 1/2\ p\ U^2 . A\ C_d \qquad (1)$$

where p = the density of seawater, A = an estimate of the projected surface area of the zoea, and the coefficient of drag for the zoea carapace, C_d, is approximated by drag on a sphere at a Reynolds number of 5 (see Table 8). Drag forces for stage I zoeae ranged from 9.03×10^{-9} to 3.80×10^{-8} N. By comparison, the drag forces encountered by stage II zoeae were substantially higher (1.51×10^{-8} to 6.66×10^{-7} N) as a result of their faster swimming velocities and greater projected surface areas. The scaling of drag to carapace volume (exponent = 2.15) and projected surface area (exponent = 3.22) suggests that stage II zoeae must expend relatively greater effort than stage I zoeae to overcome drag. Since the majority of P. producta zoeae either increased or decreased their relative swimming velocities over the observation periods, drag forces associated with acceleration are an important component of zoea locomotory behavior and will be treated separately (see below).

2. *Prey Capture by Pugettia zoeae*

Although several studies indicate that phytoplankton may be a common component of the diets of brachyuran zoeae (Lebour, 1927; Atkins, 1955; Hartman and Letterman, 1978; Incze and Paul, 1983), the majority of species are omnivorous or carnivorous (Herrnkind, 1968; Mootz and Epifanio, 1974; Sulkin, 1975, 1978; Bigford, 1978). Raptorial feeding is likely the primary mode of prey capture among brachyuran zoeae, and laboratory studies demonstrate that zoeae can capture mobile invertebrate prey including rotifers, polychaete trochophores, echinoid larvae, and crustacean nauplii (Herrnkind, 1968; Sulkin, 1975; Sulkin and Epifanio, 1975; Paul *et al*., 1979; Incze and Paul, 1983; Rumrill and Chia, 1985; Rumrill *et al*., 1985; and several studies cited therein).

Although the principal items identified from the gut contents of brachyuran zoeae collected in the field include diatoms and dinoflagellates (Bright, 1967; Incze and Paul, 1983), phytoplankton are probably conspicuous because their thecae may be difficult to digest and have long residence times. By comparison, the remains of soft-bodied prey such as ciliated invertebrate larvae or nauplii may be difficult to detect because they have few recognizable hard parts or because the hard parts may be discarded prior to ingestion.

Observations of feeding brachyuran zoeae indicate that zoeae capture and hold their prey with their mouthparts and telson (Herrnkind, 1968; Schembri, 1982) and shred portions of the prey with the mandibles. However, recognizable fragments of echinoid pluteus larvae were found in the gut contents of stage I zoeae of the grapsid crab, *Hemigrapsus nud*[illegible] at the termination of laboratory feeding experiments (Rumrill and Chia, 1985).

The feeding behavior of *Pugettia producta* zoea larvae observed in the present study is consistent with Herrnkind's (1968) observation of "tail lashing" during the capture of *Artemia* nauplii by zoea larvae of *Uca pugilator*. However, the mechanism for capturing small prey items would not have been predicted from Herrnkind's (1968) description of the use of the telson spines to pin prey against the rostrum prior to ingestion. In *P. producta*, small prey items, including asteroid oocytes and embryos, were captured out of an anteriorly directed feeding current by movements of the endopodites of the 1st maxillipeds and maxillae. There was no evidence of direct contact between the telson and prey items during bouts of feeding upon *Patiria miniata* oocytes and embryos. However, contact with the telson did occur during the capture of larger prey such as *P. miniata* bipinnaria larvae. Asteroid bipinnaria and echinoid pluteus larvae were pinned by the telson prior to ingestion in a manner similar to that reported by Herrnkind (1968; Rumrill, pers. observations). Although the concentration of prey items was abnormally high in the observation chamber, the ingestion rates by P. producta were well below saturation levels (see Rumrill, 1987).

3. Comparison between Brachyuran Zoeae and Other Aquatic Arthropods

In contrast to the wealth of information gathered concerning the swimming behavior and feeding mechanisms of copepods (Kabata and Hewitt, 1971; Strickler, 1975, 1977, 1982; Koehl and Strickler, 1981; Alcaraz et al., 1980; Andrews, 1983), cladocerans (Lehman, 1977; Lochhead, 1977; Kerfoot, 1978) and dytiscid beetles (Nachtigall, 1977; Nachtigall and Bilo, 1975), the mechanisms by which brachyuran zoea swim and capture prey are poorly understood. Comparisons of swimming and feeding between Pugettia producta zoeae and other aquatic arthropods reveal several fundamental similarities in the hydromechanics of locomotion and removal of particles from fluid at low Reynolds Numbers.

Like that of brachyuran zoeae, the swimming behavior of copepods and cladocerans can be characterized by rapid changes in direction and velocity (Strickler 1975; Lehman, 1977). Propulsive forces and changes in swimming velocity are generated primarily by movements of the antennae, mandibular palps, maxillae and thoracic legs in calanoid copepods (Gauld, 1966; Anderson, 1974; Strickler, 1975, 1977), and by oscillations of the 1st antennae, thoracic legs, and abdomen in cyclopoid copepods (Strickler and Bal, 1973). Propulsive forces are generated in cladocerans by rhythmic beating of the biramous 2nd antennae (Lochhead, 1977). In all of these microcrustaceans, the reciprocating appendages generate force vectors that propel the organism through water at cruising speeds on the order of 5 to 50 mm s^{-1}. However, instantaneous swimming velocities can reach 500 mm s^{-1} in copepods, and their rates of acceleration have been reported to be as high as 12000 mm s^{-2} (Strickler, 1975). Similarly, the velocities reached by cladocerans during escape responses are typically between 60 and 90 mm s^{-1} with acceleration rates of up to 3250 mm s^{-2} (Lehman, 1977). Although Reynolds numbers at these maximum swimming velocities approach 500, information from velocity profiles indicates that streamlines around the exoskeleton are laminar rather than turbulent (Lehman, 1977; Kerfoot _et_ _al_., 1980).

In contrast to copepods and cladocerans, propulsive forces are generated in brachyuran zoeae by oscillations of the 1st and 2nd maxillipeds. During effective strokes, lateral sweeping movements of the maxillipeds cause fluid to shear past the margins of the carapace. Beating of the telson does not appear to be essential in the generation of propulsive forces in _Pugettia_ _producta_ zoeae. The maximum swimming velocity recorded for _P_. _producta_ in the present study was 13 mm s^{-1}, although velocities as high as 22 mm s^{-1} have been reported during positive phototaxis of _Callinectes_ _sapidus_ stage VII zoeae (Sulkin _et_ _al_., 1980).

Since the swimming velocities and maximum acceleration rates of copepods and cladocerans with comparable body sizes are typically greater than those of brachyuran zoeae, the drag forces exerted by fluid against the copepod and cladoceran exoskeletons are also expected to be substantially higher. Strickler (1975) and Kerfoot et al. (1980) suggested that the teardrop and torpedo shapes of cyclopoid and calanoid copepods may reflect the importance of streamlining to reduce drag. Conversely, the relatively globose body plans of brachyuran zoeae and small dytiscid beetles (Nachtigall, 1977) are common among aquatic arthropods where drag forces take on less importance than frictional forces.

Visualization of fluid dynamics revealed that the viscous effects of seawater govern mechanisms of prey capture in calanoid copepods (Alcaraz et al., 1980; Andrews, 1983). Koehl and Strickler (1981) described the movements of feeding currents generated by beating of the 2nd antennae, mandibular palps, 1st maxillae and maxillipeds in Eucalanus pileatus. Movements of the 2nd maxillae were observed to draw fluid containing food particles toward the mouth where algal cells are captured and ingested (Alcaraz et al., 1980; Paffenhofer et al., 1982). These cinematographic studies demonstrate that algal cells are captured along with parcels of fluid by rapid movements of the 2nd maxillae. Similarly, observations of the movements of dye-marked water and episodes of feeding upon asteroid oocytes made during this study indicate that the viscosity of sea water also plays an important role in the mechanism of prey capture in Pugettia producta. The 2nd maxillae of E. pileatus and endopodites of the 1st maxillipeds of Pugettia producta are both surrounded by relatively thick boundary layers, and each appendage operates at a Reynolds number of about 10^{-2} (see Table 8). Consequently, these appendages can be expected to function similarly in their capacity to draw prey items toward the mouth along with associated parcels of viscous fluid.

Despite hydromechanical similarities in the low Reynolds number flows associated with the feeding appendages of copepods and brachyuran zoeae, several pronounced differences are apparent when comparisons are made between the feeding mechanisms of carnivorous copepods and that of Pugettia producta stage I and II zoeae. First, carnivorous cyclopoid and calanoid copepods use the 2nd maxillae to capture and hold their prey (Ambler and Frost, 1974; Landry, 1978; Lonsdale et al., 1979; Koehl and Strickler, 1981). In Cyclops scutifer, swimming prey are attacked while they are 0.5 to 2 body lengths away from the copepod, and most prey are captured within a cone-shaped region that extends anteriorly between the antennae (Kerfoot, 1978). In contrast, the majority of prey attacked by crustacean zoeae are captured after they enter a spherical region located ventrally between the endopodites of the 1st maxillipeds (Moller, 1978; Rumrill et al., 1985). Second, although C. scutifer and P. producta zoeae are both encounter predators that rely on tactile cues to detect the presence of prey, the copepods scan the water to detect disturbances with mechanoreceptors located on their 1st and 2nd antennae (Strickler, 1975; Poulet and Marsot, 1978; Andrews, 1983). In contrast, P. producta zoeae appear to detect prey via mechanoreceptors located on dorsal surface of carapace. Finally, unlike carnivorous copepods, P. producta zoeae use the telson to redirect fluid containing small prey items toward the mouth. Furthermore, the telson can also be used to capture and hold relatively large and active prey items.

During the capture of small prey items, the endopodites of the 1st maxillipeds and maxillules of P. producta zoeae select individual prey items from a passing parcel of water and manipulate them into the mouth. In contrast, herbivorous copepods, such as Eucalanus pileatus, sieve water between setae located on the 2nd maxillae, thereby retaining algal cells by a combination of active capture and filtration.

4. Importance of the Acceleration Reaction

Predatory microcrustaceans can play a major role in the regulation of species composition and demographic structure of freshwater and marine zooplankton communities (Dodson, 1974; Kerfoot, 1977, Kerfoot et al., 1980; Landry, 1978; Zaret, 1980). Recent attempts to model quantitatively the effects of selective predation in zooplankton communities are based on the simplifying assumption that predator and prey swimming speeds are constant and unidirectional in time and space (Gerritsen and Strickler, 1977; Greene, 1983). However, Daniel (1984) argues that steady-state motion is rare in aquatic locomotion; swimming organisms typically accelerate to attack prey and to escape predation. Furthermore, unsteady flow is frequently generated by oscillating paired swimming appendages during episodes of propulsive thrust and turning (Daniel, 1983). Since periodic changes in velocity are an integral component of locomotion in aquatic microcrustaceans, it is a central problem to gauge the relative importance of unsteady aspects of swimming, particularly as they apply to short-term events associated with locomotory behavior and prey capture.

The reciprocating maxillipeds of a *Pugettia producta* zoea generate instantaneous force vectors at the end of their effective strokes that propel the larva through water in a jerky manner (see Figures 18-22). Daniel (1984) pointed out the mechanism by which the acceleration reaction, or the forces that resist changes in static velocity, can be utilized by aquatic arthropods such as dytiscid beetles to generate thrust during locomotory behavior characterized by unsteady motion. In *P. producta*, the instantaneous acceleration reaction (G) can be approximated by

$$G = -L\ p\ V\ (du/dt) \qquad (2)$$

where L is the added mass coefficient for a sphere (0.5), p is the density of seawater, V is an estimate of the displacement of the zoea carapace, and du/dt is an estimate of instantaneous acceleration. The acceleration reaction can be found by integrating G over any specified time interval T, such that

$$1/T \int -L\ p\ V\ (du/dt)\ dt \qquad (3)$$

Two time intervals, T_s and T_f, are particularly relevant. The first time interval, T_s, is defined as the period of time required for a <u>Pugettia</u> <u>producta</u> zoea to accelerate from cruising to maximum swimming speed. The second time interval, T_f, is the time required for a zoea to detect and capture a prey item. In <u>P</u>. <u>producta</u>, acceleration to the maximum observed swimming speed takes from 201 to 268 ms, and the time required to capture and secure a prey item is about 300 ms. The acceleration reaction has a value of -5.99×10^{-10} N for a stage I zoea that accelerated from 2.6 to 3.7 mm s^{-1} over a period of 201 ms. Similarly, an acceleration reaction value of 8.68×10^{-9} N occurs for a stage II zoea that accelerated from 5.7 to 11.1 mm s^{-1} over a period of 268 ms. These force values are estimates of the negative resistance that must be overcome in addition to drag for the zoeae to accelerate.

The relative importance of the acceleration reaction (I) can be represented by a dimensionless ratio of the forces resisting acceleration over the total (acceleration and drag) resistive force as

$$I = G / G + D \qquad (4)$$

The ratio I has a value of 1.66×10^{-2} or approximately 1.7% for the stage I zoea over the time interval T_s. The acceleration reaction contributes 1.93×10^{-2} (1.9%) of the total resistive force in the stage II zoea. Since the ratio I can only have values between 0 and 1.0, the low values indicate that drag forces, rather than acceleration forces, dominate the swimming motion of P. producta zoeae during T_s. The resistive forces due to acceleration decrease to about 0.5% when I is figured over the time interval required to capture prey, T_f. Since laboratory observations presented here indicate that P. producta zoeae capture non-motile and slow moving prey by redirecting fluid containing prey items past the feeding appendages and mouthparts, the resistive forces that must be overcome during an encounter with a prey item are expected to be minor compared with the forces that resist changes in velocity during acceleration or escape maneuvers by zoeae in response to other zooplankton predators.

E. CONCLUSIONS

Sulkin et al. (1980) and Kelly et al. (1982) developed models for the recruitment of brachyuran larvae that are based upon ontogenetic differences in the swimming behavior of zoea stages. Similarly, Cronin (1982) and Cronin and Forward (1982) reported that differences in larval swimming behavior result in the retention of Rithropanopeus harisii zoeae within regions of a shallow estuary and net transport of Callinectes sapidus out of the estuary. The importance of zoea locomotory behavior is conspicuous in these studies, and they indicate that changes in the rate and direction of zoea swimming can play a central role in the behavioral basis of depth regulation (Sulkin, 1984). Consequently, quantitative descriptions of swimming behavior contribute to an understanding of the larval ecology of brachyurans by providing useful information about average swimming velocities and rates of acceleration within water masses.

The observations reported here corroborate previous studies of zoea behavior (Herrnkind, 1968; Schembri, 1982), and provide a more detailed description of the locomotory mechanisms utilized by brachyuran zoeae. Fluid movements around tethered zoeae have important implications concerning the maxilliped propulsion system and mechanisms of prey capture, but information concerning flow patterns around unrestrained zoeae are required to fully appreciate the range of behavioral responses and functional anatomy of the conservative brachyuran zoea body plan. Since intraspecific variation in zoea swimming behavior was considerable in _Pugettia producta_, it is premature to extrapolate the results of this study to larger groups of sibling zoeae or to the behavior of zoea populations in nearshore waters. Nevertheless, generalizations concerning average swimming velocities and mechanics of prey capture reported here may be warranted for zoeae of other brachyuran crabs. Knowledge about these fundamental aspects of larval behavior can contribute to an understanding of the complex processes affecting the selection of prey items, dietary requirements and distribution of planktonic brachyuran zoeae.

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CHAPTER V.

RECRUITMENT OF ASTERINA MINIATA (BRANDT, 1835): A POST-FACTO ASSESSMENT OF LARVAL ABUNDANCE, SUBSTRATUM SELECTION, AND LARVAL PREDATION

A. INTRODUCTION

Spatial and temporal variability in the abundance and distribution of early juveniles are prominent features of benthic marine invertebrate populations (Coe, 1956; Ebert, 1983; Caffey, 1985; Connell, 1985). General concepts of invertebrate recruitment consider interactions between events that occur in the plankton, during settlement, and on the bottom to determine patterns of juvenile distribution (Cameron and Schroeter, 1980; Cameron and Rumrill, 1982; Keough and Downes, 1982; Underwood and Denley, 1984; Connell, 1985; Gotelli, 1987). Factors that contribute to larval availability include: 1) physical and biological oceanic processes that regulate the spatial patchiness of larval populations (DeWolf, 1973; Omori and Hamner, 1982; Keough, 1983; Grosberg, 1982; Cameron and Rumrill, 1982; Emlet, 1986; Jackson, 1986), 2) rates of larval differentiation and growth (Jackson and Strathmann, 1981; Roller and Stickle, 1985; Paulay et al., 1985), and 3) mortality prior to the onset of metamorphic competence (Thorson, 1966; Hancock, 1973; Rumrill and Chia, 1985; Rumrill et al., 1985; Young and Chia, in press). Near the end of the planktonic period the availability of suitable sites for settlement (Grosberg, 1981; Young and Chia, 1982; Highsmith, 1982; Cameron and Schroeter, 1980; Breitburg, 1984) and the distribution and efficiency of benthic predators (Thorson, 1950, 1966; Wilson, 1980) regulate the initial distribution of newly settled post-larvae. Finally, the intensity of recruitment is determined after settlement by: 1) the initial abundance of post-larvae, 2) early mortality rates, and 3) immigration and emigration from the settlement site following metamorphosis (Woodin, 1976, 1978; Oliver et al., 1982; Young and Chia, 1984; Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Watzin, 1986). Complex interactions between these pre- and post-settlement events can lead to uncertainty in understanding the causes of spatial and temporal variation in the recruitment of benthic invertebrates (see Connell, 1985 for review).

Few studies of echinoderm populations distinguish between settlement, defined as the place and time when a larva becomes temporarily attached to the substratum, and recruitment, defined as the time when the smallest individuals can be accurately censused in the field. Settlement and recruitment of long-lived, iteroparous asteroids can vary markedly in space and time (Burkenroad, 1957; Loosanoff, 1964; Yamaguchi, 1973; Ebert, 1983). Consequently, it is likely that local settlement events are frequently overlooked until juveniles grow large enough to be sampled in the field. The time between settlement and recruitment can be brief or nonexistent in asteroids that brood offspring or that have macroscopic post-larvae (Chia, 1966; Menge, 1975; Strathmann et al., 1982). In contrast, the comparatively small size and slow growth rates of post-larvae that develop from planktotrophic brachiolariae typically result in long intervals between settlement and recruitment. Field studies provide inferential evidence that recruitment may be separated from settlement by 3 to 9 weeks among tropical asteroids (Yamaguchi, 1973) and by 5 to 13 months among temperate species (Vevers, 1949; Barnes and Powell, 1950; Quayle, 1954; Feder, 1970; Barker, 1977). A long interval between settlement and recruitment necessitates a post-facto approach to evaluate the importance of pre-settlement and post-settlement processes in determining spatial and temporal patterns of recruitment.

The asterinid sea star, Asterina miniata (Brandt, 1835), is a common member of shallow-water, soft-sediment, invertebrate communities along the west coast of Vancouver Island (Appendix I). In Barkley Sound, populations of A. miniata occur in protected areas adjacent to eelgrass beds (Zostera marina L.). Other conspicuous members of these soft-sediment communities include the alga, Gracilaria pacifica (Abbott, 1980), the burrowing cerianthid anemone, Pachycerianthus fimbriatus McMurrich, 1910, and the phelebobranch ascidian, Corella willmeriana Herdman, 1898. Individuals of A. miniata are predators of urchins and bryozoans in rocky subtidal habitats in southern California (Day and Osman, 1981; Schroeter _et_ _al_., 1983) and they play a major role in the dynamics and utilization of drift algae in kelp forests (Gerard, 1976). In the Pacific Northwest, individuals of _A_. _miniata_ are important scavengers within shallow-water soft-sediment estuarine communities (Rumrill, personal observations).

In this study, a heterogeneous spatial pattern of recruitment in _Asterina_ _miniata_ between adjacent estuarine inlets is described. A post-facto approach was used to evaluate pre-settlement and post-settlement factors that contribute to the differential pattern of recruitment. These factors include: 1) temporal and spatial heterogeneity of larval populations, 2) larval substratum selection, 3) predation upon larvae at the time of settlement, 4) mortality rates of juveniles, and 5) rates of juvenile immigration and emigration. Two assumptions are implicit: 1) larval behavior and substratum selection of _A_. _miniata_ do not vary significantly between successive breeding seasons, and 2) interspecific variability in predation upon larvae exceeds temporal differences in predation between conspecific suspension feeders. The results provide empirical and conceptual evidence that larval substratum selection and predation during settlement are key determinants of spatial variability in recruitment. A second conclusion is that advantages associated with repeated sampling of substrata for a suitable settlement site are offset by increasing the cumulative risk of predation by benthic suspension feeders.

B. MATERIALS AND METHODS

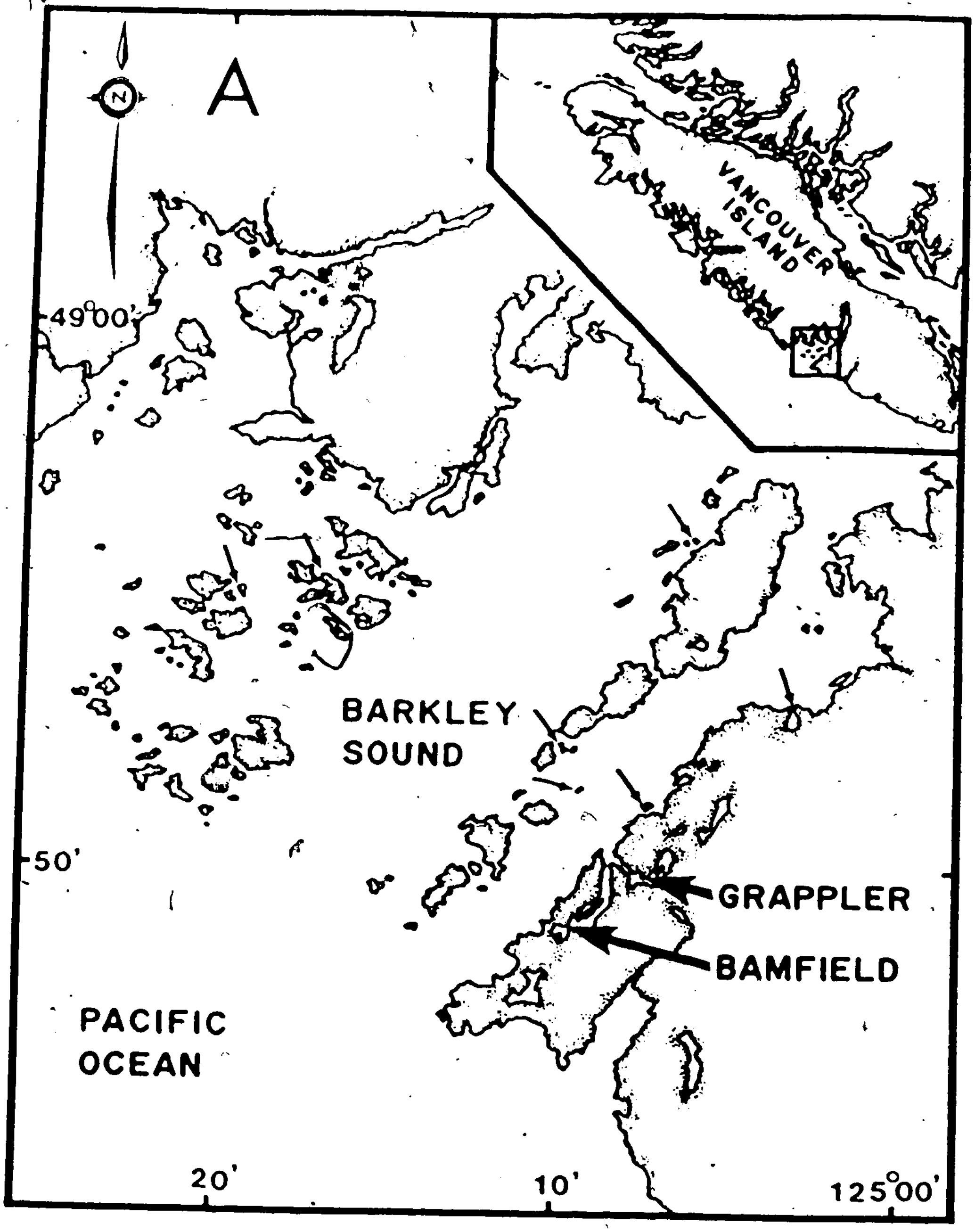
1. Study Sites

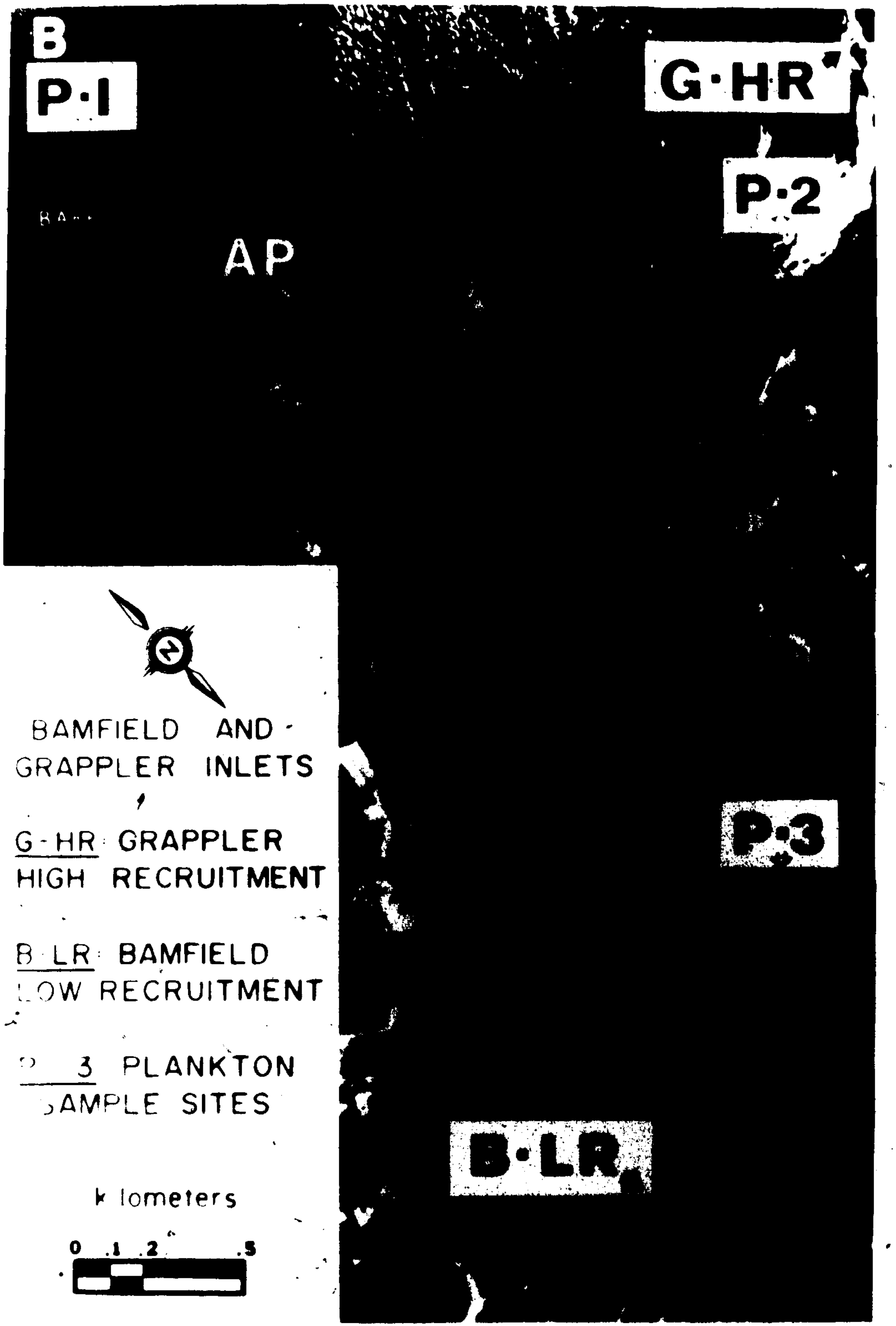
The research was carried out between March 1985 and February 1986 at 2 sites near Bamfield Marine Station, on the west coast of Vancouver Island, British Columbia (48° 50'N, 125° 08'W). Bamfield and Grappler Inlets are estuarine tidal channels that extend inland for about 2.5 km from Barkley Sound (Figure 28). Tides in the inlets are mixed and semi-diurnal with a vertical range of 3.6 m. The study sites were located at depths of 5 to 7 m on mud and cobble substrata near the heads of the inlets. Each site was inhabited by a large population of *Asterina miniata*. The nearest known other populations of *A. miniata* are located 5 and 7 km from the mouth of the inlets. Ambient surface temperature and salinity were measured at the sites at haphazard phases of the tidal cycle.

2. Abundance and Recruitment of *Asterina*

Size-frequency distributions of *Asterina miniata* populations were estimated during March through December 1985 at the Bamfield and Grappler Inlet study sites. Square quadrats (0.25 m^2) were placed in contiguous sets of 4 along 50 m transect lines to cover 50 m^2 at each study site. Size-frequency data for *A. miniata* were obtained by measuring the ray lengths of all individuals that occurred

Figure 28. Field sites in Barkley Sound, Vancouver Island, British Columbia. A. Barkley Sound. Labelled arrows show Asterina miniata study areas in Grappler and Bamfield Inlets. Unlabelled arrows indicate locations of other known populations of A. miniata. B. Bamfield and Grappler Inlets. G-HR indicates location of high recruitment site in Grappler Inlet; B-LR shows low recruitment site in Bamfield Inlet. P-1, P-2, and P-3 show zooplankton sample sites. AP indicates source of sediments for substratum selection experiments (see Tables 14 and 15).


A
N
VANCOUVER ISLAND
49°00'
BARKLEY SOUND
50'
GRAPPLER
BAMFIELD
PACIFIC OCEAN
20'
10'
125°00'


B
P·1
G·HR
P·2
AP
P·3
B·LR
BAMFIELD AND
GRAPPLER INLETS
G-HR GRAPPLER
HIGH RECRUITMENT
B LR BAMFIELD
LOW RECRUITMENT
P 3 PLANKTON
SAMPLE SITES
kilometers
0 .1 .2 .5

within quadrats. Subtidal counts and measurements of A. miniata and other benthic marine invertebrates (see Table 16) were made in situ using SCUBA. Additional A. miniata were measured at each site in May and June, 1985 during an extensive search for juveniles. Ray length measurements were recorded for all A. miniata that occurred along a second 50 m line adjacent to the initial transect.

3. Reproductive Activity of Asterina

Seasonal reproductive activity of Asterina miniata was followed to estimate the time of spawning and migration of embryos and early larval stages into the plankton. Allocation to somatic and reproductive tissue was assessed by methods outlined by Giese and Pearse (1974). Every other month, from March 1985 to February 1986, twenty-five adults of A. miniata were collected near the Grappler Inlet site. Gonads and pyloric caecum tissues were separated into pre-weighed dishes and dried at 22-24°C to constant weight. Remaining parts of the body were pooled into a third dish and dried and weighed. Gonad index and pyloric caecum index values were computed as:

(excised tissue wt./total body wt.) X 100.

4. Larval Distribution and Abundance

The abundance and distribution of asteroid larvae was estimated from a time-series of zooplankton tows. Since it was not possible to distinguish bipinnariae and brachiolariae of Asterina miniata from those of other species, total numbers of asteroid larvae were counted to obtain estimates of abundance and spatial distribution. It was assumed that the distribution and behavior of A. miniata larvae were similar to that of other species collected by plankton nets. There are no empirical data to either support or refute such an assumption. Asteroid bipinnaria and brachiolaria larvae were collected at 3 sites from zooplankton tows taken with 125 µm mesh, 0.5 m diameter standard and closing nets. During each sampling period, three replicate oblique samples were taken from the water column near the Bamfield Inlet and Grappler Inlet sites. Plankton samples were collected with a closing net at 30, 60, and 90 m depths at a site near the mouth of the inlets (Figure 28b, site P-1). Tows were taken at approximately 3 wk intervals from March, 1985 to February, 1986. No samples were taken in January, 1986. Each tow was preserved in 10% buffered formalin immediately after collection and sorted under a stereomicroscope.

5. Larval Substratum Selection

Gametes obtained from gravid Asterina miniata following injections of 10^{-5} M 1-Methyladenine or from natural spawnings were reared in the laboratory in 3.78 liter glass jars at ambient sea temperatures (11-15°C). Bipinnaria and brachiolaria larvae were cultured at densities of 100-150 larvae $liter^{-1}$ in aerated jars equipped with slowly oscillating paddles. Larvae were fed a mixture of Dunaliella tertiolecta Butch. and Pavlova lutheri Droop every 3 to 4 days at the time sea water in the culture vessels was replenished. Cultures initiated at various times throughout the study provided developmental stages for predation experiments with _Pachycerianthus_ _fimbriatus_ and _Corella_ _willmeriana_.

A series of 4 laboratory experiments examined substratum selection at settlement by brachiolaria larvae of _Asterina_ _miniata_. Settlement experiments of a multiple substratum design were conducted in glass petri dishes (10 cm diameter) coated by thin layers of 5% agar in seawater. Substrata from Grappler Inlet included sediments, bivalve shell fragments (_Tresus_ _nuttali_), rocks and 3 species of algae (_Ulva_ sp., unidentified crustose coralline algae, and _Gracilaria_ _pacifica_). Clean and aged glass were also included. Aged substrata were prepared by placing shell fragments, rocks and glass into running unfiltered seawater for 2 wks prior to the experiment; during the 2 wk period a surface film composed of bacteria, diatoms and other microorganisms developed. Substrata were arranged in the petri dishes at random according to a Latin square, and each presented a surface area of approximately 1 cm^2. Three trials were conducted with 8 substrata and 20 brachiolaria larvae per dish.

Single substratum experiments compared rates of settlement and metamorphosis on sediments collected from Bamfield and Grappler Inlets. Sediments from a third site near the entrance of Bamfield Inlet were also tested (Figure 28b, site AP). A 5 mm layer of sediment was placed at the bottom of 250 ml beakers, and each was filled with 180 ml of 1 µm filtered seawater. At the initiation of the experiment either 50 or 20 Asterina miniata brachiolariae were pipetted gently into the center of each beaker. Experiments were carried out under 16L:8D photoperiod and consisted of 4 replicates with sediment and 4 controls without sediment.

Single substratum experiments (4 replicates of each treatment, 15 larvae per trial) were also conducted to compare rates of settlement and metamorphosis between fresh and aged sediments from the entrance of Bamfield Inlet (Figure 28b, site AP). Sediments were aged in running unfiltered seawater for 9 days prior to each trial. Substrata were examined for recently metamorphosed Asterina miniata at intervals of 24 hours over a period of 3 days in all substratum selection experiments.

6. Predation upon Larvae by Benthic Suspension Feeders

Predation upon settling larvae by benthic suspension feeders was assessed by: a) the examination of gut contents, b) laboratory feeding experiments, and c) estimation of predator-prey encounter rates.

a. Analysis of Gut Contents

Gut contents of Pachycerianthus fimbriatus and Corella willmeriana were examined to determine whether the size range of prey items corresponded to that of settling larvae of Asterina miniata. Individuals of P. fimbriatus (n = 17) and C. willmeriana (n = 27) collected from Grappler and

Bamfield Inlets on August 5-6, 1985 were immediately preserved in 30% buffered formalin. Gut contents from each specimen were stained with phloxine B (Mason and Yevich, 1967) and examined at a magnification of 12X under a stereomicroscope. Although counts were made of the various taxonomic groups of prey items, only data concerning prey sizes are presented here.

b. Laboratory Predation Experiments

Laboratory feeding experiments examined the stage-specific and density-dependent (functional response, sensu Holling, 1966) characteristics of predation by *Pachycerianthus fimbriatus* and *Corella willmeriana* upon *Asterina miniata* embryos and larvae. Stage-specific feeding experiments were carried out with six developmental stages of *A. miniata* including: 1) zygotes, 2) embryos, 3) blastulae, 4) late gastrulae, 5) bipinnariae, and 6) brachiolariae (Table 9). Functional response experiments were conducted at 6 prey densities with two developmental stages (embryos and bipinnaria larvae).

Stage-specific feeding experiments were carried out with *Pachycerianthus fimbriatus* following methods developed for a terebellid polychaete (Wilson, 1980). A series of 2 liter circular aquaria were used each containing a loop of 12.7 mm diameter latex tubing. Individuals of *P. fimbriatus* constructed mucus-lined burrows in the tubes and extended their tentacles in a manner similar to that observed in the field. A few individuals were maintained in artificial

TABLE 9

Developmental stages of *Asterina miniata* used in feeding experiments with *Pachycerianthus fimbriatus* and *Corella willmeriana*. Table entries show sample size, mean and s.d. of size measurements. Measured dimensions: a, diameter; b, greatest length; c, greatest length & greatest width.

DEVELOPMENTAL STAGE	CODE	APPROXIMATE SHAPE	DIMENSION (n)	MEAN (µm)	S.D. (µm)	SWIMMING BEHAVIOR
Zygotes	ZYG	Spherical	a (34)	137	(6)	non-motile
Embryos	EMB	Spherical	a (23)	267	(26)	non-motile
Blastulae	BLS	Spheroid	b (28)	429	(28)	forward
Gastrulae II	GST	Prolate Spheroid	b (33)	526	(43)	forward
Bipinnariae	BIP	Ellipsoid	c (21)	L: 1028 W: 597	(66) (37)	forward & reverse
Brachiolariae	BCH	Elongate Ellipsoid	c (16)	L: 1194 W: 561	(72) (33)	forward & reverse & loop

tubes for over 4 months. Aquaria previously inhabited by anemones served as control chambers to assess handling losses and the effects of tubes. The experiments consisted of 5 - 10 replicate treatments with anemones and 3 - 6 controls without anemones (see Figure 37). Initial prey densities were 100 embryos of larvae liter^{-1}. Seawater in the aquaria was continuously agitated by a slow stream of small air-bubbles. The number of Asterina miniata survivors was determined after a period of 12 hrs following concentration into a small volume of seawater. Surviving embryos and larvae were fixed in buffered formalin and counted in a Bogorov tray.

Stage-specific feeding experiments with Corella willmeriana followed a modification of the design of Rumrill et al. (1985). Basal regions of the ascidians were attached to the insides of plastic jar lids with Krazy glue cyanoacrylate adhesive. The lids were sealed over 250 ml glass jars containing embryos or larvae of Asterina miniata at an initial density of 100 prey liter^{-1}. Stage-specific feeding experiments with C. willmeriana consisted of 7 replicates with ascidians and 3 controls without ascidians. Jars were fastened to a motor-driven cage and rotated continuously at 4 rpm. The number of surviving A. miniata embryos and larvae was determined after 1 hr.

Feeding experiments were carried out in a seawater flume (L:58 X W:8 X H:7 cm) to examine the responses of Pachycerianthus fimbriatus and Corella willmeriana to increasing prey density under conditions of unidirectional flow. Seawater was circulated by an airlift at a velocity of 0.3 cm s^{-1}. Individuals of <u>P. fimbriatus</u> and <u>C. willmeriana</u> were allowed to equilibrate for 4 hrs in the working section of the flume. Embryos or larvae of <u>Asterina miniata</u> were placed into a holding chamber positioned upstream from the working section. At the beginning of each trial, embryos or larvae were allowed to flow past the predator. The capture of prey and larval behavior were observed through a stereomicroscope mounted above the working section of the flume. Density-dependent feeding experiments were conducted at initial densities of 10, 25, 50, 100, 200, and 500 prey per liter, and each consisted of 3 replicates with predators and 3 controls without predators. The number of embryos or bipinnaria larvae captured was determined by subtracting the number of survivors recovered at the end of the experiment from the initial number of prey. All experiments were about 30 min in duration and were conducted under constant illumination from fluorescent lamps in a cold room at 13°C.

c. <u>Predator Encounter Rates</u>

Ambient current velocities were measured <u>in situ</u> by divers at the Bamfield and Grappler Inlet study sites on 3 occasions (June 6, 16, and August 8, 1985) during periods of peak flood and ebb tidal flow. During each series of measurements, divers released fluorescein dye from a syringe at a point 10 cm above the bottom. Advection of the dye over a distance of 50 cm was timed with a stopwatch. Current velocities were measured 5 to 9 times during each sampling period.

Size distribution, height above the substratum, and feeding posture of Pachycerianthus fimbriatus tentacles were determined for 41 animals in situ at the Grappler Inlet study area from a series of underwater photographs. All photographs included a cm scale ruler to correct for magnification errors. Densities of Corella willmeriana were estimated in Grappler and Bamfield Inlets on 5 occasions between May and December 1985 from 10 sets of 4 contiguous 0.25 m^2 quadrats placed at random points along a 30 m transect line. All ascidians within the quadrats were placed into plastic bags by divers and returned to the laboratory for counting and measurements. The body length, siphon radius, and instantaneous volume of water affected by the feeding activities of C. willmeriana were measured for 29 individuals. Measurments of siphon radii were made with an ocular micrometer while the ascidian was actively pumping seawater in the flume. Estimates of the velocity of the feeding current, and height and radius of the feeding current paraboloid (see Figure 42c) were determined by tracing the streamlines of Nile Blue dyed seawater.

The filtration efficiencies of Pachycerianthus fimbriatus and Corella willmeriana were estimated from direct observations of predation during density-dependent feeding experiments. A total of 233 embryos and 126 bipinnaria larvae of Asterina miniata were observed as they encountered the marginal tentacles of P. fimbriatus or the feeding current paraboloid of C. willmeriana. The fate of the A. miniata embryo or larva (captured or escaped) was recorded after the encounter with P. fimbriatus or C. willmeriana.

7. Juvenile Survivorship

Seven laboratory experiments during April and May 1985 assessed the susceptibility of juvenile Asterina miniata to predation by benthic macroinvertebrates and fish. Juveniles of A. miniata collected from Grappler Inlet had ray lengths between 0.8 and 2.7 cm. Predatory macroinvertebrates and fish collected near the study site included asteroids (Pisaster brevispinus, Evasterias troschelli, Dermasterias imbricata, A. miniata), cancrid crabs (Cancer productus, C. magister) and juvenile ling cod (Ophiodon elongatus). In each trial, a single predator and 5 juvenile P. miniata were placed into a plastic tub (L:55 X W:40 X H:30 cm) containing a layer of sediment from Grappler Inlet. Predation experiments with P. brevispinus and O. elongata were conducted in larger tubs (L:100 X W:70 X H:30 cm). All tubs were covered with nylon mesh and supplied with running seawater. The number of surviving A. miniata was monitored over a period of 2 to 4 weeks.

Field predation experiments were carried out with Cancer productus. Five juvenile A. miniata were placed into each of 4 cages (L:50 X W:50 X H:25 cm) covered with 0.5 cm plastic mesh. The cages were anchored along a transect line in Grappler Inlet. At the initiation of the experiment an adult male C. productus was placed into each of 3 cages. The fourth cage did not contain a crab and served as a control to assess losses due to escape from the cages. All 4 cages were retrieved after 6 days and the number of remaining A. miniata was counted.

8. Juvenile Immigration and Emigration

Rates of movement by Asterina miniata post-larvae and juveniles were measured in order to infer whether immigration or emigration could be a factor in the establishment of heterogeneous size-frequency distributions between Bamfield and Grappler Inlets. Crawling speed was measured for 37 individuals of A. miniata as they moved across detritus and mud on the bottom of glass petri dishes or a sea table. The ray lengths of A. miniata ranged from 0.6 to 2.6 cm. A. miniata that crawled continuously for less than 12 seconds were excluded from consideration

Statistical analyses were carried out following methods outlined by Snedecor and Cochran (1967), Daniel (1978), and Sokal and Rohlf (1981).

C. RESULTS

1. Study Sites

Populations of Asterina miniata occur in similar habitats at the Bamfield and Grappler Inlet study sites (Figure 28). Both populations are located near eelgrass beds and mudflats at depths of 5 to 7 m. Sea surface temperatures varied seasonally from 5.6 to 17.1 C in Bamfield Inlet and from 4.8 to 17.9 C in Grappler Inlet (Figure 29). Surface temperatures in Trevor Channel were generally 0.5^{o}C cooler than in the inlets. Surface salinities varied seasonally between 24-25 0/00 in the spring and 27-28 0/00 during late summer and fall months. Both populations of _A_. _miniata_ were exposed to similar current velocities (7-24 cm s^{-1}) during tidal exchange.

2. _Abundance_ _and_ _Recruitment_ _of_ _Asterina_

Densities of _Asterina_ _miniata_ averaged 2.69 ± 0.59 m^{-2} at Bamfield and 3.46 ± 0.65 m^{-2} at Grappler Inlet. Size-frequency analysis showed a marked difference in the size structure of _A_. _miniata_ populations between Grappler and Bamfield Inlets (Figure 30). Both populations were composed largely of adults at reproductive size with ray-lengths between 7 and 11 cm. Two distinct cohorts of small individuals occurred in Grappler Inlet. In March 1985, age-1 juveniles made up 10.2% of the sample with a mean ray length of 0.9 cm. The intermediate age-2 cohort made up 6.6% of the sample with a mean ray length of 3.1 cm. The age-1 and 2 cohorts increased steadily in size and remained nearly constant in abundance over the 12 month period of study (Table 10). The age-2 cohort merged with the adults in November and December, 1985. Growth rate data suggest that a large settlement occurred in Grappler Inlet during the fall of 1984 and in the summer or fall of 1983

Figure 29. Seasonal surface temperature and salinity measurements from January 1984 to December 1985. A, B. Bamfield Inlet. C, D. Grappler Inlet. Horizontal line indicates annual mean.

