Spring 1993

A multi-scale analysis of the population ecology of a temperate reef fish

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A multi-scale analysis of the population ecology of a temperate reef fish

Levin, Phillip S., Ph.D.

University of New Hampshire, 1993

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A MULTI-SCALE ANALYSIS OF THE POPULATION ECOLOGY OF A TEMPERATE REEF FISH

by

Phillip S. Levin
B.A. University of Texas, 1984

DISSERTATION

Submitted to the University of New Hampshire in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

in

Zoology

May, 1993

This dissertation has been examined and approved.

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20 April 1993
Date

DEDICATION

This work is dedicated to my parents

ACKNOWLEDGMENTS

Dr. Peter Sale gave me the opportunity to pursue my Ph.D. in an atmosphere that encouraged individuality, that invited thoughtful criticism, and inspired creativity. He worked to provide an intellectually stimulating laboratory, and as chair, transformed the department into one that was supportive, serious, and strove for excellence. I thank him for subtly guiding my way and for his friendship. I was lucky.

Larry Harris' love and enthusiasm for marine (and terrestrial) life was contagious. I hope that some day I can see and understand as much as he does. Art Mathieson showed me with great patience that plants aren't so bad after all, and I think he has convinced me that they're actually fascinating. Randy Olson taught me the value of being concise, of being critical and of having fun. Bob Warner, in only a few meetings, taught me an incredible amount about ecology, about thinking, and stretched my mind until it hurt. He showed me, by example, how much more I have to learn, and that the learning never ends. I would also like to thank Jon Witman for his insights about the Gulf of Maine and UNH.

Perhaps the most valuable experience of my graduate career has been forming friendships that I know will last a lifetime. Tom Good, Graham Forrester and Linda O'Brien have been with me from the beginning of my grad school experience. I sincerely appreciate their support and friendship. They were my harshest, and in many ways, my best critics, and I thank them for the time they spent thinking about the coolest fish in the North Atlantic. Very special thanks to Sara Bard who helped me to get this thing done when I thought I couldn't, and who taught me to shallow up. Also, I'd like to thank Dave Carlon, Big Geoff Trussell, Nick Tolimeri, Mike Ganger, Kelly Gestring, and Jody Berman for keeping my brain engaged and my spirits up. I'd also like to thank some of the Zoology Department faculty who helped me throughout my time at UNH, particularly Chuck Walker, Tom Kocher, "C." Jim Taylor and Marianne Litviatis. I'd especially like to thank Dr. M.P. Scott for general science-type help, for setting an excellent example and her roof.

I would also like to thank the many, many people who helped me in the field. Paul Pelletier and the crew of the Jere Chase have been and will always be awesome. The staff at the Shoals Marine Lab were invaluable and an incredible amount of fun. Thanks also to Liz Kintzing and Paul Lavoie for diving support. Wayne Chiasson and Dr. John Green collaborated on the Newfoundland work. I'd also like to thank the many divers and lab slaves who helped me. They are mentioned by name in the acknowledgments of each chapter.

Most of all I'd like to thank Marilyn Levin. She taught me to believe in myself, and she always helped me to keep things in perspective. She supported me as much as she possibly could. I deeply appreciate all she has done for and with me.

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ABSTRACT

A MULTI-SCALE ANALYSIS OF THE POPULATION ECOLOGY OF A TEMPERATE REEF FISH

by

Phillip S. Levin
University of New Hampshire, May, 1993

Using field experiments and descriptive analyses this study investigated the significance of larval settlement and post-settlement processes to populations of cunner, Tautogolabrus adspersus. At small spatial scales there was no relationship between the density of new recruits and the percent cover of kelp, foliose algae and branching algae. Crustaceans and mussels were preferred found items of juvenile cunner, and significantly greater numbers of isopods, amphipods and newly settled mussels were present in patches where fish were present than in randomly selected patches.

Experimental and correlative analyses demonstrated that variation in recruitment could not be explained by the presence of conspecifics. Manipulations of macroalgal structure showed that the distribution of fish was influenced by the algal habitat. The dispersion of macroalgae influenced the demography of cunner. Settlement was greater to randomly placed than to clumped habitats; however, no differences in recruitment between random and clumped habitat were detected. The magnitude of the change in recruit number between sampling dates did not differ between clumped and random habitats. There was no evidence of either density-dependent mortality or settlement.

A larger scale study was conducted comparing the demography of cunner in Newfoundland and the Gulf of Maine. Greater numbers of adult fish were observed in Newfoundland, but higher numbers of juveniles and recruits were found in the Gulf of

Maine. In the Gulf of Maine variation was pronounced at the site scale, while in Newfoundland variation was pronounced at both the site and location scales. Variation in recruitment was not expressed as subsequent variation in older age classes. There was no effect of topographic complexity on variation of densities of recruits or juveniles, but in Newfoundland a negative relationship between adults and topography was observed. Algal cover was not important in Newfoundland, but was important in the Gulf of Maine. Although there was consistently greater than 2 orders of magnitude difference in densities of pre-settlement fish between two locations, the location that received fewer pre-settlement fish actually had higher recruitment.

INTRODUCTION

General aim

The primary aim of this work was to define processes which limit or generate change in fish populations over a range of spatial scales. Both recruitment and post-recruitment processes may affect populations, but their relative importance may vary with spatial scale and habitat type. Using field experiments and censuses of settlers, recruits and adults, I endeavored to establish the significance of larval settlement and post-settlement processes to a demersal fish population in the Gulf of Maine. To achieve this goal I addressed the following objectives.

Objectives

1) To determine the importance of larval supply, settlement, and post-settlement mortality to variation in recruitment. At what spatial scales are these factors important? Does habitat influence the contribution of these factors to recruitment variation?

2) To determine the importance of recruitment and resources to the limitation or determination of population size in different habitats. Are populations regulated by different processes in different habitats?

Complex life cycles and the role of recruitment

Ecologists try to understand the processes that limit or generate change in populations. Previously, marine ecologists focused on processes acting on only adult populations (Connell 1975, Menge and Sutherland 1976, Paine 1977); however, this approach has led to the formation of incomplete models and to some erroneous conclusions as discussed by Dayton (1979), Sale (1980, 1984, 1988), Underwood et al. (1983), Underwood and Denley (1984), Connell (1985), Watanabe (1984), Caffey (1985), Roughgarden et al. (1985), and Menge and Sutherland (1987). Most marine species, including many demersal fishes, have complex life cycles in which different developmental stages occur in distinct habitats (Thorson 1950, Sale 1980, Roughgarden et al. 1988) (Fig. 1). Typically, demersal fishes have larvae (and often eggs) that are pelagic and widely dispersed (Barlow 1981, Cowen 1985, Doherty et al. 1985, Kingsford 1988, Thresher et al. 1989). Following the pelagic phase, larvae or already metamorphosed individuals move from the water column to the demersal habitat (*i.e.* settle, Kingsford 1988) and become relatively site-attached (Sale 1978). Thus, recruitment to demersal populations occurs by the addition of individuals through larval and post-larval settlement.

As it has been difficult to directly measure settlement, most fish ecologists have measured recruitment (but see Breitburg 1989, 1991). I operationally define recruitment as the presence of 0+ year individuals at the end of the settlement season (thus, I refer to recruits as 0+ year individuals present at the end of the settlement season)(Richards and Lindeman 1987) . Additionally, I refer to newly settled fish as settlers. Measured rates of recruitment equal the rate of settlement minus the fraction of fish which settle but die before being censused. The latter can be a significant fraction in some species particularly if several days elapse between censuses of recruits (Doherty and Sale 1986). It has generally been assumed that recruitment variation is correlated with settlement variation (Williams 1980, Doherty 1981, 1983, Victor 1983, Caffey 1985), but this is only true if post-settlement mortality is density independent (Connell 1985, McGuiness and Davis 1989).

Because of their life history, most marine populations are considered to be open populations in which local production of offspring on a scale of meters to kilometers has little to do with recruitment to that site (Cowen, 1985, Warner and Chesson 1985, Roughgarden et al. 1985, Roughgarden 1986, Doherty and Williams 1988, Mapstone and Fowler 1988, Warner and Hughes 1988). It is generally accepted that demersal fish populations consist of local sub-populations connected through larval dispersal. Thus, the arrival of pelagic propagules and subsequent mortality in the demersal population are critical demographic parameters when modeling the population dynamics of such populations (Roughgarden et al. 1985, Warner and Hughes 1988).

Resource or recruitment limitation?

Pronounced differences in recruitment and population abundance occur over a range of temporal and spatial scales in benthic invertebrates (Connell 1961, 1985, Grossberg 1982, Caffey 1985, Yoshioka 1982, Gaines et al. 1985, Olson 1985, Keough 1986, Hughes 1990, Raimondi 1990), algae (Reed et al. 1988, Deyster and Dean 1986, Levin and Mathieson 1991), tropical fishes (Williams and Sale 1981, Doherty 1983, Victor 1983, 1986, Sale and Douglas 1984, Sale et al. 1984, Schulman 1985, Doherty 1987) and temperate fishes (Hjort 1914, Choat et al. 1988, Jones 1984a,b, Kingsford et al. 1989, Carr 1989, Ebeling et al. 1980, 1985, Larson 1980, Levin 1991, in press; but see Stephens et al. 1984, Ebeling et al. 1990). How these populations are numerically regulated has become an issue of vigorous debate. Two very different schools of thought have developed; however, both include a critical role for the process of recruitment. One hypothesis, "the resource limitation hypothesis" is derived from conventional terrestrial ecology and asserts that the size of demersal fish populations is limited (i.e. the upper bound of population density is set) by the availability of resources. According to the resource limitation hypothesis, potential settlers are plentiful, and competition for resources (usually space or food) results in density dependent rates of recruitment. This model suggests that in the absence of disturbance, demersal fish populations saturate the benthic habitat. If this is true, then at small spatial scales there should be an over-abundance of new recruits (either from larval settlement or demersal migration), and rates of settlement should be density dependent (Doherty 1983). The prediction that arises from this model is that larval settlement and/or post-settlement survival is inversely related to the density of conspecifics or ecologically similar individuals (i.e. potential competitors) at the settlement site.

A more recent hypothesis, the "recruitment limitation" hypothesis, asserts that sites are undersaturated with new recruits and that upper limits of abundances are set by levels of recruitment. (Doherty 1981, 1983, Victor 1983). Additionally, an incarnation of this hypothesis, termed "recruitment determination" by Forrester (1990), suggests that populations are not only limited by recruitment, but that recruitment variation causes variation in population abundance. Thus, temporal variation in recruitment should be preserved in the age structure of the population, and spatial variation in recruitment should be reflected in subsequent patterns of abundance in demersal populations (Doherty 1987, Victor 1986, Mapstone and Fowler 1988).

The evidence

Resource limitation

Much of the evidence gathered which tests these hypotheses has focused on sessile marine invertebrates or tropical reef fishes. Numerous studies of tropical reef fish populations have failed to detect resource limitation (Robertson and Sheldon 1979, Robertson et al. 1981, Doherty 1982, 1983, Warner 1984 [cited in Doherty and Williams 1988], Munro and Williams 1985, Jones 1987; but see Schulman 1984 and Hixon and Beets 1989). Robertson and Sheldon (1979), for example, found that the removal of sleeping shelters, or the addition of fish did not affect the ability of the wrasse, *Thalassoma bifasciatum*, to find sleeping shelters. Furthermore, Robertson and co-workers (1981) conducted similar experiments manipulating the amount of coral substratum available for use by a damselfish. They found that in sites where available space was experimentally reduced by half, the damselfish population remained at an increased density, and showed no evidence over 12 months of reduced fecundity, growth or survivorship.

Manipulations have been performed in which natural reefs are denuded or artificial reefs created. Results from these studies generally show a rapid colonization that peaks within weeks (Talbot et al. 1978, Molles 1978, Schulman 1984, 1985, Bohnsack and Sutherland 1985, Hixon and Beets 1989). Individuals may colonize artificial reefs from surrounding natural habitat as well as from the pelagic larval habitat. This may be interpreted as evidence for resource limitation because fish may be responding to overcrowded conditions prior to the creation of new sites. Recruitment of larvae from the plankton to artificial reefs also may be construed as supporting space limitation since larvae are settling to previously unavailable habitat and increasing the size of the population. Only a failure to recruit to a newly available habitat can be taken as evidence that resources are not limiting the size of the demersal population. This is a most unlikely outcome. A critical problem with these studies is that small manipulations (the artificial reefs) surrounded by a large non-manipulated area that can supply colonists, by either route, will never be able to discriminate sensitively between resource limitation and recruitment limitation.

While most workers have emphasized space related resources, availability of food may also limit population abundance. Schulman (1984) found no effect of supplemental feeding on rate of settlement. However, several studies have demonstrated supplemental feeding results in increased growth and/or earlier maturation rates but not increased survivorship of recruited fish (Jones 1986, 1987, Forrester 1990). Moreover, the removal of potential competitors for food increased the growth rate of a coral reef fish (Thresher 1983). Because size and fecundity are closely related in fish, the ultimate effect of food shortages seems to be a reduction in the fecundity of populations in such conditions.

This effect is unlikely to influence local population structure since reproductive effort is exported.

Recruitment limitation

There are two general questions which have emerged from the recruitment limitation hypothesis. First, are demersal abundances limited by larval settlement? Several studies have demonstrated that densities of demersal fish populations are unstable and at a level below the carrying capacity of the environment (Williams 1980, Doherty 1983, Victor 1983, 1986, Sale and Douglas 1984). Manipulations in which groups of recruits show high survivorship even when more crowded than usually occurs naturally also indicate that the demersal habitat is under-supplied with larvae (Doherty 1983, Jones 1987, Forrester 1990). Jones (1987), for instance, artificially increased recruitment and found no consistent effects of initial recruit density on survivorship. This supports the view that recruitment rather than resource levels set the upper limit of population size (Williams 1980, Doherty 1983, Victor 1983).

The second question is, does recruitment determine population abundance of demersal populations? This question has become a focus for recent studies, and a substantial body of evidence has developed indicating that recruitment fluctuations are reflected in subsequent changes in the demersal population. For example, Davis (1988) demonstrated that post-settlement mortality of tunicate recruits is often density independent. Therefore, despite sometime high post-settlement mortality rates, the adult population reflects previous variation in larval settlement (Davis 1988). Similarly, in short-lived wrasses Victor (1983) showed that temporal variations in recruitment are reflected in the adult population. Thus, the age-structure of the population reflects its recruitment history. Cowen (1985) also showed that the age-structure of temperate labrid populations is correlated with oceanographic process which result in temporal variations in larval supply to local populations. Additionally, this study demonstrated that variation among distant locales in demersal population structure results from the frequency with which pelagic propagules are brought to a site (Cowen 1985).

A More Pluralistic Approach

It is apparent that both rates of settlement and subsequent benthic mortality due to resource limitation or other factors may contribute to fluctuations in population size in demersal fishes (Warner and Hughes 1988). While a dichotomy between resource and recruitment limitation or between density dependent and density independent processes has been manufactured, the best course may be to adopt a more pluralistic approach (Strong 1986, Warner and Hughes 1988, Forrester 1990). Single factor explanations are often too simplistic to adequately explain variability in population structure (Strong 1986, Jones 1987, 1990, 1991 Forrester 1990, Hixon 1991, Sale 1991).

Several workers have suggested that populations of a single species may be both resource and recruitment limited in different locations (Jones 1984b, Roughgarden 1986, Nisbet and Bence 1989, Hixon and Beets 1989). For organisms that are site attached, the relative importance of resources and recruitment may differ in patches which are separated by only a few meters. In addition, fluctuations in recruitment can influence density dependent post-recruitment processes (Jones 1987, 1990, Forrester 1990, Hughes 1990). Both recruitment variability and density dependent effects on juveniles contribute to variability in adult population numbers, and recruitment is just one of a number of parameters which contributes to adult population size (Jones 1987, 1988b, 1990).