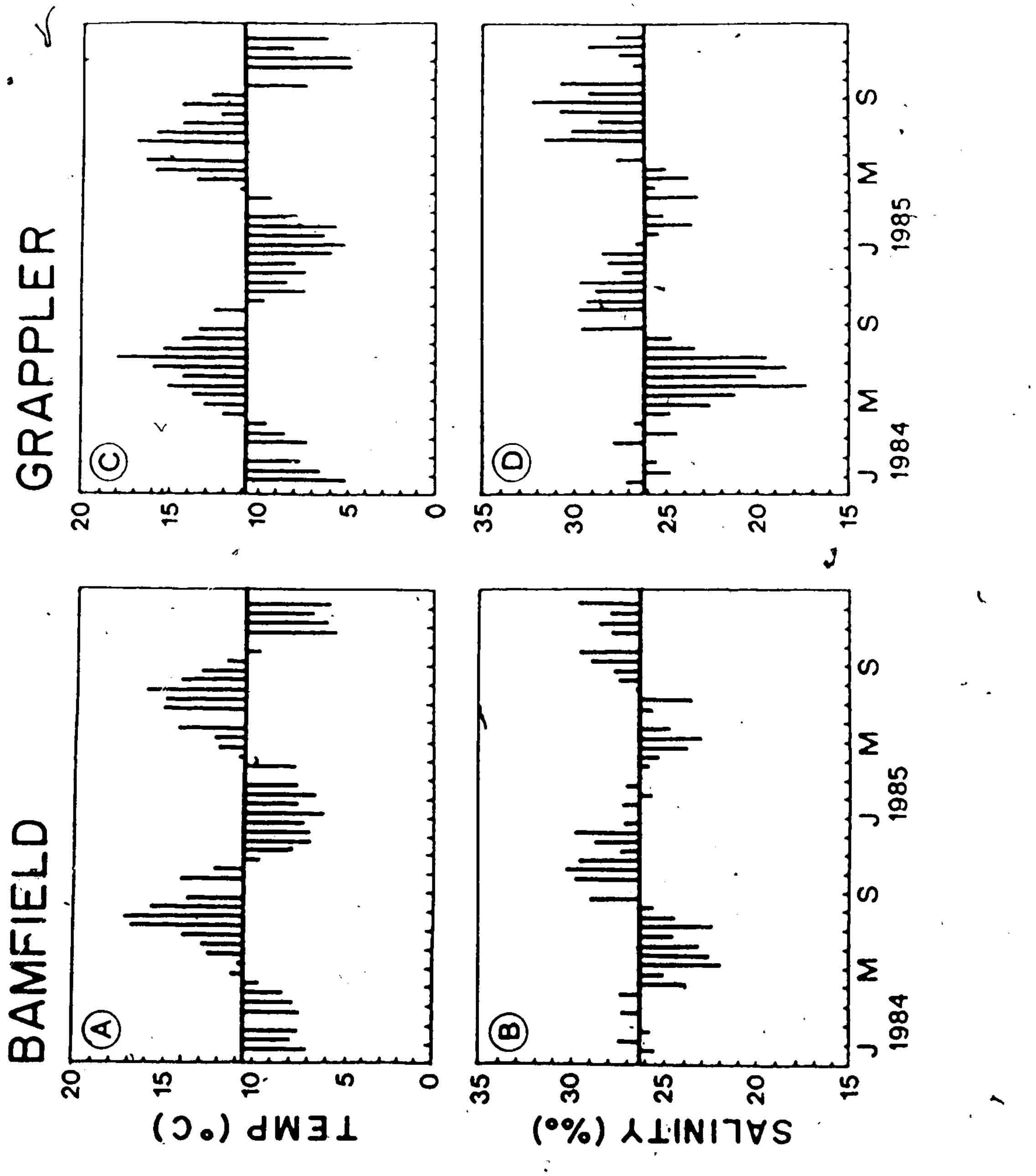

BAMFIELD
GRAPPLER
A
B
C
D
TEMP (°C)
SALINITY (‰)
20
15
10
5
0
35
30
25
20
15
J
M
S
J
M
S
1984
1985

Figure 30. Size-frequency distributions of _Asterina miniata_ from March 1985 to February 1986. Size classes = 0.2 cm. A. Grappler Inlet. B. Bamfield Inlet. Number beneath sample date indicates sample size.

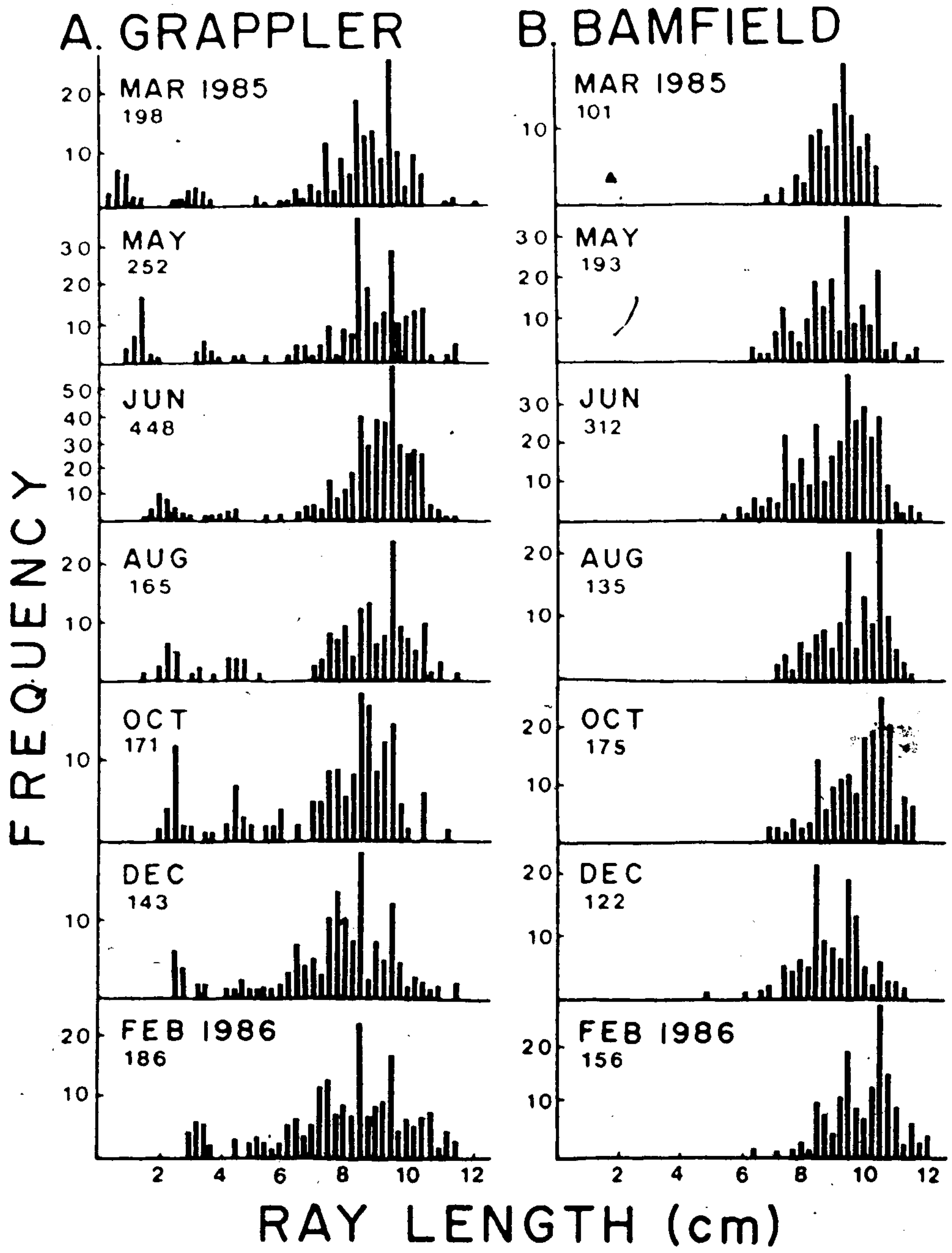

A. GRAPPLER
B. BAMFIELD
MAR 1985
198
101
MAY
252
193
JUN
448
312
AUG
165
135
OCT
171
175
DEC
143
122
FEB 1986
186
156
FREQUENCY
RAY LENGTH (cm)
2
4
6
8
10
12
10
20
30
40
50

TABLE 10

Seasonal estimates of ray length, density and percentage of the monthly population sample for age-1 and age-2 cohorts of <u>Asterina miniata</u> at the Grappler Inlet study site. Table entries show ray length values as means, standard deviations are shown in parentheses.

SAMPLE DATE	AGE-1 COHORT			AGE-2 COHORT		
	RAY LENGTH (cm)	COHORT DENSITY (#/5m2)	PERCENT OF SAMPLE (%)	RAY LENGTH (cm)	COHORT DENSITY (#/5m2)	PERCENT OF SAMPLE (%)
MAR 85	0.87 (0.24)	2.00	10.20	3.10 (0.32)	1.30	6.63
MAY	1.35 (0.24)	1.50	11.90	3.77 (0.52)	0.70	5.55
JUN	2.12 (0.34)	1.65	7.36	4.09 (0.30)	0.55	2.45
AUG	2.34 (0.43)	1.70	10.30	4.43 (0.39)	1.40	8.48
OCT	2.47 (0.32)	2.20	12.85	4.90 (0.70)	1.50	8.77
DEC	2.58 (0.71)	1.40	9.72	4.63 (0.37)	0.60	4.17
FEB 86	2.56 (1.11)	1.00	9.14	4.42 (1.55)	1.00	5.38

(Figure 31). Both cohorts of juveniles were absent from the Bamfield Inlet site.

Substantial proportions of the populations of Asterina miniata from both Grappler and Bamfield Inlets were small adults (Figure 30). Skewed size distributions were particularly evident in the June 1985 samples when the histograms included measurements for over 200 individuals. The abundance of small adults in Grappler and Bamfield Inlets suggests that recruitment may have occurred in the past at both sites.

3. Reproductive Activity of Asterina

The Grappler Inlet population of Asterina miniata showed evidence of a long breeding period (Figure 32). Peak gonad index (G.I.) values occurred in mid summer and early fall, whereas low G.I. values occurred in the late fall and winter. These results indicate that most individuals completed spawning by September and October. Mean G.I. values fluctuated between 5 and 11% of total wet-body-weight, and provide evidence for a distinct seasonal cycle (Figure 32). The G.I. frequency distributions were generally bimodal and indicate the co-occurence of gravid and depleted individuals throughout the period of study. Pyloric caeca indices (P.C.I.) fluctuated seasonally between 9 and 15% with a peak value in February and lowest values in May and July (Figure 32). A significant inverse relationship exists between the G.I. and P.C.I values (Kendall's rank correlation,

Figure 31. Growth of post-larval and juvenile *Asterina miniata*. Values shown are ray lengths for post-larvae immediately after metamorphosis in laboratory cultures (▲), ray lengths of 2 juveniles observed in Grappler Inlet prior to the onset of routine sampling (○), and mean ± S.D. for the age-1 cohort estimated from transect surveys (●).

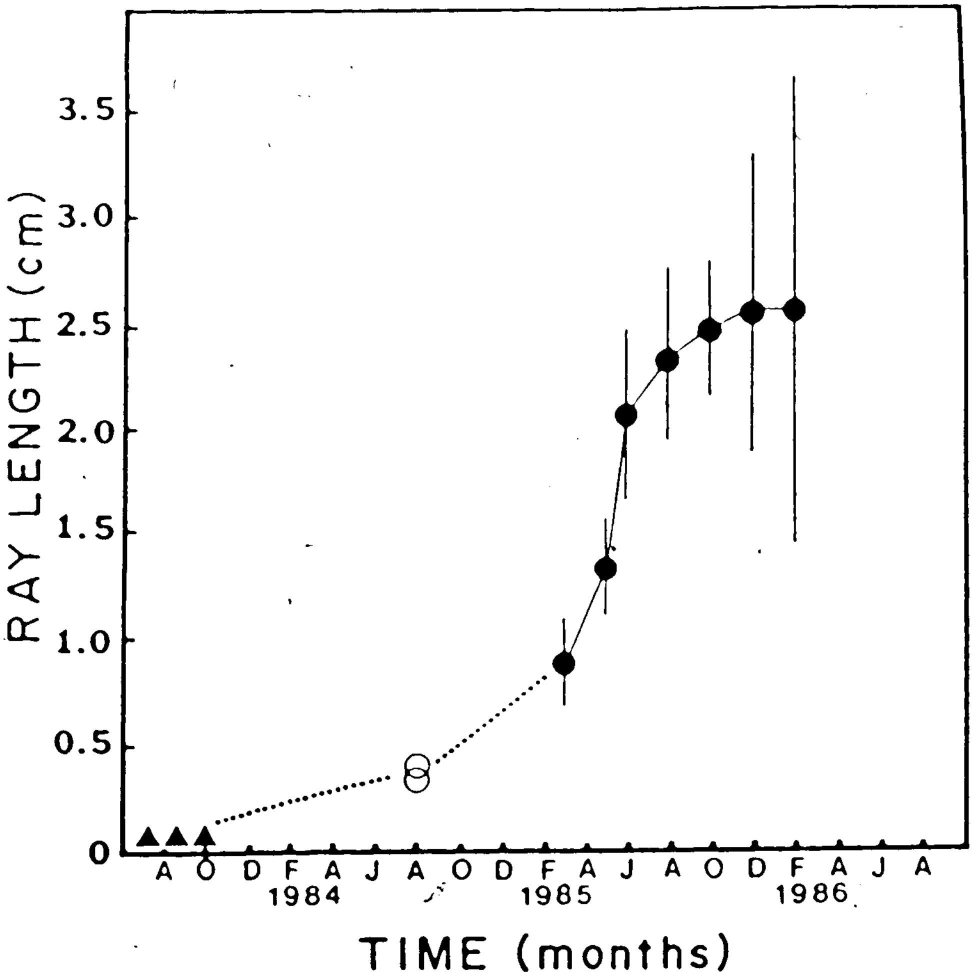
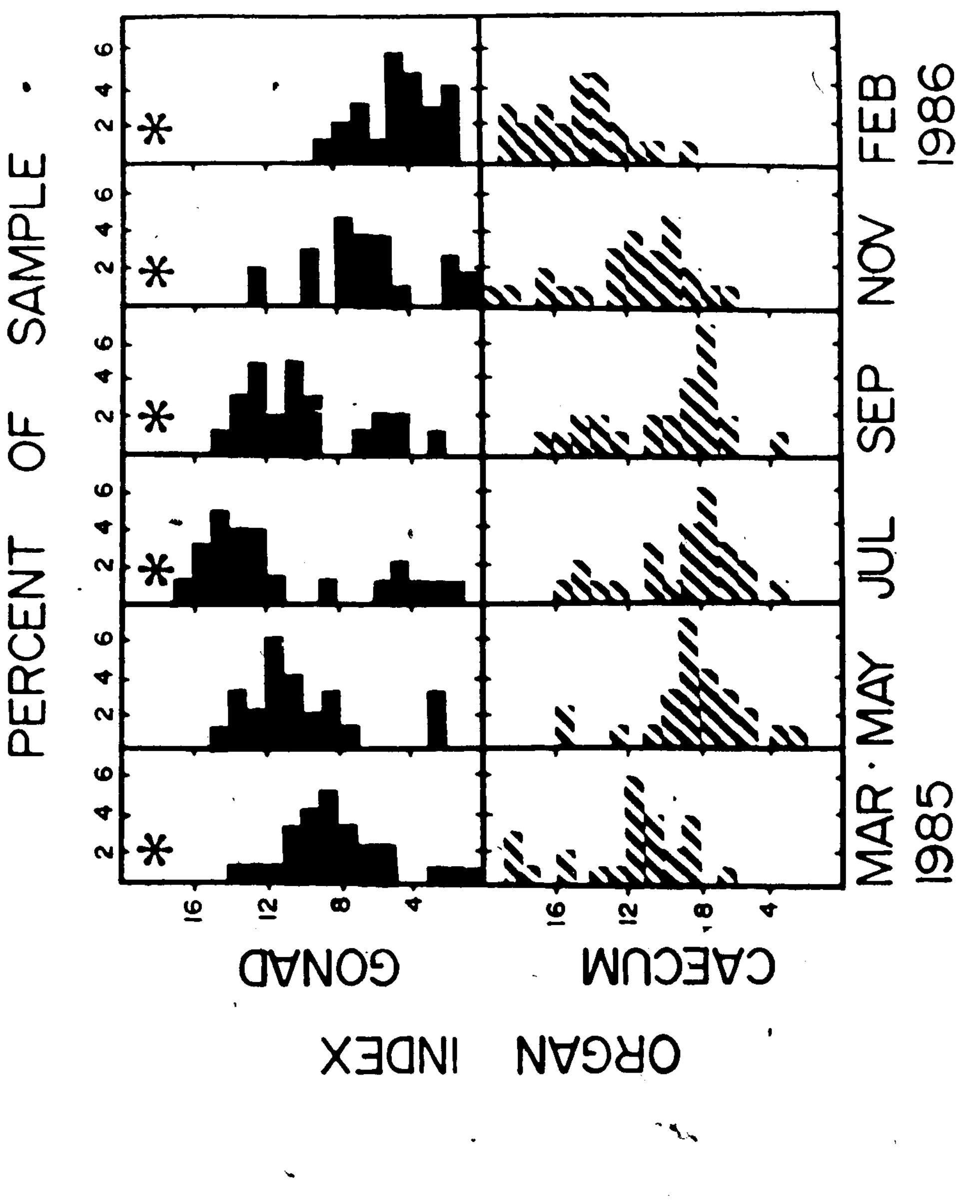

RAY LENGTH (cm)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
A
O
D
F
A
J
A
O
D
F
A
J
A
O
D
F
A
J
A
1984
1985
1986
TIME (months)

Figure 32. Gonad and pyloric caecum indices for *Asterina miniata* from March 1985 to February 1986. Specimens were collected near the Grappler Inlet study site. Histograms show percent of monthly sample; n = 25 individuals per month. Asterisks indicate months when males were observed spawning in the field. The inverse relationship between gonad and pyloric caecum indices is highly significant (Kendall's Rank Correlation, tau = -0.5097, p < 0.001).


PERCENT OF SAMPLE
2
4
6
*
MAR · 1985
MAY
JUL
SEP
NOV
FEB 1986
16
12
8
4
GONAD
CAECUM
ORGAN INDEX

tau = -0.5097, p < 0.001) suggesting that gonadal growth and vitellogenesis occur at the expense of food reserves from the pyloric caecum. Spawning of male A. miniata was observed in the field during all sampling periods except May 1985 (Figure 32).

The planktonic larval period of Asterina miniata is typical for a temperate asteroid with planktotrophic larval development. Fully hydrated ova are 137 ± 6 µm in diameter, and the embryos develop into early feeding bipinnaria larvae after about 4 days (Table 11). Development through the later bipinnaria and settling brachiolaria stages took from 44 to 67 days in cultures maintained between 11 and 19°C. Brachiolariae in substratum selection experiments first completed metamorphosis 79 days after fertilization (Table 11). These observations indicate that metamorphic competence was attained after 8 to 11 wks in the laboratory.

4. Larval Distribution and Abundance

Results from stratified plankton tows show that asteroid bipinnaria and brachiolaria larvae were more abundant in surface waters (0-30 m) than in deeper water (Table 12). The occurrence of bipinnaria and brachiolaria larvae differed significantly between depths (Kruskal-Wallis ANOVA, p < 0.05). Coefficients of variation became larger with increasing depth for both bipinnariae and brachiolariae, indicating that larval abundances were unpredictable at depths of 60 and 90 m. Bipinnariae were

TABLE 11

Schedule of development for *Asterina miniata* embryos and larvae in laboratory cultures maintained at 11 - 15°C. Times shown are minimum times required to reach a specific stage of development. Cultures were initiated following a natural spawning on May 6, 1985.

DATE	TIME	STAGE OF DEVELOPMENT
MAY 6	0	Insemination
	3 min	Fertilization envelope completed
	2 hrs	First cleavage
	5 hrs	Second cleavage
	7 hrs	Third cleavage
MAY 7	18 hrs	Morula
	26 hrs	Blastula
MAY 6	42 hrs	Hatching
	53 hrs	Gastrula I
MAY 9	71 hrs	Gastrula II
MAY 10	90 hrs	Bipinnaria (early)
MAY 11	128 hrs	Bipinnaria (late)
JUN 19	44 days	Brachiolaria (early)
JUL 6	67 days	Brachiolaria (late)
JUL 18	79 days	First larvae undergo metamorphosis
OCT 30	183 days	Last larvae undergo metamprphosis

TABLE 12

Vertical stratification of asteroid larvae in Trevor Channel (sample site P-1, Figure 28b). Values shown are means (± s.d.). All samples were collected August 20, 1985. C.V. columns indicate coefficients of variation.

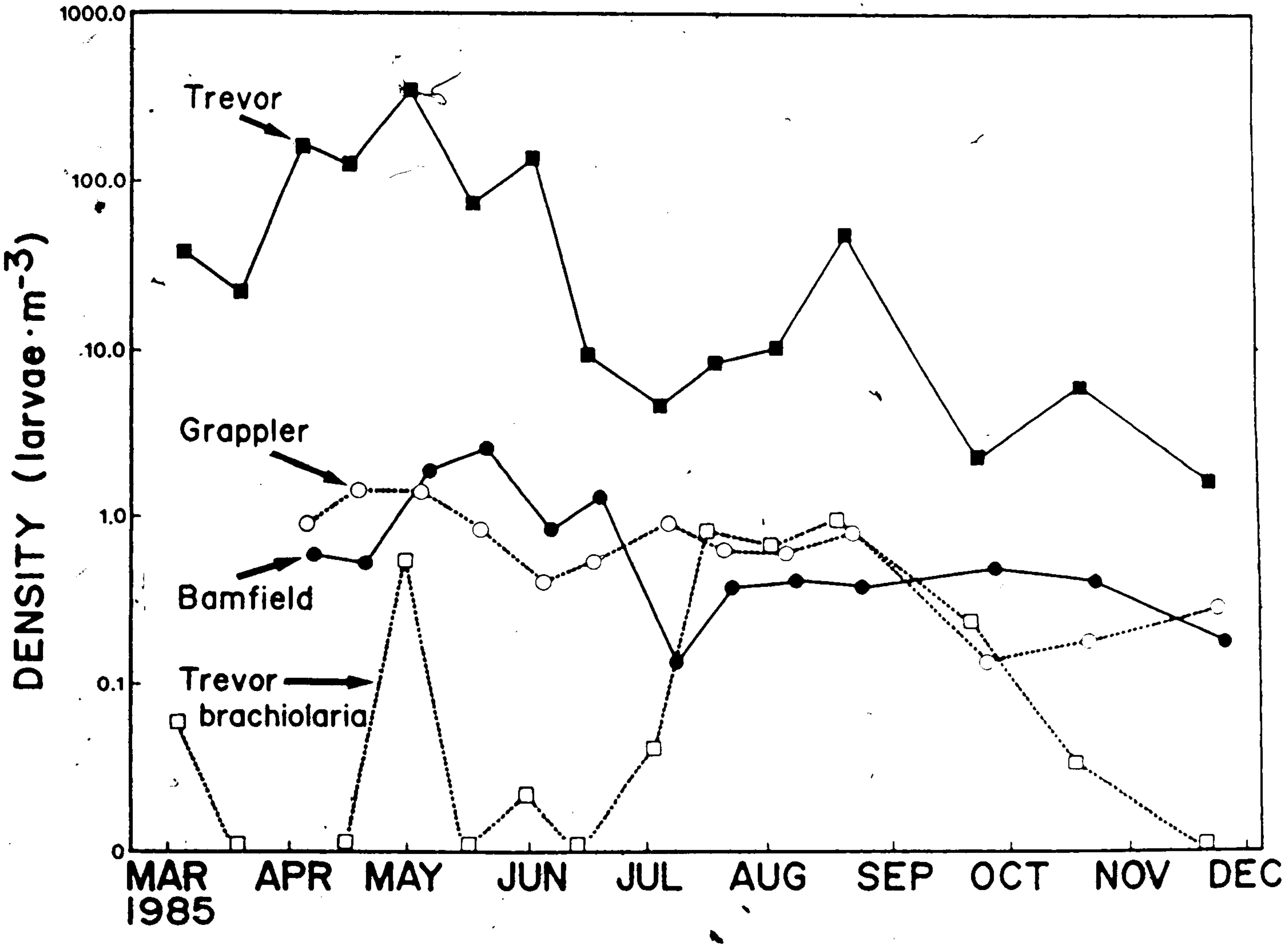
DEPTH STRATUM	# TOWS	SAMPLE VOL. m3	BIPINNARIA #/m3	BIPINNARIA C.V.	BRACHIOLARIA #/m3	BRACHIOLARIA C.V.
0 - 30 m	3	9.47 (1.36)	48.71 (6.97)	0.14	0.91 (0.63)	0.69
30 - 60 m	3	12.90 (2.52)	5.32 (3.89)	0.73	0.04 (0.04)	1.00
60 - 90 m	3	12.37 (1.91)	0.07 (0.12)	1.71	0 (0)	
KRUSKAL-WALLIS ANOVA (H)			7.38		8.27	
p			0.0249		0.0160	

tenfold more abundant than brachiolariae at the 30 and 60 m depths. Few larvae of either stage occurred in samples deeper than 60 m.

Bipinnaria larvae were significantly more abundant in Trevor Channel than in the inlets (Figure 33, Kruskal-Wallis ANOVA, $p < 0.001$). An agreement exists in the seasonal ranking of larval densities between the three sample sites (Kendall's test of concordance, $W = 0.67$, $X^2 = 24.19$, $p < 0.02$). Asteroid bipinnariae were most abundant in the spring and early summer months (Figure 33). In contrast, few brachiolariae were collected in the spring, and they reached their greatest densities during July and August. No brachiolaria larvae occurred in plankton tows collected in Bamfield or Grappler Inlet in 1985. However, two spinulosid brachiolaria larvae were identified from a series of plankton tows collected in Grappler Inlet in June 1986. No larvae were sampled in June 1986 at Bamfield Inlet.

Two lines of evidence suggest that similar numbers of asteroid larvae are transported into Bamfield and Grappler Inlets from Trevor Channel. First, pooled rank counts of bipinnariae showed no significant differences in the numbers of larvae in the inlets during the late summer when larvae are expected to enter the inlets prior to settlement (Jul - Oct, Mann Whitney 2 Sample Test, $Z = 0.8177$; $p = 0.4135$). Second, ranked counts of bipinnariae showed that larvae were equally abundant in Bamfield and Grappler

Figure 33. Seasonal abundance of asteroid larvae at 3 zooplankton sample sites in 1985. Values show density of bipinnaria larvae in Trevor Channel (■), Bamfield Inlet (●) and Grappler Inlet (○). Densities of brachiolaria larvae are shown in Trevor Channel (□). Values are mean larvae·m^{-3}, n = 3 tows per sample date.


DENSITY (larvae·m-3)
1000.0
100.0
10.0
1.0
0.1
0
Trevor
Grappler
Bamfield
Trevor brachiolaria
MAR 1985
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Inlets when densities of larvae were compared over an entire year (Z = 0.1206, p = 0.9039). The supply of planktonic larvae is apparently similar in Bamfield and Grappler Inlets due to a wind-driven advective transport mechanism that moves surface waters into the inlets from Trevor Channel. Consequently, spatial differences in the recruitment of Asterina miniata between Bamfield and Grappler Inlets cannot be attributed to differences in the spatial distribution of larvae.

5. Larval Substratum Selection

Settlement experiments in which larvae were offered a choice of substrata showed that the distribution of metamorphosed Asterina miniata was significantly different from a uniform distribution after incubation periods of 48 hrs ($X^2 = 27.1374$, $p = 0.0074$) and 72 hrs ($X^2 = 45.8608$, $p = 5.6 \times 10^{-5}$; Table 13). In contrast, counts of metamorphosed post-larvae from assays conducted after 24 hrs suggested indiscriminant site selection ($X^2 = 12.8771$, $p = 0.30$). Since metamorphosis of A. miniata brachiolariae requires 36 to 50 hrs to complete, patterns of site selection based on 24 hr counts may be biased in favor of larvae that exhibit low discrimination and complete metamorphosis rapidly.

Although Asterina miniata post-larvae occurred on 6 of 8 substrata, the number of larvae that completed metamorphosis on sediments from Grappler Inlet was significantly greater than that expected for uniform

TABLE 13

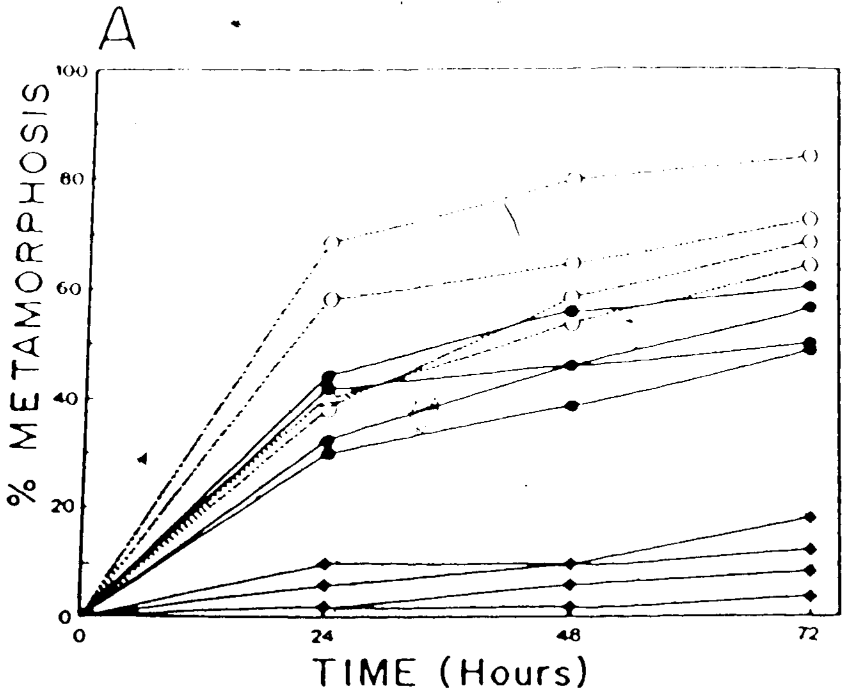
Metamorphosis of *Asterina miniata* in the multiple substratum settlement experiment. Table entries show the mean (± s.d.) number of post-larvae observed on various substrata after incubation periods of 48 and 72 hours. P values show probability levels for Mann-Whitney tests against the number of post-larvae expected for uniform settlement. Brachiolaria larvae were 79 days old at the beginning of the experiments.

SUBSTRATUM	n	NUMBER OF METAMORPHOSED POST-LARVAE			
		48 HRS	p	72 HRS	p
Glass Fragment:					
Clean	3	0.00	0.0468	0.00	0.0468
Aged	3	3.67 (3.21)	0.8802	4.33 (2.08)	0.2682
Shell Fragment:					
Tresus nuttalli	3	3.00 (1.00)	0.2668	3.33 (0.58)	0.0816
Rock Fragment:					
Aged	3	3.67 (2.08)	0.3075	3.33 (1.53)	0.4076
Soft-Sediments:					
Grappler Inlet	3	5.67 (1.15)	0.0160	6.33 (1.15)	0.0153
Rhodophyta:					
Lithothamnion sp.	3	1.00 (1.00)	0.2331	1.33 (0.58)	0.1029
Gracillaria pacifica	3	0.00	0.0468	0.00	0.0468
Chlorophyta:					
Ulva sp.	3	0.00	0.0468	0.33 (0.58)	0.0508
EXPECTED VALUE FOR UNIFORM SETTLEMENT		2.13		2.38	

settlement (Table 13). In contrast, the numbers of post-larvae on Ulva sp., Gracillaria pacifica and clean glass were significantly less than expected. These results indicate that A. miniata brachiolariae settle and complete metamorphosis non-selectively on substrata that are covered with a surface film, and that sediments offer a preferred site for metamorphosis.

Settlement experiments in which larvae were offered only a single substratum showed greater metamorphosis in treatments containing sediments collected from Bamfield and Grappler Inlets compared with treatments containing sediments from outside the inlets (Figure 34ab, $X^2 = 19.27$, $p < 0.001$; and Table 14). The number of Asterina miniata post-larvae in treatments containing sediment from Grappler Inlet was greater than that in treatments containing sediment from Bamfield Inlet (Figure 34), and sediment from Grappler Inlet appeared to be more attractive to settling larvae than sediment from Bamfield Inlet. However, the difference was only marginally significant (p values from 0.041 to 0.059, Table 14). To reduce the possibility of a Type II error (viz. erroneous acceptance of the null hypothesis that the substrata from Bamfield and Grappler Inlets did not differ as a cue for metamorphosis), the results of substratum selection experiments 1 and 2 were combined (Sokal and Rohlf, 1981). Substratum selection differed significantly when the results from Mann-Whitney U-tests were analyzed together

Figure 34. Metamorphosis of Asterina miniata in single substratum experiments. A. 84 day old larvae, 50 larvae·trial^{-1}. B. 91 day old larvae, 20 larvae·trial^{-1}. Values show % metamorphosis in treatments containing sediments collected from Grappler Inlet (○), Bamfield Inlet (●) and Aguilar Point (◆).


A
% METAMORPHOSIS
0
20
40
60
80
100
TIME (Hours)
0
24
48
72

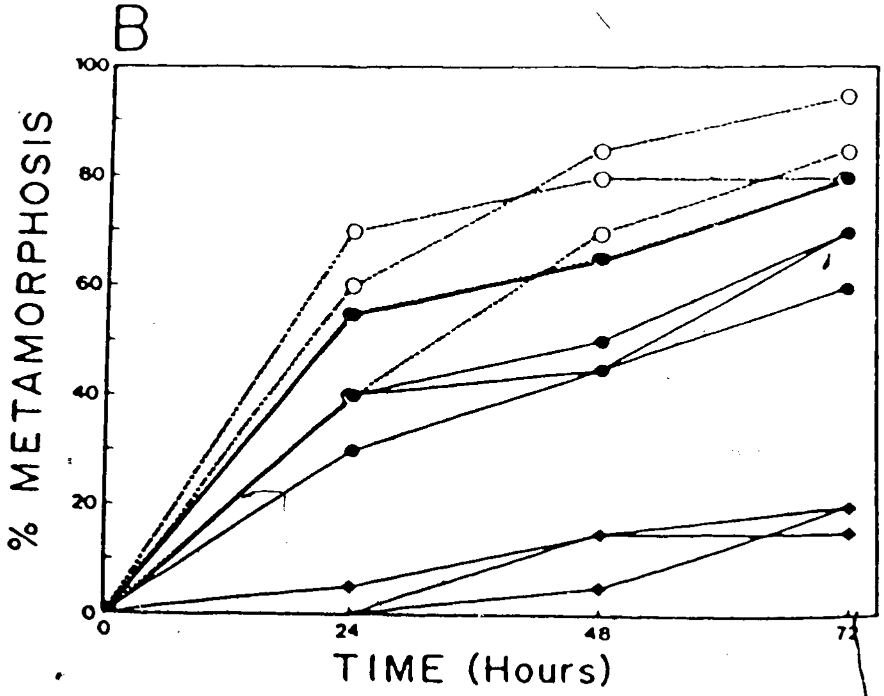

B
% METAMORPHOSIS
0
20
40
60
80
100
TIME (Hours)
0
24
48
72

TABLE 14

Metamorphosis of *Asterina miniata* in single substratum experiments. Values show Mann-Whitney U-test statistics and probability levels in two sample comparisons of the number of post-larvae observed on Bamfield and Grappler Inlet sediments. The results of Mann-Whitney U-tests are also shown for a comparison of the number of *A. miniata* post-larvae observed on sediments collected from the Inlets (pooled data) and sediments collected outside the Inlets (see Figure 28b). Combined test column indicates chi-square values and probability levels obtained by combining probabilities from Mann-Whitney U-tests.

TIME OF COMPARISON		SETTLEMENT EXPERIMENT #1	SETTLEMENT EXPERIMENT #2	COMBINED TEST #1 AND #2
BAMFIELD VS. GRAPPLER INLET SEDIMENTS:				
24 HOURS	U	1.0104	1.4884	Chi Sqr = 6.3075
	p	0.3123	0.1367	p < 0.5000
48 HOURS	U	1.8877	2.0452	Chi Sqr = 12.0552
	p	0.0591	0.0408	p < 0.0250
72 HOURS	U	1.9349	1.9349	Chi Sqr = 11.7498
	p	0.0530	0.0530	p < 0.0250
INLET SEDIMENTS VS. OUTSIDE SEDIMENTS:				
48 HOURS	U	2.6325	2.6654	Chi Sqr = 19.2684
	p	0.0085	0.0077	p < 0.0010

after 48 hrs (Table 14, $X^2 = 12.05$, $p < 0.025$) and 72 hrs ($X^2 = 11.75$, $p < 0.025$). Taken collectively, these results indicate that sediments from Grappler Inlet are more attractive as sites for settlement and metamorphosis of A. miniata brachiolariae than sediments from Bamfield Inlet.

Results from a final set of settlement experiments showed that aged-sediments induced significantly greater numbers of Asterina miniata to complete metamorphosis compared with fresh-sediments (Mann-Whitney test, $p < 0.05$; Table 15). Post-larvae were 2 - 4 times more abundant in the aged-sediment treatments than in treatments containing fresh-sediments. Presumably, aged sediments developed a surface film associated with bacteria and other microorganisms, although they were not examined specifically for bacteria. These results provide further evidence that the substratum selection response of A. miniata brachiolariae is independent of microtopographical features of the substratum including sediment grain size and texture.

6. Predation upon Larvae by Benthic Suspension Feeders

Transect surveys conducted in June 1985 showed marked differences in the abundance of benthic suspension feeders between Bamfield and Grappler Inlets (Table 16). The solitary phelebobranch ascidian, Corella willmeriana, averaged 254 individuals m^{-2} in Bamfield Inlet, but individuals were nearly absent in Grappler Inlet.

TABLE 15

Metamorphosis of *Asterina miniata* in the sediment aging experiment. Table entries show the number of *A. miniata* post-larvae on fresh and aged sediments collected outside the inlets at Aguilar Point (see Figure 28b). Values shown are means (± s.d.). The results from Mann-Whitney U-tests are also shown along with their associated probability levels.

AGUILAR POINT SEDIMENT TREATMENTS	n	INCUBATION PERIOD (Hours)		
		24	48	72
FRESH:	4	1.25 (0.50)	2.75 (1.26)	4.00 (0.82)
AGED: 9 days in running seawater	4	5.00 (1.54)	6.50 (1.73)	8.75 (2.36)
CONTROL: no sediment	4	0.00	0.25 (0.50)	0.75 (0.96)
MANN-WHITNEY U-TEST: FRESH VS. AGED SEDIMENTS				
U		2.2468	2.0578	2.1913
p		0.0247	0.0396	0.0284

TABLE 16

Densities of benthic suspension feeders in Bamfield and Grappler Inlets. Benthic transects were surveyed in June, 1985. Table entries show the mean number of individuals or colonies per square meter. Standard deviations are shown in parentheses. IND = individual; COL = Colony; PRESENT = Species present but did not occur along benthic transect line.

SPECIES	UNITS	BAMFIELD INLET		GRAPPLER INLET	
		mean	(s.d.)	mean	(s.d.)
Corella willmeriana	IND	253.8	(158.7)	0.3	(1.5)
Pachycerianthus fimbriatus	IND	6.7	(3.5)	13.2	(4.3)
Protothaca staminea	IND	2.9	(6.3)	1.3	(3.8)
Tubularia crocea	COL	0.9	(1.7)	0.4	(1.2)
Polyorchis penicillatus	IND	0.8	(2.2)	0.1	(0.7)
Metridium senile	IND	0.4	(1.2)	0.3	(1.0)
Tresus nuttalli	IND	0.1	(0.7)	0.5	(1.4)
Bugula pacifica	COL	0.1	(0.7)	0.4	(1.2)
Obelia frondosa	COL	PRESENT		0.3	(1.0)
Ptilosarcus gurneyi	IND	0.1	(0.7)		
Phoronis vancouveriensis	COL			0.1	(0.7)
Saxidomus galli	IND	PRESENT		PRESENT	

Conversely, individuals of the tube-dwelling cerianthid anemone, Pachycerianthus fimbriatus, were significantly more abundant in Grappler Inlet than in Bamfield Inlet (Mann-Whitney 2 sample test, $Z = 2.85$, $p = 0.0050$). Individuals of C. willmeriana exhibited a dramatic seasonal cycle of abundance in Bamfield Inlet (Figure 35a; $p < 0.001$) where high densities occurred during the summer months from June through October. In contrast, there were no seasonal differences in the abundance of P. fimbriatus in either Bamfield Inlet (Figure 35b; Kruskal-Wallis ANOVA; $p = 0.69$) or Grappler Inlet ($p = 0.17$). With the exception of the bivalve, Protothaca staminea, densities of other suspension feeders were low in both Inlets (Table 16). The hydromedusan, Polyorchis penicillatus, and the anthozoan, Metridium senile, were included in the survey because these cnidarians are capable of microphagous predation upon demersal zooplankton (Purcell, 1977; Arkett, 1984; Sebens and Koehl, 1984). These results suggest that the heterogeneous distribution of benthic suspension feeders may be one factor determining differential recruitment of Asterina miniata between Bamfield and Grappler Inlets.

a. Analysis of Gut Contents

Analysis of gut contents showed that a large proportion of the prey items of both Corella willmeriana and Pachycerianthus fimbriatus fall between 75 and 250 µm in length (Figure 36). Prey items greater than 375 µm are seldom ingested by C. willmeriana, but a few prey items

Figure 35. Seasonal densities of benthic suspension feeders in Bamfield (□) and Grappler (■) Inlets in 1985.
A. <u>Corella</u> <u>willmeriana</u>. Values in parentheses show density in Grappler Inlet in June and August. <u>C</u>. <u>willmeriana</u> were absent during all other sample periods.
B. <u>Pachycerianthus</u> <u>fimbriatus</u>. Histograms show mean, error bars indicate ± S.D.

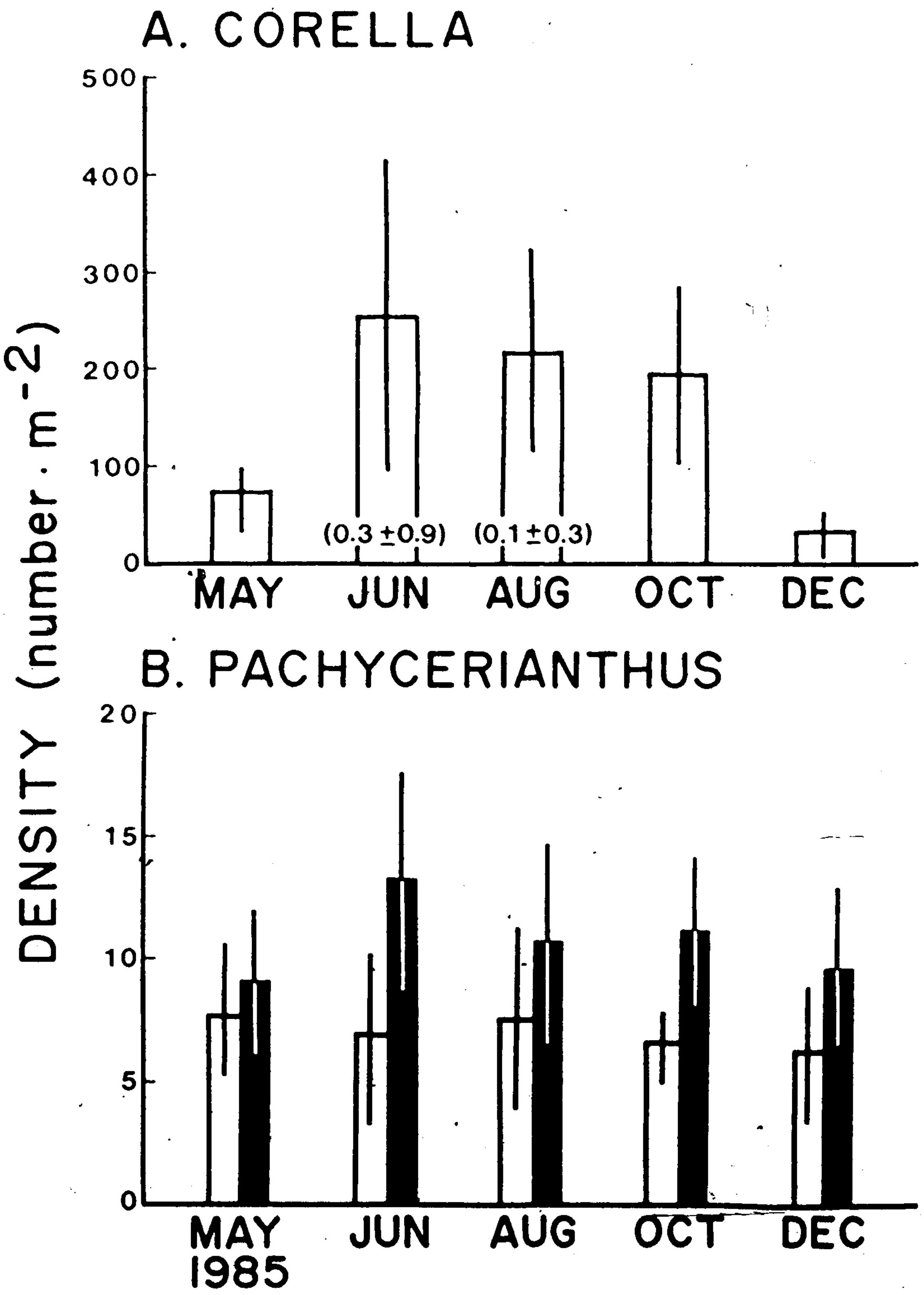
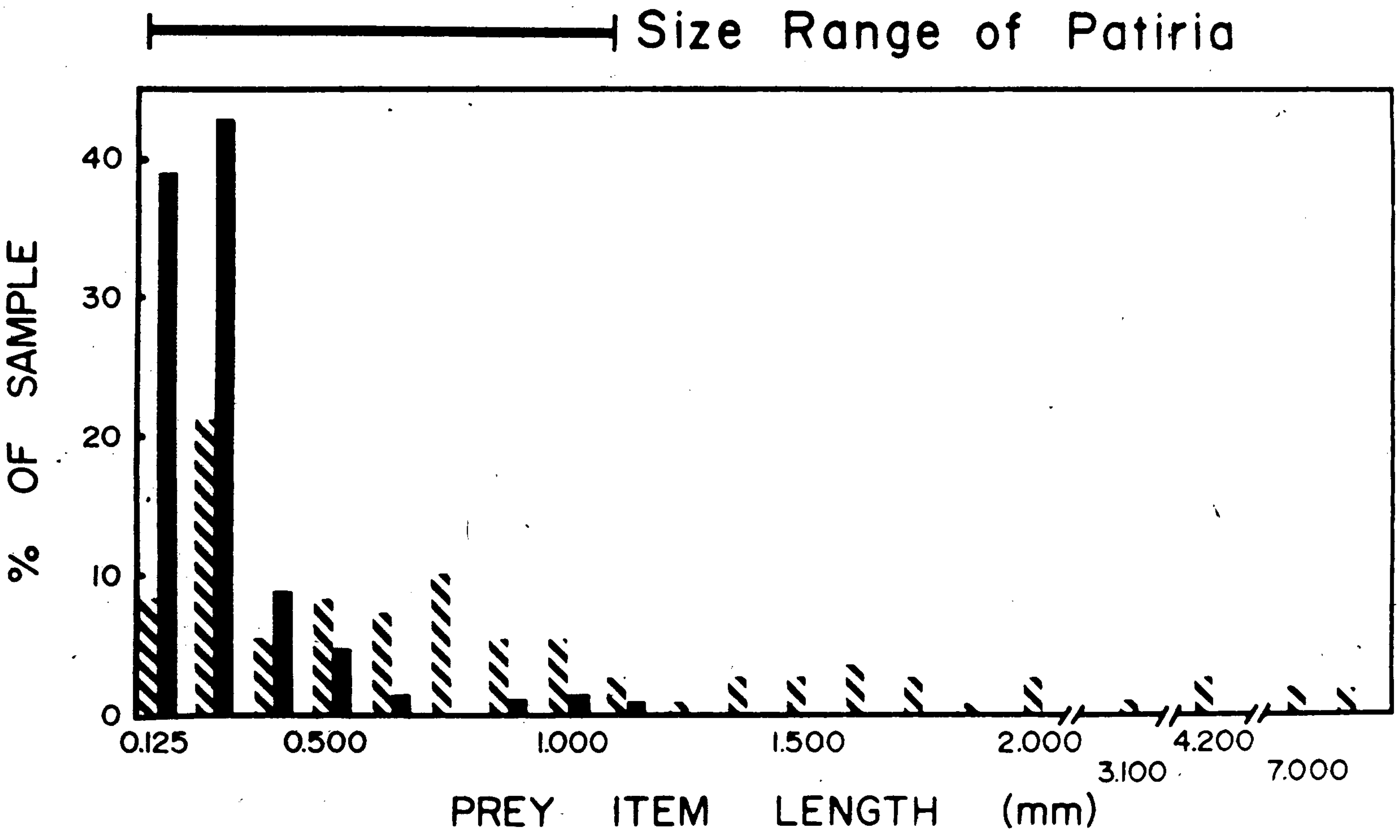

A. CORELLA
DENSITY (number · m⁻²)
500
400
300
200
100
0
(0.3 ±0.9)
(0.1 ±0.3)
MAY
JUN
AUG
OCT
DEC
B. PACHYCERIANTHUS
20
15
10
5
0
MAY
1985
JUN
AUG
OCT
DEC

Figure 36. Size distribution of prey items recovered from gut contents of *Corella willmeriana* (■, 27 individuals, n = 312 prey items) and *Pachycerianthus fimbriatus* (▨, 17 individuals, n = 109 prey items). Figure also shows overlapping size range of *Asterina miniata* embryos and larvae (see Table 9).


Size Range of Patiria
% OF SAMPLE
40
30
20
10
0
0.125
0.500
1.000
1.500
2.000
3.100
4.200
7.000
PREY ITEM LENGTH (mm)

with lengths up to 1 mm were recovered. Most prey items recovered from the gastrovascular cavity of P. fimbriatus fall between 125 µm and 2 mm in length. The majority of small prey items were diatoms, invertebrate embryos and nauplii; the larger prey items included copepods, barnacle cyprids and small polychaetes. The size range of Asterina miniata embryos and larvae overlaps with the range of prey items consumed by P. fimbriatus and C. willmeriana (see Table 9, Figure 36). Consequently, it was inferred that natural populations of these suspension feeders were capable of capturing settling A. miniata larvae in the field.

b. Laboratory Predation Experiments

Differences in the susceptibility of Asterina miniata embryos and larvae to predation were highly significant in feeding experiments conducted with Pachycerianthus fimbriatus (Figure 37, Kruskal Wallis ANOVA, $H = 19.93$, $p = 0.0013$) and Corella willmeriana ($H = 29.95$, $p < 0.001$). The percentage of early prey stages captured by P. fimbriatus (pooled mean = 16.5%) was significantly less than capture frequencies for A. miniata gastrulae (29%) and brachiolariae (30%; Student-Newman-Keuls tests, Table 17, Figure 37a). Low capture frequencies observed for bipinnariae (19%) were inconsistent with the trend toward increased susceptibility of late-stage larvae. An opposite trend, toward decreased susceptibility during development, was evident during feeding experiments conducted with

Figure 37. Mortality of various developmental stages of *Asterina miniata* during single-stage feeding experiments with benthic suspension feeders. A. Predation by *Pachycerianthus fimbriatus*. B. Predation by *Corella willmeriana*. Values shown are means, error bars indicate ± S.D. Numbers above error bars indicate sample sizes. Solid bars show capture frequencies in predator treatments; open bars indicate loss of prey in controls. The developmental stages of *A. miniata* are described in Table 9.

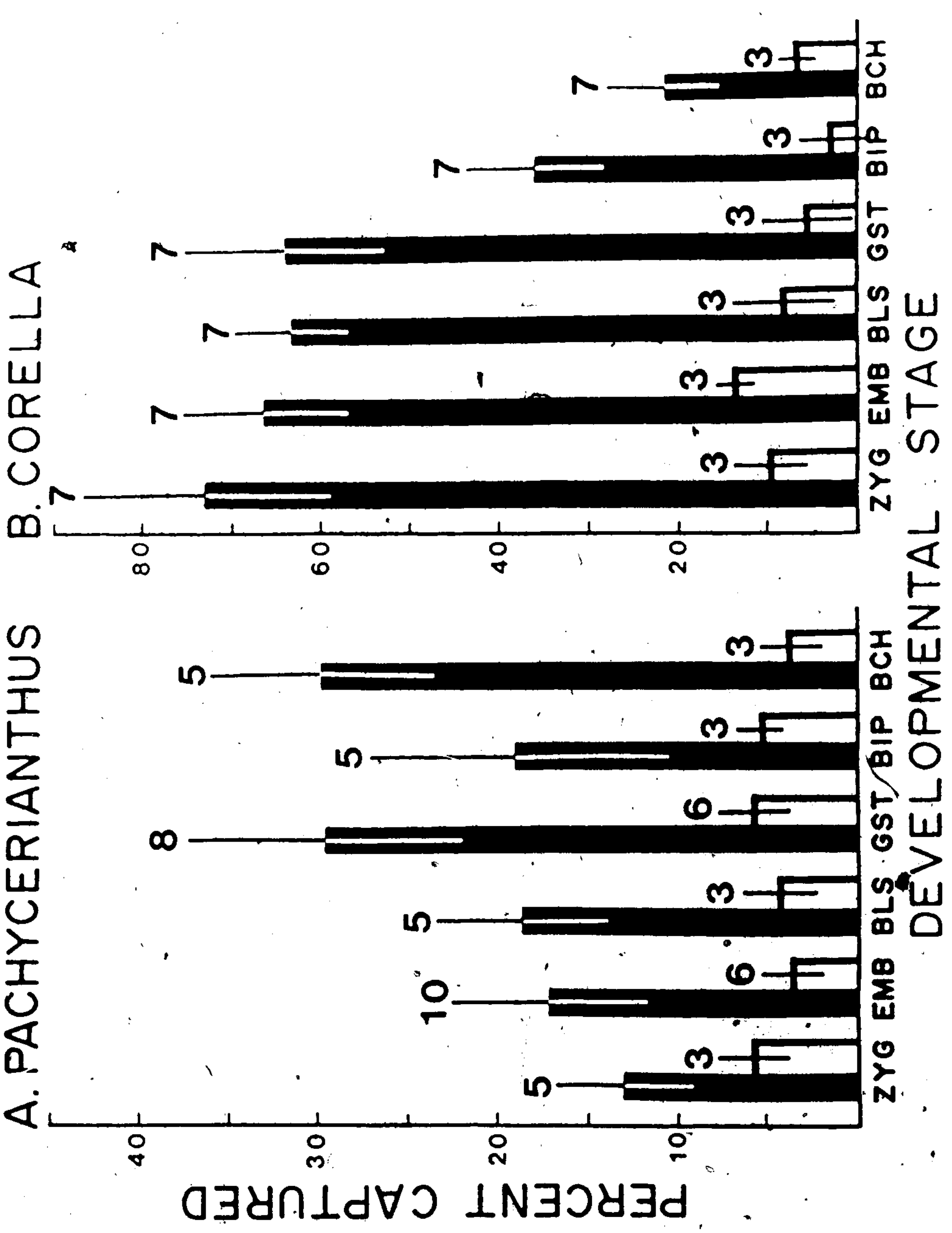

A. PACHYCERIANTHUS
B. CORELLA
PERCENT CAPTURED
DEVELOPMENTAL STAGE
10
20
30
40
20
40
60
80
ZYG
EMB
BLS
GST
BIP
BCH
ZYG
EMB
BLS
GST
BIP
BCH
5
3
10
6
5
3
8
6
5
3
5
3
7
3
7
3
7
3
7
3
7
3
7
3

TABLE 17

Summary of Student-Newman-Keuls tests of differences in capture frequencies between developmental stages of <u>Asterina miniata</u>. Upper-right region of table shows the significance levels of SNK tests for predation experiments conducted with <u>Pachycerianthus fimbriatus</u>. Lower-left region of table shows the significance levels of SNK tests for predation experiments conducted with <u>Corella willmeriana</u>.

		Pachycerianthus: DEVELOPMENT STAGE					
Corella:		ZYG	EMB	BLS	GST	BIP	BCH
DEVELOPMENT STAGE	ZYG		n.s.	n.s.	0.01	n.s.	0.05
	EMB	n.s.		n.s.	0.01	n.s.	0.05
	BLS	n.s.	n.s.		0.05	n.s.	n.s.
	GST	n.s.	n.s.	n.s.		0.05	n.s.
	BIP	0.01	0.01	0.01	0.01		n.s.
	BCH	0.01	0.01	0.01	0.01	0.05	

C. willmeriana (Figure 37b). Capture frequencies for embryonic and early larval stages (pooled mean = 67%) were significantly greater than for late-stage larvae such as bipinnariae (36%) and brachiolariae (22%, see Table 17). Losses of larvae were low in all control treatments and indicated significant predation effects for all developmental stages of *A. miniata*. Overall capture frequencies (all developmental stages) averaged 21 ± 9% (n = 38) for *P. fimbriatus* compared with a pooled mean of 54 ± 21% (n = 42) for *C. willmeriana*.

There were significant density effects in the predation rates of *Corella willmeriana* and *Pachycerianthus fimbriatus* (Figure 38, Table 18, ANOVA, $p < 0.001$). Stage-specific differences in the susceptibility of *Asterina miniata* embryos and larvae (Figure 37) were also evident in the shapes of functional response curves (Figure 38). In *C. willmeriana*, the slope of the functional response curve for non-motile embryos was significantly greater than the slope for swimming bipinnaria larvae ($t = 3.46$; $p < 0.01$), indicating higher rates of predation upon embryos compared with bipinnaria larvae. The functional response curve for *C. willmeriana* shows evidence of saturation (Holling, 1966; Type II) for embryos and larvae at initial prey densities between 100 and 200 prey liter^{-1} (Figure 38a). In contrast, the functional response curves for *P. fimbriatus* were linear (embryos: Holling Type I, Figure 38b) or showed evidence of the early region of a sigmoidal curve

Figure 38. Partial functional responses of suspension feeders to differences in the density of *Asterina miniata* prey stages. A. Predation by *Corella willmeriana*. B. Predation by *Pachycerianthus fimbriatus*. Values show the results of predation experiments (n=3 trials per initial prey density) upon *A. miniata* embryos (○) and bipinnariae (●). Solid lines show least squares regression fit to functional response data for embryos (*C. willmeriana*, $r^2 = 0.7986$; *P. fimbriatus*, $r^2 = 0.9384$) and bipinnaria larvae (*C. willmeriana*, $r^2 = 0.7556$; *P. fimbriatus*, $r^2 = 0.9369$)

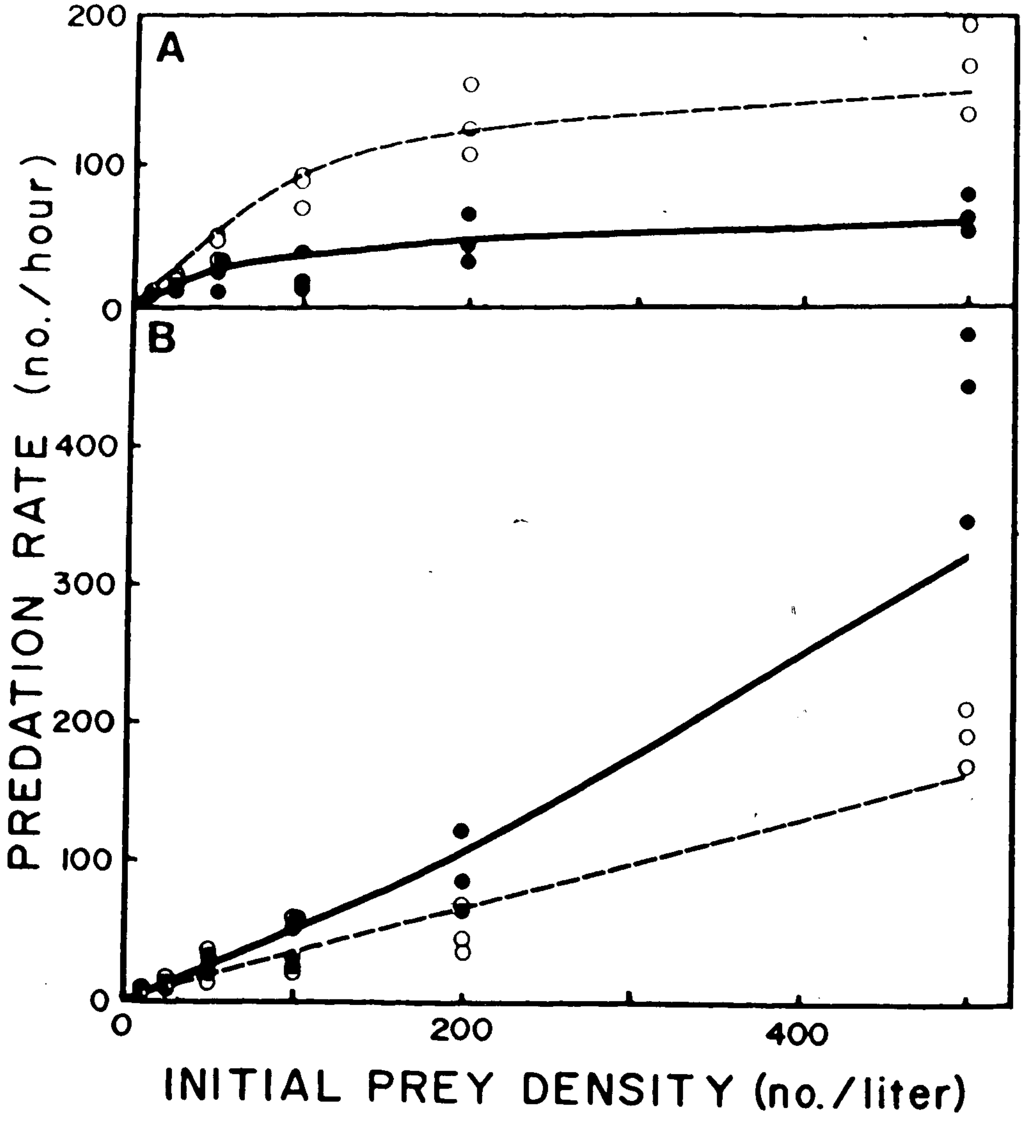

A
B
200
100
0
400
300
200
100
0
0
200
400
PREDATION RATE (no./hour)
INITIAL PREY DENSITY (no./liter)

TABLE 18

Results of single-factor ANOVA tests of the effects of prey density on predation rates upon *Asterina* embryos and larvae by *Corella* and *Pachycerianthus* during functional response feeding experiments.

PREDATOR SPECIES	PREY STAGE	SOURCE	SS	DF	MS	F-RATIO	p
Corella:							
	EMBRYOS						
		Density	61615.11	5	12323.02	44.93	p<0.001
		Error	3291.33	12	274.28		
	BIPINNARIAE						
		Density	7159.78	5	1431.96	11.05	p<0.001
		Error	1555.33	12	129.61		
Pachycerianthus:	EMBRYOS						
		Density	73516.28	5	14703.26	69.32	p<0.001
		Error	2545.33	12	212.11		
	BIPINNARIAE						
		Density	391611.6	5	78322.32	78.12	p<0.001
		Error	12030.67	12	1002.56		

(bipinnariae: Holling Type III). The slope of the predation rate curve for swimming bipinnaria larvae was significantly greater than the predation rate curve for embryos ($t = 12.38$; $p < 0.001$).

Differences in the efficiency of filtration by *Corella willmeriana* and *Pachycerianthus fimbriatus* were substantial during feeding experiments conducted with different developmental stages of *Asterina miniata* (Table 19). For example, *C. willmeriana* captured 92% of the embryos and 87% of the bipinnariae that entered the parabolic volume of seawater immediately upstream from the incurrent siphon. In contrast, *P. fimbriatus* captured only 7% of the embryos and 11% of the bipinnariae that passed through the crown of tentacles. These results are consistent with differences in embryo and larval susceptibility observed during feeding experiments (Figures 37 and 38). Taken collectively, laboratory experiments suggest that the feeding activities of *C. willmeriana* and *P. fimbriatus* may have different qualitative and quantitative effects on populations of settling *A. miniata* larvae.

Stage-specific differences in predation rates (Figures 37 and 38) reflect not only differences in the susceptibility of *Asterina miniata* embryos and larvae but also differences in the modes of feeding utilized by *Corella willmeriana* and *Pachycerianthus fimbriatus* to capture prey. Saturation characteristics illustrated by the functional response curve in *C. willmeriana* (Figure 38a)

TABLE 19

Filtration efficiencies of *Corella* and *Pachycerianthus* during flow tank feeding experiments. Encounter value indicates number of *Asterina* embryos or bipinnaria larvae whose streamline passed within the feeding current paraboloid of *Corella* or tentacle sphere of *Pachycerianthus*. Flume velocity = 4.9 mm/s.

PREDATOR SPECIES	PREY STAGE	# PREY ENCOUNTERED	# PREY CAPTURED	FILTRATION EFFICIENCY
Corella willmeriana	EMB	147	136	92.52 %
	BIP	71	62	87.32 %
Pachycerianthus fimbriatus	EMB	86	5	6.81 %
	BIP	55	6	10.91 %

appear to be related to a density-dependent decrease in the filtration efficiency of the branchial basket. After *A. miniata* embryos or larvae pass through the incurrent siphon, they become trapped in mucus and accumulate against the wall of the branchial basket where they interfere with the passage of currents through the stigmata (Figure 39). In contrast, *P. fimbriatus* captures *A. miniata* larvae with nematocysts and mucus located along the marginal tentacles (Figure 40). The tentacles of *P. fimbriatus* exhibited a characteristic feeding response (withdrawal toward the labial tentacles) after they were contacted by swimming *A. miniata* larvae. Microscopic examinations of several *A. miniata* bipinnariae recovered at the end of feeding experiments revealed the presence of stenotele nematocysts embedded in the larval epidermis (Figure 40c). Since the fate of these larvae was not followed, the long-term effects of tentacle contact and nematocyst penetration are unknown.

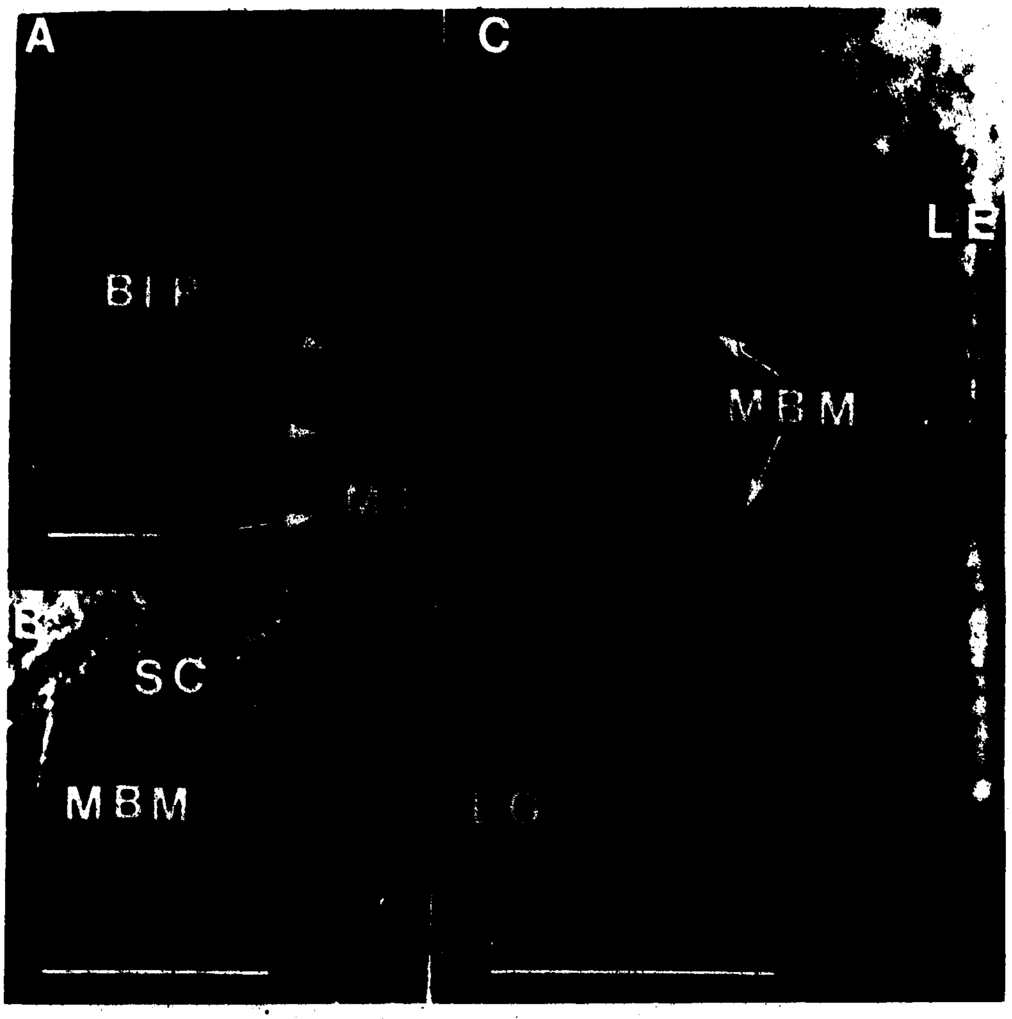
c. *Predator Encounter Rates*

The relative importance of predation upon settling *Asterina miniata* larvae was compared between Bamfield and Grappler Inlets with a random walk model (Roberts, 1975). The aerosol filtration equations used in the model were originally developed by Pich (1966), and later adapted for benthic suspension feeding invertebrates by Rubenstein and Koehl (1977) and LaBarbara (1984). The dimensionless ratio (N_{mf}) that expresses the frequency of particle capture by

Figure 39. Transverse paraffin section through the branchial basket of Corella willmeriana. The specimen was fixed after the termination of a functional response feeding experiment. The section shows several Asterina miniata ova (O) retained within the branchial basket (BB). Arrows indicate the direction of water flow during feeding. S = stigmata, AT = atrium, TU = tunic. Scale bar = 200 µm.


TU
S
BB
AT
S

Figure 40. Capture of *Asterina miniata* bipinnariae by marginal tentacles of *Pachycerianthus fimbriatus*. A. Bipinnaria larvae affixed by nematocysts and mucus to a marginal tentacle. Arrows indicate points of contact between larval epidermis and tentacle. B. Undischarged nematocysts within a marginal tentacle. C. Discharged nematocysts embedded in the epidermis of a *A. miniata* bipinnaria larva. Arrows indicate discharged nematocysts. BIP = *A. miniata* bipinnaria, MT = *P. fimbriatus* marginal tentacle, SC = spirocyst, MBM = microbasic-b-mastigophore, LG = larval gut, LE = larval epidermis. Scale bars = 100 µm.


A
BIF
B
SC
MBM
C
LE
MBM
LG

a filament such as the marginal tentacle of *Pachycerianthus fimbriatus* due to the motion of a *P. miniata* larva out of a streamline is

$$N_{mf} = D/V_o d_f \qquad (1)$$

where $D = KT/3 \Pi u dp$ (2)

(see Table 20 for definitions of symbols)

A diffusion coefficient with an external bias (Patlak, 1953; Roberts, 1975) was estimated for a planktotrophic brachiolaria (*Pisaster ochraceus*) by measuring the displacement amplitude of the larva away from a streamline over a period of 10 s. The diffusion coefficient has a value of D = 6.41 + 3.59 X 10^{-7} m^3 s^{-1}. Substitution of D into Equation 1 shows that a decrease in ambient current velocity from 0.28 to 0.01 ms^{-1} results in an increase in the time during which larval swimming takes place within the vicinity of *Pachycerianthus fimbriatus* tentacles, resulting in an exponential increase in the probability of contact and capture (Figure 41a). The increase in encounters with tentacles due to the swimming behavior of larvae only becomes important at velocities below 0.03 m s^{-1}. The model predicts similar results for the frequency of capture by a pore (Nmp) such as the incurrent siphon of *Corella willmeriana*, where

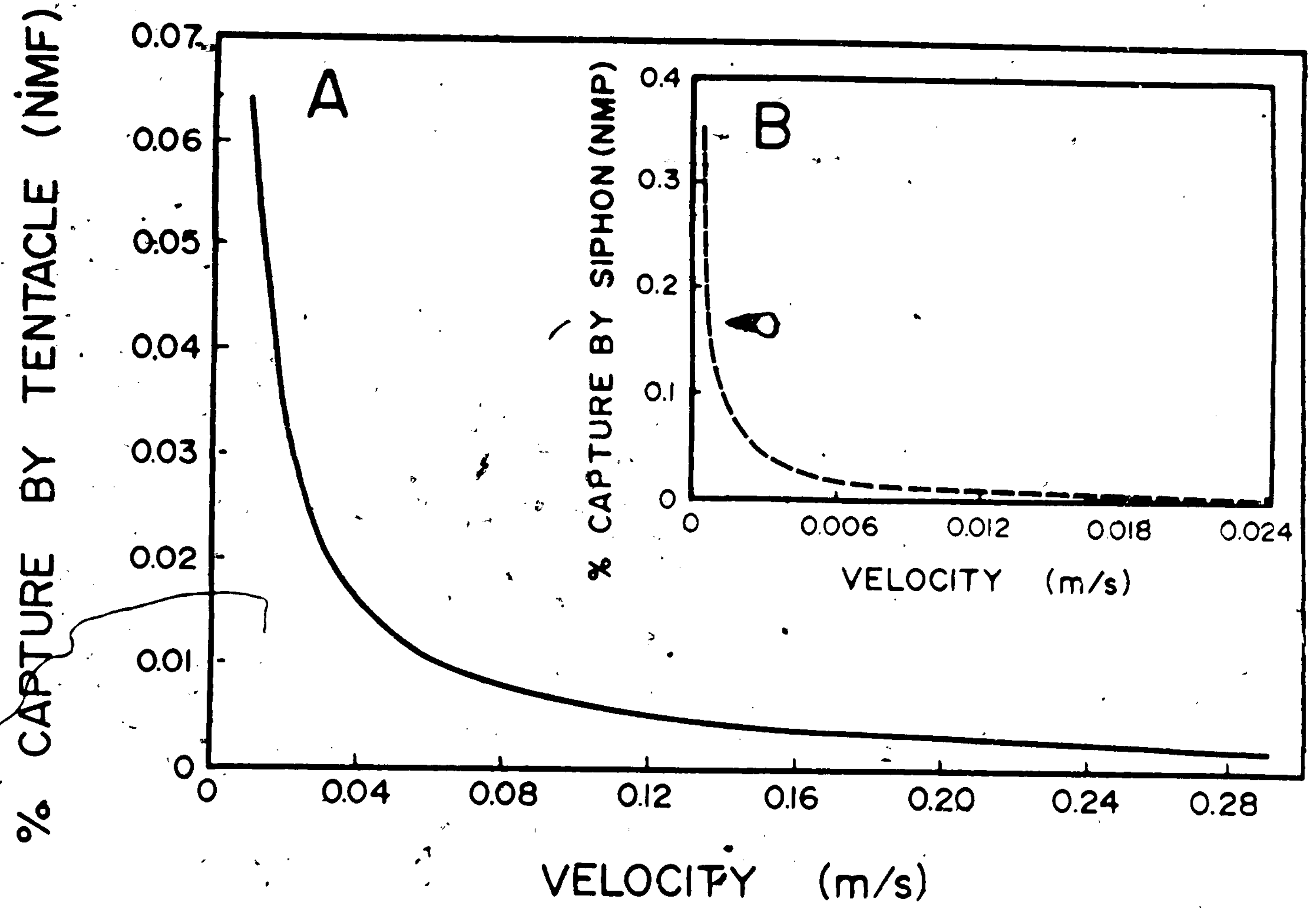
$$Nmp = (2DL)/d_c^2 V_p \quad \text{(Figure 41b)} \qquad (3)$$

TABLE 20

Definitions and units of symbols used in equations 1-8.

N_{mf} = dimensionless index describing the frequency of capture by a filament or tentacle due to the swimming behavior of a brachiolaria larva
N_{mp} = dimensionless index describing the frequency of capture by a pore or siphon due to the swimming behavior of a brachiolaria larva
D = coefficient of diffusion for a brachiolaria larva (m^3 s^{-1})
B = diffusion constant for a brachiolaria larva (J K^{-1})
V_o = ambient current velocity (m s^{-1})
V_c = current velocity at the center of the incurrent siphon (m s^{-1})
V_p = current velocity at a given point across the radius of the incurrent siphon (m s^{-1})
L = length of incurrent siphon (m)
T = absolute temperature (K)
DV_t = instantaneous displacement volume of the marginal tentacles (m^3)
DV_p = instantaneous displacement volume of the incurrent paraboloid (m^3)
R = encounter radius (m) (see Gerritsen and Strickler, 1977)
R_s = radius of incurrent siphon (m)
R_p = radius at a given point across the incurrent siphon (m)
F = filtration efficiency (%)
FV = instantaneous filter volume of tentacles or incurrent paraboloid (m^3)
$\sum FV$ = total instantaneous filter volume of tentacles and incurrent paraboloids per unit area on the benthos (m^3 m^2)
M = probability of mortality during settlement (%)
W = volume of the water column immediately above the substratum (m^3)
u = dynamic viscosity of seawater (N m^{-2} s)
h = height of tentacles or incurrent paraboloid (m)
d_f = diameter of filament or tentacle (m)
d_p = diameter of brachiolaria larva (m)
d_c = diameter of incurrent siphon (m)
r = radius of incurrent paraboloid (m)
r_1 = basal radius of tentacle or tentacle sphere (m)
r_2 = distal radius of tentacle or tentacle sphere (m)

Figure 41. Effects of current velocity on the dimensionless indicies of larval capture (N_{mf} and N_{mp}). A. Capture of <u>Asterina</u> <u>miniata</u> brachiolaria larvae by the marginal tentacles of <u>Pachycerianthus</u> <u>fimbriatus</u>. B. Capture of <u>A.</u> <u>miniata</u> brachiolaria larvae by the incurrent siphon of <u>Corella</u> <u>willmeriana</u>.

A
% CAPTURE BY TENTACLE (NMF)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
0.04
0.08
0.12
0.16
0.20
0.24
0.28
VELOCITY (m/s)
B
% CAPTURE BY SIPHON (NMP)
0.4
0.3
0.2
0.1
0
0
0.006
0.012
0.018
0.024
VELOCITY (m/s)

and the velocity profile across the siphon is approximated by Poiseuille flow as

$$V_p = V_c[1-(R_s/R_p)^2] \qquad (4)$$

(Vogel, 1981). Velocities were adjusted by a correction factor of 30% to compensate for deviation of the incurrent siphon from a circle (see Charriaud, 1982).

The relative impact of suspension feeders on larval survival in Bamfield and Grappler Inlets was compared by estimating the probability that a settling <u>Asterina</u> <u>miniata</u> larva will be captured by <u>Pachycerianthus</u> <u>fimbriatus</u> or <u>Corella</u> <u>willmeriana</u>. The instantaneous filter volume for a suspension feeder (FV) can be defined as the volume of water immediately above the substratum that is filtered during a specified period of feeding activity. If a settling larva enters FV it will be captured and ingested. Thus, FV is the instantaneous volume of water where the probability of mortality (M) is 100%, and is equivalent to the encounter radius (R) of Gerritsen and Strickler (1977).

Since the number of particles captured by a filter increases as a function of the fibre volume fraction (Chen, 1955; Rubenstein and Koehl, 1977), the impact of suspension feeding was gauged according to the instantaneous geometric displacement of water by the marginal tentacles of <u>Pachycerianthus</u> <u>fimbriatus</u>, and by the instantaneous volume of water affected by the feeding activities of <u>Corella</u>

willmeriana (Figure 42). The instantaneous displacement volume of P. fimbriatus tentacles (DV_t) can be approximated by a segment of a sphere

$$DV_t = 1/6 \Pi h(3r_1{}^2+3r_2{}^2+h^2) \qquad (5)$$

where r_1, r_2 and h are the tentacle sphere radii and height (Figure 42a). A correction factor (E) equal to the filtration efficiency of P. fimbriatus (0.11, see Table 19) must be applied to DV_t to compensate for spaces between the tentacles and for the ability of a Asterina miniata larva to escape, such that

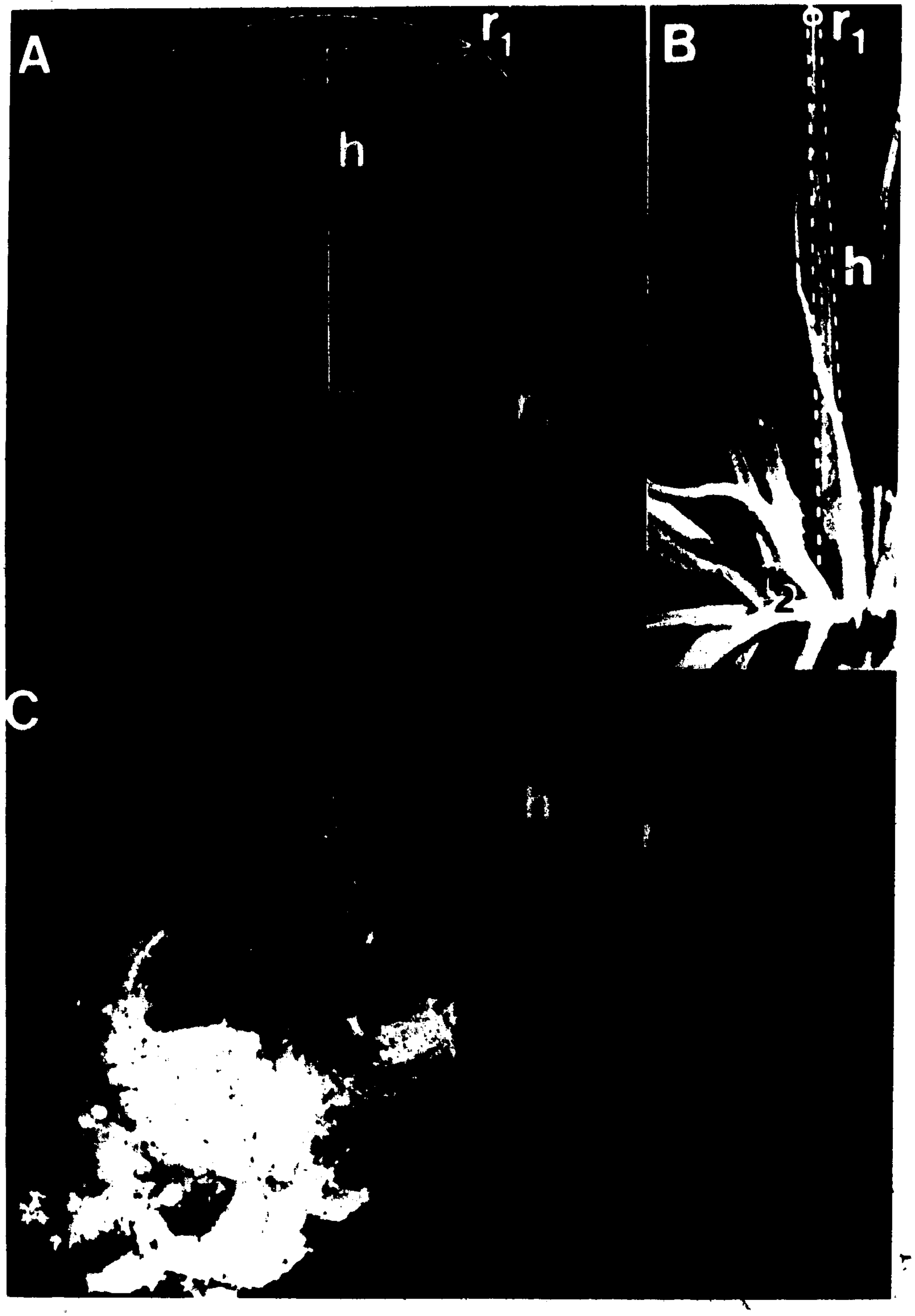
$$FV = DV_{t(\text{sphere})}(E) \qquad (6)$$

Alternatively, the corrected instantaneous displacement volume of the marginal tentacles can be obtained directly by summing the conic displacement volumes of individual tentacles (Figure 42b) as

$$DV_{t(\text{cone})} = 1/3 \Pi h(r_1{}^2+r_1r_2+r_2{}^2) \qquad (7)$$

Values for FV were determined from 41 photographs of Pachycerianthus fimbriatus taken in the field and averaged 14.8 ± 8.4 cm^3 (sphere method) and 18.8 ± 4.0 cm^3 (cone method) per anemone. In Corella willmeriana, the instantaneous displacement volume of ~~the~~ feeding currents

Figure 42. Geometric reconstructions of the instantaneous volumes of water filtered by _Pachycerianthus_ _fimbriatus_ and _Corella_ _willmeriana_. A. Segment of a sphere defined by the marginal tentacles of _P_. _fimbriatus_. B. Conic section defined by a marginal tentacle. C. Paraboloid defined by the feeding currents of _C_. _willmeriana_. See Table 20 for definitions of symbols.


A
r_1
h
B
r_1
h
r_2
C
h

(DV_p) can be approximated by a paraboloid (Figure 42c,)

$$DV_{p(\text{paraboloid})} = 1/2\,\Pi\, r^2 h \qquad (8)$$

where r and h are the radius and height above the siphon at which Asterina miniata larvae were captured during laboratory flow tank feeding experiments (Figure 38, Table 19). Values for DV_p range from 0.30 to 2.36 cm^3 per ascidian. The filtration efficiency of Corella willmeriana (E) is dependent on the developmental stage of A. miniata and has an average value of 0.87 for bipinnaria larvae (Table 19). The instantaneous filter volume for C. willmeriana (FV) is given by the product of E and $DV_{p(\text{paraboloid})}$.

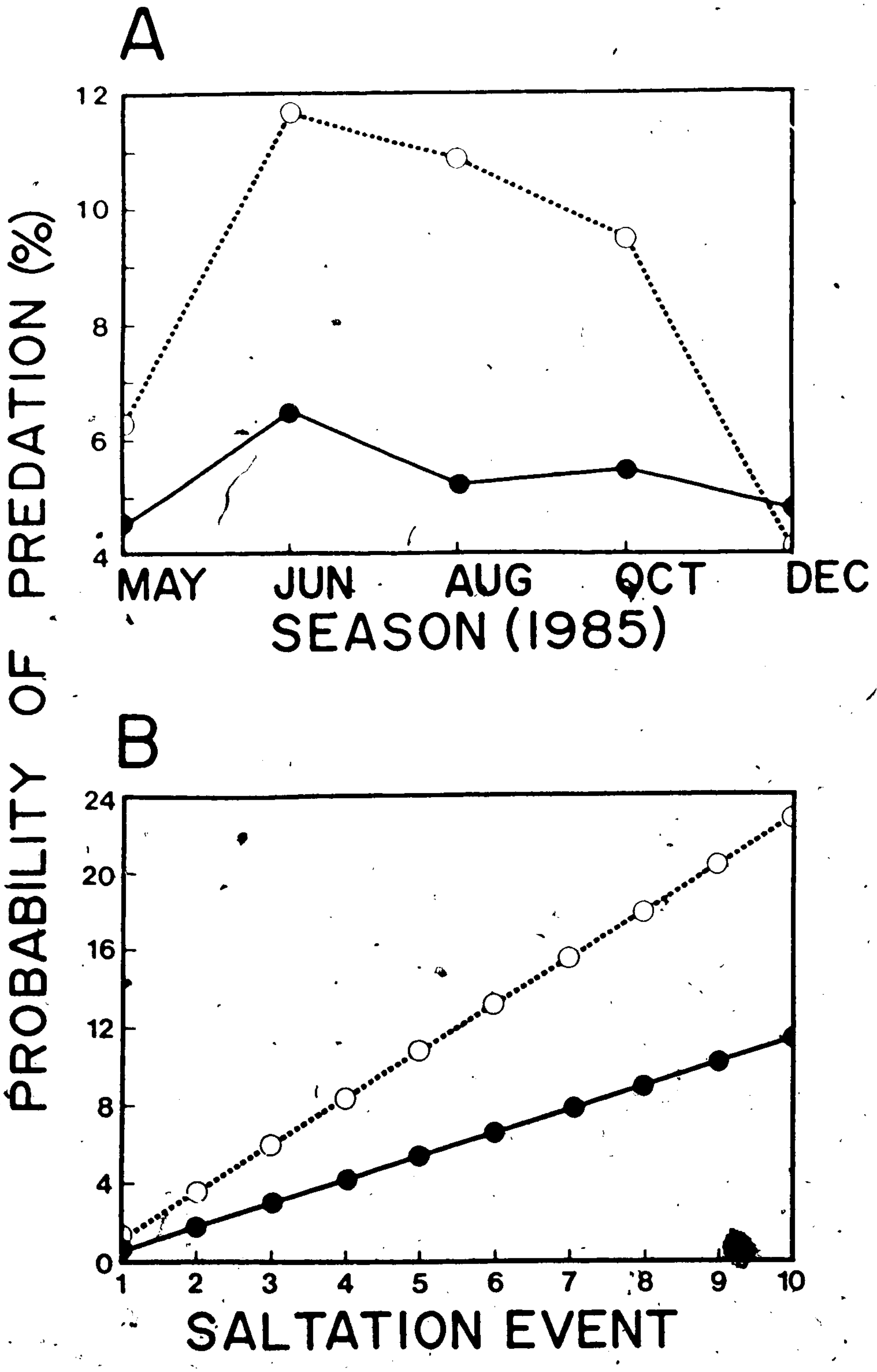
If Corella willmeriana and Pachycerianthus fimbriatus are distributed uniformly on the bottom, the instantaneous volume of water filtered per unit area ($\sum$ FV) is given by the product of FV and the densities of C. willmeriana and P. fimbriatus on the bottom of Bamfield and Grappler Inlets. Substitution of density values obtained from surveys of benthic transects (see Table 16) yields $\sum$ FV values of 3.50 X 10^{-4} m^3 m^{-2} for Bamfield Inlet and 1.95 X 10^{-4} m^3 m^{-2} for Grappler Inlet. These values indicate that the instantaneous volume of water filtered by C. willmeriana and P. fimbriatus is about 1.8 times greater in Bamfield Inlet than that filtered by suspension feeders in Grappler Inlet. Since $\sum$ FV values vary directly with seasonal changes in the density of *C. willmeriana* and *P. fimbriatus* (Figures 35 and 43a), settling *Asterina miniata* larvae are probably exposed to the greatest risk of predation by benthic suspension feeders in Bamfield Inlet as they approach the bottom during summer months when *C. willmeriana* are at their peak of abundance.