Temperate reefs

Tests of models which explain the dynamics of demersal fish populations have been conducted largely in coral reef habitats. Recently, however, some workers have addressed the roles of recruitment and post-recruitment processes on temperate rocky reefs. As in the tropics, recruitment is highly variable over a range of temporal and spatial scales (Jones 1984a,b, Cowen 1985, Ebeling and Laur 1985, Carr 1989, Keats et al. 1987, Breitburg 1989, Levin 1991, in press). Causes of spatial variation in recruitment have been shown to relate to habitat (Jones 1984a, Carr 1989, 1991) and microhabitat (Carr 1991, Levin 1991), but a few species recruit evenly across a variety of habitat types (Jones 1988, Levin in press). It is unknown if these differences reflect habitat selection by settling larvae, or differential mortality among habitats. Post-recruitment events also play a role in structuring reef fish populations. For example, Jones (1984b) found that density dependent growth and mortality restricted input into the adult population of a New Zealand labrid.

A major component of the structure of temperate reefs is macroalgal vegetation (Schiel and Foster 1986, Chapman and Johnson 1990). The macroalgal structure of temperate reefs can vary considerably in space and time and may be more ephemeral than the structure of tropical reefs (Dayton 1985, Schiel and Foster 1986, Chapman and Johnson 1990). Juvenile temperate reef fish, especially those of tropical derivation, are commonly associated with macroalgae (Pottle and Green 1979b, Wheeler 1980, Jones 1984a,b, Ebeling and Laur 1985, Keats et al. 1987, Jones 1988a, Carr 1989, DeMartini and Roberts 1990, Levin 1991). The close association of juvenile fish with macrophytes may have profound influences on the small-scale dynamics of fish populations. For example, the dispersion of juvenile fish in habitats in which algae are clumped may be aggregated (Jones 1984c, Levin in press). Consequently, the dispersion of macrophytes influences the small scale density of fish.

Habitat structure and population processes

Marine environments are composed of patches that vary in physical structure and prey availability. The trade-offs between protection from predation and quality of food and how these trade-offs govern patch selection by fish has received considerable attention (Werner et al. 1983, Ebeling and Laur 1985, Schmitt and Holbrook 1985, Werner and Hall 1988, Holbrook and Schmitt 1988). However, the ways in which population processes vary with patch structure, particularly the dispersion of habitat types, has not been directly addressed for marine fish populations.

In terrestrial systems the spatial structure within habitats has been demonstrated to have significant impacts on demographic processes (Wiens 1976, Antonovics and Levin 1980, Addicott et al. 1987). Like temperate reef fish, endophagous insects exhibit a dispersion linked to the spatial pattern of their host plants (Southwood and Kennedy 1983). Therefore, these insect populations may be analogous to temperate reef fish populations in this regard, and research on these populations is of potential importance to this research. Leafminers may suffer increased larval mortality with increased clumping (Auerbach and Simberloff 1989, Faeth 1990). For instance, Faeth (1990) demonstrated that *Cameraria* larvae suffer severe reduction in survival from increased interference competition and premature degradation of patches (i.e. leaves) when more than two individuals occupied a single leaf. By contrast Godfray (1986) showed clutch size of three larvae per leaf actually increased survivorship of the leafminer, *Pegomyza nigrotarsis*. Thus, for this species clumping has a positive effect. Clumping of larvae also may increase mortality due to predation (Itamies and Ojanem 1977) or influence parasite load (Faeth 1990). It is clear that variation in the spatial structure of the habitat can result in different degrees of aggregation by these insects, and that patterns of dispersion influence demographic processes. Similarly, it seems likely in temperate reef fishes whose dispersion, like endophagus insects, may vary as the structure of the habitat varies (Jones 1984c, Levin unpublished data), that density dependent processes (e.g. competition, predation, parasitism) may assume greater importance in some habitats than others.

Patch structure is expressed both temporally and spatially and is dependent on the scale of investigation. The answers to the questions I ask in this dissertation may be dependent on the spatial scale we define (Dayton and Tegner 1984, Wiens et al. 1986, Wiens 1989). Analyses at different spatial scales will be necessary in order to reveal scale-dependency of patterns, and suggest how the importance of pre- and post-recruitment processes in demersal fish populations vary with scale.

The Gulf of Maine - an excellent opportunity

The Gulf of Maine is a semi-enclosed basin bounded on the north and west by New England and on the east by Nova Scotia. Rocky reefs in the Gulf of Maine provide an excellent opportunity to examine the relative importance of the factors limiting or inducing changes in the structure of fish populations. As in other temperate systems, macrophytes are important features of nearshore habitats in the Gulf of Maine. At a very coarse level there are two different community types which dominate shallow rocky substrata and can be found within meters of each other (Witman 1987, Johnson and Mann 1988, Chapman and Johnson 1990). These are sea urchin (*Strongylocentrotus droebachiensis*) dominated areas (sensu Schiel and Foster 1986) in which crustose coralline algae are the primary macroalgal flora and seaweed beds which are dominated by laminarian kelps with a diverse understory of red algae. Macroalgae in kelp beds are distributed randomly throughout sites while in urchin dominated areas macrophytes are clumped (Levin in press).

Kelp beds are more productive habitats than urchin dominated areas (Mann 1972) and support rich populations of juvenile fish. Localized patches of ephemeral or unpalatable macroalgae occur in urchin dominated areas (Himmelman and Nedelec 1990). These also support aggregations of juvenile fish. These two very different habitats in close proximity to each other will allow us to answer unique questions concerning the importance of pre- and post-recruitment processes to the structure of demersal fish populations.

Cunner (Tautogolabrus adspersus) as a model species

The cunner, *Tautogolabrus adspersus* (Labridae), is an ideal species to examine recruitment processes in fish populations. Cunner occur in abundance along the Atlantic coast of North America from Conception Bay, Newfoundland to New Jersey, and are occasionally found as far south as Chesapeake Bay (Bigelow and Schroeder 1953). They are one of the most common fish in the Gulf of Maine occurring from intertidal zones (Whoriskey 1983, Ojeda and Dearborn 1990) to depths greater than 90 meters (Bigelow and Schroeder 1953). I have found juvenile cunner (12.1 mm ± 1.31) to be easily observed, collected and experimentally manipulated.

Cunner spawn during early and mid summer (Dew 1976, Pottle and Green 1979a). After a larval life averaging 18-21 days (Gleason and Reschiek 1991), fish settle to the demersal habitat. They appear to feed opportunistically on zooplankton and small benthic invertebrates (Chao 1972). Recruits are site-attached and do not stray far from cover particularly that provided by macrophytes (Bigelow and Schroeder 1953, Pottle and Green 1979b, Gleason and Reschiek 1991, M. Tupper Dalhousie University unpublished data).

As a labrid, cunner offer a unique opportunity to study a north temperate member of a well studied tropical family. The data collected concerning the importance of pre- and post-recruitment processes to the population dynamics of cunner are directly comparable to similar studies of invertebrates and tropical fishes. Additionally, differences among this study and those on invertebrates and tropical fishes may indicate that currently fashionable models need to be modified to account for the effects of habitat or spatial scale.

CHAPTER 1

SMALL-SCALE RECRUITMENT VARIATION IN A TEMPERATE FISH: THE ROLES OF MACROPHYTES AND FOOD SUPPLY

Abstract

The availability of reef-related resources, particularly food and shelter can play a significant role in determining the distribution and abundance of reef fishes. Much of the structure on temperate reefs is provided by macroalgae. Variability in the density of temperate reef fishes at large spatial scales (100's of meters) can often be explained by variation in macroalgal cover or density. In this study I investigated the role of macrophytes and associated food resources on the recruitment of a temperate fish, Tautogolabrus adspersus, at a small spatial scale (0.25 m^2). No relationship between the density of new recruits and the percent cover of kelp, foliose or filamentous algae was observed. Multiple regressions revealed that less than 8% of variability in recruitment could be explained by variability in the macroalgal assemblage. A wide variety of prey were available for use by cunner recruits; however, crustaceans and mussels were the only common components of their diet, and crustaceans were clearly the most preferred prey. The prey composition in patches where fish were present was compared to randomly selected patches. Significantly greater numbers of isopods, amphipods and newly settled mussels were present in patches where fish were present than in randomly selected patches. The data presented in this study contradict the previous work that has shown algal stucture to be important in determining patterns of abundance and food supply to be of little signifcance. A conceptual model is proppossed suggesting that settling fish select habitats in a hierarchical manner largely based on their dispersal tendencies. Hierarchical selection of habitats results in different attributes of the habitat being selecting during different life-history stages.

Introduction

The demography of fishes living on coral reefs in the tropics or on rocky reefs in temperate zones are affected by the interactive effects of patchiness in reef-related resources, particularly shelter from predators (Shulman 1984, Carr 1990, Hixon and Beets, 1993), and food (Schmitt and Holbrook 1985, Jones 1986, Forrester 1990). As juveniles, reef fishes generally have very small home ranges (Sale 1978), and some species suffer high early mortality (Shulman and Ogden 1987, Sale and Ferrell 1988, Levin 1993). The selection of appropriate habitat patches by juvenile fishes can thus have important consequences for the population dynamics of these species. Since most reef fishes have a pelagic larval phase, colonization of patches usually occurs via the settlement of post-larvae from the plankton to the demersal habitat. As a result, the covariance of larval settlement and reef-related resources is of great interest. In this paper settlement is operationally defined as the time when an individual takes up permanent residence in the demersal habitat (Keough and Downes 1982) and recruitment refers to the number of individuals surviving some arbitrary period of time after settlement (Connell 1985).

Variation in the abundance of fishes on temperate reefs, particuarlary at large spatial scales, can be often be explained by variability in macroalgal strcuture (Wheeler 1980, Jones 1988, Holbrook et al. 1990, Levin 1993). In addition, at small spatial scales the occurrence (presence/absense) of fish can be influenced by the presence of specific macroalgal habitats (Carr 1991, Levin 1991). Algal habitats serve both as a source of food and as protection from predators (Ebeling and Laur 1985, Holbrook and Schmitt, 1988). Macroalgal habitats vary extensively in space and time (Chapman and Johnson 1990, Lambert et al. 1992), thus offering associated fishes patches that differ in the quantity of food and/or quality of cover. In the few examples for temperate reefs examined thus far, effects of food resources on variability of recruitment seems slight (Jones 1984, Carr 1990), but there appears to be a strong effect of algal habitat on the intensity of predation (Carr 1990).

Although food supply has not yet been shown to influence recruitment variability, there are several reasons to suspect that it may, particularly at small spatial scales. Schmitt and Holbrook (1985) have shown that food richness rather than shelter potential is the major determinant of patch quality for juvenile black surfperch (Embiotoca jacksoni) in California. As a result, these fish choose algal patches based largely on food quality. Additionally, Jones (1986, 1987) and Forrester (1990) have shown that supplemental feeding of fish on coral reefs resulted in increased growth and/or earlier maturation rates.

While the data gathered to date suggests that large-scale variation in the abundance of recruits is affected by algal structure, a detailed study of how algal structure and associated food resources influence recruitment variation at small scales (meters) has not been conducted. In the present study I investigate patch use at a small spatial scales by a temperate demersal fish (Tautogolabrus adspersus) in the Gulf of Maine. Specifically, I ask: 1) What effect does small-scale variability in macroalgal cover have on variation in the abundance of newly recruited fish? 2) Do newly recruited fish have preferred prey? 3) Does the distribution of preferred prey influence spatial variation of recruitment? The results of this study demonstrate that small-scale variation in recruit abundance is not related to algal structure. Rather, at this scale fish appear to respond to variability in prey density.

Methods

Study species

Cunner, Tautogolabrus adspersus, are common members of rocky-reef communities in temperate waters of the western North Atlantic (Bigelow & Schroeder, 1953). Cunner occur from intertidal zones (Whoriskey, 1983) to depths greater than 90m (Bigelow & Schroeder, 1953), although newly recruited fish are most common in shallower depths (Levin, in press). In the Gulf of Maine, the most intense period of cunner spawning occurs in July and early August (personal observation). Following a 18-21 day larval life (Gleason & Reschiek, 1990), post-larval cunner settle to a wide range of habitats including both urchin-dominated areas and seaweed beds (Levin, 1991). However, they are generally associated with macroalgal microhabitats (Levin, 1991, Levin, in press). As juveniles cunner have very small home ranges and do not stray far from algal cover (Olla et al. 1975, Pottle and Green 1979). Tagging studies have shown that cunner spend their first year within an area of a few square meters (M. Tupper, Dalhousie University, unpublished data).

Adult cunner feed on a wide variety of motile and sessile invertebrates, particularly mussels (Mytilus edulis and Modiolus modiolus), urchins, (Strongylocentrotus droebachiensis), and gastropods, (Lacuna vincta and Acmaea testudinalis) (Chao 1972, Green et al. 1984). Female and non-territorial males feed throughout daylight hours, while territorial males tend to feed more in the morning (Green et al. 1984, 1985). Little published information exists on the diets of juvenile cunner. Chao (1972) found that in 8 specimens (30-50 mm standard length) that he examined, micro-crustaceans (amphipods, isopods, copepods) dominated the diet. To my knowledge, no data exist concerning the diets of newly recruited cunner (10-12 mm standard length).

Macroalgae-recruitment relationships

The relationship between macroalgal cover and the density of newly settled recruits was investigated at two sites along the southern Maine coast near York, Maine (43° 10' N, 70° 36' W). In one site (site 1), filamentous, foliose and corticated macrophytes dominated the algal assemblage, while in the other site (site 2) the flora was dominated by kelps. Both sites were ca. 6.5 m in depth. Detailed descriptions of these sites are provided elsewhere (Levin, 1991).

In order to estimate small-scale densities of cunner recruits, replicate 0.25 m^2 quadrats were placed randomly in each site. Randomization was accomplished using pairs of random numbers to indicate a compass direction and distance from a haphazard starting point. After counting all recruits, the percent cover of macroalgae in each quadrat was determined by recording the type of plant under each of 45 points created by a grid of monofilament line strung across the quadrat. Because previous work (Levin 1991, in press) has shown that erect, fleshy forms of algae are most attractive to settling fish, these were targeted in this study. Algae were grouped as kelps (Lamnaria sacharina, L. digitata, and Agarum cribrosum), foliose (Ulva lactuca) and branched (mostly Ceraminum spp., Polysiphonia spp., Desmarestia spp., Ahnfeltia plicata).

The null hypothesis that no relationship existed between algal cover and the density of recruits was examined using a multiple regression for each site. Recruit density was the response variable in these analyses, and percent cover of kelps, branched and foliose algae were independent variables. Prior to the analyses, percent covers were arcsine transformed and recruit densities were log transformed (Zar 1984).

Fish diets and prey preference

To determine the types of prey cunner recruits consume, SCUBA divers using small dip nets collected 50 fish from Appledore Island, Maine USA (42°59' N 70°36' W) in the Isles of Shoals archipelago. This site is a granite ledge, ca. 6 m deep with a dense cover of the branched alga <u>Codium</u> <u>fragile</u>. Within 15 minutes of being captured, fish were placed in 10% buffered formalin. All collections were made in the morning hours when these fish were actively foraging. As cunner have no stomach and the intestine appears to act as a storage organ (Chao 1972), the entire alimentary tract of each fish was removed. Alimentary tracts were dissected and the contents examined under a dissecting scope. Prey were classified as specifically as possible; however, the poor condition of many species, particularly crustacea, made classification to even suborder difficult. Consequently, when prey could not be identified to species, genus or family they were grouped. The most common groupings were crustaceans (isopods, amphipods, copepods, etc.), worms (annelids and non-segmented), algal fragments, and ophiuroids.

Abundances of all potential prey available in the habitat had to be assessed in order to establish prey preference. To accomplish this, at Appledore Island randomly selected, 0.0625 m^2 quadrats were scraped clean with a putty knife and all the contents were collected using an airlift fitted with a 0.5 mm mesh collecting bag. The contents were later brought to the lab where all animals and algae were separated. Algae were then damp-dried and weighed. All animals except mussels, amphipods, and isopods were then counted. As the latter animals were extremely abundant, densities were estimated from random 1/16 sub-samples taken using a Folsom plankton splitter.

Two methods were used to measure prey preference. Manly's Index α which is:

$$1$$

$$\alpha_i = r_i/n_i\,(\Sigma\, r_j/n_j) \quad \text{(Krebs, 1989)}$$

where r_i and r_j are the proportion of prey type i or j in the diet (i and j = 1,2,3...m) and n_i

and n_j are the proportion of prey types available in the environment. This index is a simple measure of preference derived from the probability that a predator will encounter a prey species and the probability of capture after encounter (Krebs 1989). The Manly's index indicates what the use of prey would be if all prey were equally available in the habitat.

As the assessment of preference is dependent upon the prey items the investigator chooses to include as "available" in the habitat (Johnson 1980), I also measured prey preference using a rank preference index. Such indices produce a ranking of relative preference of prey items included in the analysis, and is thus not influenced by the exclusion of food items that are uncommon in the diet (Krebs 1989). Johnson's (1980) rank preference index is:

$$t_i = r_i - s_i$$

where t_i is the rank difference, r_i is the rank of usage of resource types i (i= 1,2,3...m) and s_i is the rank availability of resources.

Effects of prey distribution on recruitment

In order to test the hypothesis that small-scale spatial variation in recruitment is affected by the distribution of prey, I compared the densities and sizes of prey found in habitat patches with recruits versus those selected at random at Appledore Island. Quadrats (0.0625 m^2) were sampled with an airlift as described above. It is possible that the presence of fish altered the density or size distribution of the prey. However, since all quadrats were sampled in one day, these data should provide an accurate snap-shot of the association of cunner recruits with particular habitat patches at the time the samples were collected. It is also possible that T-tests on square root transformed data (Zar 1984) were used to test for differences in the average number or size of prey in patches with fish versus those sampled at random.

Results

Macroalgae-recruitment relationships

Macrophyte cover varied greatly between the two sites. In particular, average kelp coverage at site 2 was ca. 3 times greater than that at site 1 (Fig. 1-1). Among-quadrat variation in algal cover within sites was also high; the coefficient of variation for branched, foliose and kelp plants was greater than 100% at both sites. Nonetheless, no relationship between the density of newly recruited cunner and algal coverage was apparent. (Fig. 1-1). Multiple regressions with recruit density as the response variable and the cover of kelp, foliose and branched macrophytes as predictors explained less than 8% of the variance in recruit density and were not significant ($F_{3,81} = 2.349$, $P = 0.08$ for site 1; $F_{3,75} = 0.319$, $P= 0.81$ for site 2).

Fish diets and prey preference

At Appledore Island numerous species of benthic prey were abundant and available for use by newly recruited cunner (Figs. 1-2 and 1-3). Newly settled mussels (Mytilus edulis) were common on filamentous and corticated macrophytes and were numerically dominant, with some estimates greater than 100,000 individuals 0.0625 m^{-2} (Fig. 1-3). Small crustaceans, particularly amphipods (both caprellids and gammarids) and isopods were also abundant (Fig. 1-3).

Thirty-seven of the 50 fish examined from Appledore Island (74%) had ingested material in their alimentary tracts. Despite the variety of potential prey available in the environment, crustaceans and mussels were the only common taxa in the guts of cunner recruits. Crustaceans occurred in 70% of the alimentary tracts investigated, and mussels occurred in 34% of the fish. Algal fragments were found in 10% of the fish, and 4% of the fish contained other invertebrates particularly gastropods and worms.

Three classes of prey items, crustaceans, mussels and algal fragments, were used to calculate Manly's index (α_i) values. Values above 0.33 indicate preference for a food type. Crustaceans were clearly a preferred food item ($\alpha_i = 0.96$) while mussels ($\alpha_i = 0.005$) and plants ($\alpha_i = 0.04$) were not selected as often. The same three prey groupings were used in the calculation of the rank preference index, and the results of this analysis corroborate the conclusions of Manly's Index. Crustaceans were the most preferred prey while plants were the least preferred ($t_i = -0.8$ for crustaceans, 0.86 for mussels and 2.0 for macroalgae)

Effects of prey distribution on recruitment

I was unable to detect a difference in the quantity of algae between randomly selected patches and patches where fish were present ($T = 1.26$, $P = 0.22$). The average damp-dry mass of algae in randomly selected patches was 199.25 g (24.74 SE) while in patches with fish the mass was 270.27 g (42.80 SE). There were no obvious differences in species composition of macroalgae in the patches, although this was not tested explicitly. All patches were dominated by Codium fragile.

Despite the similarity of algal habitat, there were substantial differences in the abundance of prey species in patches with fish and those selected at random (Fig. 1-4). There were ca. 4 times the number of isopods and amphipods, and more than twice the number of mussels in patches where fish were present than in randomly selected patches. The Standardized Morista's index of dispersion indicated that the prey were highly clumped in their distribution at the scale of 0.625 m^2 ($I_p = 0.61$ for isopods, 0.51 for amphipods and 0.52 for mussels).

Additionally, the sizes of amphipods and isopods in random patches tended to be larger than in patches in which fish occurred. The mean total length of amphipods in patches with fish was 2.89 mm (0.04 SE), while in randomly selected patches amphipods averaged 3.80 mm (0.59 SE). Similarly, the length of isopods in patches with fish was 4.5 mm (0.05 SE), while in randomly selected patches they averaged 5.22 mm (0.15 SE). These differences were significant ($T = 8.48$, $P < 0.001$ for amphipods, $T = 1.799$, $P = 0.001$ for isopods). No difference in the average size of mussels between the two types of patches was apparent ($T = 1.799$, $P = 0.07$). Maximum shell length of mussels averaged 0.651 mm (0.03 SE) in patches with fish, and averaged 0.606 mm (0.03 SE) in randomly sampled patches.

Discussion

Effects of macroalgae on recruitment

Macroalgae are often the major source of structure on temperate reefs. By providing juvenile fish with shelter from predation (Ebeling and Laur 1985, Carr 1991) and foraging habitat (Schmitt and Holbrook 1985, 1990), macroalgae can play a critical role in the dynamics of populations of temperate fishes. Depending upon the species under investigation, the coverage of kelp canopy or understory algae has been shown to have a dramatic influence on recruitment variability (Jones 1984, Ebeling and Laur, Jones 1988, Carr 1989, 1991, Holbrook et al. 1990, Levin 1991, in press). However, the results from this study do not conform with this pattern. No relationship between the cover of erect macrophytes and densities of recruits was observed. Rather, in the present study, the distribution of prey appears to be an important factor determining the distribution of cunner recruits.

Differences in the spatial scale of interest may be the primary reason the results from this study to not coincide with the results of previous work (Wiens 1989, Levin 1992). I focused on very small-scale variability, while most other studies have examined patterns at much larger spatial scales. For example, several workers (Jones 1984, Holbrook et al. 1990, Carr 1990) have shown that a large amount of the variability in recruitment among sites can be explained by variation in algal cover or density. The same is true for cunner: in a study in where sites were separated by 100's of meters, in 1991, more than 70% of the among-site variation in mean levels of recruitment was explained by coverage of branched algae (Levin, 1993). The data presented here are not inconsistent with these findings; instead, they suggest what types of patches within algal beds fish are using.

Experimental studies manipulating algal structure have also been carried out at larger spatial scales than this study. For example. Jones (1984) manipulated algal cover in 300 m^2 plots and found much higher densities of juvenile fish in plots with high coverage. Similarly, Carr (1989) has manipulated algal cover in 150 m^2 and 8.55 m^2 plots and Levin (in press) has manipulated algal cover in areas 28.27 m^2. The results from these studies corroborate the results of Jones (1984). However, like the descriptive studies referred to above, they did not investigate how fish were distributed within algal patches. If prey were found in aggregations within these algal plots, then the results of this study predict that fish would be found in microhabitats rich in prey.

The distribution, but not abundance, of juvenile fishes has been shown to be influenced by attributes of the algal habitat at scales comparable to those of this study (Carr 1991, Levin 1991). Levin (1991) investigated the determinants of small-scale variability in the abundance of juvenile cunner. He was only able to predict the presence or absence of recruits by microhabitat characteristics. However, differences in density among patches were not related to microhabitat structure. Thus, for cunner and perhaps for other temperate fish, macroalgae appear to influence the distribution and abundance of juveniles at larger spatial scales, but at small scales differences in density can also be attributed to the variability in prey populations.

Effects of food resources on recruitment variation

Previous work has suggested that food abundance does not explain differences in recruitment among habitats (Jones 1984, Shulman 1984, Carr 1990). Bray (1981) showed that young planktivorous reef fish (Chromis punctipinnis) would not leave shelter to forage on rich zooplankton patches although adults would. By contrast, within habitats, juvenile cunner appear to be associated with patches rich in prey. A causal relationship between prey abundance and recruitment of cunner cannot be established without experimental tests. Nonetheless, because the algal habitat was quite homogeneous at Appledore Island, it is unlikely that fish were responding directly to attributes of the algal habitat. The most parsimonious explanation for these results is that juvenile cunner are responding to small-scale patchiness of their prey, particularly crustaceans.

Hierarchical habitat selection in heterogeneous environments

The ability of an animal to select a habitat depends upon the distance it disperses relative to the size of habitat patches (Morris 1992). Fish will only be able to discriminate among habitats if they encounter alternatives (Bell and Westoby 1986). Reef fishes act out their lives on different spatial scales during their ontogeny (Sale 1991). As larvae, fish may potentially be transported 1000's of km (Kingsford 1988, Leis 1991), yet as new recruits fish may move only a few square meters (Sale 1978). A direct consequence of this life history is that the types and number of habitat patches fish encounter will vary during their development.

Results of previous work on fish-algal relationships (e.g. Jones 1984, Holbrook et al. 1990, Carr 1991a, Levin in press) within temperate zones have demonstrated that fish respond to differences in algal structure among sites at or near the time of settlement. As pre-settlement fish are advected across habitats, they have the opportunity to sample and ultimately select a habitat. Evidence that pre-settlement fish can prolong their pelagic lives (Victor 1986, Cowen 1991), presumably in the absence of appropriate conditions for settlement (Cowen 1991), supports the view that they are capable of distinguishing among habitats at relatively large spatial scales.

The present study suggests that once within an algal habitat fish respond to the presence of potential prey. Similarly, other work indicates that once within a habitat, recruits select patches with specific microhabitat characteristics (Behrents 1987, Carr 1991, Levin 1991). Since juvenile reef fish do not disperse over large spatial scales (among habitats), they only have the opportunity to select among habitat attributes that are patchy at a smaller scale than their home range. The clumped distribution of prey at scales of $0.0625\ m^2$ and algae at scales of $0.25\ m^2$ (Levin in press) suggest that juvenile cunner would be exposed to patch boundaries and have the opportunity to make choices about what patches to use.

The cost and benefits of selection of habitats at various spatial scales should vary with the dispersal ability of an individual and thus during the ontogeny of fish. For a settling larva, the benefits of choosing an appropriate habitat type where it can survive, grow and reproduce are great; whereas, the costs of a continued search may not be too extreme for a pelagic pre-settlement fish (e.g. Cowen 1991). After settlement, the cost of a large-scale search for an optimal habitat is high because it forces the fish to leave shelter and travel through poor quality habitats. However, there is little cost to searching on a small-scale for the highest quality patch since fish would never stray too far from cover. The consequences of an incorrect choice at this scale are probably not as great as the selection on an inappropriate large-scale habitat . However, the benefits of such a small-scale search are potentially great as the fish may be able to locate higher quality food patches or better shelter.

Given the potential differences in the costs and benefits of habitat selection at various spatial scales and during different ontogenetic stages, it is reasonable to hypothesize that fish recruiting to heterogeneous habitats select where to live in a hierarchical manner. Fish should first choose a habitat where there is a reasonable chance of survival. For many temperate reef fishes this is a macroalgal dominated habitat. Selection at this spatial scale would produce the among-site variation in recruitment observed by Jones (1984) and Holbrook et al. (1990). After settlement, fish should choose a patch within their home range that best meets their requirements for food and shelter. Thus, recruits should be located in specific algal patches (Carr 1991, Levin 1991) that are rich in food resources.

This model of hierarchical habitat selection is simlar to a hypothesis proposed by Bell and Westoby (1986, 1987) to explain the distribution of fish in seagrass beds. Their hypothsis suggests that post-larval fish select the first seagrass bed they encounter, regardless of the physical complexity of the bed. After settlement fish select microhabitats within the seagrass bed that provide food and a high level of cover from predation. The prediction of this hypothsis is that abudances of fish are not correlated with attributes of the seagrass at large spatial scales. However, at small scales characteristics of the seagrass influence the distribution of fish. Both the hypothesis of Bell and Westoby and the hypothesis posed in this paper suggest that fish select habitats in a hierachical manner. Nevertheless, because large-scale variation in recruitment of temperate reef fish is often related to variability in biogenic structure (Jones 1984, Holbrook et al. 1990, Levin 1993), the model of Bell and Westoby proposed for seagrass fishes is not sufficient to expalin patterns of distribution of fishes on temperate reefs.

The factors that produce variability in recruitment in demersal fishes are likely to vary with scale (Doherty and Williams 1988, Doherty 1991). The data presented here demonstrate that the well established relationship between macroalgae and recruitment of fishes on temperate reefs does not exist at small spatial scales for cunner. Rather, patchiness of food resources appears to be responsible for variability in recruit density at a scale of meters. This study underscores the importance of acknowledging that different mechanisms can produce variability in recruitment at different scales.

Acknowledgments

I thank G.E. Forrester, T.P. Good, L.G. Harris, A.E. Mathieson, R.R. Olson, R.R. Warner, J.D. Witman and especially P.F. Sale for critical comments on this work and/or early drafts of this manuscript. Erin Wright and Amy Cooke helped sort the samples. John Cobbler Maret and Dave Lockett provided diving assitance. Thanks also to Paul Pelletier and the crew of the R/V Jere Chase and the staff of the Shoals Marine Lab for outstanding logistical support. The finanical support of an NSF Graduate Fellowship and NSF grant OCE-9102927 to P.F. Sale and P.S. Levin is gratefully acknowledged.

Figure 1-1. The relationship between the density of newly recruited cunner with percent cover of kelp, foliose and branched algae are shown for two sites (site 1 - filled circles; site 2 - open circles). Variation in recruitment was not explained by variability in the algal assemblage.