Consider that a *Asterina miniata* brachiolaria larva settles through a portion of the water column immediately above the bottom (W) having dimensions of 1m X 1m X 0.08m. The probability of larval mortality during settlement (M) varies proportionately with $\sum FV$ and nears 1 as $\sum FV$ approaches W. Substitution of empirical parameters and field measurements for $\sum FV$ yields a probability of larval mortality (M) of 1.2% during a single settlement event in Bamfield Inlet compared with 0.6% in Grappler Inlet. Since larvae of many benthic marine invertebrates, including *Asterina miniata*, repeatedly sample substrata prior to metamorphosis (Crisp, 1974; Meadows and Campbell, 1974; Rumrill, personal observations), the cumulative risk of predation by benthic suspension feeders increases relative to the number of times the larvae traverses W (Figure 43b). Results from the model (Figure 43) illustrate that encounter rates between settling *A. miniata* larvae and benthic suspension feeders are greater in Bamfield Inlet than Grappler Inlet.

7. Juvenile Survivorship

Two lines of evidence indicate that mortality rates of

Figure 43. Graphical model of the pooled probabilities of predation upon brachiolaria larvae of _Asterina_ _miniata_ during settlement by _Corella_ _willmeriana_ and _Pachycerianthus_ _fimbriatus_. A. Seasonal differences in the probability of predation at the Bamfield Inlet (○) and Grappler Inlet (●) study sites. B. Expected effects of repeated sampling of substrata (saltation events) by a _A_. _miniata_ larva on the probability of predation by both _C_. _willmeriana_ and _P_. _fimbriatus_. Effects of individual predators are assumed to be additive.


A
12
10
8
6
4
MAY
JUN
AUG
OCT
DEC
SEASON (1985)
PROBABILITY OF PREDATION (%)
B
24
20
16
12
8
4
0
1
2
3
4
5
6
7
8
9
10
SALTATION EVENT

Asterina miniata may be low after juveniles reach a ray length of 0.8 cm. First, size-frequency analysis showed that juveniles of A. miniata were persistent in Grappler Inlet (Figure 30) and did not decrease in relative abundance between March 1985 and February 1986 (Table 10). Second, results from laboratory experiments indicate that juveniles of A. miniata were not susceptible to predation by several species of benthic macroinvertebrates or fish. Cancrid crabs (Cancer productus and C. magister) and juvenile ling cod (Ophiodon elongatus) did not consume any juveniles of A. miniata in feeding experiments over periods of 14 days. Juveniles of A. miniata were also not preyed upon by asteroids in experiments lasting even longer periods (Evasterias troschelli, 28 days; Dermasterias imbricata, 18 days; or Pisaster brevispinus, 31 days). Cannibalism did not occur when juveniles were confined with conspecific adults in aquaria for a period of 27 days. Only the asteroid, Pycnopodia helianthoides, preyed upon juveniles of A. miniata (Table 21).

Field caging experiments showed that losses of juvenile Asterina miniata from cages containing a male cancrid crab, Cancer productus, exceeded the loss of juveniles from a control cage. However, differences in the number of missing juveniles were not statistically significant ($t = 3.46$, $p = 0.074$). Predation upon juvenile or adult A. miniata by C. productus was never observed in natural populations during daytime SCUBA dives, and A. miniata ossicles were

TABLE 21

Percentage of juvenile *Asterina miniata* consumed by *Pycnopodia helianthoides* in a laboratory aquarium. Table entries show mean ray lengths (± s.d.) of surviving *A. miniata*.

DAY OF EXPERIMENT	# *Asterina*	PERCENT CONSUMED	RAY LENGTH (cm) Mean	(s.d.)
0	5	0	1.38	(0.15)
4	5	0	1.30	(0.07)
8	4	20	1.45	(0.13)
14	4	20	1.37	(0.15)
26	3	40	1.37	(0.15)
31	2	60	1.40	(0.14)
39	2	60	1.30	(0.14)

absent from the gut contents of 6 crabs captured near the Grappler Inlet site at night. The persistence of A. miniata juveniles in Grappler Inlet (Table 10), and the high survivorship in laboratory and field experiments suggest that predation upon juveniles of A. miniata by benthic ma[illegible]nvertebrates and fish is probably not a major source of juvenile mortality.

8. Juvenile Immigration and Emigration

Day and Osman (1981) reported a difference in habitat use between juvenile and adult Asterina miniata in a subtidal boulder field in southern California. Juveniles of A. miniata were abundant underneath boulders while adults were found in exposed habitats. The nearest boulder field analogous to the southern California nursery area is ca. 3.5 km away from the study site in Grappler Inlet. Crawling rates of A. miniata are positively correlated with ray length (Table 22), but indicate that it would take from 3 to 6 years for A. miniata post-larvae and juveniles to migrate from the nearest boulder field into the Grappler Inlet site. Growth measurements show that 3-6 year old A. miniata are typically greater than 4 cm in ray length (Figure 31), hence the cohorts of juveniles observed in Grappler Inlet (Figure 30) most likely originated from autochthonous larval settlement within the established A. miniata population.

TABLE 22

Crawling speeds of *Asterina miniata* post-larvae and juveniles in the laboratory. Individuals in size class 1 were obtained following metamorphosis of brachiolariae in substratum selection experiments. Specimens in size classes 2 - 4 were collected from Grappler Inlet.

SIZE CLASS	RAY LENGTH (cm)	n	CRAWLING SPEED (cm/min)	
			Mean	(s.d.)
1	0.06 - 0.07	8	0.09	(0.03)
2	0.24 - 0.47	14	0.26	(0.08)
3	0.71 - 1.32	6	1.80	(0.39)
4	2.42 - 2.63	9	5.61	(0.45)

KENDALL'S COEFFICIENT OF RANK CORRELATION
$W = 0.8526$ $p < 0.001$

D. DISCUSSION

The spatial pattern of <u>Asterina miniata</u> recruitment differed markedly between two adjacent inlets in Barkley Sound. Recruits were conspicuous and abundant within an established population of <u>A. miniata</u> in Grappler Inlet but were absent from a population located nearby in Bamfield Inlet (Figure 30). Several alternative hypotheses can be invoked to explain the extent to which the observed pattern of <u>A. miniata</u> recruitment reflects processes occuring within the plankton, during settlement, and after metamorphosis. These hypotheses consider: 1) the spatial heterogeneity of larval populations, 2) substratum selection preferences of settling larvae, 3) spatial differences in the susceptibility of larvae to predation at the time of settlement, 4) differential survivorship of post-larvae and juveniles, and 5) immigration and emigration away from the initial settlement site. Collectively, these hypotheses form a framework to elucidate factors that may have contributed to the abundance of <u>A. miniata</u> juveniles in Grappler Inlet.

1. <u>Reproductive Activity of Asterina miniata</u>

The population of <u>Asterina miniata</u> underwent a seasonal cycle of reproductive activity in Grappler Inlet. Pyloric caecum and gonad indices exhibited low amplitude oscillations (Figure 32) that were correlated with seasonal changes in temperature and salinity (Figure 29). Cyclic reproduction of the adult population suggests that larval stages of A. miniata may follow a similar seasonal pattern of abundance in Barkley Sound (Figure 33).

The reproductive cycle of Asterina miniata from Grappler Inlet contrasts with the poorly defined pyloric caecum and gonad index cycles reported for A. miniata from Monterey Bay, California (Farmanfarmaian et al., 1958; Nimitz, 1971; Gerard, 1976; Davis, 1985). Differences in the amplitude of organ indices between Grappler Inlet and Monterey Bay suggest that the reproductive activity of A. miniata may vary substantially in different parts of its geographical range. Crump (1971), in a similar comparison, found intraspecific differences in the relationship between pyloric caecum and gonadal tissue in the New Zealand asterinid, Patiriella regularis. He observed that gonad development was depressed in areas where the pyloric caeca showed little seasonal oscillation. Cyclic growth of gonads in A. miniata is correlated with seasonal changes in temperature and the abundance of prey items (Figures 29 and 35) as well as with changes in the production of drift algae. In contrast, aseasonal organ indices in California population may reflect a more constant food supply and a poorly defined annual temperature cycle (Gerard, 1976; Harrold and Pearse, 1980).

2. Spatial Heterogeneity of Larval Populations

The densities of asteroid larvae differed substantially between Trevor Channel, Bamfield, and Grappler Inlets (Figure 33). Asteroid larvae were consistently more abundant in Trevor Channel surface water than in shallow water near established populations of *Asterina miniata*. There were, however, no significant differences in the densities of asteroid larvae between the high and low recruitment sites. Although populations of planktonic larvae typically show year to year variability in nearshore waters, no information is available on the densities of asteroid larvae in Bamfield and Grappler Inlets in 1983 and 1984. Consequently, it was assumed that oceanographic processes that transport planktotrophic asteroid larvae into the inlets were similar between 1983 to 1985. The densities of planktotrophic asteroid larvae did not differ between Bamfield and Grappler Inlets in 1985. Thus, the differential recruitment pattern of *A. miniata* cannot be attributed to differences in the distribution or abundance of larvae.

The planktonic period of *Asterina miniata* is reported to last from 45 to 60 days (Heath, 1917; Cameron, 1983; Cameron and Holland, 1984). Although the planktonic period reported here is substantially longer (79-183 days; Table 11), it is consistent with the decreased abundance of asteroid larvae in Barkley Sound during the fall of 1985. Planktotrophic larvae of other local asteroids have planktonic periods that are similar in length to that of *A. miniata* (Greer, 1962; Strathmann, 1978; Paulay *et al*., 1985). If growth and behavior of *A. miniata* bipinnaria and brachiolaria larvae are comparable to those of other local asteroids, then patterns of larval distribution that include several species should provide an approximation of events that take place during the larval period of A. miniata.

Local wind patterns and tidal oscillations control mixing in Barkley Sound and regulate the dispersal or retention of Asterina miniata larvae in Bamfield and Grappler Inlets. Tides in the inlets are mixed and semi-diurnal with a vertical range of 3.6 m. Strathmann (1982), Boicourt (1982) and Stancyk and Feller (1986) reviewed the processes of larval retention in estuarine habitats, and maintain that larval characteristics favoring retention in estuaries include: 1) abbreviated development, 2) short planktonic periods, and 3) demersal swimming behavior. Embryos and larvae of A. miniata do not exhibit any of these traits; instead, they have planktotrophic development and a prolonged planktonic period (Table 11). These characteristics are more conducive to dispersal out of the inlets than retention.

Seasonal plankton sampling showed that bipinnaria and brachiolaria larvae were more abundant in Trevor channel than in the inlets (Figure 33). These observations suggest that metamorphically competent brachiolaria larvae most likely re-enter Bamfield and Grappler Inlets after a period of development in Barkley Sound. Prevailing winds in Barkley Sound are from the northwest, and wind-driven surface currents and the formation of a retrograde (estuarine) front may favor the accumulation of larvae near the mouth of Bamfield and Grappler Inlets. Although the evidence is indirect, local current patterns and the relatively high density of asteriod larvae in Trevor Channel may combine to enhance advection of larvae into the inlets from Barkley Sound. Data from plankton tows are sufficient to resolve large-magnitude differences in the temporal and spatial patterns of larval abundance (see Figure 33), and advective processes that influence the availability of larvae cannot provide an explanation for the observed recruitment pattern of _Asterina miniata_ between Bamfield and Grappler Inlets.

3. _Substratum Selection by Asterina Brachiolaria Larvae_

Because the spatial pattern of larval abundance (Figure 33) does not mirror the pattern of _Asterina miniata_ recruitment (Figure 30), it is likely that differences in the density of recruits observed between Bamfield and Grappler Inlets were determined during settlement or after metamorphosis. Results from larval substratum selection experiments are consistent with those of Cameron (1983), and provide further evidence that _A. miniata_ brachiolariae settle non-selectively on substrata that are covered by a surface film composed of bacteria and other microorganisms.

Induction of metamorphosis by microflora and their exudates has been demonstrated in the laboratory for larvae from several plyla including prosobranch molluscs (Scheltema, 1974), cnidarians (Spindler and Muller, 1972;

Brewer, 1976; Neumann, 1979; Sebens, 1983), bryozoans (Mihm *et al*., 1981; Brancato and Wollacott, 1982) and polychaetes (Kirchman *et al*., 1982). Barker (1977) demonstrated a preference for filmed and aged substrata during settlement of the forcipulate asteroid, *Coscinasterias calamaria*, and he observed early juveniles on a wide variety of substrata in the field. Recognition of bacterial films may be an integral step prior to metamorphosis in *Asterina miniata* and other invertebrate larvae (see reviews by Meadows and Campbell, 1972; Scheltema, 1974).

The experiments with aged substrata described here are also consistent with the hypothesis that site selection of *Asterina miniata* brachiolaria larvae is related to the development of a surface film. Aging of sediments resulted in a 2-4X increase in the number of post-larvae over treatments in which larvae were offered fresh sediments (Table 15). Since *A. miniata* brachiolariae completed metamorphosis on a variety of filmed substrata including rocks, aged glass, sediment, and shell fragments (Tables 13 and 14), cues that indicate an adequate settlement site apparently are independent of substratum microtopography.

Active choices made by settling marine invertebrate larvae play an important role in determining patterns of recruitment (Keough and Downes, 1982; Gaines and Roughgarden, 1985). Consideration must also be given to hydrodynamical phenomena that occur at the bottom boundary layer during processes of larval settlement (Hannan, 1984).

Consequently, the initial distribution of settling larvae will reflect local currents, larval substratum selection responses, and physical and biotic characteristics of the benthos.

In the present study, significantly greater numbers of *Asterina miniata* larvae completed metamorphosis in treatments containing sediments from Grappler Inlet compared with sediments from Bamfield Inlet (Figure 34, Table 14), and larval substratum selection may facilitate the high recruitment of *A. miniata* in Grappler Inlet. However, the interpretation that larval substratum selection alone can account for the differential pattern of recruitment must be viewed with caution because metamorphically competent larvae were not simultaneously offered a choice between Bamfield and Grappler Inlet sediments in settlement experiments. More importantly, the magnitude of differences in metamorphosis between Bamfield and Grappler sediment treatments cannot account for the lack of recruits in Bamfield Inlet. The substratum selection response of *A. miniata* larvae was sensitive to the biotic condition of the sediments, and perceived changes in the quality of sediments can alter larval responses over a short period of time (Table 15). Accurate assessment of substratum preferences require experiments in which larvae can discriminate between several different types of substrata. Without direct information on the substratum selection preferences of *A. miniata* brachiolariae, it is difficult to evaluate the effects of active larval choices in determining sites for settlement. The single-substratum experiments reported here indicate that bottom sediments from both Grappler and Bamfield Inlets provide adequate cues to initiate metamorphosis of A. miniata brachiolariae, and suggest that larvae may prefer sediments from Grappler Inlet.

Metamorphosis of an Asterina miniata brachiolaria larva is an irreversible ontogenetic event that requires from 36 to 50 hours to complete (Cameron, 1983; personal observations). Presumably, metamorphosis is initiated in A. miniata following the perception of stimuli by epithelial receptors located on the tips of the brachiolarian arms (see Barker, 1978). A time-dependent increase in the number of post-larvae (Figure 34, Tables 13-15) suggests that the perception of substratum quality may play a role in the delay of metamorphosis by A. miniata brachiolariae. The time-dependent increase in the number of A. miniata post-larvae may be due to variability in the delay periods among metamorphically competent sibling larvae. Bayle (1965) and Pechenik (1984) demonstrated that larvae of several species of bivalve and gastropod molluscs were able to delay metamorphosis in natural populations, but they were unable to identify a direct causal relationship between environmental conditions associated with delayed metamorphosis and the length of the delay period. The extent to which delayed metamorphosis contributes to differences in the settlement of A. miniata in Bamfield and Grappler Inlets is unknown.

Predictions about settlement preferences based on the spatial pattern of early juvenile stages are less reliable than settlement experiments because migration and mortality after settlement can significantly alter initial patterns of distribution (Young and Chia, 1982; Keough and Downes, 1982; Keough, 1984; Connell, 1985). Although no observations of Asterina miniata post-larvae could be made in the field, the distribution of juveniles on mud, cobble and algae in Grappler Inlet are consistent with nonselective larval settlement (Table 13). Unequivocal demonstrations of larval settlement preferences in P. miniata await further studies carried out in situ.

4. Predation upon Larvae During Settlement

Three lines of evidence suggest that predation upon settling Asterina miniata larvae may play a role in determining patterns of recruitment. First, bottom sediments from both Grappler and Bamfield Inlets support diverse communities of benthic suspension feeders (Table 16). Feeding activities of suspension feeders can present a threat to larvae as they settle out of the water column (Standing, 1976; MacKenzie, 1977; Purcell, 1977; Steinberg and Kennedy, 1977; Highsmith, 1982; Oliver et al., 1982; Oliver and Slattery, 1985; Cowden, et al., 1984; Sebens and Koehl, 1984; Young and Chia, in press). Gut content analysis showed that Pachycerianthus fimbriatus and

Corella willmeriana consume small infaunal invertebrates and demersal zooplankton that are similar to the size of settling A. miniata larvae (Figure 36). These findings corroborate previous studies of ascidian and cnidarian feeding; Eleftheriou and Basford (1983) reported that Cerianthus lloydi consumes a variety of zooplankton including small crustaceans and planktonic invertebrate larvae. Ross and Horridge (1957), Horridge (1958), and Arai (1965, 1972, 1973) demonstrated that feeding responses could be elicited in the marginal tentacles of ceriantheid anemones by contact with amino acids and protein homogenates from zooplankton. Phelebobranch ascidians, such as C. willmeriana, feed on suspended particulate matter and small zooplankton by pumping water through a mucus-net filter that lines the branchial basket (Kott, 1964; Millar, 1971; Charriaud, 1982; Pennachetti, 1984). The gut contents of C. willmeriana included detritus, diatoms, unidentified nauplii and invertebrate embryos. These studies indicate that P. fimbriatus and C. willmeriana are potential predators of settling A. miniata larvae.

Second, feeding experiments demonstrate that Corella willmeriana and Pachycerianthus fimbriatus prey upon Asterina miniata larvae in the laboratory. Feeding activities of C. willmeriana and P. fimbriatus had highly significant effects on the survivorship of A. miniata larvae in stage-specific and density-dependent feeding experiments (Figures 37 and 38, Table 17). Mortality rates of brachiolaria larvae were low compared with earlier larval stages in feeding experiments carried out with C. willmeriana (Figure 37b), but losses of brachiolaria larvae were nevertheless substantial (22% per hour). Rates of predation by P. fimbriatus upon brachiolaria stages were greater than rates of predation upon bipinnaria (Figure 37a). Since feeding rates varied with prey density in both C. willmeriana and P. fimbriatus (Figure 38), density-dependent predation may be a factor that favors larval dispersion away from siblings. Results from the laboratory experiments provide circumstantial evidence for predation upon A. miniata larvae in the field.

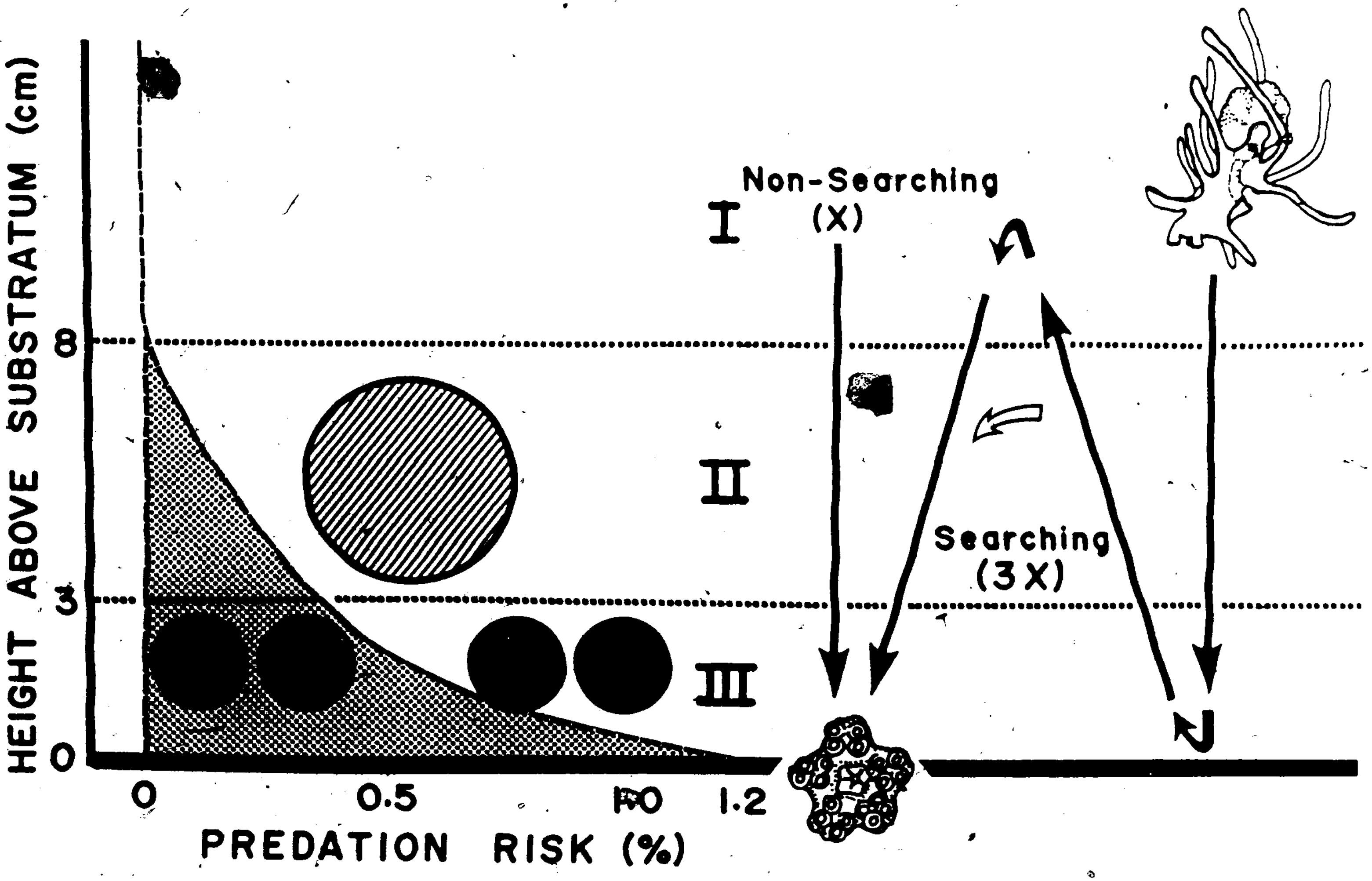
Third, estimates of encounter rates with benthic suspension feeders suggest that Asterina miniata larvae in Bamfield are exposed to greater risk than in Grappler Inlet due to differences in the feeding activities of Corella willmeriana and Pachycerianthus fimbriatus. Settling A. miniata larvae experience a 1.2% chance of predation per saltation event in Bamfield Inlet where over 71% of the encounters with benthic suspension feeders are due to C. willmeriana (Figure 43). In contrast, the probability of predation is about 0.6% per saltation event in Grappler Inlet. These estimates are conservative because they account for predation by only the 2 most abundant species from a diverse assemblage of suspension feeders (see Table 16).

The decline in the index of larvae captured as a function of current velocity (Figure 41) suggests that the swimming behavior of Asterina miniata brachiolariae may increase the probability of capture as larvae approach the bottom. Swimming of a brachiolaria larva was considered as a random walk through a three-dimensional habitat where the risk due to predation is distributed in discrete patches associated with individual suspension feeders. Movements of the brachiolaria larva outside of a streamline result in an increase in the probability of capture as the larva encounters the low Reynolds number hydrodynamic environment associated with the marginal tentacles of Pachycerianthus fimbriatus or the incurrent siphon of Corella willmeriana.

Further support for the hypothesis that the risk of predation increases as Asterina miniata larvae approach the bottom is given by the effects of vertical stratification or tiering in the community of suspension feeders in Bamfield Inlet (Figures 43 and 44). For example, in Pachycerianthus fimbriatus, the height of feeding tentacles, low capture efficiency, low species density and greater ambient current velocities, combine to suggest that the feeding activities of P. fimbriatus pose a relatively low threat to settling larvae. In contrast, the lower height, lower current velocities, greater filtration efficiency and high density of Corella willmeriana pose a relatively greater threat to settlement of A. miniata than P. fimbriatus (Figures 41, 43, 44, Table 19).

Keough and Downes (1982) proposed several qualitative

Figure 44. Graphical model of the effects of vertical tiering in the community of benthic suspension feeders and larval searching behavior on the risk of predation during settlement of *Asterina miniata* in Bamfield Inlet. I = zone where larvae are exposed to risk during the pelagic period. II = zone above substratum where larvae are exposed to risk due to the feeding activities of *Pachycerianthus fimbriatus* (▨). III = zone immediately above substratum where larvae are exposed to risk due to the feeding activities of *Corella willmeriana*. Stippled region indicates escalating risk due to *P. fimbriatus* (0.34%) and *C. willmeriana* (0.88%) during a single pass through Zones I and II (total risk = 1.22%). Sampling of the substratum once prior to settlement results in a three-fold increase in risk (3.66%). Settling larvae are less susceptible if they remain below the tentacles of *P. fimbriatus* while repeatedly sampling the substratum prior to settlement (open arrow).


HEIGHT ABOVE SUBSTRATUM (cm)
8
3
0
PREDATION RISK (%)
0
0.5
1.0
1.2
I
II
III
Non-Searching
(X)
Searching
(3X)

models to predict spatial patterns in the distribution of marine invertebrate post-larvae that are based on differences in larval settlement behavior. In the non-searching (dropped egg) model, larvae undergo metamorphosis immediately after contact with a suitable site (Figure 44). Alternatively, in the searching (ping-pong ball) model, larvae repeatedly sample the substrata prior to metamorphosis. An important consequence associated with repeated sampling of substrata by larvae prior to metamorphosis is that there is a trade-off between the advantages gained by completing metamorphosis at a favorable site and an increase in the cumulative risk of predation by benthic suspension feeders (Figures 43b and 44). The present model considers the possibility that mortality may increase in direct proportion to the number of successive larval saltation events prior to attachment of <u>Asterina</u> <u>miniata</u> larvae to the bottom.

Seasonal variation in the abundance of benthic suspension feeders may also influence the probability of predation upon <u>Asterina</u> <u>miniata</u> larvae during settlement. <u>Pachycerianthus</u> <u>fimbriatus</u> is a perennial member of benthic invertebrate communities in Bamfield and Grappler Inlets. In contrast, the population of <u>Corella</u> <u>willmeriana</u> underwent marked seasonal changes in abundance in Bamfield Inlet (Figure 35). Similar seasonal fluctuations in the abundance of <u>C</u>. <u>willmeriana</u> were reported by Lambert (1968) and Lambert <u>et</u> <u>al</u>. (1981). The cumulative probability of predation by P. fimbriatus and C. willmeriana is directly related to their densities on bottom sediments (Figure 43a), and the timing of A. miniata settlement is important in determining the likelihood that larvae are captured prior to metamorphosis. Taken collectively, the results from predator gut content analyses, laboratory feeding experiments, and estimates of predator encounter rates indicate that the assemblages of benthic suspension feeders in Bamfield Inlet may have different effects on the survivorship of metamorphically competent A. miniata larvae during settlement than in Grappler Inlet.

5. Survivorship of Post-Larvae and Juveniles

Differential post-larval mortality is a potentially important and yet poorly understood source of variability in the abundance and distribution of asteroid recruits. Demographic evidence and laboratory experiments indicate that the mortality rates of juvenile Asterina miniata (ray lengths > 0.8 cm) are probably low in Bamfield and Grappler Inlets. Size-frequency analysis showed that the density of A. miniata juveniles did not change markedly in Grappler Inlet between March and December 1985 (Table 10). Although the predatory asteroid, Pycnopodia helianthoides, had a significant effect on the survival of juvenile A. miniata in the laboratory (Table 21), adult P. helianthoides are rarely encountered in Bamfield and Grappler Inlets. Juveniles of A. miniata were not consumed by 5 other species of potential predators. Adult A. miniata are omnivorous scavengers (Anderson, 1959; Araki, 1964; Day and Osman, 1981; Schroeter et al., 1983), and it was considered possible that adults might canibalize post-larvae and small juveniles as demonstrated for other omnivorous asteroids (Scheibling, 1980). However, laboratory experiments showed that cannibalism by adult A. miniata is not an important source of juvenile mortality.

Mortality rates of recently settled Asterina miniata are unknown in Bamfield and Grappler Inlets. Consequently, the potential effects of spatial differences in post-larval survivorship cannot be compared with spatial differences in predation by benthic suspension feeders and substratum selection. Predation and disturbance by meiofauna can influence patterns of recruitment in a variety of macrofaunal invertebrates (Woodin, 1976; Oliver, 1979; Brenchley, 1981; Wilson, 1981; Oliver et al., 1982; Tamaki, 1985; Ambrose, 1984; Watzin, 1986), and it is possible that differential rates of meiofaunal predation and disturbance may contribute to low survival of A. miniata post-larvae in Bamfield Inlet compared to Grappler Inlet. Recently metamorphosed A. miniata are similar in size to prey items consumed by predatory meiofauna such as turbellarians, nematodes and polychaetes (Fauchald and Jumars, 1979; Oliver, 1979; Watzin, 1986). Experimental evidence presented here addresses the effects of benthic suspension feeders and substratum selection on settlement success prior to interactions with meiofauna. Further laboratory and field experiments are necessary to determine the relative importance of predation and disturbance by meiofauna and other sources of post-larval mortality.

Differential mortality must occur within 10 to 14 months after metamorphosis in order for juvenile mortality to be an important determinant of recruitment heterogeneity between Bamfield and Grappler Inlets. Analysis of juvenile cohorts indicate that *A. miniata* reach ray lengths of 0.3-0.6 cm after the first year and 1.9-2.8 cm in the second year following settlement (Figure 31, Table 10). These estimates are similar to growth rates observed for *Patiriella regularis* by Crump (1971). Gonads are present in individuals that have ray lengths greater than 2.7 cm. The abundance of *A. miniata* recruits in Grappler Inlet cannot be explained by differences in physical factors affecting growth or survival because post-larvae and juveniles were exposed to a similar range of temperature and salinity conditions (Figure 29). Information reported here cannot [illegible]ress the potential effects of variability in growth due to differences in the availability of food for post-larvae and juveniles.

6. Immigration and Emigration Following Settlement

Episodes of recruitment apparently are regulated in several species of asteroids by the proximity of the adult population to a nearby nursery area. For example, Birkeland *et al.* (1971) proposed that tube mats of the polychaete, *Phyllochaetopterus prolifera*, provide a nursery area for juveniles of *Mediaster aequalis*. Similarly, Barker (1979) reported that juveniles of *Stichaster australis* inhabit intertidal nursery areas composed of articulated coralline algae. Nursery areas have also been reported for *Asterina miniata* (Day and Osman, 1981) and other species of asteroids (Scheibling, 1980; Jost and Rein, 1984). The presence of an adjacent nursery could have a distinguishable affect on the size-frequency distribution of an adult population by providing an alternative habitat conducive to juvenile growth. As a consequence, juveniles would be expected to enter the adult population at a gradual rate after they have attained a relatively large body size. Jost and Rein (1984) observed immigration of juveniles into adult populations of *Astropecten aranciacus* and *A. bispinosus*, and their size-frequency data revealed a shift in mean body size reflect~~ed~~ by spatial differences between juveniles and adults. In the present study, the peripheries of adult *A. miniata* populations were searched for juveniles. However, no spatial differences in the size structure of *A. miniata* populations were detected within either the Bamfield or Grappler Inlet sites.

Among other species of asteroids, episodes of recruitment appear to be linked with local hydrographic conditions that concentrate larvae near a settlement site. Rasmussen (1973) noted large numbers of *Asterias rubens* post-larvae along the shore of a Danish fjord shortly after dense concentrations of brachiolaria larvae were seen in surface waters. Similarly, Birkeland (1982) and Yamaguchi (1973) proposed that the cyclic recruitment of Acanthaster planci in the south Pacific is linked to a series of localized events that include terrestrial runoff, nutrient levels, and growth rates of planktonic larvae in nearshore waters.

Asteroid populations that are not bordered by nursery areas would be expected to show sporadic recruitment patterns and to exhibit distinct early cohorts of juveniles. Guillou and Guillaumin (1984) presented demographic evidence of seasonal recruitment leading to normally distributed juvenile cohorts in Asterias rubens. Immigration of Asterina miniata juveniles into Grappler Inlet from an outside nursery area is unlikely because juveniles are extremely rare outside the inlets (<< 1 per 500 m^{-2}; Appendix I) and rates of juvenile movement are slow (Table 22). Subtidal boulder fields similar to those described by Day and Osman (1981) do not occur near populations of A. miniata in Bamfield and Grappler Inlets. Therefore the appearance of juvenile cohorts in Grappler Inlet is probably due to autochthonous settlement rather than immigration from an adjacent nursery area.

There have been few attempts to document the effects of predatory suspension feeders on larval settlement into echinoderm communities. Pearse et al. (1970) suggested that densities of sea urchin larvae (Strongylocentrotus franciscanus) may be reduced prior to settlement in kelp beds due to predation by kelp-associated filter feeders. However, Tegner and Dayton (1981) reported that bryozoans (*Membranipora*, *Hippothoa*, *Lichenopora*) and a polychaete (*Spirorbis*) were ineffective predators. Planktivorous fish (*Chromis*, *Brachyistius*, *Oxyjulis*) were expected to have a greater influence on the survival and spatial distribution of *S. franciscanus* larvae. Lucas *et al*. (1976) also suggested that planktivorous fish may be an important source of mortality for larvae of *Acanthaster planci*, although their conclusions are based on experiments in which agar blocks treated with larval extracts were offered to fish as prey rather than larvae. Yamaguchi (1973) found that polyps of the coral, *Pocillopora damicornis*, consumed settling larvae of the asteroids, *Acanthaster planci*, *Culcita novaeguineae* and *Linkia laevigata*. Similarly, Highsmith (1982) demonstrated that survival of settling sand dollars, *Dendraster excentricus*, can be reduced due to predation by tanaid crustaceans. These anecdotal studies provide indirect evidence that echinoderm populations may be limited by the survivorship of larval populations during the time of settlement.

Recent evidence allows the inference that echinoderm populations can also be affected during settlement by larval substratum selection responses. Larvae of temperate Pacific echinoderms settle and metamorphose in response to a variety of cues from the substratum (Birkeland *et al*., 1971; Cameron and Hinegardner, 1974; Cameron and Schroeter, 1980; Highsmith, 1982; Cameron, 1983; Mladenov and Chia, 1983; Burke, 1984). Presumably, differential availability of settlement cues could lead to a heterogeneous distribution of post-larvae (Highsmith, 1982; Barker, 1977). However, for substratum selection to be a viable explanation for recruitment patterns, densities of juveniles must directly reflect the abundance of colonizing larvae (see Connell, 1985; Gaines and Roughgarden, 1985; Yoshioka, 1986). Some evidence supports this contention for asteroids with planktotrophic larvae. For example, Rassmusen (1973) established a positive link between the occurrence of brachiolaria larvae and subsequent post-larval densities of _Asterias_ _rubens_. Barker (1977) found little evidence of mortality in _Stichaster_ _australis_ after larvae completed metamorphosis and became established at a nursery site of encrusting coralline algae. Chia _et_ _al_. (1984) recently reviewed the literature on the settlement behavior of asteroid larvae, and they proposed that post-settlement migrations are a major determinant adult spatial distribution. However, there seem to be no quantitative records of relationships between the densities of settlers, migratory movements, and subsequent recruitment for early juvenile asteroids.

Distinction between densities of post-larvae and juvenile recruits is critical to understanding patterns of juvenile distribution. The distinction is particularly important when the abundance of recruits is determined by density-dependent processes. In the present study, <u>Asterina miniata</u> larvae were captured by benthic suspension feeders in a density-dependent manner (Figure 38). However, the substratum selection response of <u>A. miniata</u> larvae was independent of larval density (Figure 34). It is not known whether sources of early <u>A. miniata</u> mortality act in a density-dependent or density-independent manner, so it is impossible to make quantitative comparisons regarding the relative importance of pre-settlement and post-settlement events.

Connell (1985) recently argued that direct assessments of factors influencing the spatial and temporal distribution of juveniles are difficult to conduct because recruitment combines settlement with early mortality. Results from the present study are consistent with two trends that emerge from Connell's (1985) review. First, laboratory feeding and settlement experiments provide post-facto evidence that the density of settlers is proportional to the density of recruits. The abundance of <u>Asterina miniata</u> recruits in Grappler Inlet was correlated with low encounter rates between larvae and benthic suspension feeders, and with the substratum selection response of settling larvae. Second, processes affecting recruitment in Grappler Inlet were consistent over at least a two year period (1983 to 84) and then changed markedly; there was no evidence of recruitment in 1985 despite extensive searches for post-larvae and juveniles. These findings suggest that mechanisms regulating recruitment of temperate asteroids such as _A_. _miniata_ may be similar to processes that control recruitment of other benthic marine invertebrates. Although interactions between events in the plankton and on the bottom may determine the extent to which juvenile distribution is due to post-settlement rather than pre-settlement events, repeated _A_. _miniata_ recruitment in Grappler Inlet is consistent with the hypothesis that biological differences among sites (e.g. intensity of predation, competition and disturbance) may be an important determinant of spatial differences in the distribution of early juveniles.

Rates of planktonic and benthic predation are pivotal in theoretical expressions of the evolution of benthic invertebrate life history traits (Vance, 1973, 1974; Chia, 1974; Strathmann, 1974, 1977; Stearns, 1976; Caswell, 1981; Grant, 1983). Risk during settlement may be considered as part of the planktonic mortality function, but predation by benthic suspension feeders is fundamentally different than predation in the water column in several respects. First, benthic suspension feeders are large and non-motile compared with predatory zooplankton. An important consequence related to body size and motility is that encounter rate equations must be modified to compensate for the greater surface area for filtration and mechanisms of particle capture found among benthic suspension feeding invertebrates. Second, not all developmental stages are exposed to equivalent risk, since predation by benthic suspension feeders is restricted largely to the periods of planktonic development shortly after spawning and during settlement. Consequently, the mortality rates of early embryos and larvae competent to metamorphose are particularly relevant in comparison with early larval stages. Finally, processes of larval settlement and predation by benthic suspension feeders take place during the transition from 3 to 2 dimensional space within shear gradients associated with bottom boundary layers (Butman, 1986; Jackson, 1986; Scheltema, 1986). Scaling the effects of larval locomotion within a velocity gradient indicates that coefficients of larval diffusion and swimming behavior gain increased importance in determining the fate of encounters with predatory suspension feeders (Figure 41).

7. Conclusions

Assessment of factors that affect the spatial pattern of _Asterina_ _miniata_ recruitment can be complicated due to: 1) substratum selection responses of larvae competent to metamorphose, 2) short-term changes in substratum quality, 3) stage-specific and density-dependent differences in the feeding responses of suspension feeders, and 4) spatial and temporal differences in the distribution of suspension feeders and settling larvae. Interactions between these factors require careful examinations to distinguish among several possible sources of recruitment heterogeneity (Weinberg _et_ _al_., 1986). Hypotheses that address the importance of substratum selection and predation of settling larvae are not mutually exclusive. Consequently, assessments of recruitment processes in benthic marine invertebrates require multifaceted approaches with particular attention to larval availability during the time of settlement and the abundance of post-larvae shortly after metamorphosis.

The principal conclusion from this study is that larval substratum selection, and the spatial distribution of suspension feeders, can be important determinants of spatial patterns of recruitment between adjacent populations of a temperate asteroid. Since embryos and early larval stages of Asterina miniata are likely to disperse out of Bamfield and Grappler Inlets shortly after spawning, feeding bipinnaria and brachiolaria larvae probably remain within Barkley Sound during the planktonic period where they are exposed to risk from pelagic predators. In late summer and fall, A. miniata larvae are transported back into the inlets on flooding tides. Advection of larvae into the inlets is facilitated during late summer by low freshwater runoff and high salinities. When A. miniata larvae settle out of the water column, they are exposed to predation by the community of benthic suspension feeders that inhabit the mud and cobble substratum on the bottom of the inlets. Benefits associated with site selection may be offset by the escalating cumulative risk of predation during the transition from planktonic to benthic life. By minimizing the number of times the benthos is sampled prior to metamorphosis, a larva will decrease the probability of encounters with suspension feeders. Differences in the perception of substratum quality, coupled with variability in the abundance and spatial distribution of benthic suspension feeders, appear to be key determinants of success or failure of settlement by _A_. _miniata_.

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CHAPTER VI.

STAGE-SPECIFIC MORTALITY OF MARINE INVERTEBRATE LARVAE: GENERAL CONCLUSIONS AND IMPLICATIONS FOR LIFE HISTORY THEORY

A. INTRODUCTION

Rates of stage-specific survivorship are a fundamental component of aquatic invertebrate population dynamics. Variability in rates of survivorship are critical to understanding the persistence of certain stages and age classes over others in a heterogeneous population. In nearshore zooplankton communities, however, it is rarely possible to monitor the survivorship of larval cohorts because the rates at which individuals enter and exit the populations are typically unknown (eg. Jorgensen, 1981). Even in species with distinct reproductive seasons and synchronous spawning, the period of gamete release is spread over several days to weeks (2.6×10^5 to 1.8×10^6 seconds). This time interval is significant compared to the duration of the planktonic period in many marine invertebrate larvae (6.1×10^5 to 6.5×10^6 seconds). Consequently, variation in the timing of spawning alone is sufficient to produce a heterogeneous age structure among larval populations.

The basic pattern of stage-specific survivorship for any marine invertebrate larva is influenced by several different parameters including: 1) relative and absolute body size, 2) morphological traits, 3) swimming velocities and behavior, and 3) biochemical composition. These parameters are augmented by the presence or absence of defensive mechanisms that function to reduce the probability of larval mortality (Pennington and Chia, 1984; Pennington et al., 1986; Rumrill et al., 1985). Previous attempts to estimate rates of larval mortality have been hampered by the lack of an underlying conceptual framework from which to view temporal changes in the abundance and stage structure of larval populations (Strathmann, 1985; Hines, 1986).

In this final chapter, I develop the basis for an alternative methodology to estimate age and stage-specific mortality rates of marine invertebrate larvae. The approach is based on knowledge of: 1) the distribution of ontogenetic stages within natural populations of larvae, and 2) the relative risk of mortality associated with each developmental stage. I present information on short-term temporal changes in the abundance of echinoderm larvae, and integrate these findings with results from a broad survey of larval susceptibility patterns to provide a new perspective for estimating rates of mortality among natural populations.

B. MATERIALS AND METHODS

The research was carried out from July 1983 to September 1985 at Bamfield Marine Station, British Columbia

(48°50'N, 125°08'W).

1. Intensive Sampling of Larval Populations

Populations of larval echinoids were sampled on 63 consecutive days from February 24 to April 26, 1984. All samples were collected with 125 µm mesh, 0.5 m diameter standard and closing nets. Each day during the study period three replicate samples were collected from surface (0-30 m) and mid (30-60 m) depths. Each tow was chilled on ice and returned immediately to the laboratory for sorting. With the exception of a few samples, the majority of tows were sorted live. All sorting was carried out in a Bogorov Tray, and larval echinoids were identified on the basis of skeletal characteristics, overall morphology and pigmentation (Strathmann, 1979).

2. Differential Susceptibility of Echinoderm Larvae

The relative susceptibility of echinoderm embryos and larvae was assessed by a series of laboratory feeding experiments. Embryos and larvae from 17 different species of echinoderms were tested as prey for 34 different species of planktivorous invertebrates and fish (see Table 24). Feeding experiments with particular predator-prey combinations were carried out according to methods described by Rumrill *et al*. (1985; Chapters 2 and 3). Embryonic and larval echinoderms were placed into 1 or 3.7 liter glass jars along with an individual predator and agitated continuously for 12 to 24 hrs. All feeding experiments were conducted in an incubator maintained near ambient temperatures (10 - 14^{O}C). In most cases 5 or 6 different developmental stages were tested as prey. An effort was made to include representatives of species with planktotrophic and lecithotrophic larvae, although the majority of prey species had planktotrophic development due primarily to the extended breeding periods of certain echinoids and asteroids.