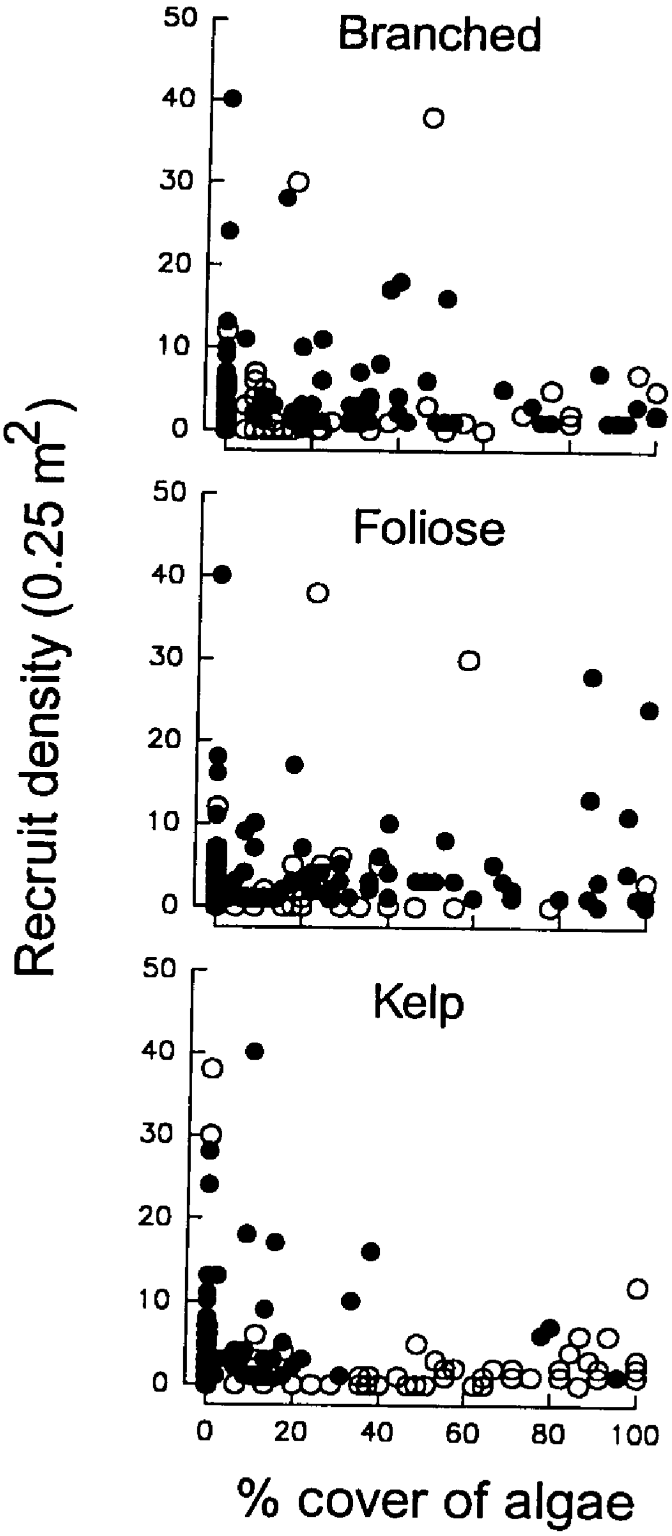

Branched
Foliose
Kelp
Recruit density (0.25 m^2)
% cover of algae
0
10
20
30
40
50
0
20
40
60
80
100

Figure 1-2. The mean density (± 1 standard error) of potential prey for newly recruited cunner collected from Appledore Island. Samples were collecting using an airlift fitted with a 0.5mm mesh bag. Densities of amphipods, isopods and mussels were determined by sub-sampling and results are shown in figures 3 and 4.

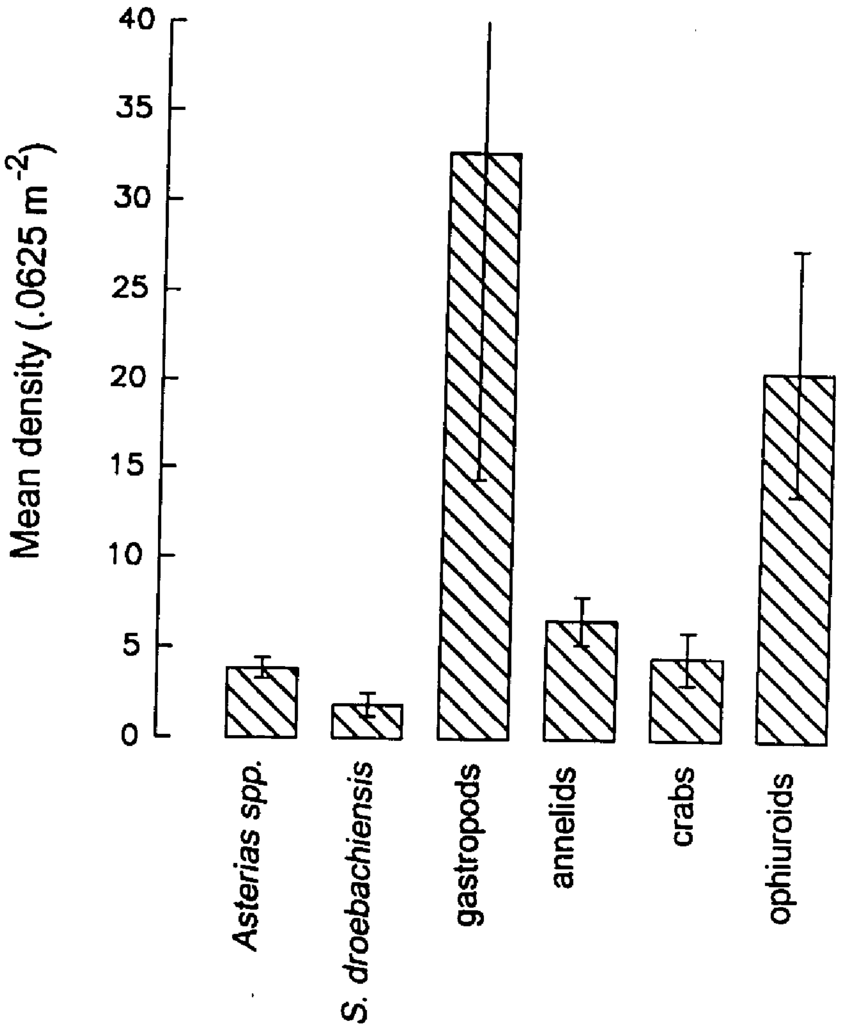

Mean density (.0625 m-2)
40
35
30
25
20
15
10
5
0
Asterias spp.
S. droebachiensis
gastropods
annelids
crabs
ophiuroids

Figure 1-3. The mean proportion (± 1 standard error) of mussels, crustaceans (amphipods, isopods) and other organisms found by random sampling of the environment and in the alimentary tracts of newly recruited cunner. Manly's α indicates that crustaceans were the preferred item for cunner recruits.

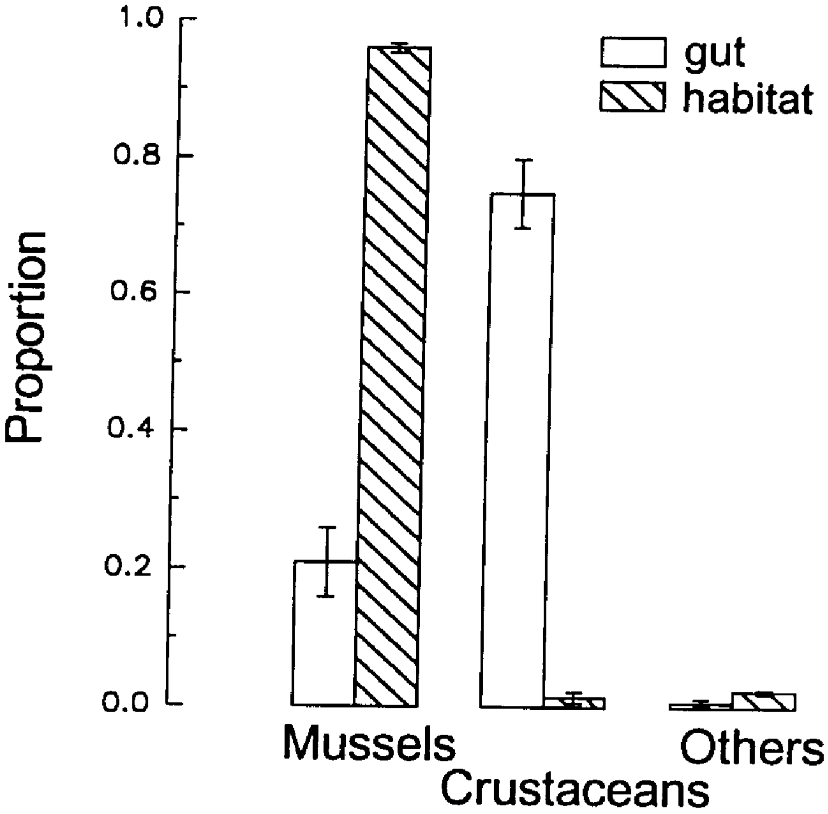
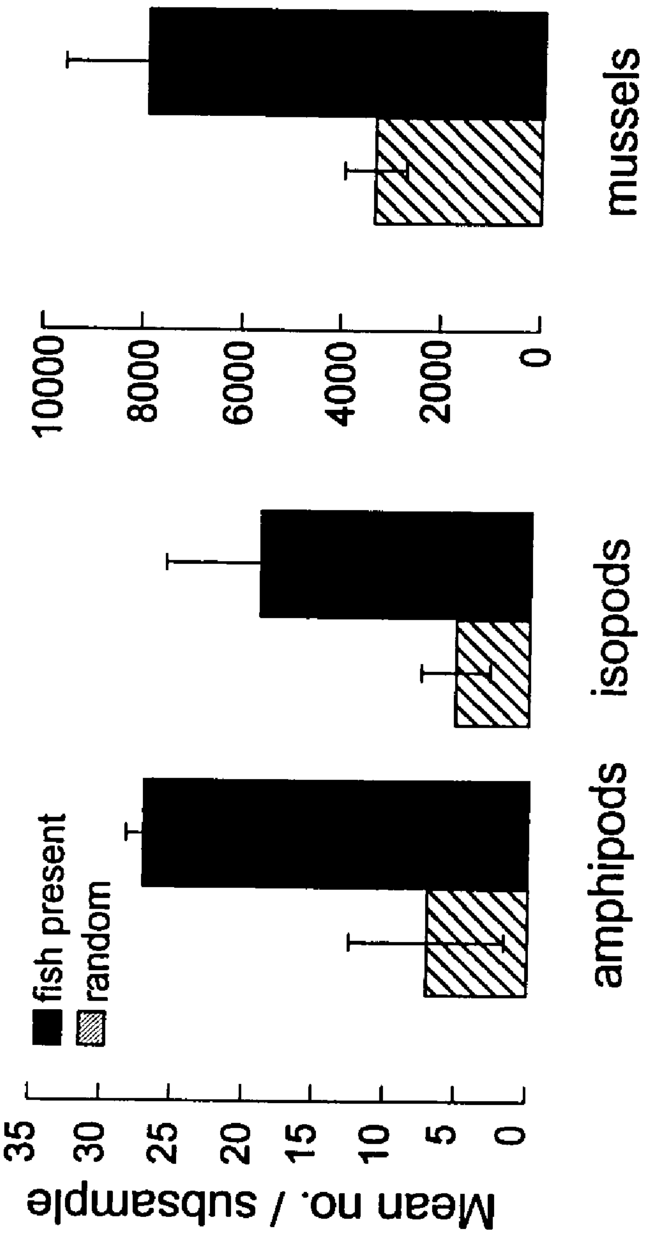

1.0
0.8
0.6
0.4
0.2
0.0
Proportion
gut
habitat
Mussels
Crustaceans
Others

Figure 1-4. The mean number (± 1 standard error) of amphipods, isopods and mussels in random 1/16 sub-samples of 0.0625 m^2 quadrats. For all species there were significantly more individuals found in quadrats with fish present versus those that were randomly sampled ($T = 4.66$, $P < .001$ for amphipods; $T = 3.38$, $P = .002$ for isopods; $T = 1.26$, $P = .015$ for mussels).


Mean no. / subsample
35
30
25
20
15
10
5
0
■ fish present
▨ random
amphipods
isopods
10000
8000
6000
4000
2000
0
mussels

CHAPTER 2

HABITAT STRUCTURE, CONSPECIFIC PRESENCE AND SPATIAL VARIATION IN THE RECRUITMENT OF A TEMPERATE REEF FISH

Abstract

Pronounced spatial variation in recruitment occurs in many marine invertebrate and fish populations and is thought to be critical to the demography of these species. In this study I examined the importance of habitat structure and the presence of conspecific residents to spatial variation in larval settlement and recruitment in a temperate fish Tautogolabrus adspersus. I define settlement as the movement of individuals from the water column to the benthic habitat, while I refer to recruitment as numbers of individuals surviving some arbitrary period of time after settlement. Experiments in which standard habitats were stocked with conspecifics showed that resident conspecifics were not an important factor contributing to small-scale variability in recruitment. Further correlative analyses demonstrated that large-scale variation in recruitment could not be explained by variability in older age classes. By contrast, manipulations of macroalgal structure within a kelp bed demonstrated that recruitment was significantly higher in habitats with a dense understory of foliose and filamentous algae than in habitats with only crustose algae. Understory algae varied in their pattern of dispersion among sites, and the dispersion of fish matched that of the plants. In order to determine the effects of differences in patterns of algal dispersion on the demography of associated T. adspersus populations, I used experimental habitat units to manipulate patterns of dispersion. Settlement was significantly greater to randomly placed versus clumped habitats; however, no differences in recruitment between random and clumped habitats were detected. Because recruitment is a function of the numbers of settlers minus the subsequent loss of settlers, rates of mortality or migration must have been higher in the randomly placed habitats. These results are counter to the current paradigm for reef fishes which suggests that larval settlement is the crucial demographic process producing variability in population abundance. In this experiment patterns of settlement were modified by varying the patch structure of the habitat.

Introduction

Landscapes in both terrestrial and marine environments are composed of patches of habitat which vary in their physical and biogenic structure (e.g. Paine and Levin 1981; Addicott et al. 1987; Wiens 1989). Differential use of patches by individual organisms as well as the consequences of environmental heterogeneity on the structure of populations and communities have received increasing attention by both marine and terrestrial ecologists (Sale 1977, 1978; Sousa 1984; Fowler 1988; Wiens and Milne 1989; Moller 1991). Nonetheless, population models for reef fishes largely overlook how variability in the mosaic of patches forming the habitat may influence the dynamics of populations.

Reef fish generally have complex life cycles during which larvae and often eggs are pelagic and widely dispersed (Sale 1980). Following the pelagic phase, larvae or metamorphosed individuals settle (move from the water column to the benthic habitat). Thus, recruitment occurs by the addition of individuals to benthic populations through larval and post-larval settlement. In this context, I operationally define settlement as the permanent movement of individuals from the pelagic to benthic habitat and recruitment as the addition of individuals to the benthic population.

Recently, it has been argued that settlement of individuals from the water column to the adult habitat is the most important demographic process for both benthic and demersal marine populations (Underwood and Fairweather 1989; Doherty and Williams 1988). Consequently, emphasis has been placed on variability in the availability of pelagic propagules and subsequent variation in recruitment (e.g. Williams 1980; Grossberg 1982; Doherty 1983; Victor 1983; Gaines et al. 1985). In particular, the recruitment limitation model (Doherty 1981) asserts that sites are undersaturated with new settlers, and thus population density increases or decreases as settlement increases or decreases (Williams 1980; Doherty 1981, 1983; Victor 1983). Another incarnation of this model suggests that sizes of demersal populations are determined by the strength and variability of settlement and post-settlement processes (Forrester 1990). The distinction between these two, often confused, versions of recruitment limitation is critical (Forrester 1990). The former version predicts that abundances of cohorts generated at settlement are not substantially modified by processes occurring after settlement. However, the latter interpretation proposes that the size of a demersal population may be affected by post-settlement processes, particularly if they are stronger or less variable than processes influencing settlement. (Forrester 1990).

Implicit in these models of recruitment limitation is that density-dependent interactions between demersal individuals and new settlers are of little importance. Resident conspecifics thus should not influence levels of recruitment. These models also make no allowance for the effects that variability in the structure of the habitat have on settlement. Therefore, the demography of local populations inhabiting areas which differ only in their patch structure (e.g. the sizes or dispersion of habitat patches) should not vary.

In this study I investigate the juvenile demography of a temperate reef fish, and ask if attributes of the habitat, including the presence of conspecifics can influence the relative contribution of pre- and post-settlement processes to variation in population abundance. Using both experimental and descriptive analyses, this study asks the following specific questions: 1) Are aggregations of recruits the result of attributes of the habitat? 2) Are settling post-larvae attracted to conspecifics? 3) Do differences in the dispersion of the habitat patches affect the relative importance of settlement and post-settlement mortality to variation in recruitment?

Methods

Study species

Cunner, Tautogolabrus adspersus (Pisces:Labridae), are common members of shallow subtidal communities in the Northwest Atlantic, occurring from intertidal zones (Whoriskey 1983) to depths greater than 90m (Bigelow and Schroeder 1953). They occur in abundance from Conception Bay, Newfoundland, to New Jersey, and are occasionally found as far south as a Chesapeake Bay (Bigelow and Schroeder 1953).

Cunner spawn in early and mid summer (Dew 1976; Pottle and Green 1979). After a larval life averaging 18-21 days (Gleason and Reschiek 1990), fish settle to the demersal habitat. In the Gulf of Maine, cunner generally spawn in July and thus settlement of cunner occurs predictably in late summer, almost entirely in early August (Levin unpubl.). Young-of-the-year cunner appear to feed opportunistically on zooplankton and small benthic invertebrates (Chao 1972; Levin unpubl.). As juveniles, cunner are site-attached and do not stray far from cover, particularly that provided by macrophytes (Olla et al. 1975; Pottle and Green 1979; Levin 1991).

General methods

Field experiments and descriptive investigations were conducted during August and September of 1990 and 1991. Descriptive investigations were conducted at two spatial scales. For the purposes of this study, "small-scale" is defined as a scale of meters and "large-scale" refers to a scale of hundreds of meters. I refer to pigmented young-of-the-year fish as "recruits", 1+ year old fish as "juveniles", and individuals >= 2 years old as "adults".

Censuses of cunner were conducted at seven sites in the Gulf of Maine. These sites are numbered and described in table 2-1 and are representative of shallow subtidal habitats in the Gulf of Maine (Witman 1987, Chapman and Johnson 1990).

Quantifying patterns of recruitment

To determine large scale (among site) patterns of recruitment, densities of each age class were quantified by visually censusing randomly placed 15 X 1 m band transects in seven sites (Keast and Harker 1977; Lincoln-Smith 1988). Three to five minutes after the transect line was extended a diver carrying a 1 meter wide T-shaped bar to delineate the transect width swam over the line at a rate of eight to ten meters per minute and counted all fish (Sale et al. 1984). The three to five minute interval between extending and sampling the transect allowed fish to resume their normal behavior.

Additionally, the dispersion of fish within sites was examined. Two methods were used to assess patterns of dispersion in cunner recruits. Smaller scale patterns were determined at 5 sites by counting the number of recruits in randomly placed 0.25 m^2 quadrats. Larger scale patterns were also investigated at 4 sites by censusing numbers of recruits in randomly placed 15 x 1m strip transects.

The standardized Morisita index of dispersion (I_p) was used to determine patterns of dispersion from both quadrat and transect data (Krebs 1989). This index ranges from -1.0 to +1.0, with 95% confidence limits at +0.5 and -0.5. I_p values > 0 indicate aggregated patterns of dispersion, values < 0 indicate a uniform pattern, and values = 0 indicate a random pattern. Because this index is both independent of sample size and the density of the population, Myers (1978) argued that this index is one of the least biased measures of dispersion.

Dispersion of macrophytes was also quantified at two spatial scales. Percent covers of algae were enumerated by recording the type of algae under each of 45 points created by a grid of monofilament strung across randomly placed 0.25 m^2 quadrats. Dispersion of the coverage of upright (i.e. non-encrusting) macrophytes was determined using the standardized Morisita index of dispersion. Larger scale spatial patterns were also examined for the dominant macrophytes in the study sites. The T-square sampling procedure was used to assess the spatial pattern of these plants (Krebs 1989). This procedure compares the distance from a random point to the nearest plant with the distance from this plant to its nearest neighbor. The hypothesis of a random spatial pattern is tested using the Hines' test statistic for randomness (H_t). This sampling procedure samples a large area and is statistically robust (Krebs 1989).

Large-scale effects of conspecifics of recruitment

The effect of conspecifics on recruitment was assessed by examining the patterns of co-occurrence of recruits with juveniles (1+ yr) and with subadults/adults (> 2+yr) at all seven study sites. In August, recruits average 12mm standard length (SL) (Levin, unpubl.), juveniles are greater than 51mm SL (Bigelow and Schroeder 1953), and subadults/adults are at least 100mm SL (Bigelow and Schroeder 1953). Because of the large size differences of these age classes, it was possible to unambiguously distinguish them while visually censusing transects.

A two factor analysis of covariance was used to simultaneously examine the effects of site, adult densities and juvenile densities on variation in recruitment (Winer et al. 1991). Prior to the analysis data were log transformed.

Small-scale effects of resident conspecific juveniles

Twelve standard habitat units (SHUs, after Sweatman 1985) were constructed and half of these were allocated equally between 2 sites. SHUs consisted of 2cm diameter

PVC pipe frames (1m X 0.5m) with five pieces of rope strung across each frame and 2 kelp fronds (Lamanaria saccharina) attached to each strand of rope. SHUs were fitted with PVC legs so they stood 0.5m above the substratum to prevent burial in sandy areas. SHUs were isolated by at least 4m from natural macrophytic structure and from each other.

All fish were removed from SHUs using the anaesthetic quinaldine at the start of the experiment. Six recruits were added to 3 SHUs at each site. This represented 1 standard deviation above the mean recruit density observed at site 1 in 1989. The remaining 3 SHUs at each site were left as controls. After adding recruits to SHUs, I observed that fish sought immediate shelter in the algae. The day following the addition of the recruits, I examined all SHUs. In all cases recruits had remained on the SHUs. The SHUs were censused for cunner recruitment three weeks (August 30, 1990) and five weeks (September 13, 1990) after the experiment was initiated. As cunner settle primarily during the month of August (Levin, unpubl.), the experiment was conducted during the entire settlement season for this species.

The hypothesis that recruitment to the SHUs did not vary between sites or experimental treatments was tested using a two-factor analysis of variance (ANOVA). Each sampling date was analyzed separately. A model I ANOVA was used in which both site and the addition of conspecific juveniles were considered fixed factors (Winer et al. 1991). Prior to analyses data were log transformed to meet the assumptions of parametric analyses (Winer et al. 1991).

Effects of macrophytes on recruitment

Previous descriptive work (Levin 1991) has shown that the presence or absence of cunner recruits could be predicted by the nature of the macroalgal assemblage at very small spatial scales. In particular, recruits were associated with fleshy upright algae rather than crustose species. An additional experiment was performed in August 1990 in order to determine if differences in the type of macroalgal cover could influence the density of recruits.

In this experiment, I manipulated the percent cover and type of macroalgae present within a kelp bed (site 2). In July 1990, immediately before cunner settlement had occurred, two circular plots 6m in diameter with an area of 28.26 m^2 were created for each of three treatments. The first treatment consisted of removing all algae from the plot using putty knives and wire brushes. In the second treatment the kelp canopy was eliminated leaving only the filamentous and foliose understory. Because of the lack of canopy shade, this treatment became dominated by sun-tolerant filamentous and foliose species. In the final treatment, the control, macrophytes were not manipulated. One plot for each treatment were created in each of two areas. Within each area, plots were separated by at least 10m, and the two areas were separated by 60m. The surrounding habitat (kelp bed) was equivalent for all treatments.

At the end of the settlement season, four 0.25m^2 quadrats were placed randomly within the central 12.56 m^2 of each of the 2 plots for each treatment. All recruits were visually censused within each quadrat. A one-way ANOVA with quadrats as replicates and areas as a blocking factor was used to test the null hypothesis that the density of recruits did not differ among treatments.

Consequences of small-scale patterns of dispersion

To determine the effects of habitat dispersion on the demography of juvenile cunner, an experiment was performed in which the spatial pattern of the macroalgal habitat was experimentally manipulated using SHUs. The SHUs used in this experiment were 0.5m x 0.5m with 0.5cm^2 wire mesh across the top. Kelp was not attached, but filamentous algae was allowed to naturally colonize the SHUs. The experiment was performed adjacent to site 6 (Table 2-1) in Gosport Harbor at the Isles of Shoals, Maine. This site provided a protected and relatively level plain with sandy substrata at a depth of 4-10m below mean low water. Forty eight contiguous plots (36 m^2) were established and 4 SHUs were positioned within the central 9 m^2 of each plot so that groups of SHUs were at least 6m apart. Positioning of SHUs within active zones depended on treatment: 1) clumped - 4 SHUs were adjacent and touching to form a 1 m^2 square within the active zone; or 2) random - 4 SHUs were placed randomly within the active zone except that they were separated from each other by at least 1m.

Each treatment was assigned randomly to half of the plots. The experiment was monitored on 11 of the 17 days of cunner settlement in 1991, and 2 days shortly after the settlement season. The number of translucent fish (settlers) and the number of pigmented young-of-the-year cunner (recruits) were recorded on each occasion. Settlers were assumed to remain translucent for no more than 24 hours. Because of the close association of juvenile cunner with cover, the loss of fish between censuses was assumed to be due to mortality rather than demersal migration.

Prior to the analysis of settlement and recruitment SHUs, differences due to positioning of replicates within the study site were investigated. The study site was divided into 8 quadrants representing different compass directions. No differences in either settlement ($F=.798$ $p=.57$) or recruitment ($F=1.54$ $p=.23$) were detected in different quadrants. Settlement was correlated with depth ($r = .731$, $p<.001$); however, the study site was divided into three depth ranges (4-6m, 6-8m, 8-10m) and I ensured that equal numbers of replicates from each treatment were allocated to each depth zone.

Hypotheses about effects of experiment factors on demographic variables were tested using ANOVA. All analyses used a model where the experimental factor (clumped vs. randomly placed SHUs) was considered fixed and different sampling dates were considered random effects and a repeated measure (Winer et al. 1991). This model tested for differences in settlement or recruitment between experimental treatments over all dates sampled.

Results

Large-scale (among site) patterns of abundance

Recruitment varied significantly among sites (Fig 1a, $F_{6,193}=14.39$, $p<.001$). Sites 1, 2 and 3, averaged greater than 33 recruits per transect and received significantly higher recruitment than the other four sites (Tukey's HSD, $p< .05$). Additionally, sites 4, 5 and 7 averaged between 18 and 25 per transect and were statistically indistinguishable (Tukey's HSD $p > .05$); however, recruit densities at these sites were significantly greater than the density of recruits at site 6 (Tukey's HSD, $p< .05$).

Adult and juvenile densities also varied among sites (Figs. 1b and 1c; for adults, $F_{4,\ 169}=17.49$, $p<.001$; for juveniles $F_{4,\ 162}=8.145$, $p <.001$). Mean juvenile densities (3-4 fish per transect) were highest at sites 2 and 5 (Tukey's HSD $p< 0.05$). Mean juvenile densities between 0.5 and 2 fish per transect were observed at sites 1, 6, and 7, and these were significantly lower than the densities observed at sites 2 and 5 (Tukey's HSD $p< .05$). No juveniles were observed at sites 3 and 4. Sites 1 and 2 had the highest mean adult density with >2 fish per transect (Tukey's HSD, $p< 0.001$). Sites 5, 6, and 7 had similar mean adult densities of <1 fish per transect (Tukey's HSD $p> 0.3$). Adults were not observed at sites 3 and 4.

Small-scale (within site) patterns of abundance

At the small spatial scale examined (0.25 m^2), cunner recruits exhibited an aggregated pattern of dispersion in sites 1 ($I_p = .510$), 5 ($I_p = .512$) and 6 ($I_p = .541$); however in sites 2 ($I_p = .490$) and 7 ($I_p = .490$) fish were randomly dispersed. Recruits in sites which were separated by relatively small distances showed different dispersion patterns. Sites 1 and 2, for example were separated by ca. 100 m, yet fish at site 1 were aggregated and fish at site 2 were dispersed randomly. Cunner recruits were clumped at the larger spatial scale examined (15 m^2) at all 4 sites investigated (site 1 $I_p = .521$; site 2 $I_p = .532$; site 5 $I_p = .510$; site 6 $I_p = .516$).

Large scale effects of conspecifics on variation in recruitment

Variability in recruitment was not consistently explained by variation in either juvenile or adult cunner abundance. A two factor analysis of covariance revealed that there were significant differences among sites in recruitment, but not a significant effect of juveniles or adults (Table 2-2). Sites 3 and 4 were omitted from this analysis because no juveniles or adults were present at these sites. Despite the absence of older stage from these sites, there was still variability in recruitment comparable to other sites (Fig. 2-2-1).

There was also no relationship observed between numbers of recruits and the density of older stages among sites. Regression analyses of the mean density of recruits for each site versus the average density of both juveniles and adults were not significant ($P >> .05$).

Small-scale effects of resident conspecifics

Recruitment of cunner to SHUs did not vary significantly between sites on either date examined (Fig. 2-2). Additionally, no significant differences in recruitment were evident between those SHUs stocked with conspecifics and those left as controls (Fig. 2-2). On August 30, the mean number of recruits at on SHUs stocked with conspecifics was 39.5 (SE 3.96), versus 46.5 (SE 3.16) on SHUs which were not stocked.

There was a substantial decline in the number of recruits present on the SHUs after two weeks; however, the difference in recruitment between experimental treatments remained non-significant (Fig. 2-2). On September 13, SHUs stocked with conspecifics averaged of 16.83 (SE 2.65) recruits, and SHUs left as controls had a mean of 15.83 (SE 3.01) recruits.

Effects of macrophytes on recruitment

The field manipulation of algal cover indicated that the presence of an understory without a kelp canopy increased recruitment of cunner (Fig. 2-3). While no difference in recruit density was detected between habitats without algae and those left as controls, there was significantly greater recruitment to habitats in which the canopy was removed than to those in which all algae was removed (Fig. 2-3, $F_{2,21}=3.51$, $p=.048$) The density of recruits averaged 8.75 (SE 2.2) fish/0.25m^2 in plots where only the canopy was removed, while in plots in which all algae were eliminated the mean was 4.00 (SE 1.3) recruits/0.25m^2. Thus, the enhancement of the understory algal assemblage via canopy removal or the simply the absence of the kelp canopy resulted in a substantial increase in recruit density.

There was also a strong relationship between the dispersion of macroaglae and the dispersion of fish. At the smaller scale examined there was a high correlation (Spearman rank correlation coefficient = .895) between the standardized Morista's index for algae and for fish (Fig. 2-4). Because two different methods were used to assess algal and fish dispersion at the larger scale examined, I did not perform a correlation analysis; nonetheless, both algae and fish were clumped at this scale for each site investigated.

Consequences of small-scale patterns of dispersion

Both numbers of settlers and recruits on SHUs varied significantly during the sampling period (Table 2-3). These differences were due ostensibly to daily variability in the supply of pre-settlement fish and the subsequent accumulation of fish in the demersal habitat.

The relative importance of initial patterns of settlement and of mortality immediately after settlement varied between experimentally produced clumped and random habitats. Overall, there was significantly greater settlement to the random than the aggregated habitats (Fig. 2-5, Table 2-3). The total number of settlers observed averaged 54.75 (SE 5.96) on the random replicates versus 28.41 (SE 4.86) on the clumped SHUs. However, differences in the intensity of settlement between treatments varied with the sampling date (Table 2-3). As figure 5 illustrates there were some dates when settlement to the two treatments was similar, while on others settlement was higher to the random SHUs.

In contrast to patterns of settlement, no difference in the numbers of recruits over all dates was detected between random and aggregated habitats (Fig. 2-6, Table 2-3). Only on August 7, one day following the greatest pulse of settlement, was there a substantial difference in recruitment between the treatments. Although on 12 of 14 of the sampling dates the average number of recruits was higher on random SHUs than on clumped habitats, high variability within treatments resulted in a non-significant statistical result.