C. RESULTS AND DISCUSSION

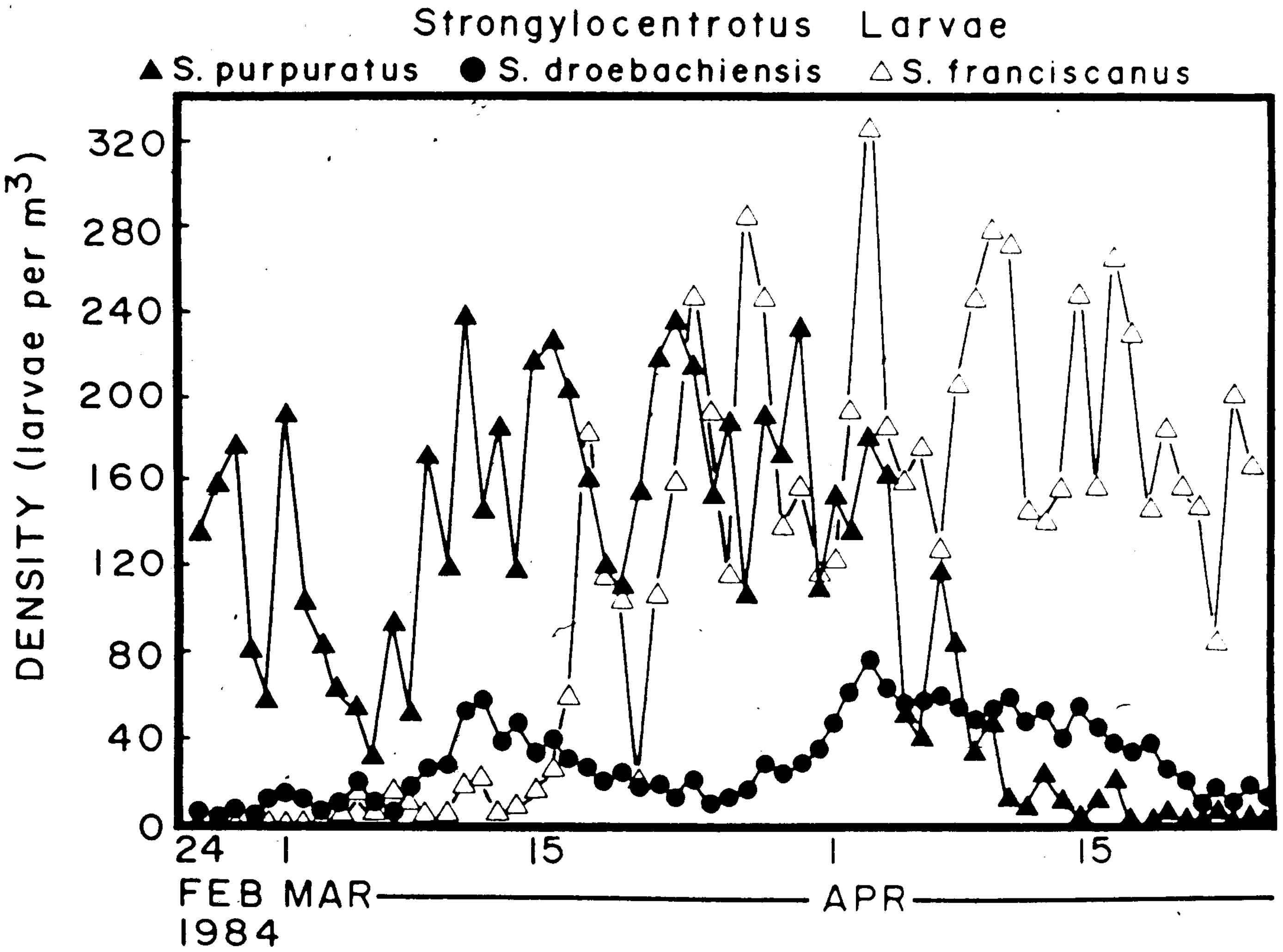
Optimization of the developmental patterns of marine invertebrate larvae can be phrased in terms of the maximization of larval survival. The selective pressure on any particular life history parameter is given by the sensitivity of overall fitness to that parameter. Consequently, the task of larval ecologists concerned with larval survivorship and population dynamics becomes one of estimating the relationship between overall fitness and larval mortality.

1. Intensive Sampling of Larval Populations

Attempts to monitor the population dynamics of marine invertebrate larvae by periodic sampling with zooplankton nets cannot adequately address small scale immigration and emigration because the sampling frequency of most field studies is typically too long to allow the assumption of continuity to be warranted. However, even when a sampling interval of 1 day is used, net sampling techniques do not provide sufficient resolution to distinguish between emigration and mortality (see below). Estimates of field mortality rates obtained from periodic zooplankton samples typically assume: 1) that marine invertebrate larval populations exist at equilibrium densities, 2) that rates of net emigration and immigration are zero, and 3) that the probability of mortality is distributed equally among the various developmental stages. The inferential strength of most field estimates of larval mortality is seriously limited because they do not take into account the size and age structure of the larval population. In the majority of cases information is also lacking about rates of larval growth and variability in the length of the planktonic period.

In the present study, the abundance of larval echinoids varied substantially on a daily basis in Barkley Sound (Figure 45). Two species, Strongylocentrotus purpuratus and S. franciscanus, occurred in relatively high densities in shallow water (0-30 m). The third species, S. droebachiensis, occurred at roughly half the density of S. purpuratus and S. franciscanus (Figure 45). Both S. purpuratus and S. franciscanus were characterized by high day to day differences in density; in contrast, daily differences in the abundance of S. droebachiensis were substantially lower. Despite these differences in abundance, the overall coefficients of variation were nearly equivalent for all species (S. purpuratus, C.V. = 0.74; S. franciscanus, C.V. = 0.82;

Figure 45. Daily variation in the density of echinoid larvae collected from shallow (0 - 30 m) depths in Trevor Channel, Barkley Sound. Values show mean density of larvae from 3 tows.


Strongylocentrotus Larvae
▲ S. purpuratus
● S. droebachiensis
△ S. franciscanus
DENSITY (larvae per m^3)
320
280
240
200
160
120
80
40
0
24
1
15
1
15
FEB MAR
APR
1984

S. droebachiensis, C.V. = 0.64).

Differences in the abundance and stage structure of Strongylocentrotus droebachiensis larval populations are shown in in more detail in Figure 46. Larvae exhibited bimodal changes in abundance with an initial peak during the second week of March and a more substantial peak during early April. These changes in density were accompanied by changes in the stage structure of the larval population. Samples of S. droebachiensis were dominated by 4-armed and 6-armed echinoplutei from late February to early April. Six-armed echinoplutei increased in relative abundance from 16% of the sample on February 27 to 39% on March 11 and 72% by March 23 (Figure 46).

Is the increase in 6-armed echinoplutei a reflection of the rate of growth in a stable population? The 4-armed echinoplutei sampled in February were at least 1 wk old, and perhaps as much as 2 wks. Larvae grew to an early 6-armed stage over a period of 10 to 12 days in laboratory cultures (Table 23), and the 8-armed stage was reached after 27 days. Thus, the shift from 4-armed to 6-armed echinoplutei in nature was slow in comparison to the rate of growth in the laboratory. With the exception of 2 larvae sampled March 19, 8-armed echinoplutei were absent from most samples collected during February and March. Even with slow rates of growth 8-armed echinoplutei would be expected to occur in greater abundance in the March samples.

The virtual absence of 8-armed echinoplutei and the

Figure 46. Daily variation in the density of *Strongylocentrotus droebachiensis* echinoplutei collected from shallow (0 - 30 m) depths in Trevor Channel, Barkley Sound. Values show mean density of larvae from 3 tows; error bars indicate ± 1 standard deviation. Pie diagrams indicate the proportion of the larval population composed of 4, 6 and 8 armed echinopluteus larvae.

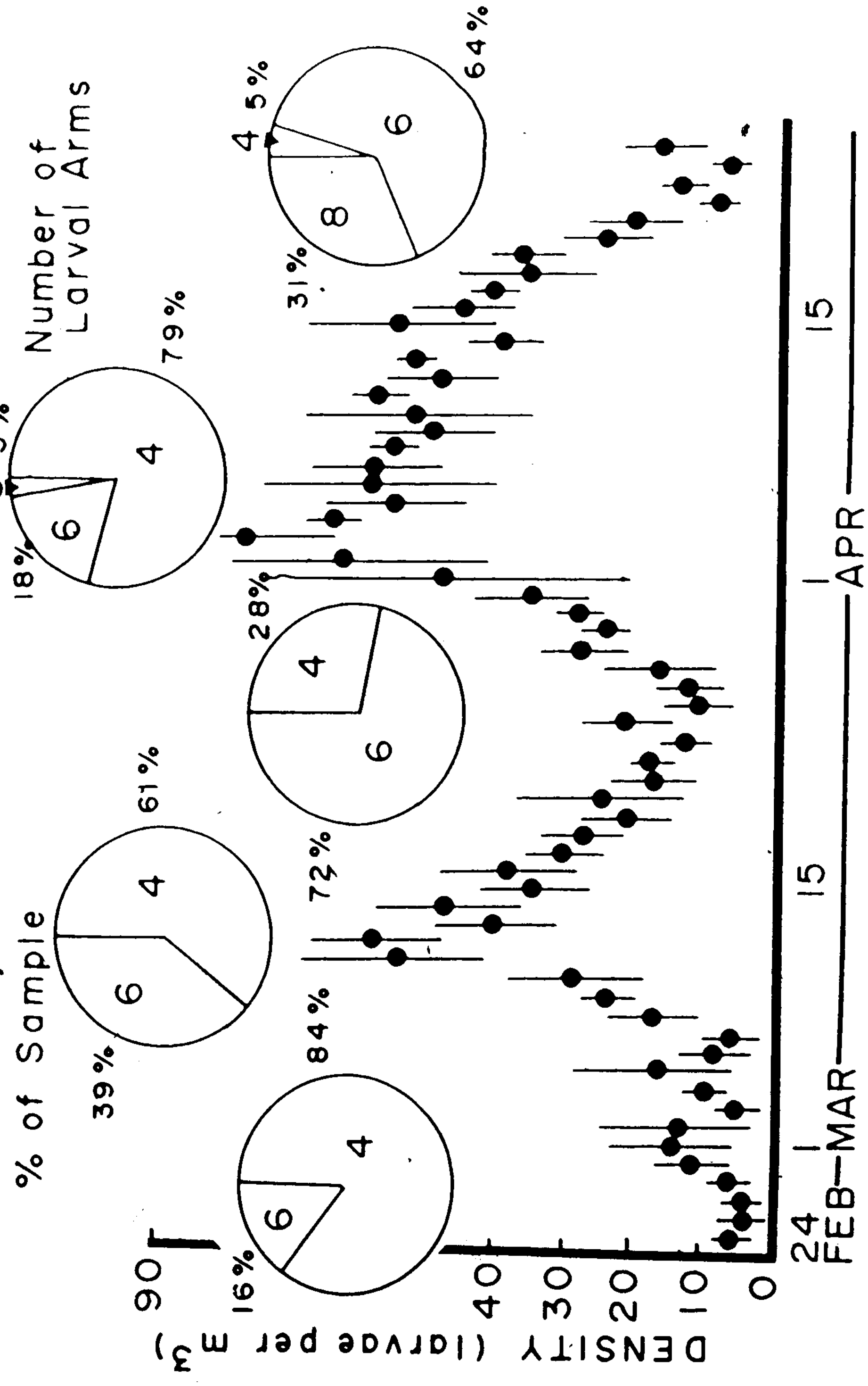

% of Sample
Number of Larval Arms
DENSITY (larvae per m3)
90
40
30
20
10
0
24
FEB
1
MAR
15
1
APR
15
16%
84%
6
4
39%
61%
6
4
72%
28%
4
6
18%
79%
3%
8
6
4
31%
5%
64%
4
8
6

TABLE 23

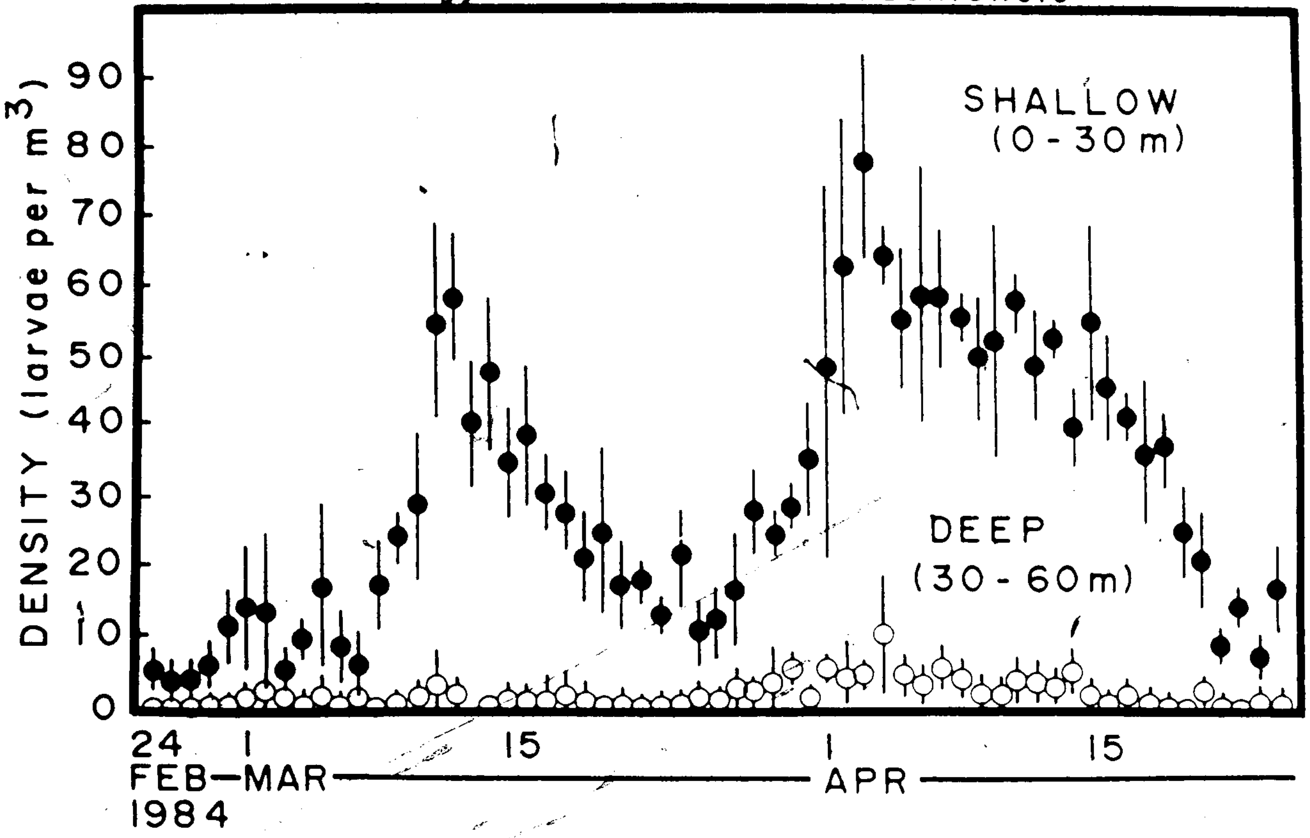
Comparison of laboratory and field growth rates of *Strongylocentrotus droebachiensis*. Table entries indicate number of days necessary to reach 4, 6, and 8 armed stages, and total days to metamorphosis. Values in parentheses are alternative times provided by the authors.

TEMP °C	DAYS TO ECHINOPLUTEUS STAGE 4 arm	6 arm	8 arm	Metamorphosis	Reference
Laboratory:					
4 - 7				56	Turner, '65
8	7 (12)				Stephens, '72
4	11 (20)				Stephens, '72
7 - 13				51 - 152	Strathmann, '79
9 - 11	7				Roller & Stickle, '85
8 - 10	6	10	27	47	This study, '84
Field:					
7 - 9			42-56	61	This study, '84

general decline in larval abundance in late March was not due to migration of larvae into deeper water (Figure 47). The density of *Strongylocentrotus droebachiensis* echinoplutei at mid depths (30-60 m) was always low and reflected the abundance of larvae in shallow water. Following the drop in larval abundance at the end of March, densities of *S. droebachiensis* echinoplutei increased rapidly to a second peak by early April (Figure 46). Densities of *S. droebachiensis* approached 80 larvae m^{-3} during the first week of April and averaged about 60 larvae m^{-3} until April 15. Eight-armed echinoplutei made up 3% of the sample on April 6 and 31% of the sample on April 24. The increased abundance of 8-armed echinoplutei during April is consistent with the hypothesis that the April samples of *S. droebachiensis* were composed primarily of new individuals that entered the population by immigration from an adjacent source. Rates of growth to the 8-armed stage in the laboratory, however, suggest that it is unlikely the second peak of larval abundance was due entirely to input of new individuals by a second period of spawning activity. The relative abundance of 8-armed echinoplutei in late April suggests that these larvae may have grown rapidly from earlier stages originating in March.

There are several alternative perspectives from which to view these short-term changes in larval abundance and stage structure. Temporal variation in density may

Figure 47. Daily variation in the density of Strongylocentrotus droebachiensis echinoplutei collected from shallow (0 - 30 m) and deep (30 - 60 m) water in Trevor Channel, Barkley Sound. Values show mean density of larvae from 3 tows; error bars indicate ± 1 standard deviation.



DAILY VARIATION IN LARVAL DENSITY

Strongylocentrotus droebachiensis

reflect: 1) small scale patchiness in the distribution of larval populations, 2) short term differences in larval concentration due to immigration and emigration of individuals, and 3) decreases in density due to the effects of starvation, predators and settlement out of the water column. Similarly, changes in the stage structure of larval populations may be caused by factors including those affecting density as well as others relating to rates of larval growth and differences in the susceptibility of embryonic and larval stages to predation and starvation. Determining the actual causes of short-term temporal changes in larval populations is thus beyond the resolution of net-sampling techniques and will require careful and concurrent investigation of several sensitive parameters.

Given the technical problems associated with net sampling, daily differences in the abundance of strongylocentrotid echinopluteus larvae shown in Figure 45 provide an opportunity to investigate rates of loss from natural populations over relatively short periods of time. Data from Figure 45 allow comparisons between 3 case histories in which larval populations exhibited net decreases in density. The first example is shown by the decline in _Strongylocentrotus purpuratus_ larval density over a period of 25 days from April 2 to 26. Daily differences in density ranged from a +284.2% increase in the population day^{-1} to a -92.3% decrease in the population day^{-1}. Net losses averaged over longer periods of time ranged from -5.6% day^{-1} over 7 days, -6.5% day^{-1} over 14 days, and -3.9% day^{-1} over 25 days. Similar results were obtained from investigations of daily and net losses from populations of S. droebachiensis (Figure 45). The second example is shown by the decline in S. droebachiensis echinopluteus density over a period of 14 days from March 11 to 25. Daily differences in density ranged from a +65.0% increase in the population day^{-1} to a -50.4% decrease in the population day^{-1}. Net losses averaged over longer periods of time ranged from -7.4% day^{-1} over 7 days to -5.8% day^{-1} over 14 days. The third example is shown by the decline in S. droebachiensis echinopluteus density over a period of 14 days from April 12 to 26. Daily differences in density ranged from a +136.7% increase in the population day^{-1} to a -57.3% decrease in the population day^{-1}. Net losses averaged over longer periods of time ranged from -4.2% day^{-1} over 7 days to -5.3% day^{-1} over 14 days.

Although these estimates of loss from larval populations can be attributed to many different causes, they are roughly equivalent to the losses of 3 to 12% day^{-1} reported for a variety of larval forms by Pennington (1986) and to the estimate of 13% per day reported for larvae of Mytilus edulis by Jørgensen (1981). It must be noted, however, that none of these estimates of loss from larval populations distinguish between declines in abundance due to emigration, settlement, starvation and predation.

2. Differential Susceptibility of Echinoderm Larvae

The local coexistence of echinoderm larvae and predatory zooplankton in nearshore waters poses several questions regarding the relative benefits of a dispersive larval stage and the associated risks of larval mortality. Different types of larval forms may exist because they confer different advantages to the adults, such as differences in the probability of larval survival to metamorphosis and the frequency of recruitment. Coexistence of larvae and predatory zooplankton may also occur if predators have a negligible impact on larval populations, either through low encounter rates (Gerritsen and Strickler, 1977) or through selective feeding on other more abundant prey.

Type A: High Susceptibility of Early Embryos and Larvae

Microcrustaceans including omnivorous and carnivorous copepods, decapod zoeae, mysids, and euphausids are the dominant planktivores that feed upon echinoderm embryos and larvae in the nearshore waters of Barkley Sound (Table 24). These groups of predators are referred to as cruising raptorial feeders by Greene (1985) and they rely primarily upon mechanical sensory cues for prey detection. Selective feeding by these groups of predators results in a typical pattern of prey mortality in laboratory experiments that is characterized by high susceptibility of embryos and early larval stages and lower susceptibility of later larvae. I

TABLE 24

Summary of predators used in feeding experiments. List includes 34 species of planktivorous invertebrates and fish, and their encounter and handling tactics. Planktivore functional groups are those described by Greene (1985).

PREDATOR Phylum & Class		Genus & species	Functional Group
Cnidaria: Hydrozoa		Polyorchis penicillatus	Cruising Entangling
		Aequorea victoria	Cruising Entangling
		Gonionemus vertens	Cruising Entangling
		Phialidium gregarium	Cruising Entangling
		Sarsia apicula	Cruising Entangling
		Velella vellata	Cruising Entangling
		Nanomia cara	Cruising Entangling
Ctenophora:	Tentaculata	Pleurobrachia bachei	Ambush Entangling
	Lobata	Bolinopsis infindibulum	Cruising Raptorial
Arthropoda:	Crustacea	Calanus marshallae	Cruising Raptorial
	(copepods)	Calanus pacificus	Cruising Raptorial
		Eucalanus elongatus	Cruising Raptorial
		Acartia longiremis	Cruising Raptorial
		Pseudocalanus sp.	Cruising Raptorial
		Corycaceus sp.	Cruising Raptorial
		Epilabidocera longipedata	Cruising Raptorial
		Euchaeta elongata	Cruising Raptorial
		Centropages abdominalis	Cruising Raptorial
		Tigriopus californicus	Cruising Raptorial
	(mysid)	Neomysis rayi	Cruising Raptorial
	(euphausiids)	Euphausia pacifica	Cruising Raptorial
		Thysanoessa raschii	Cruising Raptorial
	(cladocera)	Podon leukarti	Cruising Raptorial
	(amphipod)	Parathemisto pacifica	Cruising Raptorial
	(decapod zoea)	Pugettia producta	Cruising Raptorial
		Hemigrapsus nudus	Cruising Raptorial
		Cancer productus	Cruising Raptorial
		Cancer magister	Cruising Raptorial
		Pinnixa faba	Cruising Raptorial
Chaetognatha:	Sagittoidea	Saggitta elegans	Ambush Raptorial
		Eukronia hamata	Ambush Raptorial
Chordata:	Osteichthyes	Engraulis mordaux	Cruising Suction
		Clupea harengus	Cruising Suction
		Aulorhynchus flavidus	Cruising Suction

TABLE 24 (continued)

Summary matrix of predator-prey experiments conducted with 34 species of planktivorous invertebrates and fish and 17 species of echinoderms. See text for description of Type A, B, C, D, and 0 susceptibility patterns. Species codes are provided in Appendix 1, Table 30.

PREDATOR	PREY:									
	ECHINOIDS				ASTEROIDS					
Genus & species	Sf	Sp	Sdr	De	Po	Pb	Ok	Ph	Pm	Di
Polyorchis penicillatus	C	C		C	C	C	C		C	
Aequorea victoria	A	A	A	A	A	A	A			
Gonionemus vertens	C	C	C	C	C	C	C	C	C	
Phialidium gregarium	C	C	C	A	A	A	A	A	A	
Sarsia apicula	C			C	C	C	C		C	
Vellella vellata		0	0	0						
Nanomia cara	C			C						
Pleurobrachia bachei	C	C	C	C	C	C	C	C	C	
Bolinopsis infindibulum	0	0		0					0	
Calanus marshallae	A	A	A	A	A	A	A	A	A	
Calanus pacificus	A	A	A	A	A	A	A	A	A	
Eucalanus elongatus		A			A	A	A			
Acartia longiremis		A		A					A	
Pseudocalanus sp.	A	A	A	A	A	A	A	A		
Corycaceus sp.				A					A	
Epilabidocera longipedata	A			A	A	A	A		A	
Euchaeta elongata	C	C	C	C	C	C	C	C	C	
Centropages abdominalis		A							A	
Tigriopus californicus	0	0			0	0	0			
Neomysis rayi	A/C	A/C		F	F	F	F	F	F	F
Euphausia pacifica				A						
Thysanoessa raschii	A	A		A	A	A	A	F	A	
Podon leukarti	A			A					A	
Parathemisto pacifica	B	B	B	B	B	B	B	B	F	F
Pugettia producta	A	A	A	A	A	A	A	A	A	A
Hemigrapsus nudus	A	A		A						
Cancer productus	A			A						
Cancer magister				A	A	F	A		A	
Pinnixa faba	A	A		A						
Saggitta elegans	B	B	B	B	B	B	B	B	B	
Eukronia hamata					B	B	B			
Engraulis mordaux		C			C	C	C			
Clupea harengus		C			C	C	C			
Aulorhynchus flavidus	C									

TABLE 24 (continued)

Summary matrix of predator-prey experiments conducted with 34 species of planktivorous invertebrates and fish and 17 species of echinoderms. See text for description of Type A, B, C, D, and 0 susceptibility patterns. Species codes are provided in Appendix I, Table 30.

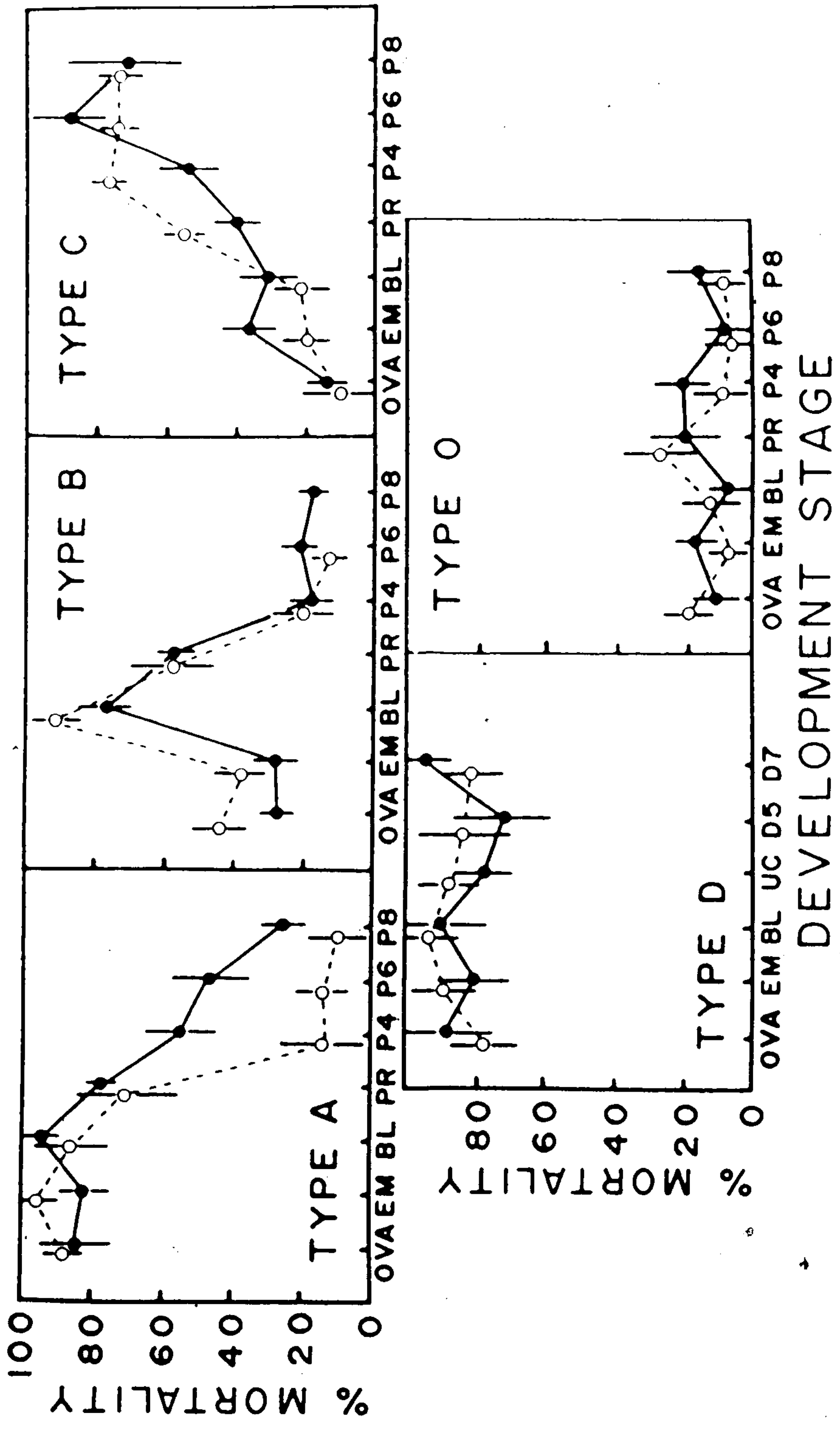
PREDATOR:	PREY: ASTEROIDS			HOLOTHUROIDS		OPHIUROID	CRINOID	
Genus & species	Ss	Hl	Cp	Pc	Cm	Oa	Fs	TOTALS
Polyorchis penicillatus	D	D	D	C		C		12
Aequorea victoria				0				8
Gonionemus vertens	D	D	D			C	0	14
Phialidium gregarium	D	D			D	C	A	14
Sarsia apicula					B			7
Vellella vellata	C			0				5
Nanomia cara								2
Pleurobrachia bachei	C	C		D	D	D		14
Bolinopsis infindibulum					0			5
Calanus marshallae		0			0	A		12
Calanus pacificus	0	0	0	A	0	A		15
Eucalanus elongatus				A	0			6
Acartia longiremis					0			4
Pseudocalanus sp.	0	0		A	0	A		13
Corycaceus sp.								2
Epilabidocera longipedata								6
Euchaeta elongata		0		C	A	C		13
Centropages abdominalis								2
Tigriopus californicus								5
Neomysis rayi						F		10
Euphausia pacifica			0					2
Thysanoessa raschii	0	0	0			A		12
Podon leukarti	0					A		5
Parathemisto pacifica					0	B	D	13
Pugettia producta	0			F		A	D	14
Hemigrapsus nudus								3
Cancer productus					0			3
Cancer magister								5
Pinnixa faba					0			4
Saggitta elegans	0	0	0	B	0	B	D	16
Eukronia hamata								3
Engraulis mordaux								4
Clupea harengus								4
Aulorhynchus flavidus								1

refer to this pattern of prey susceptibility as a "Type A" pattern (Table 24, Figure 48). Among echinoids, ova and embryonic stages were usually preyed upon at the greatest rate followed by early, larval stages such as gastrulae and prism larvae. Echinopluteus larvae having 4, 6, and 8 arms were typically preyed upon at relatively low rates. Similar results were evident during feeding experiments with planktotrophic asteroids, an ophiuroid, and a holothuroid (Table 24). In these taxa susceptibility to predation usually decreased after development to the late bipinnaria, ophiopluteus or auricularia stages. Among the 133 predator-prey combinations that included microcrustaceans, over 66% resulted in Type A susceptibility patterns. In the remaining predator-prey combinations, microcrustaceans did not have significant effects on larval populations (Type O susceptibility pattern, 20%) or fed primarily on later larval stages (Type C pattern, 8%).

<u>Type B: High Susceptibility of Motile Hatching Stages</u>

High susceptibility is shifted towards larger and more active prey stages in laboratory experiments with predatory chaetognaths and hyperiid amphipods (Table 24). Non-motile stages such as eggs and embryos were relatively less susceptible than the motile stages immediately following hatching. In most cases blastulae and gastrulae were captured at high rates; susceptibility to capture typically decreased for the later echinopluteus, ophiopluteus, bipinnaria, brachiolaria and auricularia stages. I refer to

Figure 48. Differential susceptibility of embryos and larvae. Values show standardized mean (± s.d.) % mortality in laboratory feeding experiments. Development stages: OVA = unfertilized ova; EM = embryo; BL = blastula; PR = prism larvae; P4 = 4 arm pluteus; P6 = 6 arm pluteus; P8 = 8 arm pluteus; UC = uniformly ciliated larvae; D5 = 5 day doliolaria; D7 = 7 day doliolaria. Type A: High susceptibility of embryos and early larvae of Strongylocentrotus franciscanus in feeding experiments with Cancer productus (open circles) and Calanus marshallae (closed circles). Type B: High susceptibility of blastulae and prism larvae of S. franciscanus in feeding experiments with Parathemisto pacifica (open circles) and Sagitta elegans (closed circles). Type C: High susceptibility of echinopluteus larvae of S. franciscanus in feeding experiments with Phialidium gregarium (open circles) and Pleurobrachia bachei (closed circles). Type D: High susceptibility of all developmental stages of Florometra serratissima in feeding experiments with Pugettia producta (open circles) and Parathemisto pacifica (closed circles). Type O: Low susceptibility of all developmental stages of S. purpuratus (open circles) and S. franciscanus (closed circles) in feeding experiments with Bolinopsis infindibulum.


TYPE A
TYPE B
TYPE C
TYPE D
TYPE O
% MORTALITY
100
80
60
40
20
0
OVA EM BL PR P4 P6 P8
OVA EM BL PR P4 P6 P8
OVA EM BL PR P4 P6 P8
OVA EM BL UC D5 D7
OVA EM BL PR P4 P6 P8
DEVELOPMENT STAGE

this pattern of prey susceptibility as a "Type B" curve (Table 24, Figure 48). Chaetognaths and hyperiid amphipods conform to the description of ambush raptorial feeders given by Greene (1985). The increase in susceptibility following hatching suggests that blastulae and gastrulae are detected primarily on the basis of motion as they increase their encounter rates with the stationary predators.

Type C: High Susceptibility of Later Larval Stages

High susceptibility is shifted further towards larger and older larval stages in feeding experiments with planktivores that locate their prey with visual cues and by those that employ cruising and ambush entangling tactics to capture prey. These groups of predators include planktivorous fish, hydromedusae, and siphonophores. I refer to this pattern of prey susceptibility as a "Type C" curve (Table 24, Figure 48).

Types D and O: Uniform High and Low Susceptibility

A few planktivores such as the tentaculate ctenophore Pleurobrachia bachei and several hydromedusae consumed all echinoderm developmental stages at equally high rates in the laboratory feeding experiments (Table 24). I define uniformly high susceptibility as a "Type D" (death) pattern. In contrast, several predators (viz. Vellella vellata, Calanus pacificus, Pseudocalanus sp., Thysanoessa raschii, and Saggitta elegans) did not consume any prey stages during feeding experiments with certain species of echinoderms; in these cases echinoderm embryos and larvae appear to be virtually immune from predation. Uniformly low susceptibility is referred to as a "Type O" (nil) pattern (Table 24, Figure 48).

3. Implications for Life History Theory

Hines (1986) recently argued that "larval mortality is the most difficult life history variable to measure" and that "good estimates of larval mortality or, conversely, survivorship to settlement are critical to progress in analyzing the evolution of life histories." Because estimates of net reproductive rate and age-specific reproductive value are dependent on estimates of larval survivorship, the relationship between juvenile fitness and larval mortality must be considered for species with contrasting modes of development. Results from the survey of predator-prey interactions demonstrate that the patterns of susceptibility exhibited by species with planktotrophic and lecithotrophic development are fundamentally different (Table 24). About half of the species with planktotrophic development exhibited Type A susceptibility patterns (48%) with the remainder exhibiting Type B (12%) and Type C (28%) patterns. In contrast, species with lecithotrophic development generally have Type O (59%) and Type D (28%) pattetns.

These differences in the susceptibility of planktotrophic and lecithotrophic larval forms have widespread implications for contemporary life history theory. For example, the predominance of Type A susceptibility patterns among species with planktotrophic development suggests that rapid morphogenesis through the critical early stages should be favored. I have demonstrated that the cumulative loss of embryos and larvae increases proportionately with increased development time in response to predation pressures by a brachyuran zoea (Chapter 3). Opposite results, however, are expected in response to predation by planktivores that feed at high rates upon later larval stages. The predominance of Type O patterns among species with lecithotrophic development provides support for the contention that there is an inverse relationship between egg size and mortality. The proportion of species interactions resulting in Type D susceptibility patterns is nevertheless substantial (28%), suggesting that lecithotrophic embryos and larvae may be at risk due to predation by certain planktivores. In particular, gelatinous hydromedusae and tentaculate ctenophores may consume large numbers of lecithotrophic embryos and larvae in nature; similar results have been gathered by Bailey (1984) and Purcell (1985) during investigations of predation upon relatively large and yolky fish eggs.

Predatory zooplankton may be able to detect regions of high embryo and/or larval density and selectively forage within patches. Nearly all species of planktivores increased their ingestion rates with increasing prey density (see functional response data, Chapters 2, 3, and 5). The observations of increased risk with higher larval abundance suggest that larval dispersion away from siblings should be favored. Increased rates of feeding at high prey densities should also favor rapid development to a motile hatching stage to facilitate the diffusion of dense patches. Finally, density-dependent feeding responses are expected to result in homogeneous patterns of spatial distribution among larval populations in nearshore zooplankton communities where predators are often more abundant than prey.

Estimation of the extent to which predatory zooplankton and fish reduce the density of echinoderm larvae in Barkley Sound is difficult because larval populations change daily in abundance and distribution (Figure 45). The impact of carnivorous copepods and decapod zoeae on populations of echinoderm larvae with planktotrophic development is expected to be quite different from that of hydromedusae and planktivorous fish (Table 24). Differences in the shapes of stage-specific susceptibility curves, coupled with information regarding encounter rates, will ultimately provide the foundation for evaluating the impact of predators on natural populations of larvae.

4. Contributions to the Study of Larval Mortality

In this thesis I have used a multifaceted approach to study various aspects of larval mortality. Information presented here outline general principles and guidelines for future research, and they highlight my contributions to date concerning patterns of larval susceptibility.

In this final chapter, I describe a series of experimental observations to test the hypothesis that rates of embryo and larval mortality are inversely correlated with initial egg size and mode of development. The life history patterns and differential susceptibility of planktotrophic and lecithotrophic larvae to predation by carnivorous zooplankton support the size-mortality hypothesis, although stage-specific differences in embryo and larval susceptibility were found to vary substantially between species.

Small-scale biogeographical shifts in the proportions of species that exhibit planktotrophic, lecithotrophic and brooding modes of development are described in Appendix I for echinoderm faunal assemblages from a variety of marine and estuarine habitats within Barkley Sound, British Columbia. Shifts in the predominance of planktotrophic and lecithotrophic species within Barkley Sound are similar to larger-scale latitudinal trends among faunal assemblages along the north-east Pacific coast. The similarity in life history trends on vastly different spatial scales emphasizes the point that life history patterns are sensitive to local differences in species richness and diversity, and that the life history traits of adult echinoderms may reflect local differences in conditions for larval and juvenile survivorship.

A series of microcosm feeding experiments were used to provide the pioneering demonstration of stage-specific differences in the susceptibility of echinoderm embryos and larvae to predation by carnivorous zooplankton (Chapter 2). The occurrence of similar stage-specific susceptibility curves among phylogenetically divergent larval forms (Chapters 2, 3 and 5) allow predator-prey interactions to be assessed at a functional-group level that recognizes 5 distinct patterns of larval susceptibility (Chapter 6). The fixed shape of stage-specific susceptibility curves at ambient thermal extremes suggests that cumulative losses of embryos and larvae to predation are directly related to rates of larval development in nearshore waters (see Chapter 3).

Stage-specific differences in embryo and larval susceptibility depend in part upon differences in the feeding modes of predatory zooplankton and benthic suspension feeders. A hydromechanical analysis of locomotion and prey capture was completed for a raptorial microcrustacean (Chapter 4). The analysis revealed that differences in the behavior of echinopluteus larvae can be an effective deterrent to predation at low Reynolds numbers. In contrast, the swimming behavior of asteroid brachiolaria larvae was found to increase ~~their~~ probability of capture by two species of benthic suspension feeders. These studies provide an indication that although the outcome of larval behavioral patterns varies predictably with the feeding mode of the predator (see Table 24, Chapter 6), stage-specific feeding rates can differ between predators by orders of magnitude. Consequently, ontogenetic differences in echinoderm larval behavior cannot be used to infer rates of natural mortality.

A post-facto assessment of pre-settlement and post-settlement sources of variation in the spatial distribution of larval and juvenile asteroids is described in Chapter 5. Results from this study suggest that predation upon larvae may be an important parameter in determining spatial patterns of recruitment. Differences in the field distribution of juven[illegible] asteroids, coupled with information from zooplankton tows and laboratory feeding and substratum selection experiments, support the hypothesis that communities of benthic suspension feeders can have a significant impact on the survivorship of asteroid larvae during settlement.

Taken collectively, results from the investigations presented in this thesis show that rates of echinoderm larval mortality depend on complex interactions between the ontogeny of behavioral and morphological traits, the feeding mechanism of the predator, and local habitat conditions within the water column and near the benthos. As a consequence of the ecological complexity of these predator-prey interactions, patterns of larval mortality cannot be predicted solely on the basis of egg size and energetic expenditure per offspring.

5. Recommendations for Future Research

Several alternative and competing explanations for the bentho-pelagic life cycles of echinoderms and other metazoa may be clarified by future investigations of larval susceptibility to predation. Determination of the actual risk of mortality due to capture and ingestion, however, requires information about several related parameters. These include: 1) knowledge about breeding seasons, ova sizes, modes of larval development, behavior and morphology of larval stages, 2) results from feeding experiments to assess the relative risk associated with various developmental stages, 3) determinations of the distribution and abundance of predators in nearshore waters to allow for the calculation of encounter rates, 4) investigations of the effects of ambient environmental conditions on cumulative larval mortality, and 5) knowledge about the feeding behavior of functional groups of predators, particularly as they relate to predator-prey interactions with mixed populations of larvae. Information is also needed regarding the swimming velocities, prey capture mechanics, detection distances, and feeding and retention efficiencies for planktivores. Furthermore, it is desirable to determine the relative importance of predation in the water column compared with risk near the bottom. I have endeavored to shed some light on these subjects, and hope that the research presented in this thesis stimulates further interest in resolving the complex problem of mortality among populations of marine invertebrate larvae.

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APPENDIX I.

SMALL SCALE BIOGEOGRAPHICAL VARIATION IN LIFE HISTORY DIVERSITY AMONG ECHINODERM FAUNAL ASSEMBLAGES FROM BARKLEY SOUND, BRITISH COLUMBIA

A. INTRODUCTION

Causes of geographic variability in the life history traits of terrestrial and aquatic invertebrates have been debated for over three decades (Cole, 1954; Vance, 1973a,b; Schaffer, 1974; Frank, 1975; Stearns, 1976; Pechenik, 1979; Wilbur, 1980; Caswell, 1981, 1982). Most investigations of variability among benthic marine invertebrates have focused on large scale latitudinal trends (100-1000 km, Ockelmann, 1965; Jablonski and Lutz, 1983) or onshore-offshore changes in life history traits associated with depth (Dell, 1972; Schoener, 1972; Hansen, 1978, 1980). Typically the proportions of faunal assemblages that exhibit planktonic (planktotrophic or lecithotrophic) and benthic (direct) modes of larval development are compared. A limitation of this approach is that the scale of resolution largely pre-determines the range of possible explanations for the observed patterns. Not surprisingly, geographical variability in the frequency of marine invertebrates with planktonic and benthic modes of development has also been attributed to phenomena that differ along large spatial scales.

Geographic variability in the life history traits of benthic marine invertebrates can occur on large or small spatial scales. For example, Jackson (1974), Scheltema (1975), Schopf and Dutton (1976), Rex and Warén (1982), and Levin (1984) reported differences in reproductive traits between littoral and sublittoral habitats. Marine habitats are spatially heterogeneous and can be exposed to a wide range of environmental conditions (Dayton, 1971; Sousa, 1979). Consequently, patterns of life history observed on small spatial scales may elucidate factors that influence larger-scale patterns.

In the Pacific Northwest, the nearshore echinoderm fauna consists of over 80 species with representatives from 5 classes (Austin et al., 1971; Austin and Haylock, 1973; Lambert, 1981). These species have variable modes of development, ova sizes, and breeding seasons (Chia, 1966a,b; Strathmann, 1978; McEuen, 1986; Strathmann and Rumrill, in press; Strathmann, in press), and they occupy several different types of habitats ranging from exposed rocky intertidal headlands to protected estuarine mudflats. Within this range of habitats, differences in the distribution of species with lecithotrophic, planktotrophic and brooding modes of development can be striking. Consequently, the Pacific Northwest echinoderm fauna is a convenient group in which to examine life history patterns on a small spatial scale.

This investigation compares small and large-scale zoogeographical patterns of echinoderms with planktotrophic, lecithotrophic and brooding modes of development. Species diversity and abundance are described for echinoderms along an exposure gradient within Barkley Sound, British Columbia. A comparison is drawn between the small-scale pattern of life history diversity observed within Barkley Sound and the larger-scale zoogeographic pattern of life history diversity among asteroid faunal assemblages from 4 biogeographic regions along the north-east Pacific continental shelf. Results from this study illustrate the role of species richness and diversity in determining relationships between larval trophic mode and distribution.

B. MATERIALS AND METHODS

1. Description of Study Areas

The research was carried out from May 1984 to June 1986 at 3 study areas within Barkley Sound, on the west coast of Vancouver Island, British Columbia (Figure 49). Intertidal and subtidal surveys were conducted along benthic transect lines at Taylor Island (48°49'50"N, 125°11'53"W), Bamfield Inlet (48°49'30"N, 125°08'30"W), and Grappler Inlet (48°49'52"N, 125°07'45"). The study areas (Table 25) were selected because they were representative of local sites inhabitated by echinoderms, and because they were exposed to a gradient of waves and surf (Table 26).

A general description of marine benthic environments within Barkley Sound is given by Austin et al. (1971).

Figure 49. Location of study areas within Barkley Sound. Arrows indicate the locations of Taylor Island, Grappler Inlet, and Bamfield Inlet.

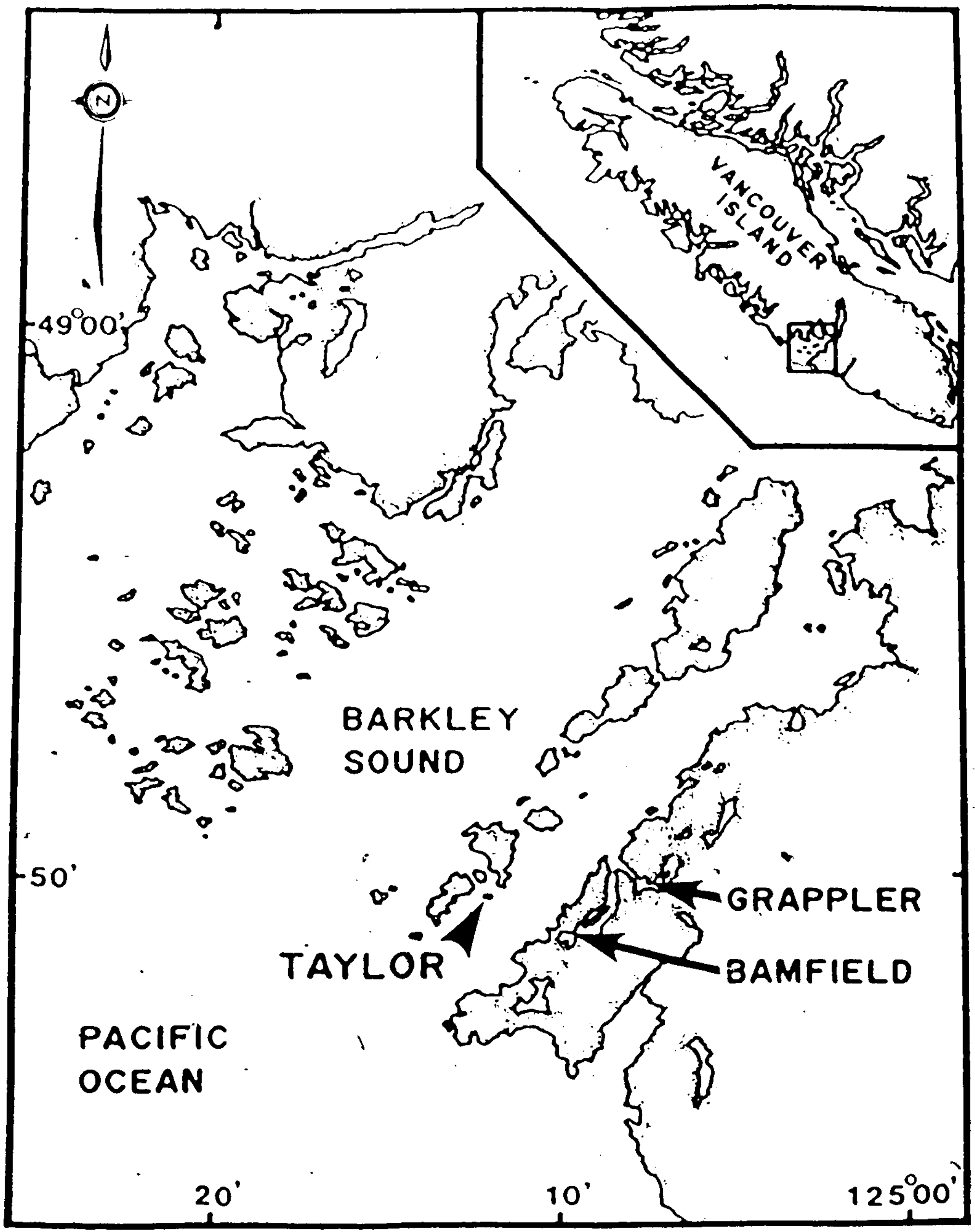

N
49°00'
50'
20'
10'
125°00'
VANCOUVER ISLAND
BARKLEY SOUND
GRAPPLER
BAMFIELD
TAYLOR
PACIFIC OCEAN

TABLE 25

Comparison of study areas, habitats and vertical ranges sampled by benthic transect lines at the Taylor Island, Bamfield and Grappler Inlet study sites.

STUDY SITE	#. TRANSECT CODE	DESCRIPTION OF HABITATS	VERTICAL RANGE (ft)	
Taylor Island	1. TI.PO.E	Intertidal: Rock wall	+ 0.7	+ 0.3
	2. TI.PO.N	Intertidal: Boulder field	+ 0.2	- 0.1
	3. TI.10.AB	Subtidal: Cliff face	-11	-16
	4. TI.35.AB	Subtidal: Boulder field	-37	-42
	5. TI.50.AB	Subtidal: Sand & Rubble	-50	-52
Bamfield Inlet	6. BI.COB.AB	Intertidal: Cobble shelf	+ 0.9	+ 0.4
	7. BI.MUD.AB	Intertidal: Mudflat	+ 0.6	+ 0.3
	8. BI.15.AB	Subtidal: Mud & cobble	-12	-16
	9. BI.40.AB	Subtidal: Mud & silt	-36	-42
	10. BI.85.AB	Subtidal: Mud & silt	-85	-92
	11. BI.PILE.AB	Subtidal: Wharf pilings	-38	-47
Grappler Inlet	12. GI.COB.AB	Intertidal: Cobble shelf	+ 1.1	+ 0.8
	13. GI.MUD.AB	Intertidal: Mudflat	+ 0.5	+ 0.3
	14. GI.20.AB	Subtidal: Mud & cobble	-16	-22
	15. GI.35.AB	Subtidal: Boulder field	-31	-39
	16. GI.40.AB	Subtidal: Mud & silt	-38	-47
	17. GI.60.AB	Subtidal: Mud & silt	-58	-63

Taylor Island is located near the southern entrance to Barkley Sound (Figure 49). Intertidal substrata at Taylor Island consist of rocky cliffs and boulder fields protected by outlying reefs. The subtidal topography at Taylor Island is heterogeneous; cliffs and bedrock are interspersed with sloping boulder fields and regions of sand and shell rubble. In the summer of 1984, five 50 m transect lines were established at Taylor Island. Two of the lines were laid in the intertidal, the first along a rock wall and the second through an adjacent boulder field (Figure 50). Three additional transect lines were established subtidally at average depths of 14, 37 and 54 ft below Mean Lower Low Water (MLLW: Canadian Datum).

Bamfield and Grappler Inlets are less exposed to waves than Taylor Island (Figure 51). Substrata located along sheltered intertidal regions of the inlets range from rock and boulders to cobble and mud. Intertidal mudflats are located at the head of each inlet, and gravel and mud bottoms are prevalent in the shallow and deeper subtidal regions. A series of six transect lines were established within each inlet (Table 25). A major difference between the two inlets is that subtidal boulder fields near the mouth of Grappler Inlet are inhabited by an invertebrate and algal community typical of the open-coast whereas most species that inhabit Bamfield Inlet are characteristic of more protected marine habitats.

The Taylor Island, Bamfield Inlet and Grappler Inlet

Figure 50. Locations of 5 transect lines laid at Taylor Island. Lines 1 and 2 traverse intertidal habitats. Lines 3-5 traverse subtidal habitats. The number beside each transect line corresponds to descriptions listed in Table 26 and elsewhere throughout the text. Each transect line is 50 m in length.

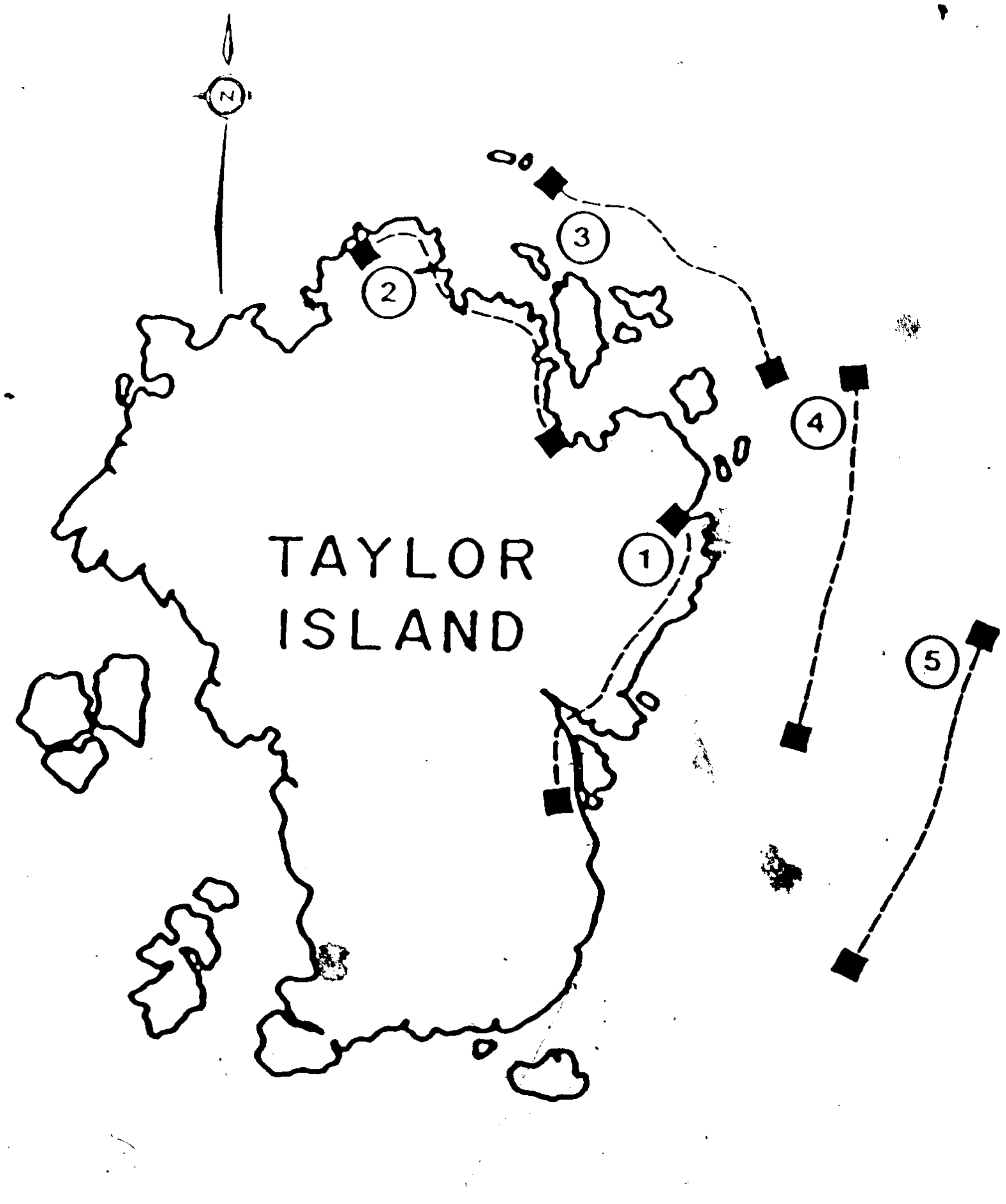
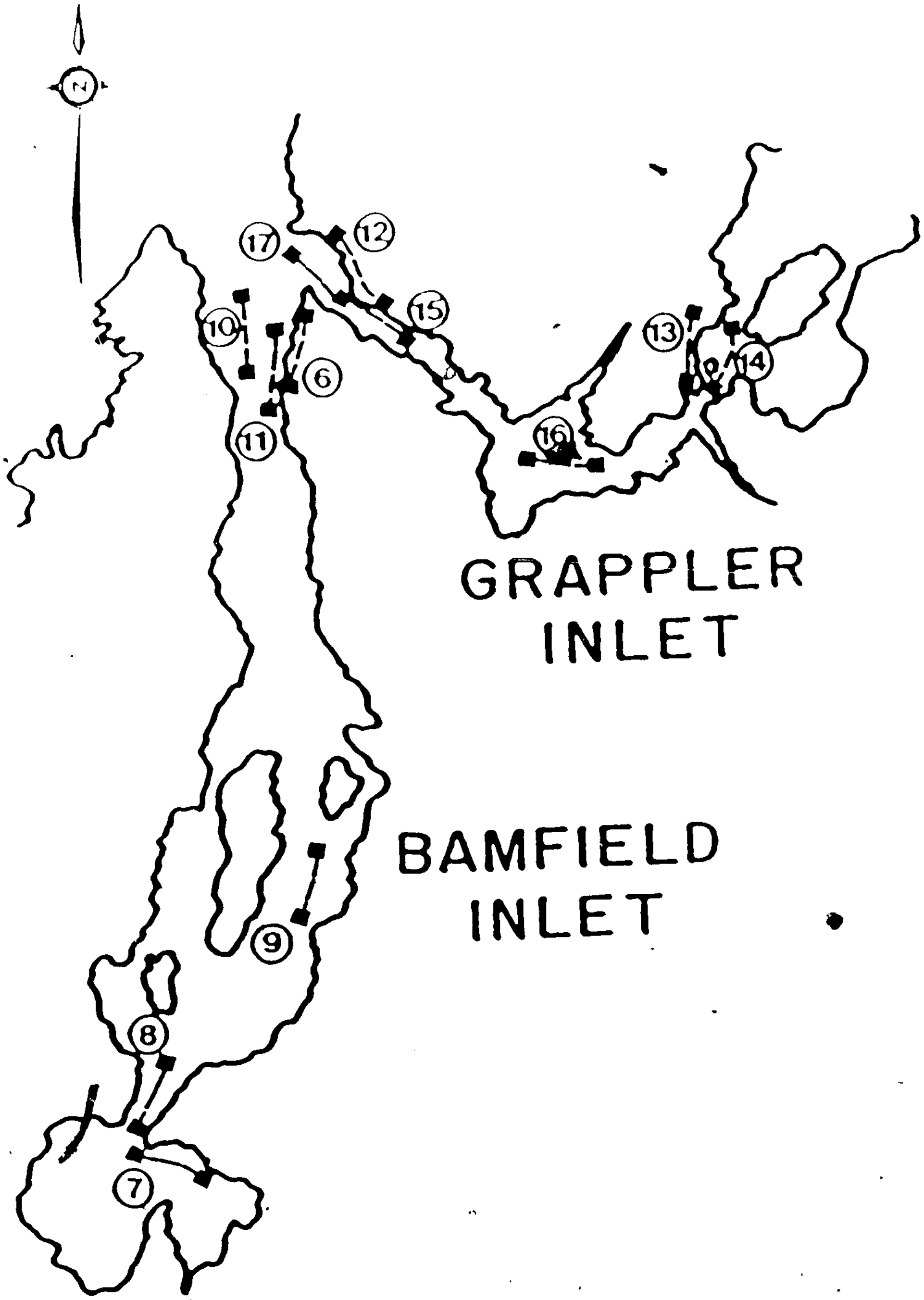

N
TAYLOR ISLAND
1
2
3
4
5

Figure 51. Locations of 12 transect lines laid within Grappler and Bamfield Inlets. Lines 6,7 12 and 13 traverse intertidal habitats. All other lines are subtidal. The number beside each transect corresponds with discriptions listed in Table 26 and elsewhere throughout the text. Lines 7 and 13 are 30 m in length. All other lines are 50 m in length.


N
17
12
15
10
6
11
13
14
16
GRAPPLER INLET
BAMFIELD INLET
9
8
7

study sites occur along a conspicuous environmental gradient. Differences in the relative degree of exposure between the sites are related to differences in the intensity of wave action, physical disturbance, sediment grain size, and depth. No single parameter can provide a reliable index of the position of a particular site along the environmental gradient. In this study, three indices were used to evaluate the relative degree of exposure at each transect line. The first index was a subjective assessment of local exposure based on experience acquired during surveys of transect lines. The second index was an estimate of the range of sediment grain sizes. Sediments were sampled at each transect (June 16-18, 1986) and brought into the laboratory where they were dried and sorted through a series of sediment sieves. Differences in sediment grain sizes were analyzed according to the Wentworth scale (Holme and McIntyre, 1971). The third index estimated the relative degree of wave action along each transect by determining the weight loss of Plaster of Paris casts according to the methods of Muus (1968) and Doty (1971). At three times during the study (July 19, September 21, 1985 and June 18, 1986), six replicate plaster-casts were anchored to the substratum adjacent to each transect line. The casts were recovered after one tidal cycle, rinsed in distilled water, and air-dried at room temperature to constant weight. Sea surface temperature and hydrometer measurements of salinity were made at approximately monthly intervals at each of the three study areas.

2. Surveys of Benthic Transects

Densities of echinoderms were estimated along the 17 transect lines with a standardized sampling procedure. All individuals encountered within contiguous 0.25 or 1.0 m^2 quadrats were identified to species, counted and measured in situ with calipers. The effects of quadrat size were analyzed by plots of species richness (S) and number of individuals (N) versus quadrat area (A: cm^2). The census technique was evaluated for rocky-bottom habitats with preliminary data from a 50 m transect line (TI.10.AB) laid at Taylor Island at a depth of 13-17 ft ($S = -1.54 + 0.36 \ln A$, $r^2 = 0.8602$; $N = -0.33 + 1.27 \times 10^{-3} A$, $r^2 = 0.9290$). Quadrat size was evaluated for soft-substratum habitats with data from a 50 m transect (GI.20.AB) at a depth of 19 ft in Grappler Inlet ($S = -1.09 + 0.29 \ln A$, $r^2 = 0.4120$; $N = 1.00 + 2.17 \times 10^{-4} A$, $r^2 = 0.6156$). The lengths of transect lines (30 or 50 m) were determined by the position of asymptotes on plots of the cumulative number of species encountered along each transect line (Figures 55-57).

Disruptive sampling techniques were used to quantify the abundance of cryptic species following the initial non-destructive surveys. Densities of infaunal ophiuroids and holothuroids were determined from a set of 8-12 randomly placed coffee-can cores (248 cm^2; see Oliver and

Slattery, 1985). Densities of juvenile echinoderms were determined along each transect during the initial surveys, and from a series of 9 - 12 randomly placed 0.25 m^2 quadrats. The cryptic behavior and small size of juveniles required that careful searches be made of understory algae and cobble during initial surveys of adult echinoderms. Repeated sampling of particular quadrats by successive divers revealed that small juveniles were often overlooked during the surveys of adults. In a second survey designed to sample cryptic juveniles, substratum samples were collected with an airlift suction device. All mobile and encrusting invertebrates and foliose algae were removed from each 0.25 m^2 quadrat and collected in 1 mm mesh bags. The contents of the bags were returned to the laboratory and sorted under a stereomicroscope. Some of the juvenile echinoderms collected by the airlift were too small to be identified to species. These individuals were raised in a laboratory nursery until their identification could be confirmed.

Several indices of diversity were calculated from estimates of species abundance and richness along the intertidal and subtidal transects (Pielou, 1966a,b, 1975; Loya, 1972; Krebs, 1978). Species richness (S) was simply the cumulative number of species encountered along each transect line. Estimates of species richness are dependent upon sample size (Figures 55-57) and do not distinguish between abundant and rare species. In most cases, S underestimated the actual number of species within a particular habitat, although only 2 to 3 species known to occur along the transect were missing from the quantitative samples (Tables 27 and 28). Simpson's Index (D_n) was calculated from the number of individuals for a particular species as:

$$D_n = 1 - \sum_{i=1}^{S} (p_i)^2$$

where p_i is the proportion of individuals of species i in the sample.

A third measure of diversity was the Shannon-Wiener Index, H_n, where:

$$H_n = - \sum_{i=1}^{S} (p_i) \ (\mathrm{Ln}\ p_i)$$

The final indices were ranks of relative species variety, V, where:

$$V = (S - 1) / (\mathrm{Ln}\ N)$$

and community diversity, α, where:

$$S = \alpha\ \mathrm{Ln}\ (1 + (N / \alpha\ )$$

and N is the total number of individuals encountered along the transect (Margalef, 1958). Although the diversity indices were not always in agreement in their ranking of particular transects, the general pattern of echinoderm species diversity was nearly identical (Figure 59).

3. Echinoderm Life History Traits

Quantitative information was gathered for several life history traits including ova size, fecundity and larval development mode for 36 species of echinoderms (Table 29). Most observations of reproductive traits were made during early spring (April and May, 1984-85) when adults were gravid and spawning individuals were observed in the field. Measurements of ova sizes were made during February, 1985 for species that breed during winter (Table 30). Estimates of the number of ova per female were obtained by two methods. In the first method, direct counts of ova were made following spawning in laboratory aquaria. Ova were counted in Sedgewick-Rafter chambers that contained 1 ml aliquots of the spawn suspension. In the second method, ova were counted from suspensions prepared by maceration of gravid ovaries. Only mature ova were included in the counts. Although both methods underestimate the number of eggs released during a period of spawning activity, the latter technique usually yielded greater fecundity values due to the inclusion of residual oocytes and ova. Ova sizes were measured in ocular units along their greatest diameter at a magnification of 40X. Modes of larval development were determined from direct observations of embryos and larvae in laboratory cultures, or inferred from measurements of ova diameter (see Table 29).

4. Large Scale Shifts in Echinoderm Life History Traits

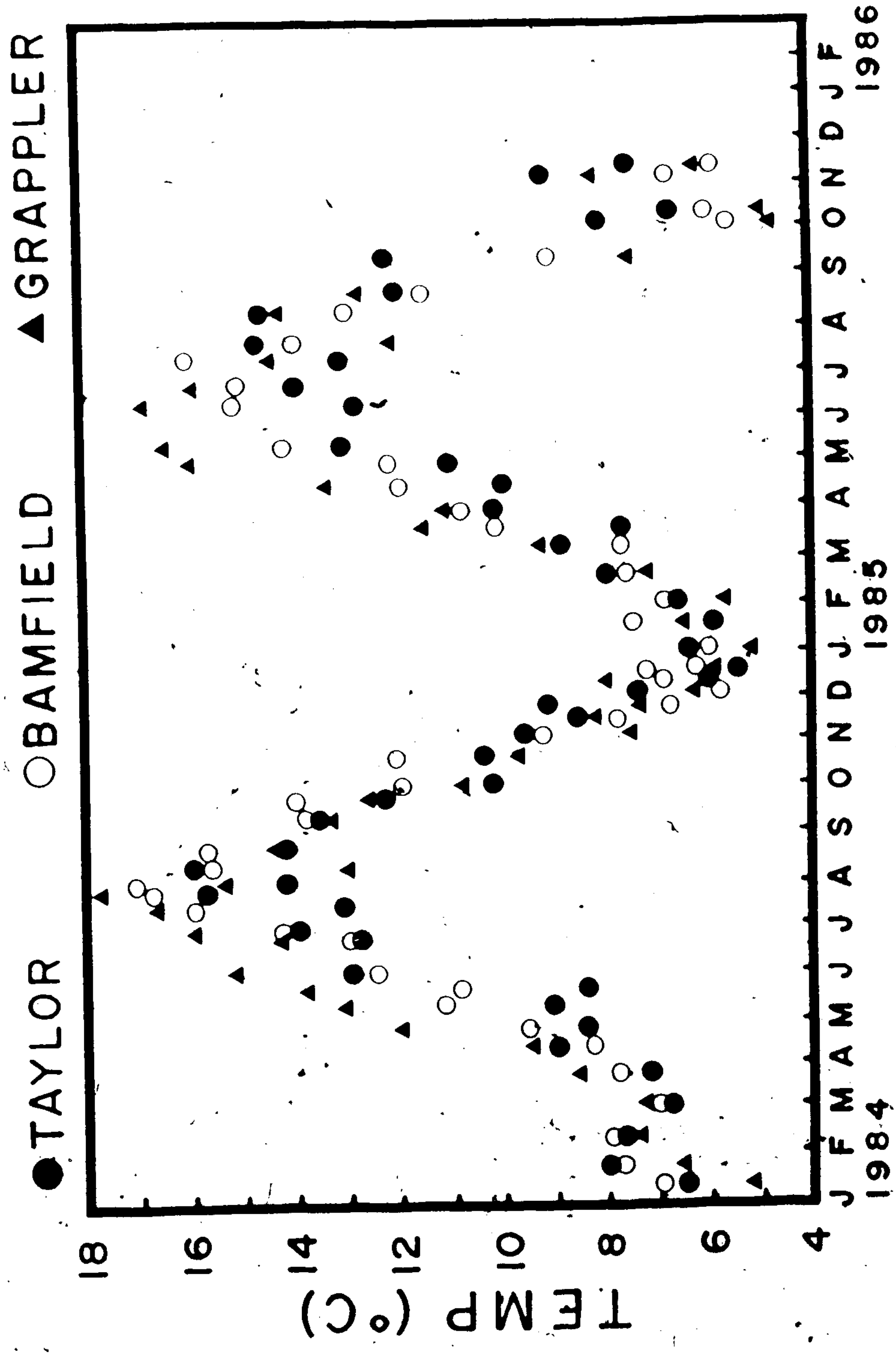
Latitudinal shifts in modes of development were analyzed for assemblages of asteroids within 4 biogeographic regions including: 1) Baja - Southern California (25-35°N Lat.), 2) Central California - Oregon (35-45°N Lat.), 3) Washington - British Columbia (45-55°N Lat.), and 4) Aleutian - Bering Sea (55-65°N Lat.). These biogeographical boundaries are consistent with differences in the distribution of marine fish, invertebrates, and algae along the temperate and boreal east Pacific coast (Dodimead et al., 1963; Valentine, 1966; Briggs, 1974; Hayden and Dolan, 1976; Horn and Allen, 1978; Murray et al., 1980; Hartman and Zahary, 1983). Frequencies of asteroid species with planktotrophic, lecithotrophic and brooding modes of development were calculated only for species whose mode of development is known rather than inferred from egg size.

C. RESULTS

1. Comparison of Study Areas

Ambient sea surface temperatures varied seasonally from 6° to 16°C in 1984 and from 5° to 14°C in 1985 at Taylor Island (Figure 52). Surface temperatures in Bamfield and Grappler Inlets were slightly greater than temperatures at Taylor Island during the summer months of 1984-85, and all three sites showed a marked seasonal cycle (Figure 52).

Figure 52. Seasonal surface temperatures over two consecutive years at Taylor Island and within Bamfield and Grappler Inlets.


● TAYLOR
○ BAMFIELD
▲ GRAPPLER
TEMP (°C)
18
16
14
12
10
8
6
4
J F M A M J J A S O N D J F M A M J J A S O N D J F
1984
1985
1986

Salinities averaged 30.2 ppt at Taylor Island, and periods of low salinity (< 28-30 ppt) occurred occasionally during winter and spring (Figure 53). In contrast, salinities varied seasonally from 17 to 30 ppt during 1984 and from 23 to 32 ppt during 1985 in Bamfield and Grappler Inlets (Figure 53). Salinities in the inlets during late summer and fall were similar to those at Taylor Island, and low salinities (< 25 ppt) occurred in winter and spring during periods of heavy rainfall.

The exposure gradient along the 17 benthic transect lines is characterized at one extreme by a wave-swept rocky intertidal wall and at the other by quiet water soft-sediment habitats. Sediment particle sizes ranged from boulders and coarse sand at the Taylor Island site to cobble, fine sand and silt at the Bamfield and Grappler Inlet sites (Table 26). The degree of exposure to ocean swells and wave surge also differed between the study areas (Figure 54). A Kendall's test of concordance indicated that there was significant agreement in the weight-loss of plaster casts between sample dates (Figure 54; W = 0.89, $p < 0.005$). Pooled weight-loss rates of plaster casts were greatest at Taylor Island, intermediate at Bamfield Inlet, and lowest in Grappler Inlet (Kruskal-Wallis ANOVA, H = 168.48, $p < 0.001$). There was an inverse correlation between cast weight-loss and transect depth at all three study areas. Differences in depth accounted for 70% of the variance in weight loss values at Taylor Island, 10% at

Figure 53. Seasonal surface salinities over two consecutive years at the Taylor Island, Bamfield and Grappler Inlet Study sites.

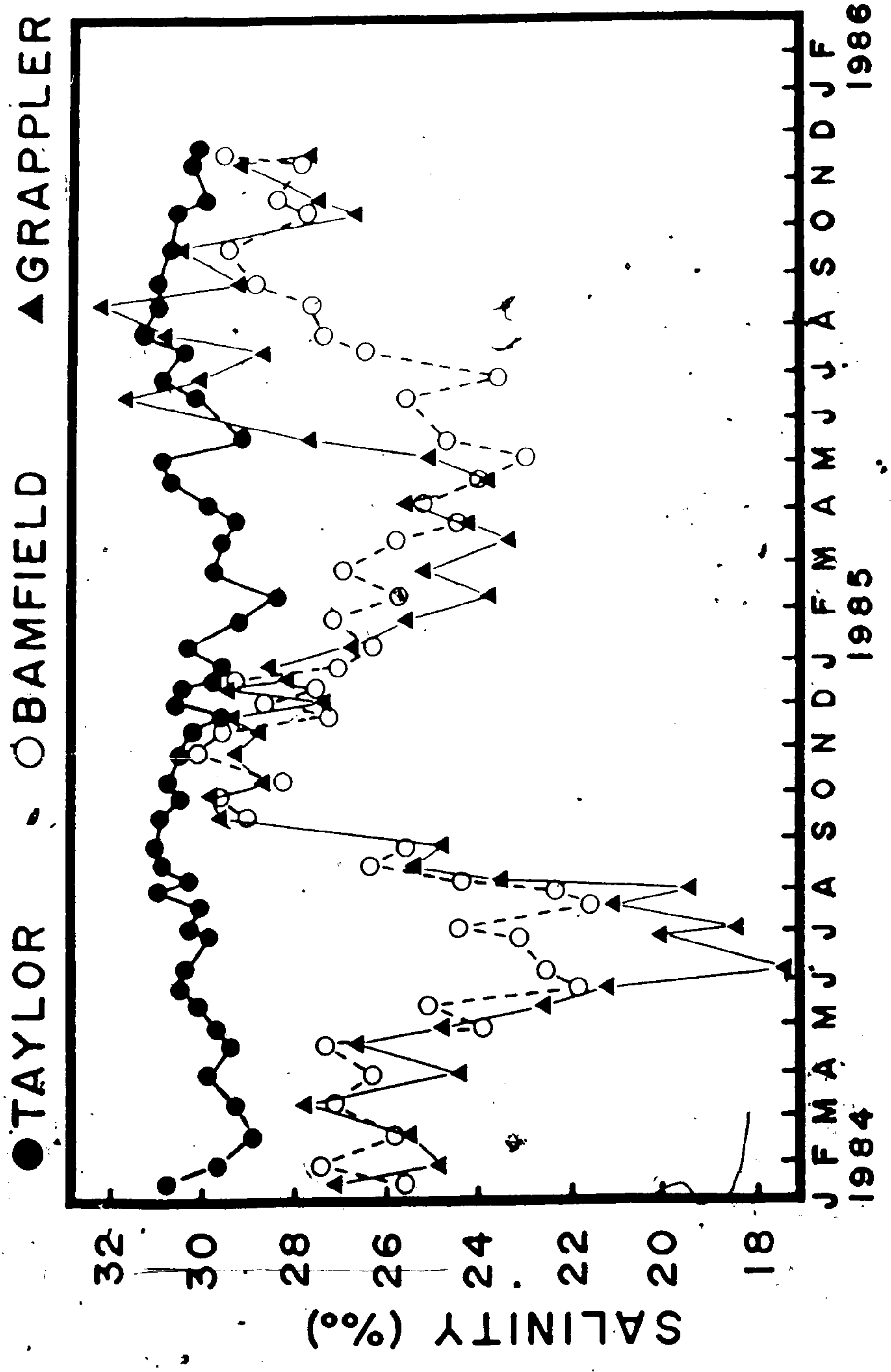
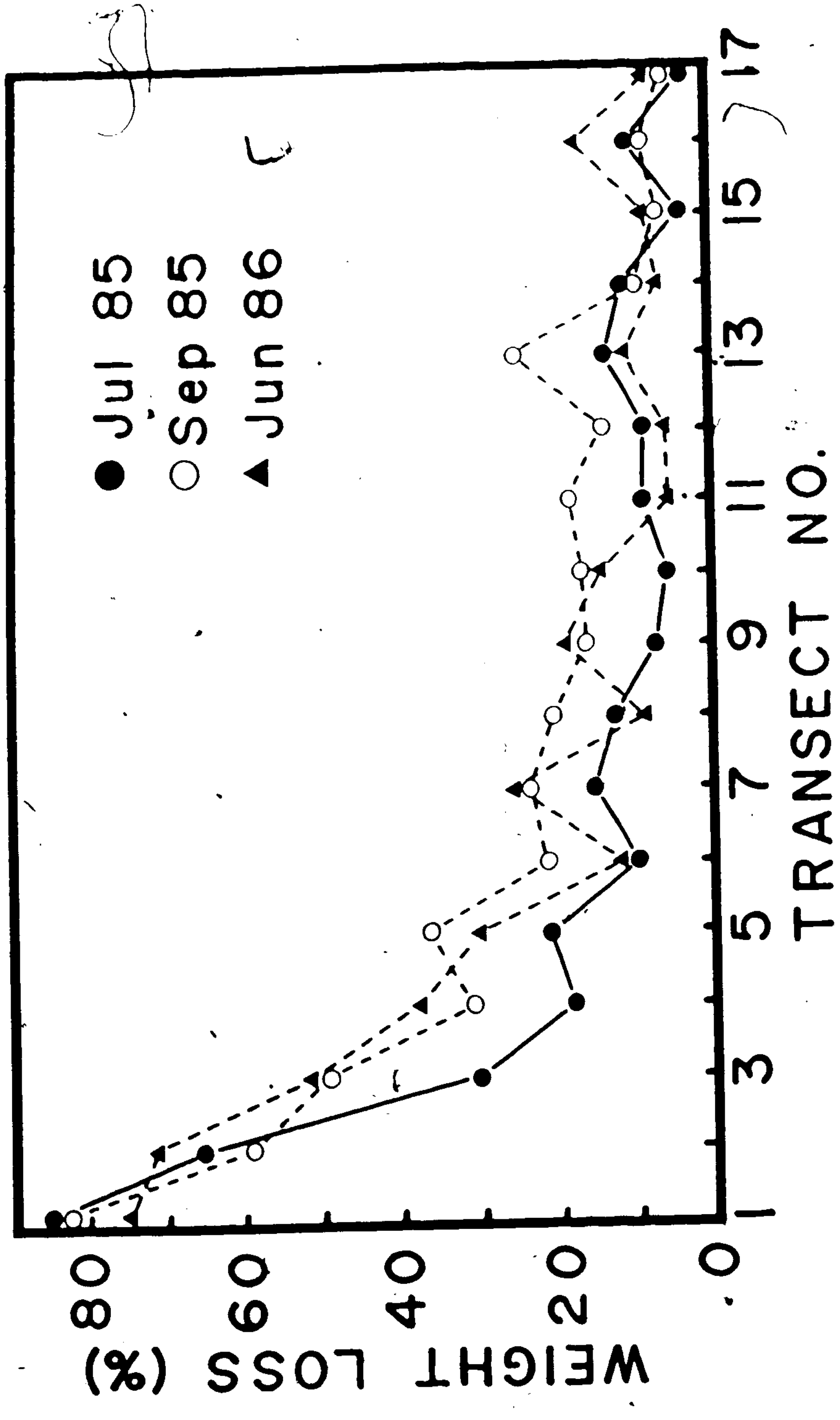

● TAYLOR
○ BAMFIELD
▲ GRAPPLER
SALINITY (‰)
32
30
28
26
24
22
20
18
J F M A M J J A S O N D J F M A M J J A S O N D J F
1984
1985
1986

TABLE 26

Comparison of the relative positions of 17 benthic transect lines along the environmental gradient. Positions are based on a subjective rank of exposure, sediment particle grain size, and percent weight loss of plaster casts. Sediment particle size categories are shown according to the Wentworth Scale (boulder > 256 mm, cobble > 64 mm, coarse sand 1-0.5 mm, fine sand 0.25-0.12 mm, silt 0.06-0.004 mm). Plaster cast index values show ranked sums pooled fro 3 sample-periods and mean percent weight loss averaged over one tidal cycle.

STUDY SITE	#	TRANSECT CODE	SUBJECTIVE INDEX	SEDIMENT PARTICLE SIZE (%)	PLASTER CAST (% loss)
Taylor Island	1.	TI.PO.E	1. very exposed	boulder (100)	1 (81)
	2.	TI.PO.N	2. very exposed	boulder (100)	2 (65)
	3.	TI.10.AB	3. exposed	boulder (100)	3 (44)
	4.	TI.35.AB	4. exposed	boulder (94)	5 (28)
	5.	TI.50.AB	7. semi-protected	coarse sand (91)	4 (29)
Bamfield Inlet	6.	BI.COB.AB	5. exposed	cobble (96)	8 (16)
	7.	BI.MUD.AB	12. protected	silt (98)	6 (22)
	8.	BI.15.AB	14. protected	silt (86)	9 (15)
	9.	BI.40.AB	16. very protected	silt (72)	10 (14)
	10.	BI.85.AB	9. semi-protected	silt (78)	12 (11)
	11.	BI.PILE.AB	11. semi-protected	fine sand (74)	14 (10)
Grappler Inlet	12.	GI.COB.AB	6. exposed	cobble (83)	15 (10)
	13.	GI.MUD.AB	13. protected	silt (94)	7 (17)
	14.	GI.20.AB	15. protected	silt (81)	13 (10)
	15.	GI.35.AB	8. semi-protected	cobble (69)	17 (5)
	16.	GI.40.AB	17. very protected	silt (96)	11 (12)
	17.	GI.60.AB	10. semi-protected	silt (82)	16 (6)

Figure 54. Exposure gradient within Barkley Sound estimated by the proportional weight loss of plaster casts along each of 17 transect lines located at various sites within Barkley Sound (see Table 26). Transects 1-5 are characterized by high exposure, 6-11 by intermediate exposure, and 12-17 by low exposure. Weight loss values indicate the mean percent loss of 3-6 casts over one complete tidal cycle. Dates indicate months when rates of weight loss were recorded.


● Jul 85
○ Sep 85
▲ Jun 86
WEIGHT LOSS (%)
80
60
40
20
0
TRANSECT NO.
1
3
5
7
9
11
13
15
17

Bamfield Inlet and 15% at Grappler Inlet. The positions of transects along the exposure gradient illustrated by the subjective ranking, sediment grain size and plaster cast indices are consistent with changes in the distribution of intertidal invertebrates and algae (Austin _et al_., 1971), and suggest that the exposure gradient shown in Figure 54 is a persistent feature among the study sites in Barkley Sound.

2. Diversity and Abundance of Barkley Sound Echinoderms

A total of 37 species of echinoderms were encountered during transect surveys at Taylor Island, Bamfield Inlet and Grappler Inlet. Counts of the cumulative number of species encountered along each transect are shown in Figures 55-57. The total number of species typically reached an asymptote after 20-24 successive quadrats in habitats occupied by less than 15 species. Asymptotes were reached after about 35 successive quadrats in habitats occupied by more than 15 species. The greatest number of species occurred along rocky bottom subtidal transects at Taylor Island and Grappler Inlet, and among wharf pilings at the Bamfield Inlet study area (Figures 55-57). Intertidal mud flats and rocky cliffs were inhabited by the lowest number of species.

Figure 58 shows the proportion of the echinoderm fauna composed of echinoids, asteroids, holothuroids, ophiuroids, and crinoids at each of 17 transects. Asteroids were found along all transect lines and composed the greatest

Figure 55. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Taylor Island study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 50).

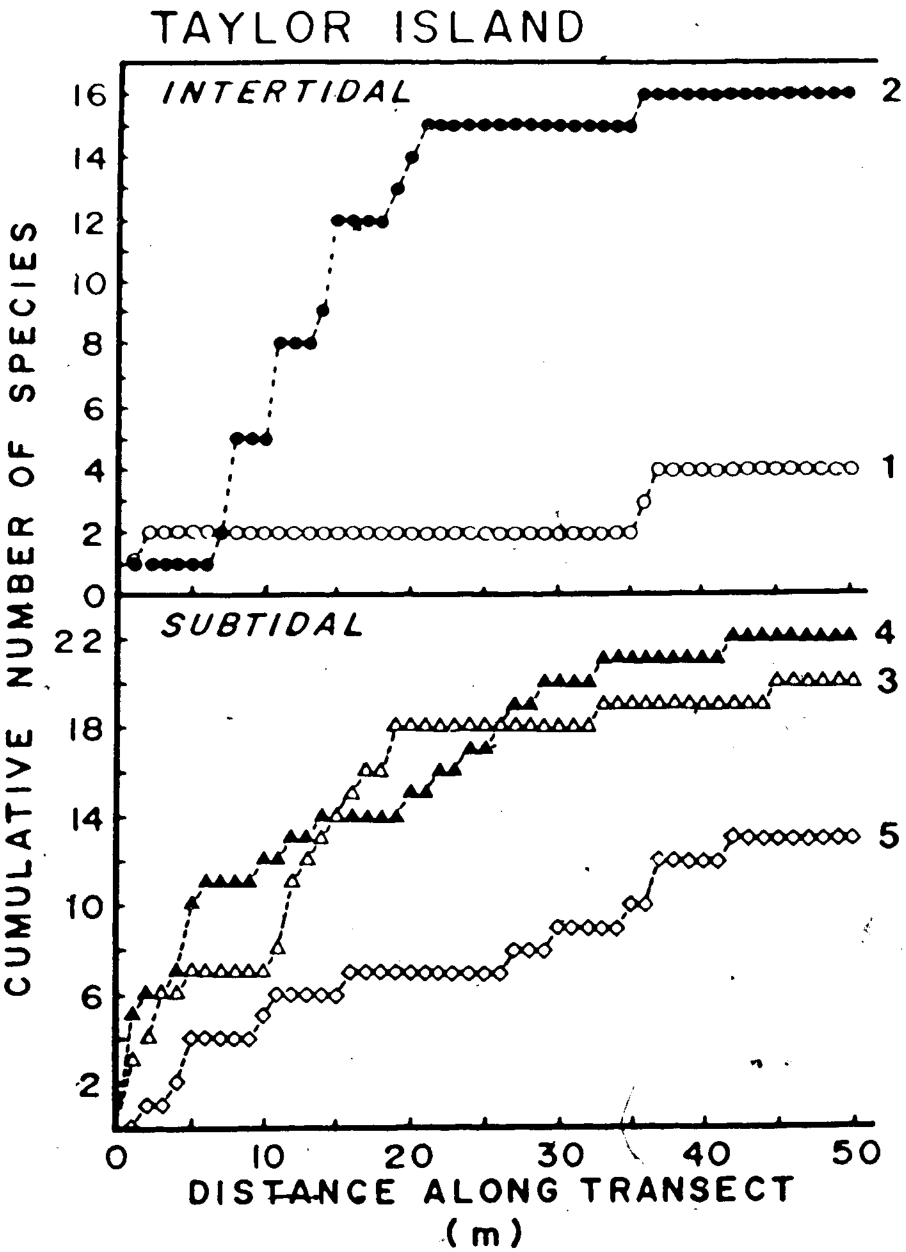

TAYLOR ISLAND
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
0
2
4
6
8
10
12
14
16
2
6
10
14
18
22
DISTANCE ALONG TRANSECT (m)
0
10
20
30
40
50
1
2
3
4
5

Figure 56. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Bamfield Inlet study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 51).

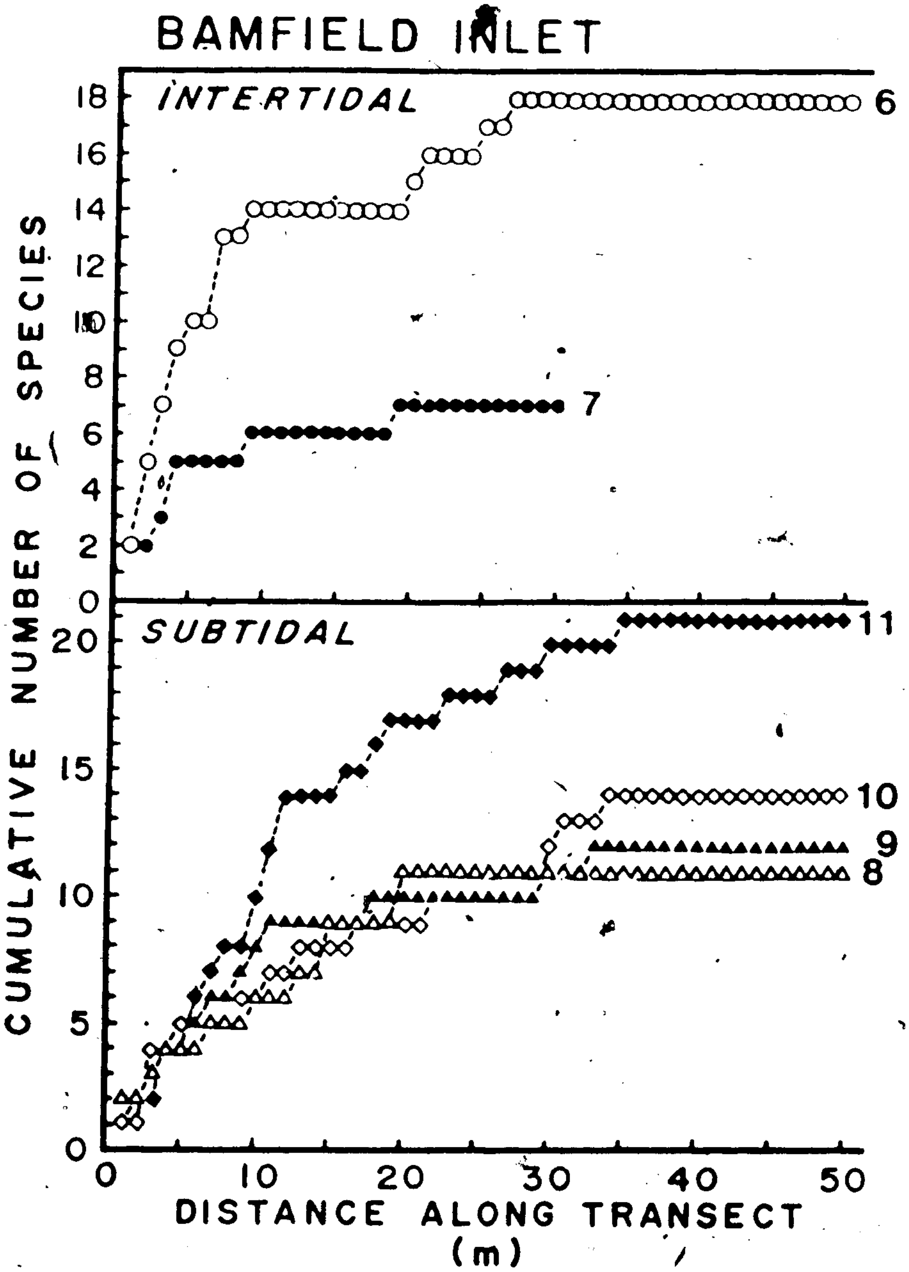

BAMFIELD INLET
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
6
7
11
10
9
8
0
10
20
30
40
50
DISTANCE ALONG TRANSECT
(m)

Figure 57. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Grappler Inlet study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 51).