Recruitment is a function of the numbers of settlers minus the subsequent loss of settlers due to mortality and migration. Because I could not detect a difference in recruitment between the treatments, yet settlement was higher on random than clumped SHUs, mortality or migration of newly settled fish must have been greater on the randomly placed SHUs. Moreover, as censuses of the SHUs were performed frequently (often daily, Figs. 5 and 6) differential loss of newly settled fish must have occurred soon after settlement. Consequently, the difference between the clumped and random treatment which was set by settlement was subsequently reduced by differential mortality or migration.

Potential demersal predators occupying the SHUs were also enumerated. Sculpins Myoxocephalus aeneus were the only demersal predators observed and their densities did not vary between the treatments (T=.84, p=.41). The only other common animal inhabiting the SHUs was the crab Cancer irroratus and no difference in their densities was detected between the treatments (T= .397, p=.70,).

Discussion

Spatial pattern of recruitment

Fish settling from the water column to the benthos require habitats in which they can obtain adequate food and cover so that they may mature and reproduce. By selectively settling in the presence of conspecifics these larvae would colonize sites where conspecifics have been successful in acquiring food and protection from predation. This appears to explain aggregated settlement in many sessile invertebrates and some reef fish (e.g. Highsmith 1982; Sweatman 1985). However, the clumped distribution of cunner recruits cannot be explained by this mechanism. In the present study, I did not detect higher recruitment on experimental habitats "seeded" with conspecifics, nor was any association of recruitment and conspecific density observed within or among sites.

These results corroborate the findings of several workers. Doherty (1983) performed experiments on the damselfish Pomacentrus wardi, in which the removal of resident conspecifics had no effect on levels of recruitment. Likewise, Jones (1984a) found that the removal of adult Pseudolabrus celidotus (Labridae) on temperate reefs had no effect on recruitment. By contrast, the presence of resident conspecifics enhanced recruitment of the damselfishes Dascyllus aruanus (Sweatman 1983, 1985, Forrester 1988), Dascyllus retuculatus (Sweatman 1985), Dascyllus albisella (Booth 1991), and Chromis caerula (Sweatman 1985) to experimental coral heads.

The experiments of Sweatman (1983, 1985) and Forrester (1988) were procedurally similar to mine; however, the results of this study differ in several respects from their findings. Densities of cunner recruits, corrected for differences in the sizes of the experimental habitats, were generally greater than Sweatman (1985) or Forrester (1988) observed for D. aruanus and D. retuculatus. Additionally, spatial variation in recruitment was much higher for D. aruanus (Forrester 1988) than for cunner. These differences may be the result of differences in the length and periodicity of the settlement season of the two species. All recruitment of cunner occurs within a one month period (Levin, unpubl.), whereas the recruitment season of D. aruanus is much longer (Sweatman 1985). As a result the outcome of an entire settlement season was observed in this study with only a relatively short time for high densities of fish to be lowered by mortality or emigration.

A strong relationship between the density of recruits and older stages could arise from a preference of settling fish for conspecifics, or could indicate that attributes of a habitat make it attractive to settling fish and provide resources necessary for survival to maturity. Species which use the same habitat throughout their life should show a positive relationship between the density of recruits and older stages as long as resources are not in short supply. Thus, for species such Dascyllus aruanus, in which recruits and adults occur in the same habitat, adults would be a reliable indicator of appropriate habitat.. However, ontogenetic changes in resource requirements would make the presence of older conspecifics poor indicators of habitat quality for recruits. The absence of a relationship between recruits and older stages would thus be expected. For example, cunner recruits prefer macroalgal microhabitats, as is the case in many other fishes on temperate reefs (Wheeler 1980; Jones 1984a; Ebeling and Laur 1985; Carr 1989; DeMartini and Roberts 1990; Holbrook et al. 1990). However, as cunner grow, their dependence on macroalgal cover decreases and adults can often be seen in urchin dominated habitats where algal cover is sparse (Fig. 2-2., Pottle and Green 1979). Consequently, the presence of adult conspecifics would not be a reliable indicator of appropriate habitat for newly recruited cunner. Thus, unless older conspecifics, themselves, confer some fitness advantage, there is no expectation that cunner recruits, or recruits of other species with changing resource requirements, would be associated with older conspecifics.

It is more likely that settling larval cunner respond directly to attributes of the habitat than to the presence of conspecifics. Newly recruited cunner were found in higher densities in habitats in which the canopy was removed and only understory was present. This result agrees with previousl work which demonstrated an association of cunner results with microhabitats dominated by filamentous and foliose algae (Levin 1991). Additional laboratory experiments suggest this association is at least partially the result of active choice (Levin unpubl.). The role of differential mortality or migration among habitats was not investigated in this study and may also be important in determining patterns of recruitment. In addition, patterns of dispersion of recruits corresponded exactly to those exhibited by macrophytes in natural habitats or experimentally created habitats. Consequently, the dispersion of recruits at different spatial scales seems to be a response to patchiness of macrophytes.

Studies in other temperate systems have also noted that the dispersion of recruits appears to be influenced by habitat patchiness. On oyster reefs in Chesapeake Bay, Breitburg (1989, 1991) found that aggregation patterns of recently settled gobies Gobiosoma bosci were affected by topographic relief provided by rocks and the oyster reef. Jones (1984b), working on rocky reefs in New Zealand, found that 0+ year wrasses Pseudolabrus celidotus exhibited clumped patterns of dispersion, and suggested that the over-dispersion of these fish was, in part, a response to patchiness of appropriate habitat. Some plant species also show highly aggregated patterns of recruitment, and these also appear to the result of the dispersion of favorable microsites rather than effects of conspecifics (Fowler 1988). The present study, as well as those cited above, suggest that spatial patterns of variation in recruitment in many species may, in fact, be more predictable than current thinking would suggest.

Consequences of the spatial pattern of habitat on recruitment

In experimentally created habitats, settlement was higher to randomly placed than clumped habitats. However, no statistical differences in recruitment were detected between the two treatments. Consequently, initial patterns of settlement were modified by mortality or emigration to a greater extent in the random than in the clumped habitats.

The mechanisms producing these differences were not investigated; however, several non-mutually exclusive possibilities seem likely. First, although the actual areas of habitat were equal between the random and clumped treatments, if the attractiveness of the habitat extended some distance beyond their borders, than dispersed habitats would present a larger target to pelagic, pre-settlement fish. Therefore, a randomly moving pre-settlement fish would more likely encounter a random treatment than a clumped treatment, just as a propagule is more likely to colonize a larger than smaller island (MacArthur and Wilson 1967).

Second, while the densities of demersal predators did not vary between treatments, large schools of pelagic predators, particularly pollock Pollachius virens, were common. I frequently observed large schools of pollock feeding on cunner recruits living on SHUs and in natural habitats. As these predators moved through the experimental area, they too may come upon the randomly placed SHUs more frequently than the clumped ones. Larger aggregations of recruits may also suffer lower rates of predation due to the increased vigilance of the group or decreased foraging efficiency of the predator in large aggregations of fish (Hobson 1978). As a result, post-settlement mortality due to predation may have been greater on random than clumped SHUs.

Third, it is also conceivable that density dependent mortality due to competition or predation modified initial patterns of settlement. The best evidence for density dependence in reef fishes involves competition for food resources, which appears to affect growth rate more than mortality (Thresher 1983; Jones 1986, 1987; Forrester 1990); thus, it seems unlikely that competition was important to mortality occurring within the first 24 hours after settlement. However, if predators respond to variability in the number of cunner recruits, density dependent mortality due to predation may be important (Gendron 1987).

Fish ecologists have investigated how the trade-offs between protection from predation and the quality of food govern patch selection (Mittelbach 1981, Werner et al 1983, Schmitt and Holbrook 1985, Holbrook and Schmitt 1988). However, to my knowledge, the ways in which demographic processes vary with patch structure, particularly the dispersion of habitat types, had not been directly addressed for reef fish until this study. In terrestrial systems the spatial structure within habitats has been demonstrated to have significant impacts on demographic processes (Wiens 1976, Antonovis and Levin 1980, Addicott et al. 1987). Moller (1991), for example, found the patch structure of the habitat affected nest predation for several bird species. Variation in the spatial structure of the habitat can result in different degrees of aggregation in endophytophagus insects (Southwood and Kennedy 1983) and these differences may influence survival (Godfray 1986, Auerbach and Simberloff 1989, Faeth 1990), predation rates (Itamies and Ojanem 1977) or parasite load (Faeth 1990). Given the evidence gathered in other systems, it is not surprising that the dispersion of the habitat influenced the demography of juvenile cunner. However, counter to much current thinking, this result suggests that in order to understand the population dynamics of reef fishes, knowledge of what habitats settlers use and how subsequent losses vary with structural aspects of those habitats is critical.

Implications for models of recruitment-limitation

One generally accepted feature of reef fish populations is that they exhibit dramatic spatial and temporal fluctuations in recruitment (Doherty and Williams 1988). The significant spatial variation of recruitment in cunner certainly conforms with this belief. Nonetheless, the question relevant to the dynamics of populations is "does variability in recruitment exclusively determine abundance of demersal populations?" For this to be the case, settlement must be independent of the size of the resident population, and population size must be dependent on levels of settlement (Jones 1991).

No measurable effects of variability in the size of conspecific populations on recruitment were found in this study. This is consistent with the first requirement of recruitment-limitation. The second criterion of the model, however, is clearly not met. When the dispersion of patches was experimentally manipulated, variability in settlement between experimental treatments was not reflected as variation in the population of older fish (i.e. recruits). In this case density independent loss which was influenced by patch structure, or density dependent mortality or migration modified patterns of settlement differently in the two experimental habitats.

It is apparent that both rates of settlement and subsequent benthic mortality or migration may contribute to population fluctuations in demersal fishes (Warner and Hughes 1988). Recently several workers have called for a more pluralistic approach to the study of populations of reef fish (Warner and Hughes 1988; Jones 1987, 1990, 1991; Forrester 1990; Connell and Jones 1991, Sale 1991). The data presented here strongly support this argument. This study demonstrated that the relative importance of settlement and post-settlement mortality or emigration varies among experimental habitats of different structure, and it is evident that a single-process model cannot adequately explain the population dynamics of different reef fish species or of populations of single species in different habitats.

Acknowledgments

To P.F. Sale, T.P. Good, G.E. Forrester, L.G. Harris, A.C. Mathieson, R.R. Olson, R.R. Warner, and J.D. Witman, I offer gratitude for extensive comments on various aspects of this work. I thank P.F. Sale, M.A, Hixon, T.P. Good, R.R. Warner, and an anonymous reviewer for their comments on the manuscript. Thanks also to the staff of the Shoals Marine Lab, Capt. P. Pelletier and the crew of the R/V Jere Chase for providing logistical and moral support. Many thanks also to the divers who assisted me in the field, particularly J. Maret, L. Saabe, E. Wright, D. Lockett, B. McCarthy, and L. Neaveu. Most of all thanks to M.J. Levin. This work was supported by a development grant from New Hampshire/Maine Seagrant and NSF grant OCE-9102027 to P.F. Sale and P.S. Levin.

Table 2-1. Location and description of sites used in this study.

Site	Location	Description
1	Cape Neddick, ME 43°10'N 70°36'35"W	rock ledge/urchin dominated area with sparse coverage of ephemeral and unpalatable algae
2	Nubble Island, ME 43°10'N 70°36'30"W	rock ledge with high(>80%) cover of Laminaria spp.) and a rich understory of red algae, mostly Chondrus crispus
3	Fort Point, NH 43°05'N 70°44'W	sandy substratum with few large boulders surrounded by Zostera marina bed
4	Fort Foster, ME 43°04'N 70°42'W	sandy/cobble substratum with Zostera marina, Chondrus crispus and scattered Laminaria spp.
5	Appledore Island, ME 42°59'N 70°37'W	rock ledge with moderate cover of (ca. 50%) Laminaria spp. as well as a dense understory of Codium fragile and Chondrus crispus
6	Haley's Cove, NH 42°59'N 70°36'30"W	rock ledge with dense cover of Codium and numerous filamentous species
7	Smuttynose Island, NH 42°59'N 70°36'W	rock ledge/large boulders, dominated by urchins with very sparse cover of ephemeral algae

Table 2-2. Two factor analysis of covariance testing the effects of site, juvenile density and adult density on recruit abundance. Sites 3 and 4 were omitted from the analysis because there was no variation in juvenile or adult density at these sites. Data were log (x + 1) transformed for the analysis.

source	SS	df	MS	F	P
site (s)	67.376	4	16.844	11.982	< 0.001
adult (a)	0.232	1	0.232	0.165	0.69
juvenile (j)	0.806	1	0.806	0.573	0.45
s x a	6.362	4	1.591	1.131	0.34
s x j	10.258	4	2.564	1.824	0.13
a x j	0.014	1	0.014	0.01	0.92
s x a x j	6.817	4	17.04	1.212	0.31
error	224.923	160	1.406		

Table 2-3. Repeated measures analysis of variance of settlement and recruitment on treatment (clumped vs. random) and sampling date.

A. Settlement

source	SS	df	MS	F	P
Between subjects:					
treatment	23.24	1	23.24	10.53	.006
error	30.92	14	2.208		
Within subjects:					
date	55.06	10	5.506	.84	<.001
date* treatment	37.19	10	3.719	.27	.001
error	159.23	140	1.14		

B. Recruitment

source	SS	df	MS	F	P
Between subjects:					
treatment	6.88	1	6.88	.77	.40
error	115.53	13	8.89		
Within subjects:					
date	17.18	11	1.56	2.50	.007
date * treatment	2.63	11	.24	.38	.96
error	89.51	143	.63		

Figure 2-1. Mean density per 15 x 1m strip transects of three age classes of T. adspersus at seven sites in the Gulf of Maine. Letters indicate sites which could not be distinguished statistically. Error bars represent ± 1 standard error.