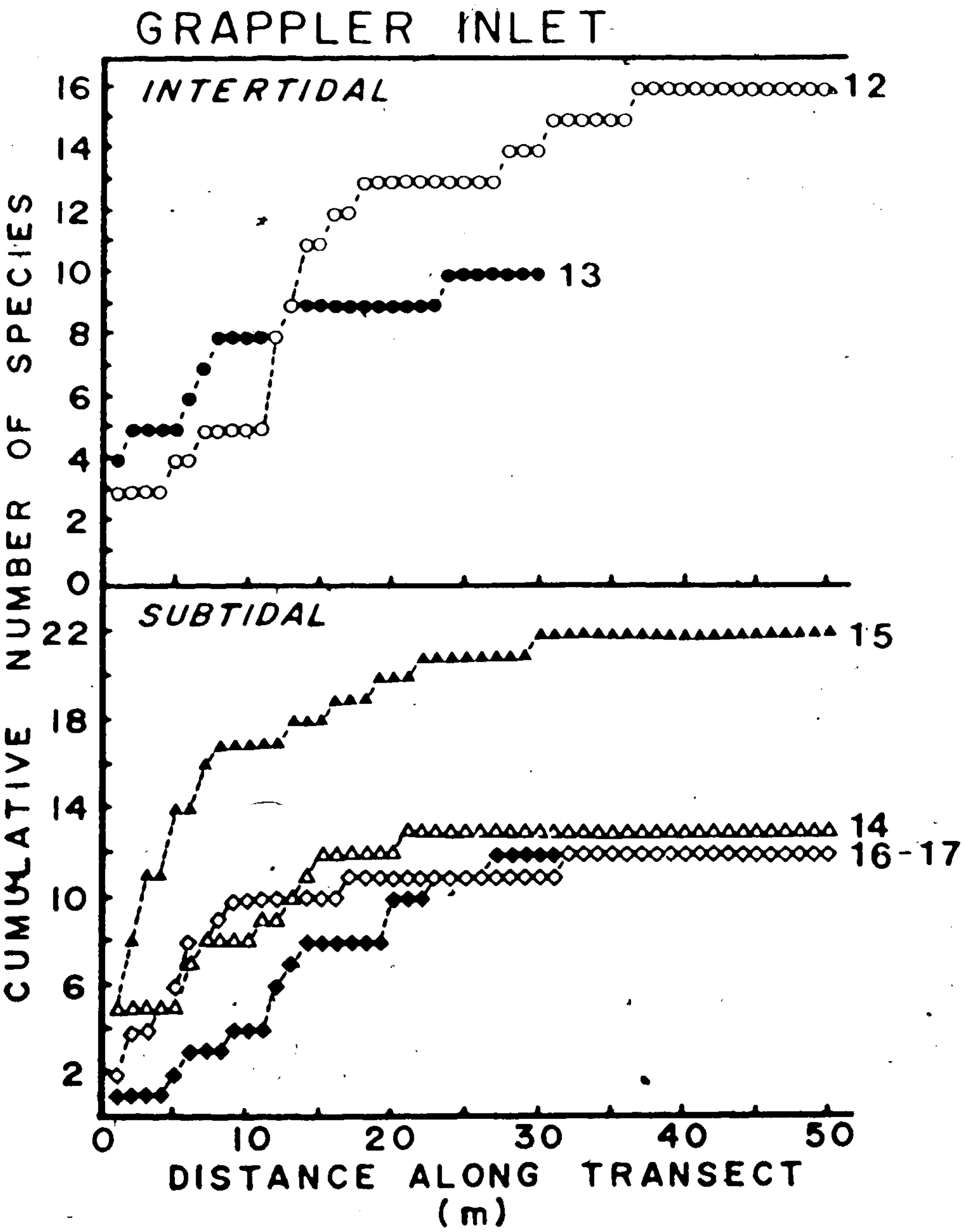
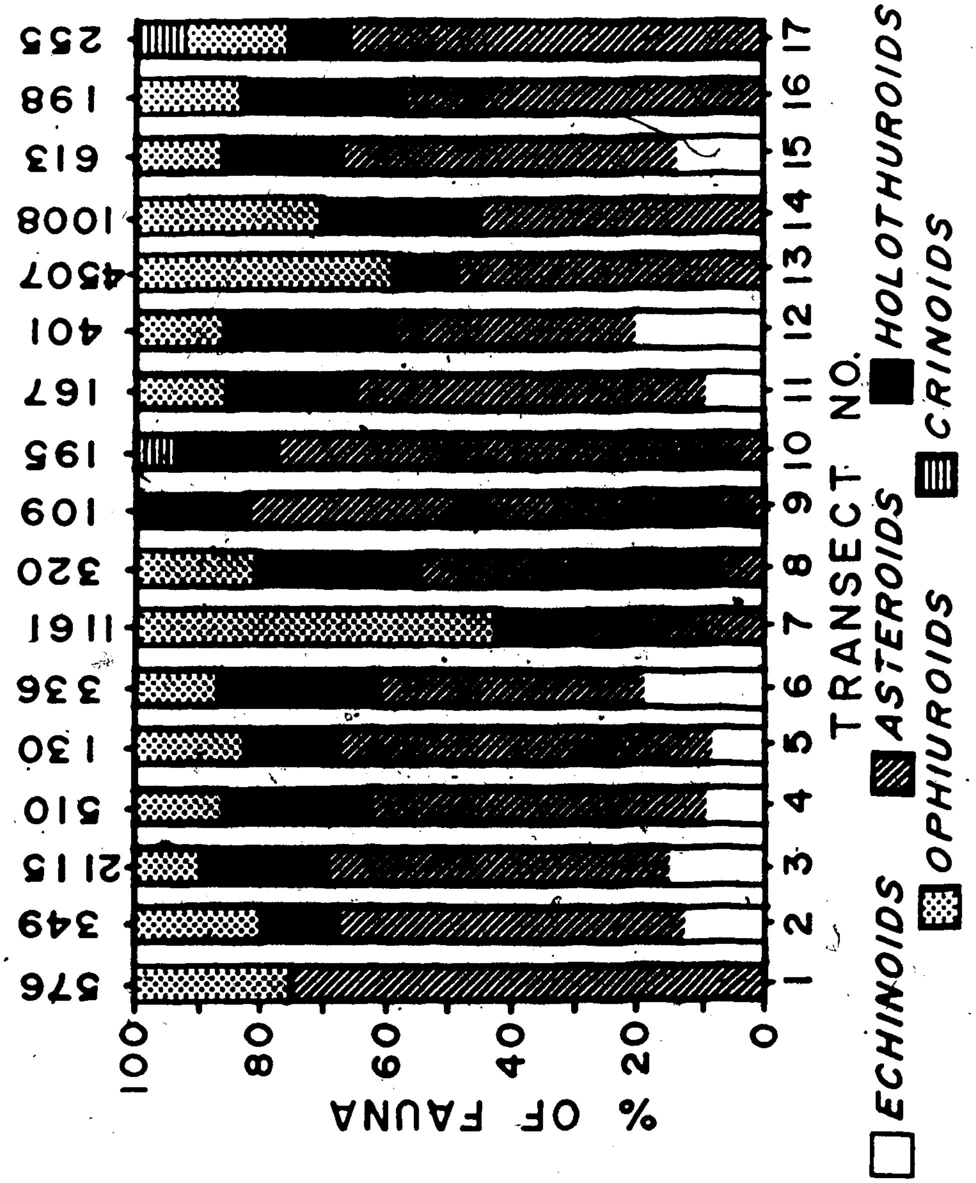

GRAPPLER INLET
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
0
2
4
6
8
10
12
14
16
2
6
10
14
18
22
12
13
15
14
16-17
0
10
20
30
40
50
DISTANCE ALONG TRANSECT
(m)

Figure 58. Proportions of the echinoderm fauna composed of echinoids, asteroids, holothuroids and crinods. Transect numbers refer to transect lines listed in Table 26. The number above each bar indicates the total number of individuals on which each proportion is based.


% OF FAUNA
100
80
60
40
20
0
TRANSECT NO.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
576
349
2115
510
130
336
1161
320
109
195
167
401
4507
1008
613
198
255
ECHINOIDS
ASTEROIDS
HOLOTHUROIDS
OPHIUROIDS
CRINOIDS

proportion of the echinoderm fauna at 16 sites. Echinoids were represented at 8 sites by 3 species, and the comatulid crinoid, <u>Florometra serratissima</u>, occurred in deep water at two sites (Figure 58). Holothuroids were a conspicuous component of the echinoderm fauna along all transect lines except one that traversed an exposed rocky intertidal habitat. Ophiuroids were found in 15 of 17 sites (Figure 58), and they were abundant along with infaunal holothuroids in protected mud-flat habitats.

The distribution and densities of 37 species of echinoderms are listed in Tables 27 and 28. Seven species of sea urchins occur within Barkley Sound (Austin and Deutsch, 1978). However, only 3 species were encountered during quantitative sampling along benthic transects. Both the red urchin, <u>Strongylocentrotus franciscanus</u>, and the purple urchin, <u>S. purpuratus</u>, were abundant in shallow water at Taylor Island (Table 27). Densities of <u>S. franciscanus</u> averaged 174 ± 44 and 17 ± 6 per 10 m^2 along the 15 and 35 ft depth contours, respectively. Purple urchins averaged 19 ± 24 per 10 m^2 at 15 ft below MLLW, but their densities decreased rapidly in deeper water. The green urchin, <u>S. droebachiensis</u>, was common on wharf pilings and a variety of hard substrata ranging from exposed bedrock to cobble habitats in sheltered locations (Tables 27 and 28).

Although asteroids were found along all transect lines, only 2 species, <u>Pycnopodia helianthoides</u> and <u>Dermasterias</u>

TABLE 27

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did n[illegible]ppear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ECHINOIDEA: SF	SP	SDR	ASTEROIDEA: PO	PB	PG	OK	STY	ET	LH	PH	DI	SS	SO	SPAX
Taylor Island																	
	1.	TI.PO.E	0	0	0	107.6 50.2	0	0	0	0	0	3.8 8.5	0	0	0	0	0
	2.	TI.PO.N	0.6 0.9	18.8 23.6	+	32.0 28.7	0	0	0.4 0.5	0	0.8 1.3	5.4 4.0	0.2 0.5	0.2 0.5	0	0	0
	3.	TI.10.AB	173.7 44.9	42.0 19.3	0.8 0.8	0.4 0.5	0.1 0.3	0	1.0 1.2	0	0.1 0.3	1.2 1.1	1.4 1.3	0.4 0.7	0.1 0.3	0.6 0.9	0
	4.	TI.35.AB	17.1 5.6	0.1 0.1	0	0	0.3 0.5	0	0.8 1.0	0.3 0.5	0.2 0.4	0	0.4 0.7	0.1 0.3	0.6 0.9	0.3 0.5	0
	5.	TI.50.AB	7.0 9.4	0	0	0	0.1 0.3	0.1 0.3	0.4 0.7	0	0	0	0	0	0.1 0.3	1.0 1.4	0

TABLE 27 (continued)

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ASTEROIDEA: SE	LOF	CP	HL	HNS	HA	PT	MA	PM	HOLOTHUROIDEA LA	PC	CM	CFIP	EO	PSOL	LC
Taylor Island	1.	TI.PO.E	0	0	0	0	0.6 1.3	0	0	0	0	0	0	0	0	0	0	0
	2.	TI.PO.N	0	0	0	0.2 0.5	0.4 0.9	0	0	0	0.4 0.5	0	0	3.2 5.1	0	0.6 1.3	0	0
	3.	TI.10.AB	0	0 +	0	1.4 1.8	0.2 0.4	0	0	0	0	0	2.1 4.0	1.9 2.3	0.2 [illegible]	0.6 0.9	+	0
	4.	TI.35.AB	0	0	0	5.4 3.0	0.2 0.4	0	0.2 0.4	0.2 0.4	0	0	1.8 1.1	13.7 22.8	1.6 1.5	0.8 1.1	3.9 3.9	0
	5.	TI.50.AB	0	0	0.3 0.7	0.2 0.4	0.1 0.1	0	0	0	0	+	1.4 1.2	+	+	0.1 0.3	0	0

TABLE 27 (continued)

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	OPHIUROIDEA: OA	AO	AU	AP	AX	CRINOIDEA: FS	INDEX OF DIVERSITY: TOTAL # Spp.	SHANNON Hn	SIMPSON Dn	COMMUNITY α	VARIETY J
Taylor Island	1.	TI.PO.E	0	0	0	0	3.4 1.7	0	4	0.30	0.13	0.58	1.09
	2.	TI.PO.N	1.0 1.7	0.2 0.5	0	0	5.4 2.9	0	16	1.60	0.72	3.46	5.89
	3.	TI.10.AB	35.8 37.5	+	0	0	113.7 68.3	0	20	0.66	0.31	3.06	5.71
	4.	TI.35.AB	10.2 6.0	3.5 3.7	0	0	6.2 6.7	0	22	1.77	0.75	4.68	7.26
	5.	TI.50.AB	+	5.8 4.0	0	0	7.1 6.2	0	13	1.17	0.50	3.60	5.68

TABLE 2B

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets. Table entries show the mean and s.d. (below) number of individuals per 10 square meters. A (+) symbol indicates species was present at the site but did not appear within a quadrat. Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ECHINOIDEA: SF	SP	SDR	ASTEROIDEA: PO	PB	PG	OK	STY	ET	LH	PH	DI	SS	SC	SPAX
Bamfield Inlet	6.	BI.COB.AB	0.6 0.9	7.8 6.2	1.4 1.5	16.6 6.2	0	0	0.6 0.9	0	0	27.4 13.6	+	0.8 0.8	0	0.2 0.4	0
	7.	BI.MUD.AB	0	0	0	0	+	0	0	0	0.4 1.3	0	0	0.4 0.9	0	0	0
	8.	BI.15.AB	0	0	0	0	0.4 0.5	0	0	0	0.4 0.5	0	0.4 0.7	0.5 0.7	0	0	0
	9.	BI.40.AB	0	0	0	0	3.0 2.3	0	1.0 0.7	0	1.5 1.3	0	1.8 1.5	0.6 0.5	0.2 0.4	0.1 0.3	0
	10.	BI.85.AB	0	0	+	0	0.2 0.6	0	1.0 0.3	0	+	0	0.1 0.3	0	0.4 0.7	0.6 0.8	0
	11.	BI.PILE.AB	0.3 0.7	0	0.1 0.3	+	0.5 0.7	0	0.7 0.8	0	0.3 1.0	+	2.7 2.2	1.6 1.2	0.6 0.8	0.2 0.4	0.1 0.3
Grappler Inlet	12.	GI.COB.AB	0.6 0.9	18.4 15.1	2.6 1.8	4.2 4.6	0	0	0.2 0.4	0	0	10.4 6.2	0	1.0 0.7	0	0	0
	13.	GI.MUD.AB	0	0	0	0.5 1.1	+	0	0	0	0	0.7 2.1	0.4 0.9	0.4 0.9	0	0	0
	14.	GI.20.AB	0	0	0	0.6 0.7	1.2 0.4	0	+	0	0.9 1.0	0	1.6 1.3	1.6 1.3	0	0	0
	15.	GI.35.AB	0.8 1.0	0.3 0.5	2.4 2.5	0	0.4 0.5	0	+	0	0.2 0.4	0	2.1 1.4	1.1 1.0	0.3 0.5	0.2 0.4	0
	16.	GI.40.AB	0	0	0	0	1.3 0.9	0	0.1 0.3	0	0.2 0.4	0	1.3 1.2	0.5 0.5	0.5 0.7	0	0
	17.	GI.60.AB	0	0	0	0	0.3 0.5	0	0	0	0.7 1.1	0	0.4 0.5	0	0.2 0.4	0.2 0.6	0

TABLE 28 (continued)

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets. Table entries show the mean and s.d. (below) number of individuals per 10 square meters. A (+) symbol indicates species was present at the site but did not appear within a quadrat. Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ASTEROIDEA: SE	LOF	CP	HL	HNS	HA	PT	MA	PM	LF	HOLOTHUROIDEA: PC	CM	CPIP	FD	PSOL	LC
Bamfield Inlet																		
	6.	BI.COB.AB	0	0	0	1.0 1.0	0.6 0.9	0	0	0	0	0	0.2 0.4	2.1 1.2	0.4 0.6	1.0 1.4	+	0
	7.	BI.MUD.AB	0	0	0	0	0	0	0	0	+	0	+	0	0	0	0	132.2 68.1
	8.	BI.15.AB	0	0	0	+	0	0	0	+	14.1 3.6	0	0.2 0.4	0.9 1.7	+	0	0	4.3 8.6
	9.	BI.40.AB	0.1 0.3	0	0	0.6 0.7	0	0	0	0	0	0	1.3 1.2	0.1 0.3	+	0	0	0
	10.	BI.85.AB	+	0.2 0.6	1.4 1.2	0.8 1.0	0	0	0.2 0.4	11.2 5.1	0	0.1 0.3	1.4 1.3	0	0.3 0.5	0	0	0
	11.	BI.PILE.AB	0	0	0.2 0.6	2.2 1.7	0	0.1 0.3	0	1.2 1.4	0	0	1.2 1.0	1.6 1.7	0.4 0.7	0.5 0.7	+	0
Grappler Inlet																		
	12.	GI.COB.AB	0	0	0	0.8 1.3	16.6 16.9	0	0	+	0	0	0	8.6 6.8	0.4 0.6	1.0 1.0	0.6 1.3	0
	13.	GI.MUD.AB	0	0	0	0	0	0	0	0	0.8 2.1	0	+	0	0	0	0	407.3 229.6
	14.	GI.20.AB	0	0	0	0	0	0	0	0	61.3 21.5	0	1.1 1.1	1.7 6.1	0	0	0	632.3 356.4
	15.	GI.35.AB	0.1 0.3	0	0.7 0.7	7.0 3.6	5.9 3.8	0	0.1 0.3	2.2 2.4	0	0	2.3 1.9	11.1 2.6	1.4 1.4	0	2.6 2.7	0
	16.	GI.40.AB	0	0	0	0	0	0	0	0	4.3 1.6	0	1.7 0.9	0.9 1.9	0.2 0.4	0	0	0
	17.	GI.60.AB	0	+	1.5 1.1	0.6 0.7	0	0	0	15.2 7.8	0	+	0.6 0.7	0	0	0	0	0

TABLE 28 (continued)

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets. Table entries show the mean and s.d. (below) number of individuals per 10 square meters. A (+) symbol indicates species was present at the site but did not appear within a quadrat. Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	OPHIUROIDEA: OA	AO	AU	AP	AX	CRINOIDEA: FS	INDEX OF DIVERSITY: TOTAL # Spp.	SHANNON Hn	SIMPSON Dn	COMMUNITY α	VARIETY V
Bamfield Inlet													
	6.	BI.COB.AB	1.4 1.5	4.7 3.9	0.1 0.2	+	5.2 5.4	0	18	1.79	0.75	4.57	6.73
	7.	BI.MUD.AB	0	14.3 12.7	5.1 3.8	0.9 1.2	1.3 4.[illegible]	0	7	0.42	0.21	0.99	1.96
	8.	BI.15.AB	0	14.4 7.2	0.1 0.4	0	0.7 1.3	0	11	1.17	0.60	2.21	3.99
	9.	BI.40.AB	0	0.4 0.6	+	0	0	0	12	1.98	0.83	3.44	5.40
	10.	BI.85.AB	0	0	0	0	0	0.3 0.5	14	1.42	0.56	3.46	5.68
	11.	BI.PILE.AB	1.1 1.0	0.1 0.3	0.	0	0.2 0.4	0	21	2.65	0.91	6.35	9.00
Grappler Inlet													
	12.	GI.COB.AB	4.4 4.6	16.8 7.4	0	0	10.4 8.3	0	16	2.13	0.85	3.33	5.76
	13.	GI.MUD.AB	0	157.2 122.3	1.3 4.2	6.3 14.2	16.7 17.6	0	10	0.79	0.45	1.22	2.46
	14.	GI.20.AB	0	1216 708	2.0 4.4	40.5 128.2	445.9 403.1	0	13	1.36	0.59	2.11	3.99
	15.	GI.35.AB	12.8 13.4	405.3 573.2	+	0	851.2 905.4	0	22	2.47	0.89	4.46	7.53
	16.	GI.40.AB	0	3.6 1.9	+	+	108.8 213.7	0	12	1.92	0.79	2.81	4.79
	17.	GI.60.AB	0	202.7 393.9	+	+	486.4 912.4	0.2 0.4	12	1.44	0.60	2.61	4.57

imbricata, occurred at 12 or more sites. The common species of asteroids occurred at 5 - 11 sites (mean = 8, s.d. = 2), and rare species were encountered at 1 or 2 sites (Tables 27 and 28). The density of Pisaster ochraceus exceeded 10 m^{-2} along rocky intertidal habitats at Taylor Island and averaged about 2 m^{-2} along a cobble transect in Bamfield Inlet. Two species of forcipulate asteroids, Leptasterias hexactis and P. ochraceus made up 12 to 50% of the total echinoderm fauna at three of the intertidal sites (1:TI.POE, 2:TI.PON, 6:BI.COB). Predatory asteroids were represented by 9 to 11 species along muddy bottom habitats at depths greater than 40 ft in Bamfield Inlet where Pisaster brevispinus, Orthasterias koehleri, Evasterias troschelli, and Pycnopodia helianthoides occurred at densities from 1 to 3 per $10m^2$. The valvatid species, Mediaster aequalis, and the circumboreal spinulosid species, Crossaster papposus, were both common on shell rubble and worm tubes of Phyllochaetopterus prolifera in deep water. Other asteroids found occasionally in deep water included Solaster paxillatus and Lophaster furcilliger. Six species of asteroids were found at a single site (Tables 27 and 28). One of these, Pisaster giganteus, is at the northern extreme of its geographic range in Barkley Sound, and is infrequently reported north of Cape Flattery, Washington (Feder, 1980).

The greatest diversity of ophiuroids (4 species) occurred along transect lines that sampled mudflats and shallow subtidal habitats within Bamfield and Grappler Inlets. Densities of the amphiurid ophiuroids, Amphiodia (Diamphiodia) occidentalis, A. urtica, A. periercta, and Amphipholis (Axiognathus) squamata were greater within mudflats and shallow soft-substratum habitats in Grappler Inlet than within similar habitats in Bamfield Inlet (Tables 27 and 28). Individuals of A. occidentalis were also abundant at the 35 and 50 ft depth contours at Taylor Island. Two species of ophiuroids (A. occidentalis and A. squamata) occurred along 16 out of 17 transects. The absence of A. squamata from 40 and 85 foot depths in Bamfield Inlet was unexpected because this species was abundant at similar depths in Grappler Inlet and at Taylor Island (Tables 27 and 28).

Holothuroids occurred in nearly equal abundance and diversity along three transect lines. These included the subtidal rock wall and boulder field habitat at Taylor Island, and the cobble and wharf piling habitats at Bamfield Inlet (Tables 27 and 28). The diversity of holothuroids was also similar within the cobble habitat in Grappler Inlet. The deposit feeding aspidochirote holothuroid, Parastichopus californicus, was common in subtidal habitats at depths greater than 12 ft below MLLW.

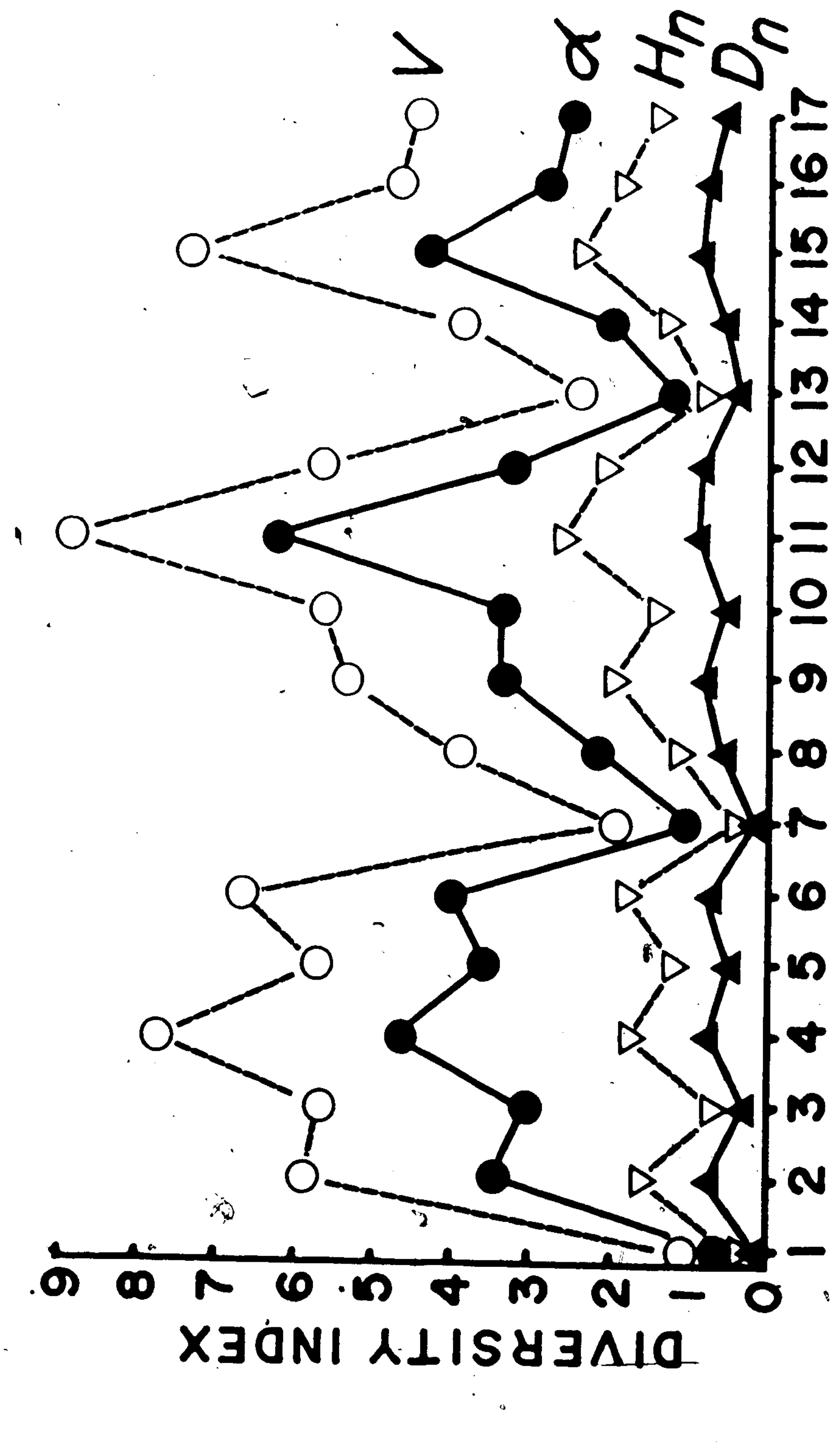
Low numbers of the comatulid crinoid, Florometra serratissima, occurred in deep water near the confluence of Bamfield and Grappler Inlets (Tables 27 and 28). These populations of F. serratissima were probably established during 1960 - 1970 by the release of dredged specimens. The typical habitat of F. serratissima is along deep water hard substratum pinnacles and rock walls swept by persistent currents.

Differences in species composition and abundance were striking between Bamfield and Grappler Inlets despite their close proximity and similar types of habitats (Tables 27 and 28). Five species of ophiuroids and the infaunal holothuroid, Leptosynapta clarki, were generally more abundant in Grappler Inlet than Bamfield Inlet. Only Amphiodia urtica occurred in greater densities in Bamfield Inlet (7:BI.MUD.AB) compared to a similar habitat in Grappler Inlet (13:GI.MUD.AB). Predatory asteroids were abundant in Grappler Inlet along transects that sampled intertidal mudflats and subtidal soft substratum habitats. In contrast, the densities of echinoids and asteroids were similar along intertidal cobble transects within Bamfield and Grappler Inlets.

Three sites were exceptional in the number of species encountered during quantitative sampling of the transects. The boulder field habitats located at Taylor Island and Grappler Inlet were each inhabited by 22 species of echinoderms. A third site among wharf pilings (11:BI.PILE.AB) was occupied by 21 species (Tables 27 and 28).

Figure 59 summarizes the diversity index values obtained for each of the 17 transect lines. All 4 indices

Figure 59. Comparison of four measures of echinoderm faunal diversity along 17 transect lines. V = index of faunal variety, α = index of community diversity, H_n = Shannon-Wiener index of diversity, D_n = Simpson's index of diversity. Equations for the various diversity indices are provided in the text. Transect numbers refer to transects listed in Table 26.


DIVERSITY INDEX
0
1
2
3
4
5
6
7
8
9
TRANSECT NUMBER
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
V
α
Hn
Dn

gave low rankings to the intertidal rock wall at Taylor Island (1:TI.PO.E) and the intertidal mudflats in Bamfield and Grappler Inlets (7:BI.MUD.AB and 13:GI.MUD.AB). High diversity index values were obtained for the transect that sampled subtidal wharf pilings in Bamfield Inlet (11.BI.PILE.AB) and for the subtidal boulder field in Grappler Inlet (15:GI.35.AB). High diversity ranks were also given to the intertidal (2:TI.PO.N) and subtidal (4:TI.35.AB) boulder field habitats at Taylor Island. The results from these diversity indices are similar to ranks based on species richness (Tables 27 and 28), and all of the measures showed similar patterns of diversity in their assessment of the transect lines.

The value of diversity indices depend upon their capacity to provide reliable and meaningful comparative descriptions within particular habitats. With the exception of 2 sites (8:BI.15.AB and 14:GI.20.AB), quantitative surveys of the transect lines were completed on a single occasion. Sampling heterogeneous echinoderm assemblages at a single point in time provides a snapshot view of the communities. Consequently, it is not possible to evaluate the variance associated with the diversity index values shown in Figure 59. Two measures were used in later evaluations of community patterns obtained from the static sample. Both Simpson's Index (D_n), and the Shannon-Wiener Index (H_n) were used to analyze relationships between life history traits and community composition because they are sensitive to the distribution of individuals among faunal assemblages (Levins 1966; Loya, 1971; Krebs, 1978).

3. Echinoderm Life History Traits

Ova sizes and modes of development differ among members of the Barkley Sound echinoderm fauna (Table 29); 17 species have planktotrophic development (47%), 15 species have lecithotrophic development (42%), and 4 species brood their offspring (11%). The distribution of ova diameters is bimodal (Figure 60). Species with planktotrophic development have ova ranging from 85 to 200 µm in diameter. Small ova from the viviparous hermaphroditic ophiuroid, Amphipholis squamata, occur in the first mode along with planktotrophic species in Figure 60. Ova from the remaining species range from 200 to 1300 µm in diameter. This group includes 16 lecithotrophic species and 3 brooding species (Table 29, Figure 60). The planktotrophic and lecithotrophic species are gonochoric and free-spawning with external fertilization and development. Most of the brooding species are also gonochoric, and either brood benthic external egg masses (Leptasterias hexactis and Henricia sp. nov.) or incubate their offspring internally within the coelom (Leptosynapta clarki).

The breeding seasons of 32 species of echinoderms are shown in Table 30. The majority of species breed during the spring and early summer months from March to June. Three species, Amphiodia occidentalis, Leptasterias hexactis, and Leptosynapta clarki breed primarily during winter. The

TABLE 29

Comparison of larval trophic modes, larval types, ova diameters, and maximum fecundities of echinoderms from Barkley Sound.

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter (µm) n	 mean ± (s.d.)	Fecundity Max. # Ova per Female
Echinoidea:				
Strongylocentrotus franciscanus	P: echinopluteus	100	152 ± (4)	2.9 X 10^7
Strongylocentrotus purpuratus	P: echinopluteus	100	85 ± (5)	1.7 X 10^7
Strongylocentrotus droebachiensis	P: echinopluteus	100	156 ± (4)	3.8 X 10^5
Holothurqidea:				
Parastichopus californicus	P: auricularia doliolaria	50	189 ± (9)	2.6 X 10^6
Cucumaria miniata	L: doliolaria	24	525 ± (9)	1.6 X 10^5
Cucumaria piperata *	L: doliolaria	21	540 ± (10)	9.2 X 10^3
Eupentacta quinquesimita *	L: doliolaria	18	392 ± (16)	3.8 X 10^4
Psolus chitonoides	L: doliolaria	34	630 ± (7)	1.5 X 10^4
Leptosynapta clarki *	B: vitellaria pentacula	22	302 ± (17)	1.2 X 10^3
Ophiuroidea:				
Ophiopholis aculeata	P: ophiopluteus	50	115 ± (6)	2.5 X 10^5
Amphiodia occidentalis	P: ophiopluteus	50	103 ± (5)	7.8 X 10^4
Amphiodia urtica *	P: ophiopluteus ?	26	101 ± (8)	
Amphiodia periercta *	P: ophiopluteus ?	32	96 ± (6)	
Amphipholis squamata *	B: vestigial ophiopluteus	9	98 ± (6)	11

TABLE 29 (continued)

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter (µm) n	 mean ± (s.d.)	Fecundity Max. # Ova per Female
Asteroidea:				
Pisaster ochraceus	P: bipinnaria brachiolaria	100	160 ± (6)	5.6 X 10^6
Pisaster brevispinus	P: bipinnaria brachiolaria	32	156 ± (4)	9.3 X 10^5
Orthasterias koehleri	P: bipinnaria brachiolaria	100	139 ± (5)	9.4 X 10^5
Stylasterias forreri *	P: bipinnaria brachiolaria	28	152 ± (5)	
Evasterias troschelli	P: bipinnaria brachiolaria	47	144 ± (3)	2.4 X 10^7
Leptasterias hexactis	B: modified brachiolaria	49	986 ± (21)	921
Pycnopodia helianthoides	P: bipinnaria brachiolaria	40	134 ± (4)	12.7 X 10^7
Dermasterias imbricata	P: bipinnaria brachiolaria	100	172 ± (7)	1.3 X 10^7
Solaster stimpsoni	L: modified brachiolaria	36	922 ± (21)	7.2 X 10^4
Solaster dawsoni	L: modified brachiolaria	29	962 ± (13)	3.1 X 10^4
Solaster paxillatus *	L: modified brachiolaria	18	900 ± (41)	
Solaster endeca *	L: modified brachiolaria	14	1112 ± (37)	
Lophaster furcilliger *	L: modified brachiolaria ?	12	354 ± (16)	
Crossaster papposus	L: modified brachiolaria	25	820 ± (8)	427
Henricia leviuscula	L: modified brachiolaria	25	605 ± (13)	

TABLE 29 (continued)

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter* (µm)		Fecundity
		n	mean ± (s.d.)	Max. # Ova per Female
Henricia sp. nov.	B: modified brachiolaria	25	891 ± (12)	
Henricia asthenactis *	L: modified brachiolaria ?	17	865 ± (15)	
Pteraster tesselatus	L: modified brachiolaria	12	1327 ± (30)	2.7 X 10^3
Mediaster aequalis	L: modified brachiolaria	37	1049 ± (68)	1.4 X 10^3
Patiria miniata	P: bipinnaria brachiolaria	100	137 ± (6)	4.4 X 10^5
Luidia foliolata *	P: bipinnaria	45	154 ± (4)	
Crinoidea:				
Florometra serratissima	L: doliolaria	39	216 ± (8)	1.1 X 10^4

Most ova measured from natual spawnings that occurred in laboratory aquaria. Asterisk (*) indicates ova measured from excised gravid ovaries. P = planktotrophic, L = lecithotrophic, B = brooding. Question mark indicates species where larval trophic mode and type are inferred from ova diameter.

Figure 60. Distribution of ova diameters among 36 species of echinoderms listed in Table 29. The distribution is best fit by a log-normal curve ($chi^2 = 14.11$, $p < 0.001$); ln transformed data are strongly bimodal.

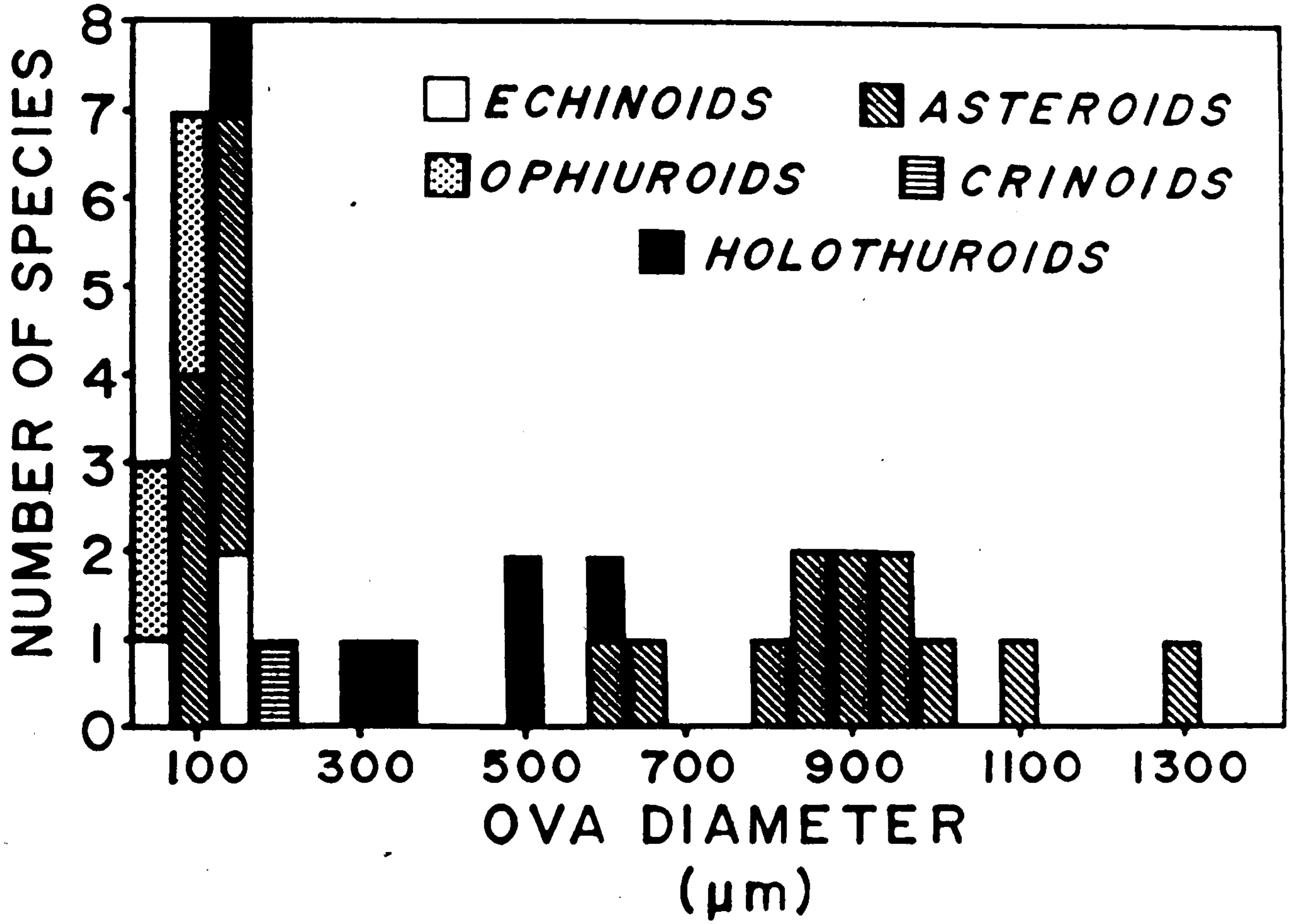
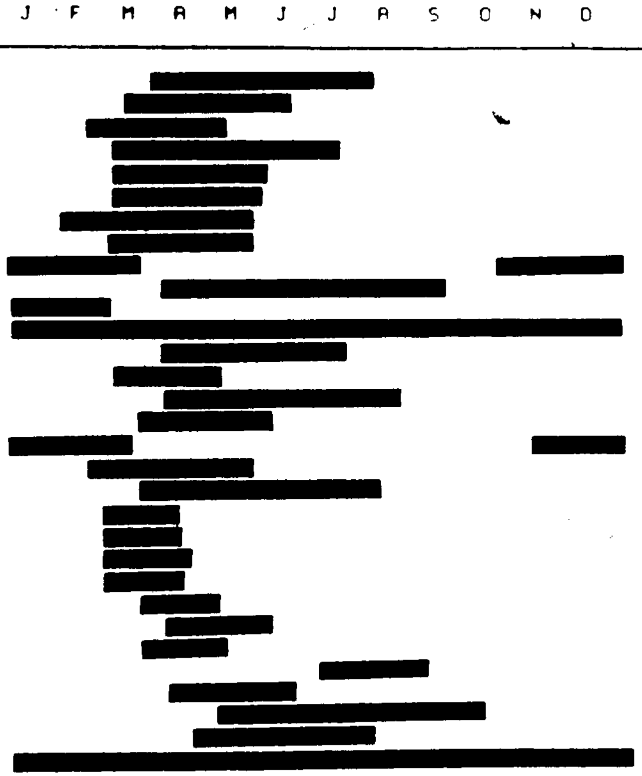

NUMBER OF SPECIES
0
1
2
3
4
5
6
7
8
100
300
500
700
900
1100
1300
OVA DIAMETER
(μm)
□ ECHINOIDS
▨ ASTEROIDS
▩ OPHIUROIDS
▤ CRINOIDS
■ HOLOTHUROIDS

TABLE 30

Breeding seasons of echinoderms from Barkley Sound.
Code column indicates species abbreviations used elsewhere in the text.