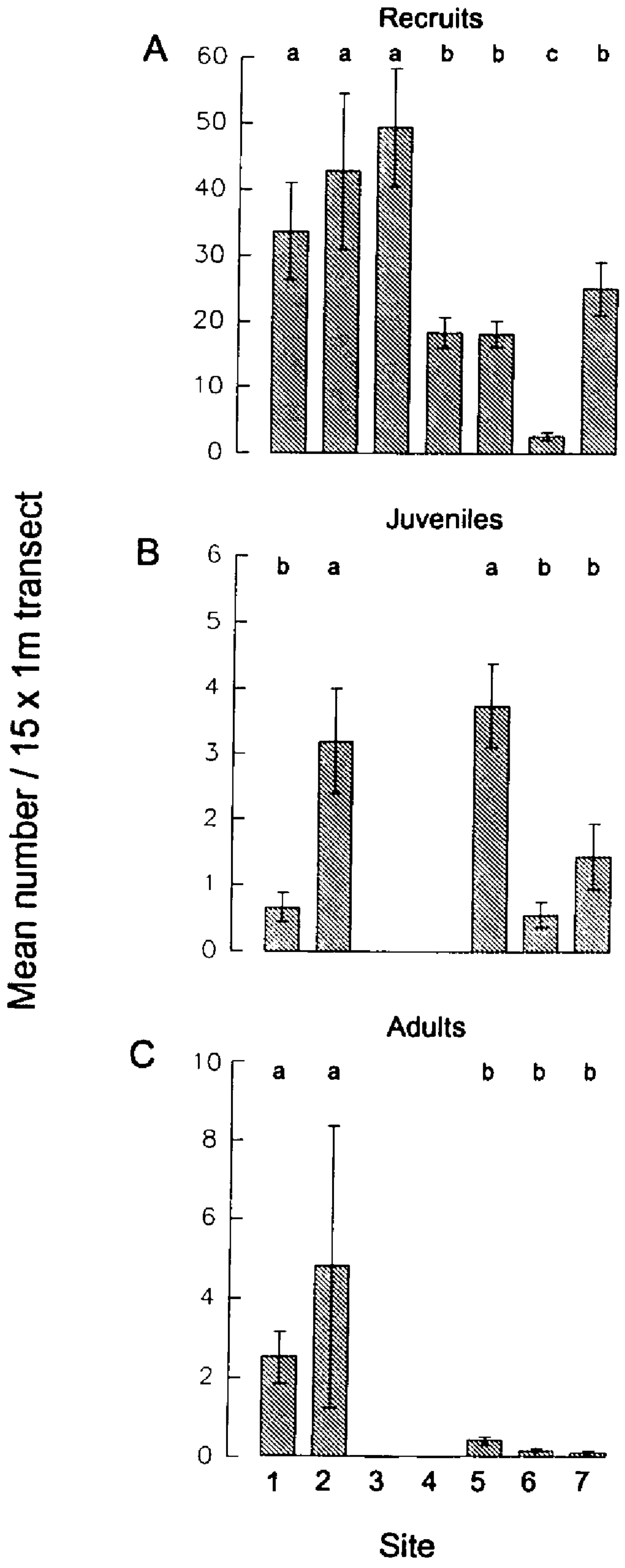

Recruits
A
60
50
40
30
20
10
0
a a a b b c b
Juveniles
B
6
5
4
3
2
1
0
b a a b b
Adults
C
10
8
6
4
2
0
a a b b b
Mean number / 15 x 1m transect
1 2 3 4 5 6 7
Site

Figure 2-2. Mean density of T. adspersus recruits at 2 sites on standard habitat units (SHUs) to which conspecifics were added or left as controls. Using a two way ANOVA, no difference was detected in recruit density either between treatments (F = 1.56, P = .24 for 30 August; F = .116, P = .74 for 13 September), or between sites (F = .344, P = .57 for 30 August; F = 2.22, P = .17 for 13 September). Error bars represent ± 1 standard error.

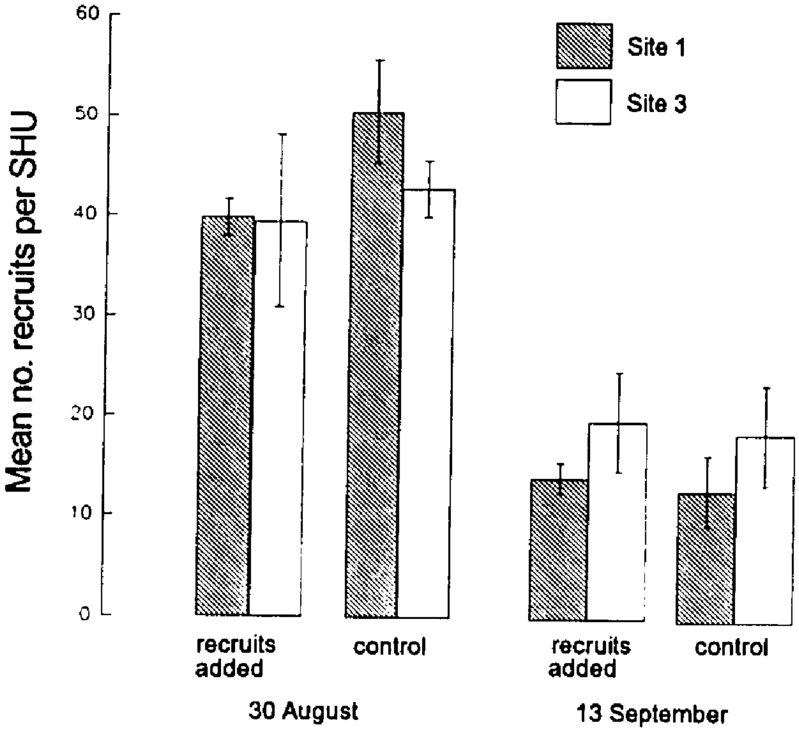

Mean no. recruits per SHU
60
50
40
30
20
10
0
Site 1
Site 3
recruits added
control
recruits added
control
30 August
13 September

Figure 2-3. Mean density of T. adspersus recruits in replicate experimental plots in which only the kelp canopy was removed, all fleshy algae was removed, and no algae was removed (control). Horizontal lines join bars which were not significantly different (Tukey's HSD $p > 0.05$). * indicates significance at $p < .05$. N = 8 quadrats for each treatment. Error bars represent ± 1 standard error.

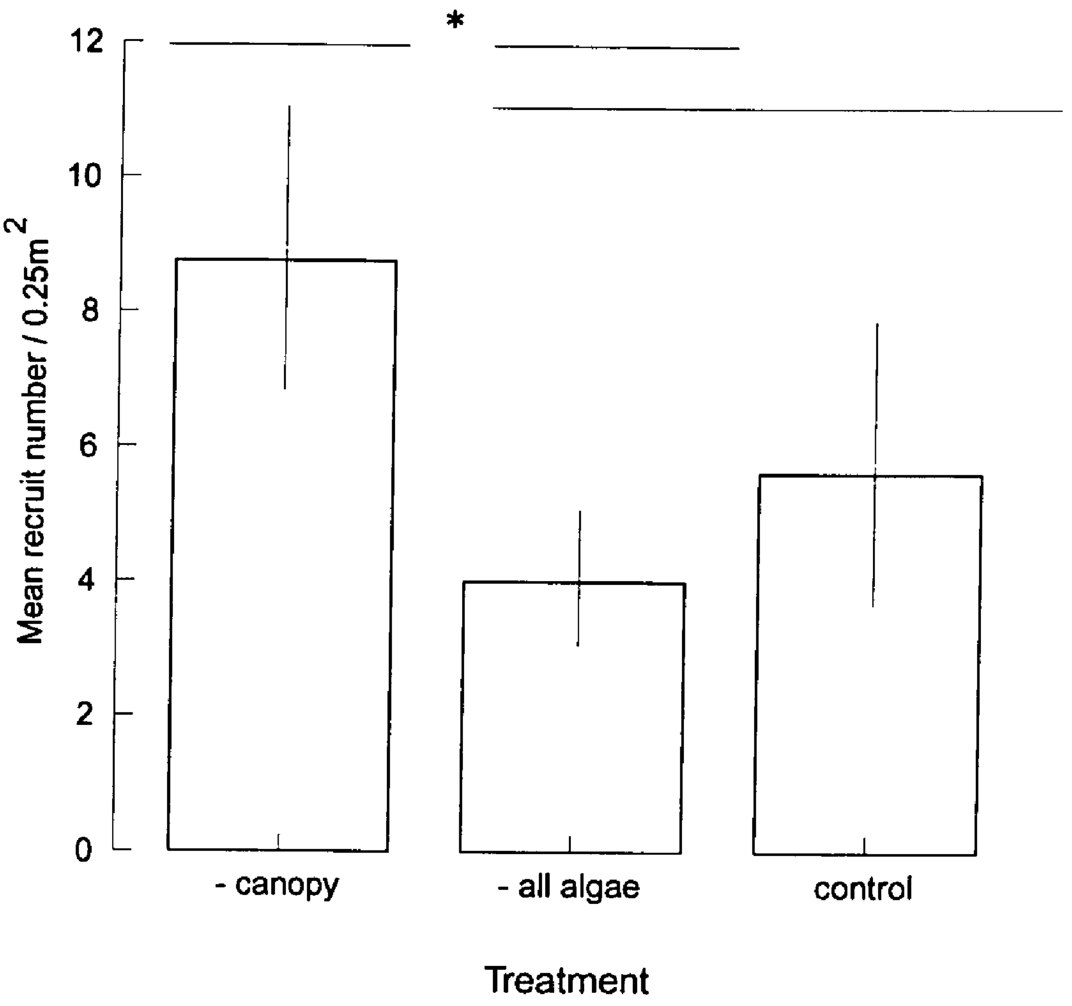

*
12
10
8
6
4
2
0
Mean recruit number / 0.25m^2
- canopy
- all algae
control
Treatment

Figure 2-4. The standardized Morisita's index of dispersion (I_p) for fish is plotted against the I_p for macroalgae for 5 sites. The spatial pattern for fish is highly correlated with that of the algae (Spearman rank correlation coefficient = .895)

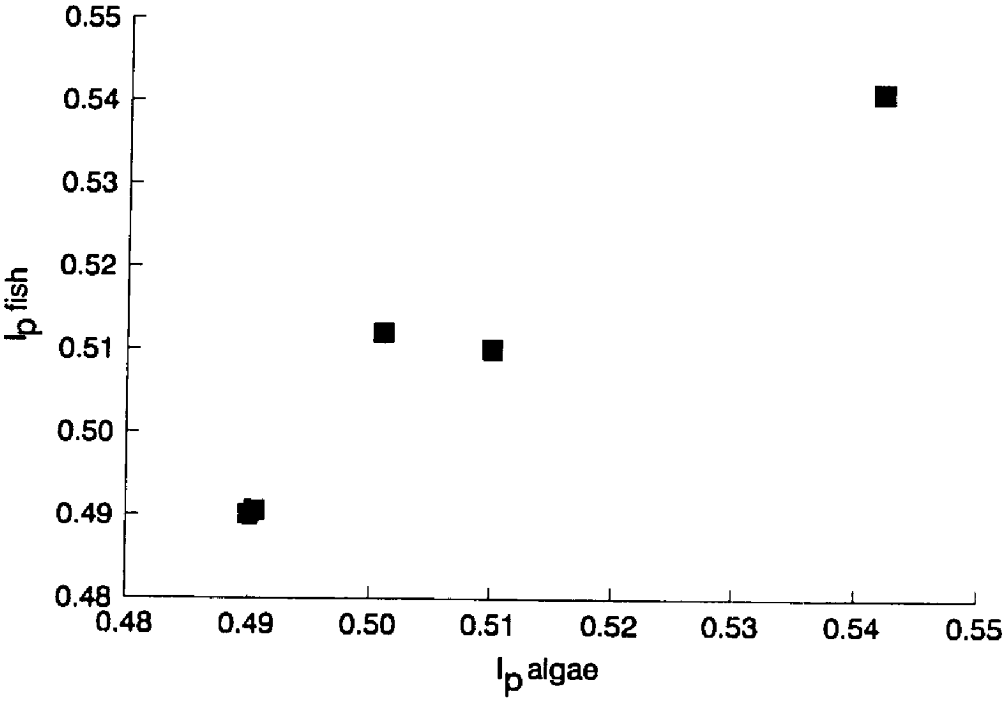

0.55
0.54
0.53
0.52
0.51
0.50
0.49
0.48
I_p fish
0.48
0.49
0.50
0.51
0.52
0.53
0.54
0.55
I_p algae

Figure 2-5. Mean number of newly settled T. adspersus on randomly placed versus clumped sets of standard habitat units (SHUs)(area = $1 m^2$). *, and ** indicate significance at $p < .05$ and $p < .01$ respectively by T tests for each date. Results from repeated measures ANOVA determining significance over all dates are presented in table 2-3a. Error bars represent ± 1 standard error.

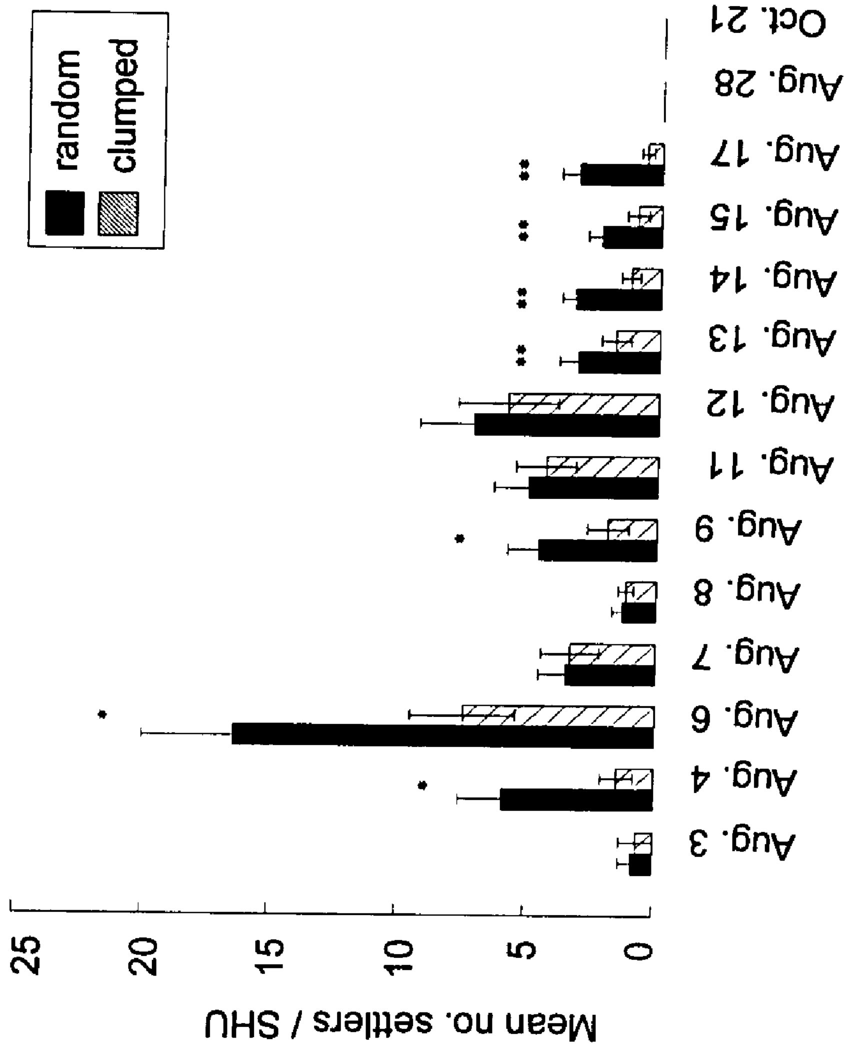
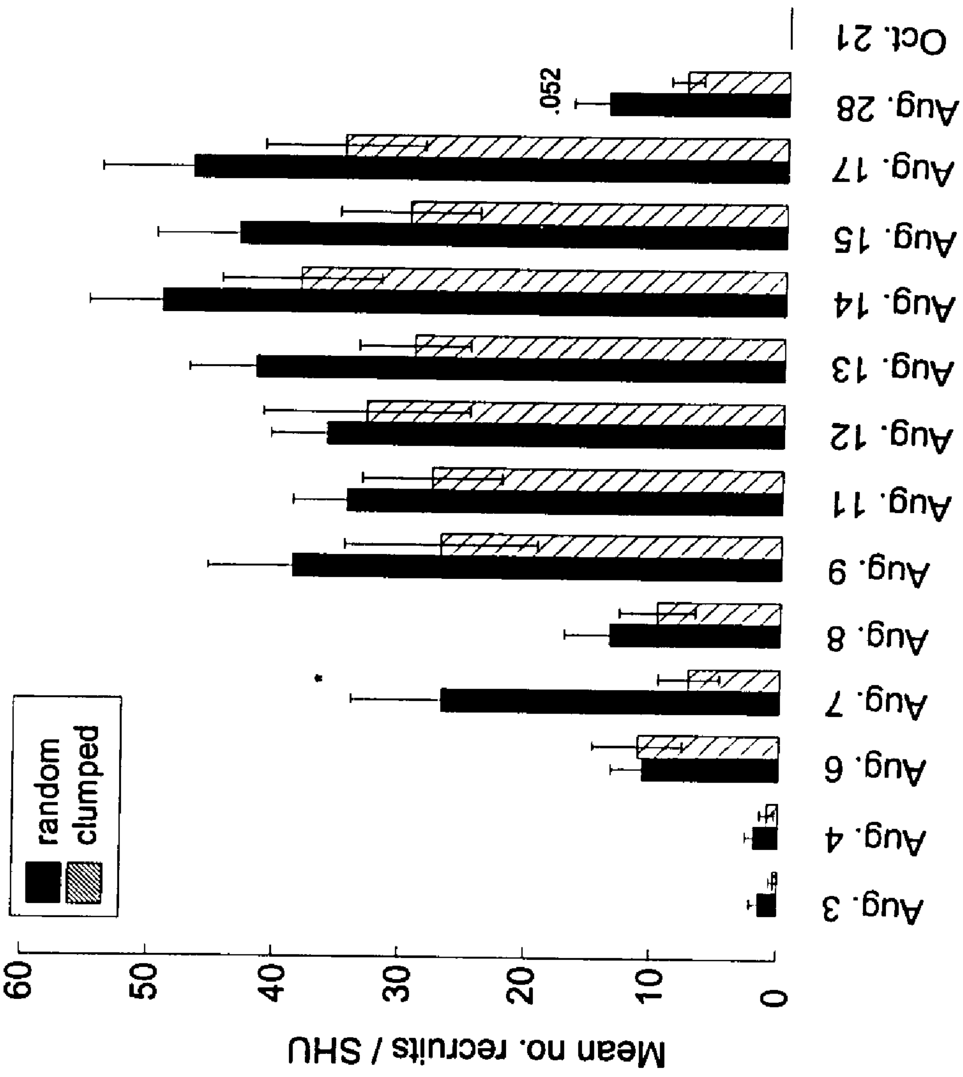

Mean no. settlers / SHU
0
5
10
15
20
25
Aug. 3
Aug. 4
Aug. 6
Aug. 7
Aug. 8
Aug. 9
Aug. 11
Aug. 12
Aug. 13
Aug. 14
Aug. 15
Aug. 17
Aug. 28
Oct. 21
*
*
*
**
**
**
**
■ random
▨ clumped

Figure 2-6. Mean number of T. adspersus recruits on randomly placed versus clumped sets of standard habitat units (SHUs) (area = $1 m^2$). * indicates significance at $p < .05$ by T test for each date. Results from repeated measures ANOVA determining significance over all dates are presented in table 3-3b. Error bars represent ± 1 standard error.