CODE	Genus and species	REFERENCE
SF	Strongylocentrotus franciscanus	Bennett and Giese, 1955
SP	Strongylocentrotus purpuratus	Cochran and Engelmann, 1975
SDR	Strongylocentrotus droebachiensis	Himmelman, 1978
PC	Parastichopus californicus	McEuen, 1986
CM	Cucumaria miniata	personal observations
CPIP	Cucumaria piperata	McEuen, 1986
EQ	Eupentacta quinquesemita	McEuen, 1986
PSOL	Psolus chitonoides	McEuen, 1986
LC	Leptosynapta clarki	McEuen, 1986
OA	Ophiopholis aculeata	personal observations
AO	Amphiodia occidentalis	Rumrill and Pearse, 1985
AX	Amphipholis squamata	Rumrill and Pearse, 1985
PO	Pisaster ochraceus	Mauzey, 1966
PB	Pisaster brevispinus	personal observations
OK	Ort[illegible] koehleri	personal observations
ET	Evas[illegible] tros[illegible]lli	Strathmann (in press)
LH	Leptasterias hexactis	Chia, 1966a
PH	Pycnopodia helianthoides	Greer, 1962
DI	Dermasterias imbricata	personal observations
SS	Solaster stimpsoni	S. Carson, pers. comm.
SD	Solaster dawsoni	S. Carson, pers. comm.
SPAX	Solaster paxillatus	S. Carson, pers. comm.
SE	Solaster endeca	S. Carson, pers. comm.
CP	Crossaster papposus	Strathmann (in press)
HL	Henricia leviuscula	Strathmann (in press)
HNS	Henricia nov. sp.	personal observations
PT	Pteraster tesselatus	Chia, 1966b
MA	Mediaster aequalis	Lambert, 1981
PM	Patiria miniata	Rumrill, 1987
LF	Luidia foliolata	Lambert, 1981
FS	Florometra serratissima	Mladenov, 1980

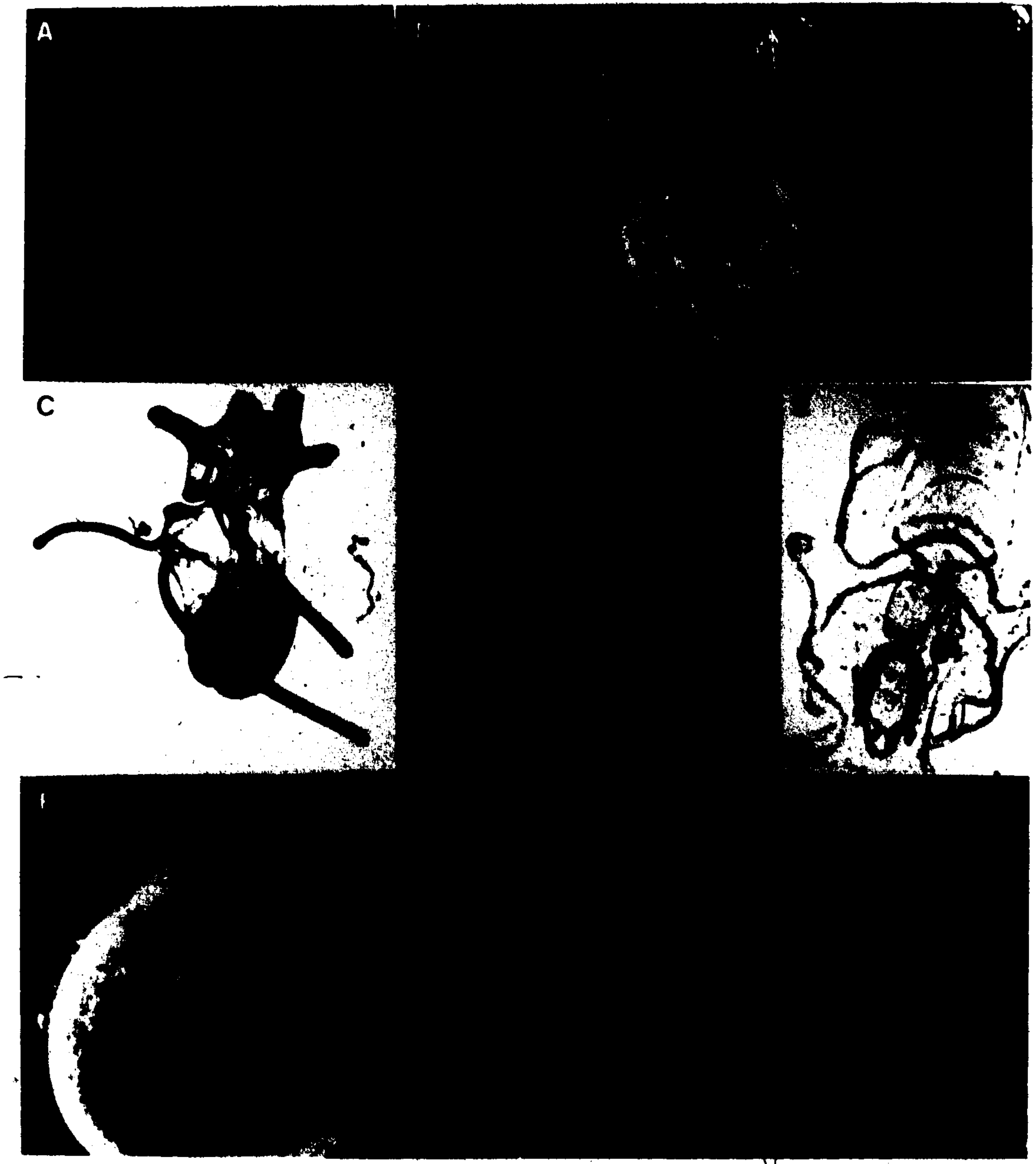
* Abbreviation codes for other species listed in Tables 27 and 28 include: PG = Pisaster giganteus, STY = Stylasterias forreri, LOF = Lofaster furcilliger, HA = Henricia asthenactis, AU = Amphiodia urtica, AP = Amphiodia periercta.

species with lecithotrophic development generally have short breeding seasons and reproduce early in the spring. In contrast, species with planktotrophic development have longer (3-5 month) breeding periods. Two species, Amphipholis squamata and Florometra serratissima, reproduce throughout the year (Table 30).

Morphological characteristics of the various types of echinoderm larvae are illustrated in Figure 61. All types of echinoderm larvae swim with cilia. In the planktotrophic echinopluteus, ophiopluteus, auricularia and brachiolaria larvae the cilia are concentrated along an elaborate looping band. In contrast, the cilia of lecithotrophic holothuroid and crinoid larvae are organized into rings that encircle the larval body. Finally, in the modified brachiolaria of lecithotrophic asteroids the cilia are scattered throughout the larval epidermis. Maximum body lengths of the metamorphically competent larval stages approach 1 mm in the planktotrophic species and range from 1 to 2 mm in the lecithotrophic species.

Estimates of the maximum number of ova per female are shown for 26 species in Table 29. These estimates underestimate the number of ova spawned during an extended period of reproductive activity. Maximum numbers of ova among planktotrophic species ranged from 78 thousand ova per female in the ophiuroid, Amphiodia occidentalis, to 127 million ova per female in the asteroid, Pycnopodia helianthoides. Maximum numbers of ova among the species

Figure 61. Diversity of echinoderm larvae among the Barkley Sound fauna. A. Planktotrophic echinopluteus of *Strongylocentrotus droebachiensis*. B. Unidentified planktotrophic ophiopluteus. C. Planktotrophic brachiolaria of *Pisaster ochraceus*. D. Lecithotrophic modified brachiolaria of *Henricia leviuscula*..Photograph by R. Koss. E. Planktotrophic auricularia of *Parastichopus californicus*. F. Lecithotrophic doliolaria of *Psolus chitonoides*. Photograph by F. McEuen. G. Lecithotrophic doliolaria of *Florometra serratissima*. Photograph by R. Koss.


A
C

with lecithotrophic development ranged from 427 ova per female in the asteroid, Crossaster papposus, to 160 thousand in the holothuroid, Cucumaria miniata. The maximum numbers of ova among brooding species ranged from 11 in Amphipholis squamata to 1,200 in Leptosynapta clarki (Table 29).

Intraspecific differences in the number of ova per female were observed between habitats in two species of forcipulate asteroids. Significantly greater numbers of ova were obtained from gravid females of Pisaster ochraceus collected from Taylor Island compared with females from Grappler Inlet (t = 3.3051, p = 0.0018). The inverse trend was evident for brood counts of Leptasterias hexactis where significantly larger broods occurred in Grappler Inlet (t = 4.0274, p = 0.0003). Numbers of ova per female were independent of habitat in Orthasterias koehleri (Taylor vs. Bamfield, t = 0.5790, p = 0.5666) and Patiria miniata (Bamfield vs. Grappler, t = 0.7141, p = 0.4834). In addition, there were no significant differences in the numbers of ova obtained from gravid females of Strongylocentrotus franciscanus collected from 3 different depths at Taylor Island (12 vs. 35 ft, t = 0.1493, p = 0.8821; 35 vs. 54 ft, t = 0.6075, p = 0.5495; 12 vs. 54 ft, t = 0.7654, p = 0.4493).

4. Relationships Between Species Diversity, Life History Traits and Distribution

Relationships between modes of development and habitat parameters were examined by Spearman's and Kendall's tests of rank correlation (Table 31). The proportion of species with planktotrophic development was not significantly correlated with species richness, diversity, exposure or depth (Table 31). In contrast, the proportion of species with lecithotrophic development was positively correlated with species richness, diversity, and depth, and negatively correlated with habitat exposure. Brooding species showed an inverse trend and were negatively correlated with species richness, habitat diversity and depth, and positively correlated with exposure. The high frequency of brooding species in intertidal and shallow subtidal habitats is primarily due to the distribution patterns of Leptasterias hexactis and Leptosynapta clarki (See Tables 27 and 28).

Although there were differences in the relative degree of exposure between Taylor Island and Bamfield and Grappler Inlets (Figure 54), comparisons of life history patterns made along the entire exposure gradient within Barkley Sound are misleading because they combine trends within outer coast and estuarine habitats. Correlations that include the entire range of species richness, species diversity and depth values are valid because these parameters are distributed heterogeneously among the 17 transects (see Tables 26 - 28, Figure 59).

Figures 62 and 63 show that the distribution of echinoderms with planktotrophic, lecithotrophic and

TABLE 31

Summary of comparisons between life history traits and species richness, diversity and exposure. Exposure values are dissolution rates of plaster casts. Table entries show results of Spearman's and Kendall's rank correlations and their associated probability values. Probability values > 0.05 are listed as not significant (n.s.). Sample size is 17 for all comparisons except Ova Diameter X Depth (n=36).

COMPARISON	SPEARMAN'S rho	p	KENDALL'S tau	p
Diversity (Hn) X # Species	0.6215	0.001	0.5114	0.005
Diversity (Dn) X # Species	0.5760	0.010	0.4362	0.010
Diversity (Hn) X Exposure	-0.6511	0.005	-0.5092	0.005
Diversity (Dn) X Exposure	-0.6266	0.005	-0.4945	0.005
No. Species X Exposure	-0.2426	n.s.	-0.2340	n.s.
No. Species X Depth	0.1313	n.s.	0.1369	n.s.
% Planktotrophy X # Species	-2.993	n.s.	-0.2491	n.s.
% Planktotrophy X Diversity (Hn)	0.1815	n.s.	-0.1255	n.s.
% Planktotrophy X Diversity (Dn)	-0.0564	n.s.	-0.0812	n.s.
% Planktotrophy X Exposure	0.1202	n.s.	0.0741	n.s.
% Planktotrophy X Depth	-0.2985	n.s.	-0.2090	n.s.
% Lecithotrophy X # Species	0.6204	0.005	0.4886	0.005
% Lecithotrophy X Diversity (Hn)	0.6331	0.005	0.4777	0.005
% Lecithotrophy X Diversity (Dn)	0.5347	0.025	0.4329	0.010
% Lecithotrophy X Exposure	-0.5437	0.025	-0.4270	0.010
% Lecithotrophy X Depth	0.6724	0.005	0.4906	0.005
% Brooding X # Species	-0.4414	0.050	-0.3422	0.050
% Brooding X Diversity (Hn)	-0.6077	0.010	-0.4684	0.010
% Brooding X Diversity (Dn)	-0.5242	0.025	-0.3941	0.025
% Brooding X Exposure	0.4435	0.050	0.2687	n.s.
% Brooding X Depth	-0.7921	0.001	-0.6316	0.005
Ova Diameter X Depth	0.3876	0.025	0.2799	0.010

Figure 62. Shifts in the proportions of the echinoderm fauna composed of planktototrophic, lecithotrophic and brooding species along the exposure gradient at Taylor Island. Exposure rank values are based on the average rank given to each transect line by the relative weight loss of plaster casts (see Table 26). The numbers above each set of bars indicate habitat depth.

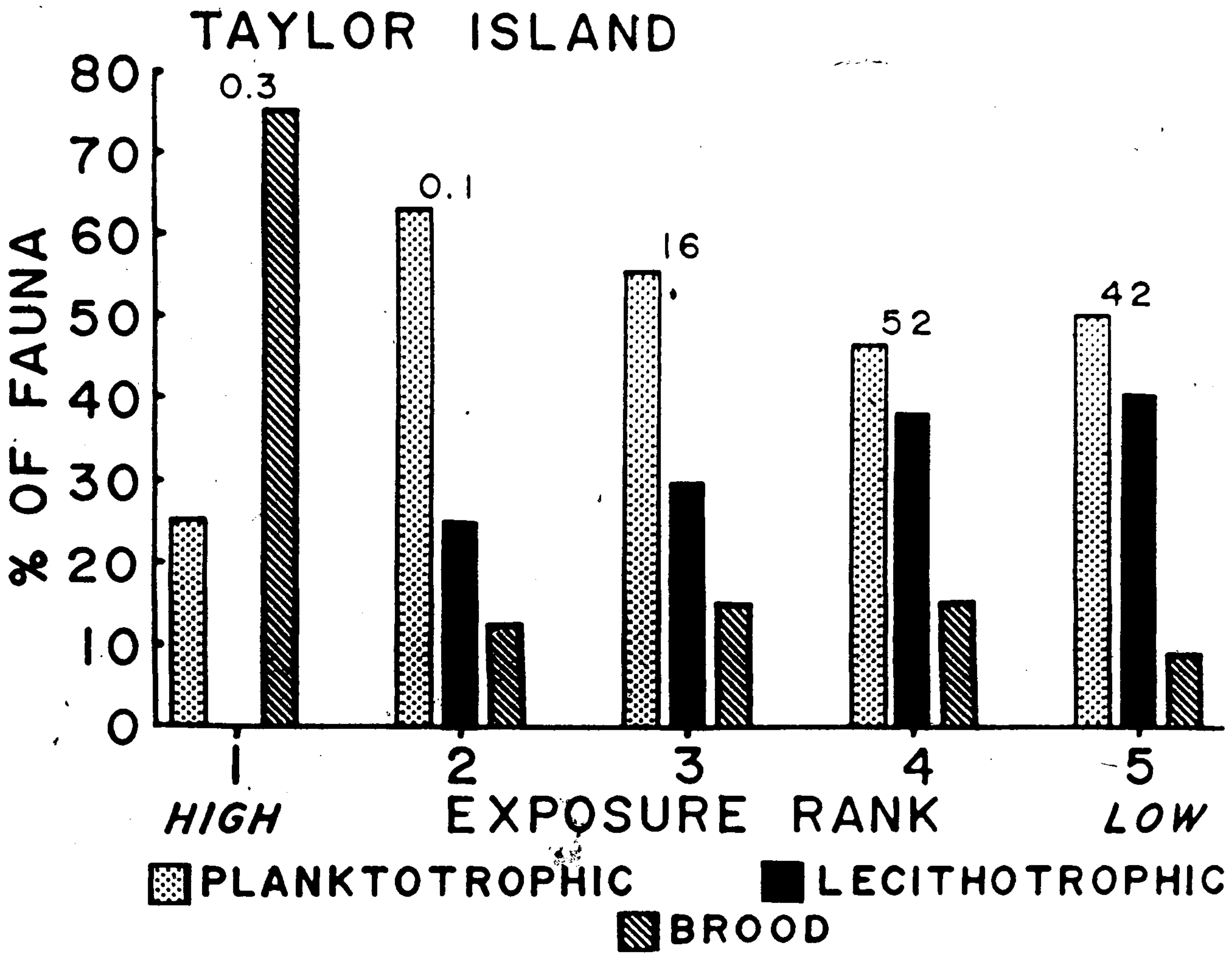
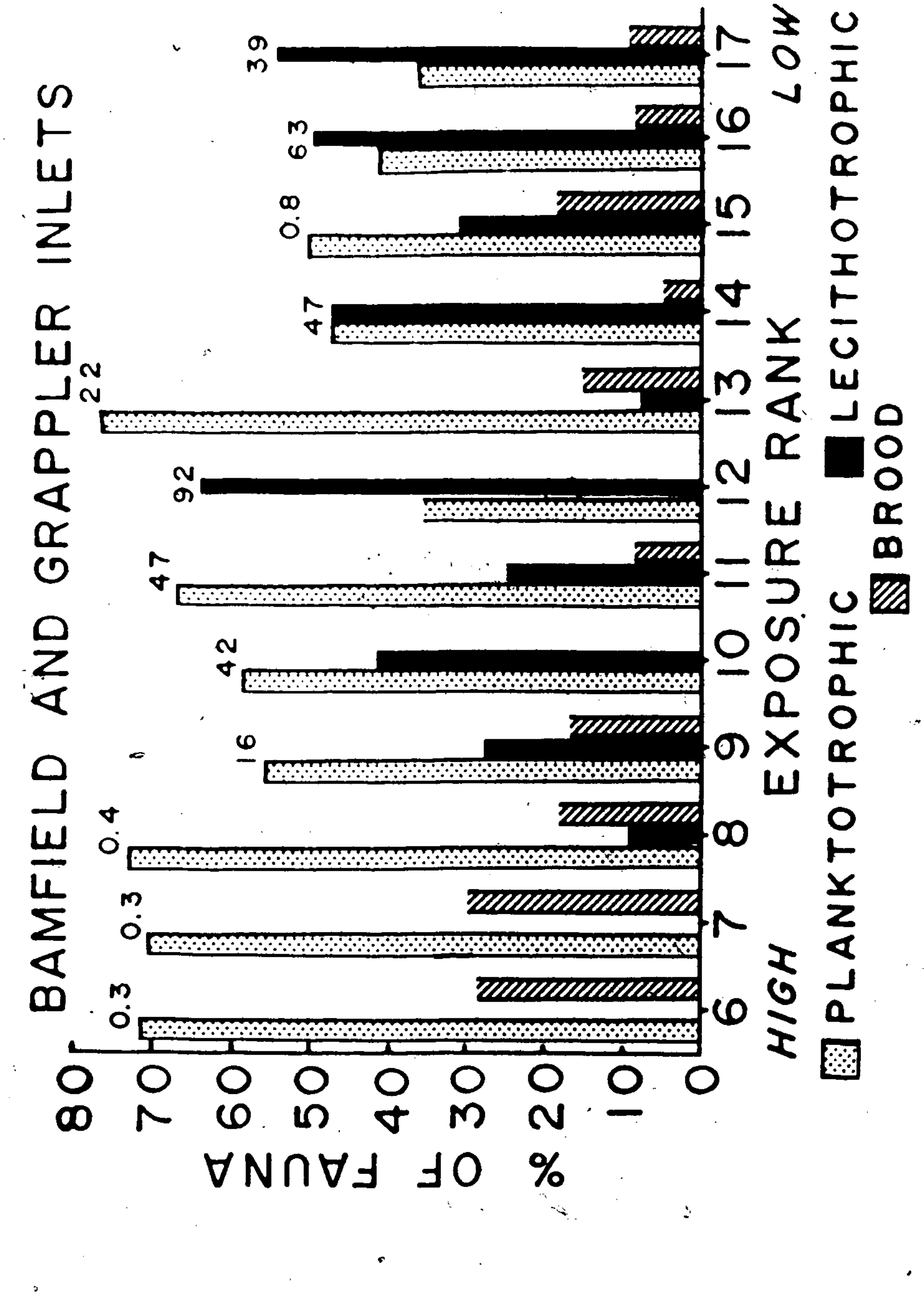

TAYLOR ISLAND
% OF FAUNA
80
70
60
50
40
30
20
10
0
0.3
0.1
16
52
42
1
2
3
4
5
HIGH
EXPOSURE RANK
LOW
PLANKTOTROPHIC
LECITHOTROPHIC
BROOD

Figure 63. Shifts in the proportions of the echinoderm fauna composed of planktototrophic, lecithotrophic and brooding species along the exposure gradient at Bamfield and Grappler Inlets. Exposure rank values are based on the average rank given to each transect line by the relative weight loss of plaster casts (see Table 26). The numbers above each set of bars indicate habitat depth.


BAMFIELD AND GRAPPLER INLETS
% OF FAUNA
0
10
20
30
40
50
60
70
80
0.3
0.3
0.4
16
42
47
92
22
47
0.8
63
39
6
7
8
9
10
11
12
13
14
15
16
17
HIGH
EXPOSURE RANK
LOW
PLANKTOTROPHIC
LECITHOTROPHIC
BROOD

brooding modes of development are neither uniform nor random within Barkley Sound. Consistent trends were evident when comparisons were made between transect lines at Taylor Island (Figure 62) and between transect lines at Bamfield and Grappler Inlets (Figure 63). There was a general trend toward an increase in the frequency of species with lecithotrophic development with increasing depth and decreasing exposure. Relationships between depth and habitat exposure were also significant for species that brood their offspring. Although correlations between habitat depth, exposure and the frequency of planktotrophic and brooding species were not significant due to the low number of transects at Taylor Island, the frequency of lecithotrophic species showed perfect negative rank correlations with increasing habitat depth and exposure. Similar changes in the frequency of planktotrophic and lecithotrophic species were evident within Bamfield and Grappler Inlets (Figure 63). The proportion of species with planktotrophic development increased significantly along transects with successively greater exposure (rho = 0.6340, p = 0.025), while lecithotrophic species became relatively more abundant in habitats characterized by low exposure (rho = -0.7263, p = 0.01). Changes in the frequency of brooding species were not significantly correlated with exposure within Bamfield and Grappler Inlets (rho = 0.4429, $p > 0.05$).

The diameters of echinoderm ova are positively correlated with the depth at which adults reached their maximum abundance (Figure 64, Table 31). The relationship is significant only when data from all 37 species listed in Table 29 are considered ($\rho = 0.3876$, $p < 0.025$). Ova diameters among the four brooding species show a negative correlation with depth, although the vertical range of the two subtidal brooding species extend into the intertidal (see Tables 27 and 28). The similar relationship between ova diameter and habitat depth on small and large geographical scales suggests that mechanisms responsible for the generation of large scale variability may be at least partially explained by analogy with local patterns.

Faunal records and published descriptions of larval development provide sufficient information to compare latitudinal shifts in the life history patterns of asteroids from 4 zoogeographical regions located along the north-east Pacific coast (Figure 65). Planktotrophic species composed about 60% of the fauna between 25 and 45°N (latitude), 47% of the fauna between 45 and 55°N, and 14% of the fauna above 55°N. Conversely, lecithotrophic species composed an increasingly greater proportion of the asteroid fauna between 35 and 65°N. Brooding species averaged about 9% of the fauna between 25 and 55°N and increased to 26% above 55°N.

The latitudinal shift in the frequency of asteroid species with planktotrophic and lecithotrophic development (Figure 65) is similar to the local pattern observed for

Figure 64. Relationship between ova diameter and the habitat where species reach their greatest abundance. Densities of species are provided in Tables 27 and 28. The overall correlation between ova diameter and depth of maximum species abundance is significant (Spearman's rho = 0.3876, $p < 0.025$; Kendall's tau = 0.2799, $p < 0.01$). Trends within planktotrophic, lecithotrophic and brooding species are not significant ($p > 0.05$). Dotted line separates intertidal (left) and subtidal (right) habitats.

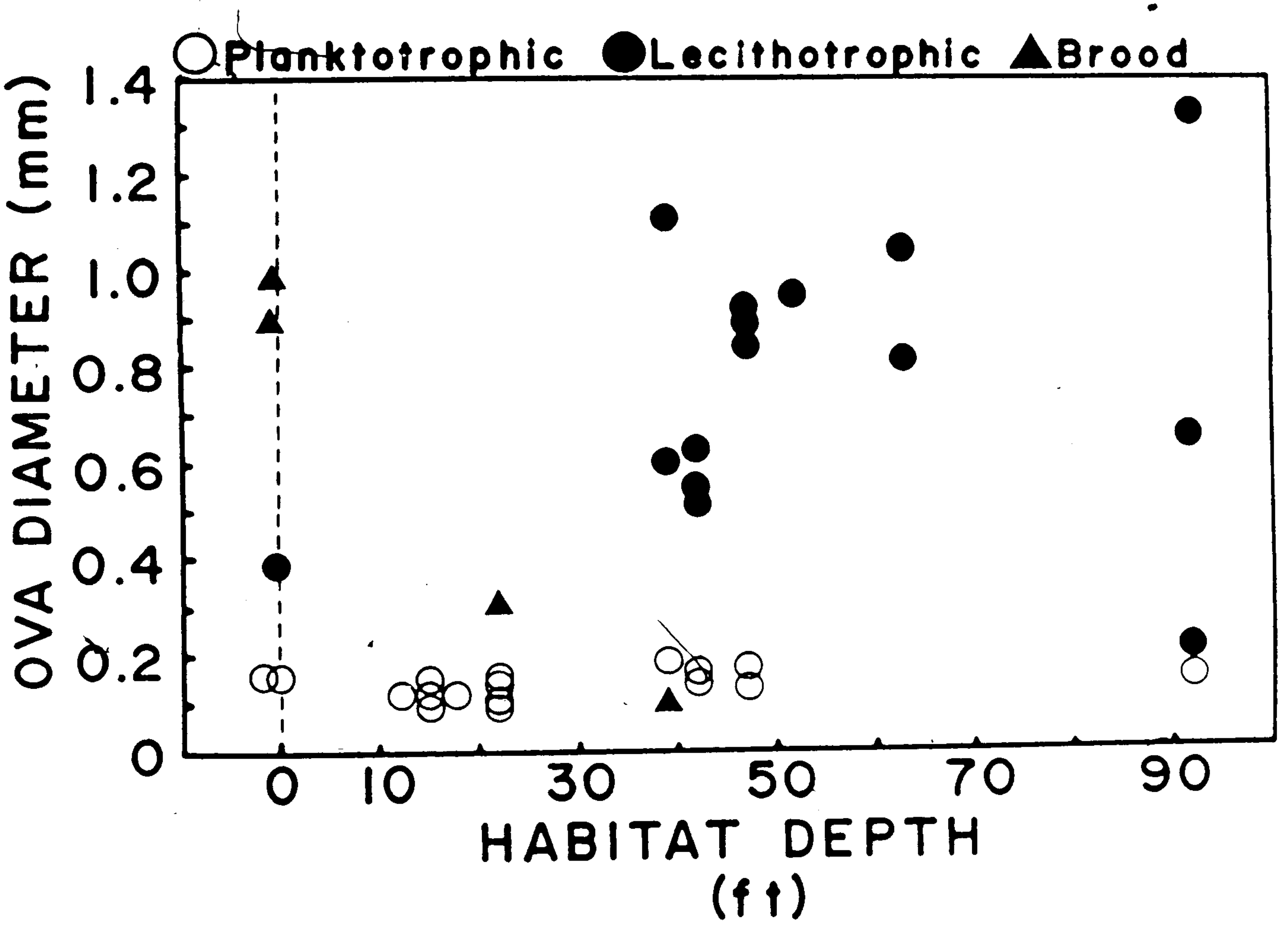
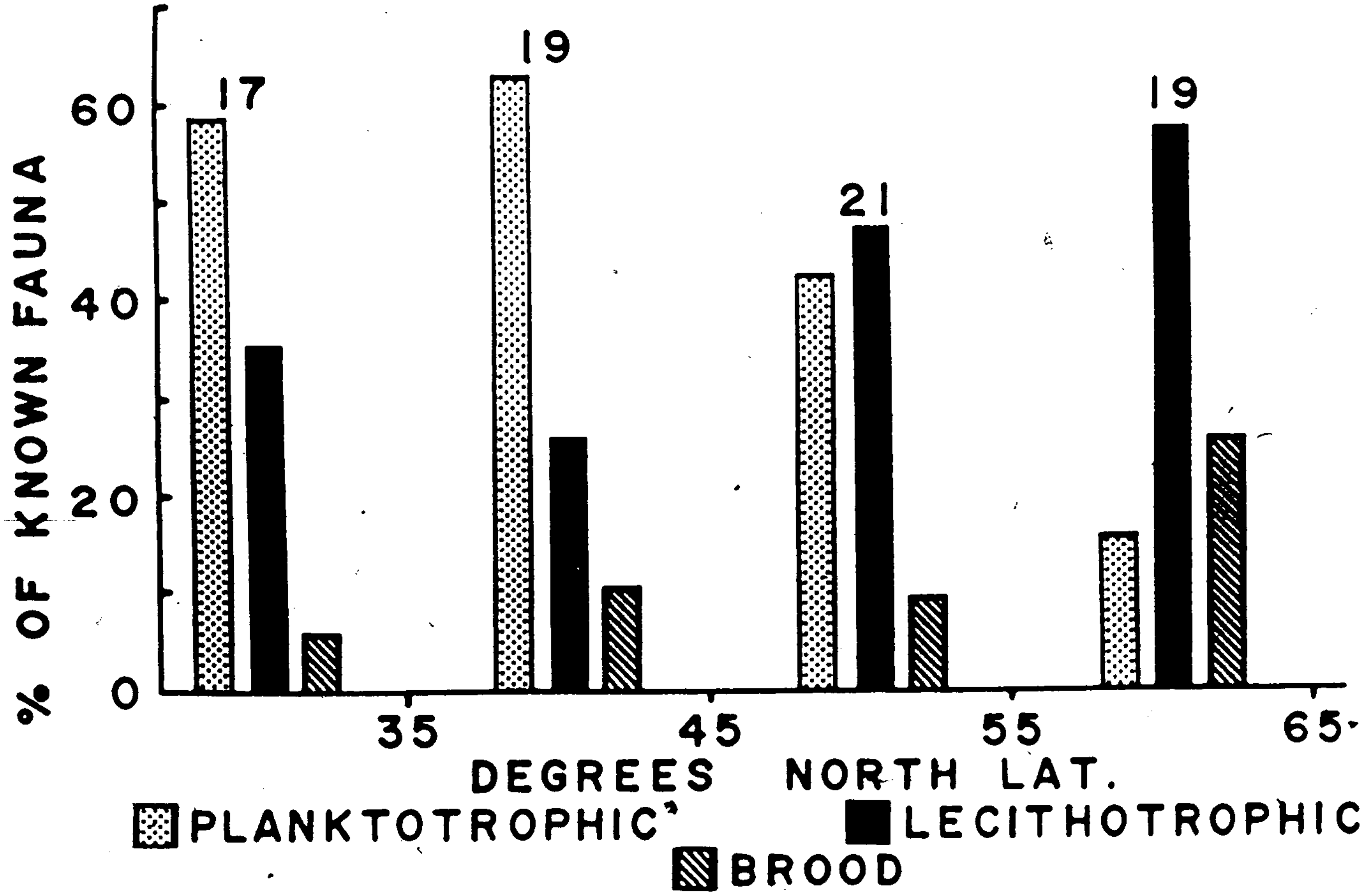

○ Planktotrophic
● Lecithotrophic
▲ Brood
OVA DIAMETER (mm)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0
10
30
50
70
90
HABITAT DEPTH
(ft)

Figure 65. Latitudinal shifts in the proportions of asteroid faunal assemblages composed of planktotrophic, lecithotrophic and brooding species along the north-east Pacific coast. Descriptions of faunal assemblages were compiled from Verrill (1914), Fisher (1940), McLaughlin (1963), Austin and Deutsch (1978), Feder (1980), and Lambert (1981). Modes of development are listed by Emlet *et al*. (1987). The numbers above the bars indicate the number of species on which the proportions are based.



ASTEROIDEA: NORTH-EAST PACIFIC

echinoderms within Barkley Sound (Figures 62 and 63). Similarity between these large and small scale patterns suggests that geographical shifts in echinoderm life history traits may result from a common mechanism that operates on substantially different spatial scales. An alternative hypothesis is that the geographical patterns in the distribution of echinoderm life history traits may be fortuitous. Detailed information concerning small scale geographical patterns in life history traits are needed for faunal assemblages from other locations to distinguish between these two alternatives.

D. DISCUSSION

Life history traits of echinoderms are traditionally compared according to the morphology and trophic modes of larvae (Chia, 1974). In the Pacific Northwest, the majority of species reproduce by means of: 1) obligate planktotrophic larvae, which are released in great numbers and feed upon algal cells during the planktonic period, 2) lecithotrophic larvae, which are produced in fewer numbers and do not feed on exogenous materials, or 3) brooded offspring, which can be produced in intermediate or low numbers and whose nourishment for development is generally incorporated within the egg. Other modes of development among echinoderms from the Pacific Northwest include the production of facultative planktotrophic larvae and viviparous development (Strathmann, 1978; Strathmann and

Rumrill, in press). In Barkley Sound, 47% of the echinoderm fauna is composed of species with planktotrophic development, 42% of the species have planktonic lecithotrophic larvae, and 11% of the species brood their offspring.

Latitudinal variability in marine invertebrate life history traits has received widespread attention (Fisher, 1940; Thorson, 1950; Ocklemann, 1965; Spight, 1977, 1981; Clark and Goetzfried, 1978; Hansen, 1980; Jones and Simons, 1983; Jablonski and Lutz, 1983; Emlet et al., 1987). Studies of geographical variability in the life history traits of prosobranch and bivalve molluscs reveal a general increase in the proportion of species with non-dispersive development at higher latitudes. Analogous data have been collected for echinoderms (Ericksen, 1940; Valentine and Jablonski, 1983; McEuen, 1986; Emlet et al., 1987) and several other taxa (Jones and Simons, 1983; Valentine and Jablonski, 1983). Since changes in latitude cannot directly affect the life history patterns of marine invertebrates, differences in environmental parameters that vary with latitude are implicated as the mechanism responsible for shifts in the proportions of faunal assemblages that exhibit particular life history traits. Relationships between life history traits and distribution have not been thoroughly investigated on smaller geographic scales. In addition, trends in life history traits based on latitudinal differences have not been compared among faunal assemblages in which the proportions of planktotrophic, lecithotrophic and brooding species are known.

Thorson (1950, 1965) reported a decrease in the proportion of marine prosobranch molluscs with planktonic larvae and a corresponding increase in the proportion of species with benthic development with increasing latitude within level bottom communities along the temperate Atlantic coast. Mileikovsky (1971) called the phenomenon "Thorson's Rule" and he evaluated several other cases where the proportions of species with planktonic and benthic development changed along a latitudinal gradient (Eriksen, 1940; Ocklemann, 1965). The traditional explanation for Thorson's Rule is that the decrease in the proportion of species with planktotrophic development is related to the short period when phytoplankton are available as a source of food. Menge (1975) pointed out several inconsistencies with Thorson's hypothesis, the most serious of which is that while the number of species with planktotrophic development decreases at higher latitudes, individuals of such species can occur in great abundance. Menge's criticism highlights the importance of considering both species richness and the distribution of individuals within a benthic community in estimates of faunal diversity. Thorson's Rule has recently been interpreted as a mathematical artifact of sampling faunal assemblages from sites positioned at non-random points along the geographical ranges of species with planktonic and benthic development (Jablonski and Lutz, 1983; Lindberg, 1985). Carefully designed sampling programs are necessary to determine the relative importance of sampling biases on latitudinal trends in the proportions of planktotrophic, lecithotrophic and brooding species among assemblages of benthic marine invertebrates.

Transect surveys conducted in Barkley Sound indicate that species with planktotrophic, lecithotrophic and brooding modes of development are distributed heterogeneously among marine habitats. The frequency of species with lecithotrophic development was positively correlated with species richness and with estimates of faunal diversity. Brooding species were negatively correlated with species richness, diversity, and depth, and positively correlated with habitat exposure (Table 31). Changes in the relative frequency of species with planktotrophic, lecithotrophic and brooding modes of development were consistent among the Taylor Island, Bamfield and Grappler Inlets study sites (Figures 62 and 63). Small scale biogeographical patterns observed within Barkley Sound are similar to large scale latitudinal shifts in the life history characteristics of echinoderms (Valentine and Jablonski, 1983; Emlet et al., 1987). Similar patterns in the reproductive characteristics of echinoderm faunal assemblages on small and large spatial scales suggests that mechanisms that contribute to the formation and maintenance of variable life history patterns may depend on factors that regulate species richness and diversity.

Several factors influence the frequency of species that have planktotrophic, lecithotrophic and brooding modes of development within Barkley Sound. Probably the most important factor is the type of habitat in which the surveys were conducted. Relationships between habitat and mode of development were influenced by depth and exposure, and they are also linked with substratum characteristics. The use of plaster cast as a measure of current velocity should be viewed with caution because the dissolution rates of plaster casts are dependent upon temperature, susceptibility to abrasion, local flow directions, and inherent variability in the plaster mixture (Muus, 1968; Denny, 1985). However, the plaster casts provided a reliable index of relative habitat exposure within Barkley Sound that was consistent with subjective ranks of exposure and with differences in sediment particle sizes. Correlations between developmental mode and exposure rank were nearly identical to correlations between development mode and depth. The consistently high relative weight loss values at intertidal and shallow subtidal transects provide an indication that these habitats are characterized by persistent wave surge and turbulent flow conditions.

The frequency of species that exhibit contrasting modes of development probably shift seasonally within several habitats in Barkley Sound. For example, individuals of

Pisaster ochraceus are less abundant along intertidal transects during fall and winter months when they migrate subtidally. Surveys of transect lines conducted during winter would be expected to show a relative decrease in the frequency of planktotrophic species at the most exposed sites and a corresponding increase at the less exposed shallow subtidal sites. The proportions of planktotrophic and lecithotrophic species are also sensitive to the appearance of rare species. For example, one individual of Pisaster giganteus occurred along a transect line at a depth of 54 ft at Taylor Island. Similarly, a single individual of Pteraster tesselatus occurred at Taylor Island along a transect 35 ft below MLLW. In each case, the proportions of planktotrophic and lecithotrophic species were influenced little by the appearance of rare species because each site was inhabited by relatively large numbers of species (Table 27). However, the influence of rare species would be greater along transects inhabited by few species.

An additional factor that may influence the proportions of planktotrophic and lecithotrophic species within a particular habitat is that the reproductive modes of resident species may be responsive to local conditions that influence survival of their offspring. Stearns (1976, 1977) proposed a bet-hedging model to predict that fewer offspring are favored in habitats where juvenile mortality is highly variable and of greater magnitude than adult mortality. The relatively low number of planktotrophic species encountered along the deep protected transects and within estuarine habitats may be related to high rates of larval and post-larval mortality. For example, planktotrophic echinoderm larvae are generally smaller in size than lecithotrophic larvae, and they rely on elaborate ciliary bands to swim and capture algal cells. Zooplankton samples collected near the bottom showed that the abundance of predatory demersal zooplankton is greater within the estuarine habitats in Bamfield and Grappler Inlets compared to Taylor Island. As a consequence, small planktotrophic larval stages may risk greater mortality in the estuaries compared with the more oceanic waters that surround Taylor Island. In addition, the silt substratum and high concentrations of suspended particulate material present in the deep water protected habitats may interfere with feeding and growth of planktotrophic larvae. Presumably, particulate material does not influence the survivorship of lecithotrophic echinoderm larvae. Little information is available concerning the mortality rates of pelagic planktotrophic and lecithotrophic larvae. Although differences in larval mortality due to demersal predators and siltation may be partially responsible for differences in the proportion of planktotrophic and lecithotrophic species between Taylor Island and Bamfield and Grappler Inlets, differential larval mortality cannot explain shifts in development mode among the Taylor Island or Inlet study sites.

Previous authors have described correlations between modes of development and depth among bivalves, prosobranch molluscs, and asteroid and echinoid echinoderms (Thorson, 1950; Ockelmann, 1965; Jackson, 1974, Jablonski and Valentine, 1981; Rex and Warén, 1982; Emlet _et al_., 1987). These studies document a general trend toward increased lecithotrophy with increasing depth among bivalves and echinoderms. An inverse trend was reported for prosobranch gastropods by Rex and Warén (1982), although the trend was largely restricted to a single family (Turridae). Rex and Warén (1982) suggested that the inverse relationship between reproductive mode and depth among turrids may be related to selective pressures that favor the dispersal of offspring in deep sea habitats.

The trend toward increased lecithotrophy with depth among echinoderms from Barkley Sound is consistent with the large scale pattern reported for asteroids and echinoids by Emlet _et al_. (1987). In Barkley Sound, the frequency of species with lecithotrophic development increased with depth, although brooding species were negatively correlated with habitat depth. The frequency of species with planktotrophic development was not correlated with habitat depth (see Figure 64, Table 31). These relationships are independent of variation in faunal diversity because species richness was not correlated with habitat depth (Table 31).

Processes that affect the distribution and abundance of adult echinoderms can also contribute to small scale biogeographical shifts in the frequency of planktotrophic and lecithotrophic species. In the Pacific Northwest, echinoderms are ubiquitous members of intertidal and subtidal marine invertebrate communities where they can be influential as ecologically dominant or keystone species (Paine, 1974; Estes and Palmisano, 1974; Duggins, 1980, 1981). Echinoderm communities can be influenced by several processes including: 1) predatory interactions and mutual accomodation (Paine, 1966; Mauzey et al., 1968; Paine and Vadas, 1969; Paine, 1976; Estes and Palmisano, 1974; Duggins, 1980; Tegner and Levin, 1982; Whitman, 1985), 2) the frequency and intensity of physical disturbance (Paine, 1966; Dayton, 1971; Sousa et al., 1981), and 3) links between trophic modes and habitat heterogeneity (Menge and Sutherland, 1976). Differences in the distribution and abundance of echinoderm populations can also result from variation in the spatial patterns and intensity of settlement events (Keough and Downes, 1982; Gaines and Roughgarden, 1985). Processes that influence temporal and spatial variability in settlement are particularly important because settlement events establish the initial distribution patterns upon which subsequent processes can act (Birkeland and Chia, 1971; Cameron and Schroeter, 1980; Tegner and Dayton, 1981; Young and Chia, 1982; Connell, 1985).

In spite of the enormous complexity of interactions that regulate the abundance an composition of echinoderm communities within Barkley Sound, the proportions of lecithotrophic and brooding species changed predictably with depth and exposure. However, shifts in the frequency of lecithotrophic and brooding species were also influenced by factors that regulate species richness and faunal diversity. In contrast, the frequency of species with planktotrophic development was independent of species richness and faunal diversity. These relationships indicate that care must be exercised to sample faunal assemblages from habitats characterized by similar depth and exposure, and that are represented by comparable numbers of species and faunal diversity.

Results from this investigation suggest that the relative frequency of echinoderms that exhibit planktotrophic, lecithotrophic and brooding modes of development vary along latitudinal, depth, exposure and substratum gradients due to differences in species richness and faunal diversity. Since the life history traits of other benthic marine invertebrates also vary along latitudinal and depth gradients, it is predicted that their patterns of life history diversity may also be correlated with geographic variability on smaller spatial scales.

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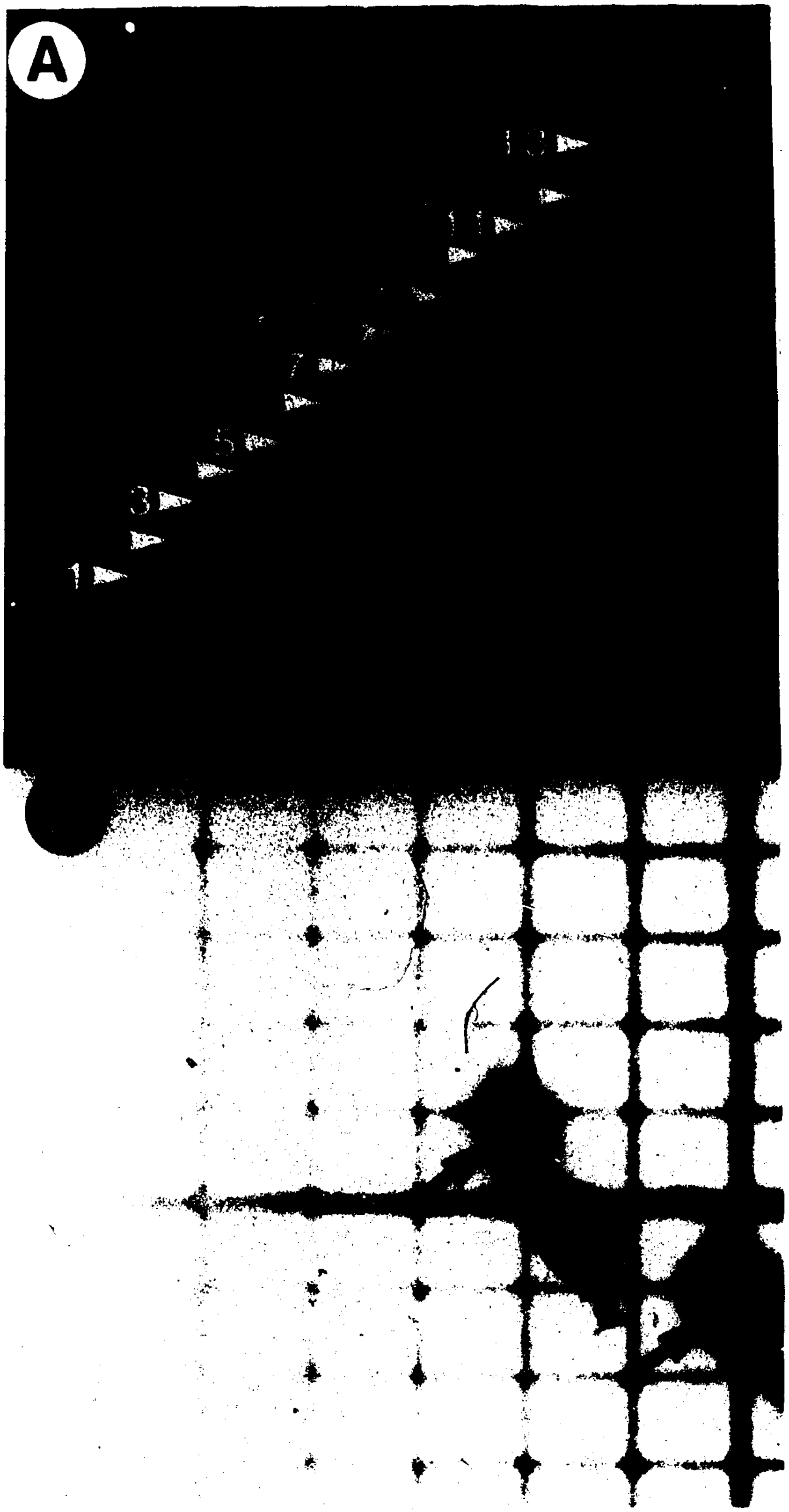
Appendix II. A. Stroboscopic photograph of a *Pugettia producta* stage I zoea. Arrows and numbers indicate successive images of the zoea over a period of 4 seconds. Instantaneous velocities and acceleration values are obtained by measuring the distances between successive images of the swimming zoea. B. Shadow triangulation of a stage I zoea in an observation chamber. Arrows point to twin shadows created by light directed at the center of the chamber through fibre optic glass. Grid = 1 mm.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