Mean no. recruits / SHU
0
10
20
30
40
50
60
random
clumped
Aug. 3
Aug. 4
Aug. 6
Aug. 7
Aug. 8
Aug. 9
Aug. 11
Aug. 12
Aug. 13
Aug. 14
Aug. 15
Aug. 17
Aug. 28
Oct. 21
*
.052

CHAPTER 3

FINE-SCALE TEMPORAL VARIATION IN RECRUITMENT OF A TEMPERATE DEMERSAL FISH: THE IMPORTANCE OF SETTLEMENT VERSUS POST-SETTLEMENT LOSS

Abstract

In order to understand variability in recruitment to populations of benthic and demersal marine species, it is critical to distinguish between the contributions due to variations in larval settlement and in post-settlement mortality. In this study, fine-scale (1-2 days) temporal changes in recruit abundance were followed through an entire settlement season in a temperate demersal fish in order to determine 1) how dynamic the process of recruitment is on a daily scale, 2) whether settlement and post-settlement mortality are influenced by habitat structure and conspecific density, and 3) how the relationship between settlement and recruitment changes over time. "Settlement" is considered to be the arrival of new individuals from the pelagic habitat, and "recruitment" is defined as the number of individuals surviving arbitrary periods of time after settlement.

The study species, cunner, Tautogolabrus adspersus Walbaum, is a common demersal fish in the Northwest Atlantic, particularly on rocky reefs and near other physical structures such as wharfs. Replicate standardized habitat units were placed in 2 spatial configurations (clumped and randomly dispersed) and monitored visually every 1-2d throughout the settlement season. The process of recruitment in T. adspersus was highly variable at a fine temporal scale. Changes in the numbers of recruits present on habitat units were due to both settlement of new individuals and mortality of animals previously recruited. The relative importance of these two processes appeared to change from day to day. The magnitude of the change in recruit number did not differ between the clumped and random habitats. However, post-settlement loss was significantly greater on randomly dispersed than clumped habitats. During several sampling dates, the extent of the change in recruit abundance was correlated with the density of resident conspecifics; however, on other dates no such relationship appeared to exist. Despite the presence of significant relationships between the change in recruit number and density, there was no evidence of either density-dependent mortality or settlement. Initially, there was a strong relationship between settlement and recruitment; however, this relationship weakened over time. Within 2 months after the cessation of settlement post-settlement loss was greater than 99%, and no correlation remained between recruitment and the initial pattern of settlement.

Introduction

The ways in which animals respond to environmental heterogeneity has important implications for a diversity of topics in ecology. Habitats are frequently composed of mosaics of patches, some of which are used by a particular species while others are not (Addicott et al., 1987). Variation in the dispersion of preferred habitat patches within a habitat can have important consequences for the demography of many taxa. Theoretical studies have demonstrated the importance of the spatial arrangement of habitat patches for the persistence (Lomnicki, 1980) as well as abundance (Taylor & Taylor, 1977; Hanski 1985) of populations. Additionally, empirical investigations have shown that differences in the degree of spatial aggregation of individuals within a habitat can influences survivorship (Godfray 1986; Auerbach & Simberloff 1989; Faeth 1990), predation rates (Itamies and Ojanem, 1977; Moller 1991) and parasite load (Faeth 1990).

Fish ecologists have investigated how trade-offs between securing protection from predation and gaining high quality food govern patch selection (Mittlelbach, 1981; Werner et al., 1983; Schmitt & Holbrook, 1985; Holbrook & Schmitt, 1988). However, the ways in which demographic processes vary with the patch structure of a habitat, particularly the dispersion of preferred habitat types, has received surprisingly little attention for demersal marine fishes.

Pronounced differences in recruitment and subsequent local population abundance occur over a range of temporal and spatial scales in benthic invertebrates (Connell, 1961; Grosberg, 1982; Caffey, 1985; Olson, 1985; Raimondi, 1990), algae (Deyster & Dean, 1986; Reed et al., 1988; Levin & Mathieson, 1991) and demersal fishes (Williams & Sale, 1981; Doherty, 1983; Victor, 1983; Jones, 1984; Sale et al., 1984; Choat et al., 1988; Levin, 1991). Predictive models for dynamics of populations of reef fish have recently emphasized the relative importance of larval supply, the settlement of larval and post-larval fish, and post-settlement growth and mortality (Jones, 1991; Hixon and Beets, 1993). As it has been difficult to directly measure settlement of fish in the field (but see Breitburg, 1989, 1991), most fish ecologists have measured recruitment. I define settlement as the time when an individual takes up permanent residence in the demersal habitat (Keough & Downes, 1982), and recruitment as numbers of individuals surviving some arbitrary period of time after settlement (Connell, 1985). Measured rates of recruitment equal the rate of settlement minus the fraction of fish that settle but die before being censused. The latter can be a significant fraction in some species, particularly if several days elapse between censuses of recruits (Doherty & Sale, 1986; Sale & Ferrell, 1988; Booth, 1991).

How demersal fish populations are numerically regulated has become an issue of vigorous debate. Historically, three hypotheses have been posed to predict variability in the distribution and abundance of fish. I present these hypotheses as alternatives;

however, recent work has emphasized the need to adopt a more pluralist approach that does not view them as mutually exclusive (Doherty & Williams 1988; Warner & Hughes, 1988; Doherty, 1991; Hixon, 1991; Jones, 1991). One hypothesis, the "resource limitation hypothesis" is derived from classical terrestrial ecology and asserts that the size of benthic populations is limited by the availability of resources. According to this model potential settlers are plentiful, and competition for resources (usually space or food) results in density dependent rates of recruitment. The prediction from this model is that larval settlement and/or post-settlement survival is inversely related to the densities of conspecifics or ecologically similar individuals at the settlement site (Doherty, 1983).

An alternative hypothesis, the "recruitment limitation" hypothesis, asserts that sites are undersaturated with new recruits and that sizes of populations are limited or determined by levels of recruitment (Doherty 1981, 1983; Victor 1983). This model predicts that settlement and post-settlement mortality are independent of the densities of conspecifics or potential competitors, and variation in settlement is expressed as variability in older age classes (Doherty 1983).

A third alternative, the "predation hypothesis" suggests that piscivores strongly influence the abundances of demersal fishes (Hixon, 1991; Hixon and Beets 1993). This hypothesis asserts that predation pressure on individual fish is intense and abundances are kept low enough that non-refuge resources are seldom limiting. Thus variation in recruitment should result from variability in predation pressure.

Tests of these models for demersal fish populations have been conducted largely in coral reef habitats (e.g. Doherty, 1983; Victor, 1986; Jones, 1987, 1990; Forrester, 1990; Hixon and Beets, 1993). Recently, however, some workers have addressed the roles of settlement and post-settlement processes on temperate rocky reefs (Jones, 1984a,b; Carr, 1989, 1991; Levin, in press). A major component of the structure of temperate reefs is macroalgal vegetation, and juvenile temperate reef fish are commonly associated with macroalgae (Wheeler, 1980; Jones, 1984a,b; Carr, 1989, 1991; Levin, 1991; in press). The macroalgal structure of temperate reefs can vary considerably in space and time and may be more ephemeral than the structure of tropical reefs (Dayton, 1985; Chapman & Johnson, 1990; Lambert et al., 1992). The close association of juvenile fish with macrophytes may have profound influences on the demography of fish populations. For example, the dispersion of juvenile fish in habitats in which algae are clumped may be aggregated (Jones 1984c, Levin, in press) thus influencing the small-scale density of fish.

The purpose of this study is to test the predictions of population models for reef fishes using a temperate demersal fish in habitats of different patch structure. Changes in recruit abundance due to settlement, post-settlement loss or both were observed at a fine temporal scale (1-2 d) to determine the importance for changes in the size of the recruit population of habitat structure and of resident fish densities to . Specifically, I ask: 1) Are fine-scale temporal changes in recruit number influenced by the dispersion of habitat patches? 2) Are changes in recruit abundance affected by the density of resident conspecifics? 3) What are the consequences of fine-scale temporal changes in recruit abundance for the interpretation of the recruitment-settlement relationship?

Methods

Study species

Cunner Tautogolabrus adspersus Walbaum are common members of shallow subtidal communities in the Northwest Atlantic, occurring from intertidal zones (Whoriskey 1983) to depths greater than 90m (Bigelow and Schroeder 1953). They occur in abundance from Newfoundland, Canada to New Jersey, U.S.A. (Bigelow and Schroeder 1953). The larval life of cunner averages 18-21 days (Gleason & Reschick, 1990), and they settle to macroalgal habitats dominated by foliose and filamentous algae (Levin, 1991; Levin, in press). In the Gulf of Maine, cunner usually spawn in July and thus settlement occurs in late summer (Levin, in press). As juveniles, cunner are site-attached and do not stray far from cover (Olla et al., 1975; Pottle and Green, 1979; Levin 1991). Recent tagging experiments (M. Tupper, Dalhousie University, unpublished data) have shown that cunner spend their first year within a few square meters . Even as adults, home ranges of cunner are quite small (< 3000 m^2) with most of their activity limited to core areas averaging < 100 m^2. (Pottle and Green, 1979; C. Bradbury, 1993). Cunner overwinter in a torpid state within their home ranges (Green and Farwell, 1971).

General methods

The study was conducted in April-October, 1991 in Gosport Harbor, Isles of Shoals, New Hampshire, USA (42°59'N 70°37'W). This site provided a protected, relatively level plain with sandy substrata at a depth of 4-9m mean low water. In April an experiment commenced using standard habitat units (SHUs). SHUs were constructed from 0.5 cm wire mesh placed across a 0.5m X 0.5m frame fashioned from 1cm diameter PVC pipe. Filamentous algae were allowed to colonize the mesh, and thus they provided a habitat similar to the one naturally used by young cunner. Levels of algal colonization to different SHUs appeared to be approximately equal. To prevent burial by shifting sand, legs were attached to SHUs so they stood 0.5m above the substratum. SHUs were placed in two spatial patterns: 1) clumped - 4 SHUs adjacent and touching to form a 1m X 1m square; and 2) random - 4 SHUs placed randomly except that they were separated from each other by no more than 1-2m. Each set of 4 SHUs was separated from other sets and from natural habitat by at least 6m. There were 12 replicates of each of the spatial patterns. As settlement and recruitment are negatively correlated with depth (Levin, in press), I ensured that equal numbers of replicates were allocated to each of 3 depth zones (4-6m, 6-8m, 8-10m). Because juvenile cunner are extremely site-attached and SHUs were separated from each other and natural habitat, additions to the SHUs were expected to be the result of larval settlement rather than demersal migration.

SHUs were visually censused on 11 of the 17 days when cunner settlement was observed in 1991 (August 1-17) and on 2 more dates following the settlement season (August 28 and October 21). On August 26 Hurricane Bob passed approximately 4 miles from the study site. Thus, this sampling period included a potentially major disturbance. Visual censuses consisted of a diver counting all the fish while slowly circling the SHUs. Due to difficulties in locating all replicates, not all replicates were censused on the first 2 sampling periods. Since settling individuals are translucent and appear to assume full pigmentation 24 hours after settling, fish were scored as settlers only if they were translucent. My index of settlement underestimated settlement, but should have done so in a uniform fashion among replicates. Fish were recorded as recruits if they were fully pigmented.

Data analysis

Changes in recruit abundance for each group of 4 SHUs were determined by subtracting the recruit number counted on one day from the recruit number counted on the next census (1 or 2 days later). The hypothesis that changes in recruit abundance were affected by the dispersion of habitat patches was tested using an analysis of variance in which the experimental factor (clumped vs. randomly placed SHUs) was considered a fixed factor and different sampling periods were considered a random factor and a repeated measure (Winer et al. 1991). Each group of 4 SHUs was considered a replicate. Data were log transformed to meet the assumptions of analysis of variance.

To determine if changes in recruit number were associated with the density of conspecifics on each set of 4 SHUs, regression analyses were performed in which the change in recruit number between two successive sampling periods was the response variable and the density estimated during the earlier period was the independent variable. In this analysis, the change in recruit number results from two different processes, settlement and post-settlement loss, that may act simultaneously and have opposite effects. The measured daily change is thus an index of the relative importance of settlement versus post-settlement loss during the sampling interval. This analysis is limited, however, since it masks the precise mechanisms producing the observed changes. Because changes in recruit density are influenced by both settlement and post-settlement loss, variation in the response variable is not constrained by the density of the resident population. For all regression analyses, residuals were examined to ensure they were approximately normally distributed, had a constant variance and were independent (Wilkinson, 1990). Analysis of covariance was used to compare the slopes and intercepts of the regression lines for the clumped and random treatments.

Two null hypotheses were tested with the regression analyses. First I tested the null hypothesis that the slope of the regression line did not differ from zero. A significant positive slope indicates that there was greater growth in numbers of resident recruits on SHUs with higher resident densities. Similarly, a significant negative slope indicates that there was greater loss of recruits on SHUs with higher densities.

A significant result from this analysis does not demonstrate density dependence, since greater post-settlement loss is expected on replicates with more fish. To test for density dependence, I further analyzed data for those sampling periods in which the slope of the line as significantly different from zero. My working hypothesis was that the slope of the regression line had a greater negative slope than the line expected from simply higher loss with higher densities. The expected line was generated from the data by determining the average proportional change in recruit number over the entire settlement season and then multiplying this value by a range of densities. A one-tailed t-test was then used to test the hypothesis that the observed regression line had a more negative slope than the expected line.

To investigate how these patterns of change might influence the recruit-settler relationship, I examined the relationship between the number of settlers I observed from August 1 through August 17 and the number of recruits on August 17, 28 and October 21. August 1 was the first date I observed a newly settled fish, and August 17 was 2 days after the last appearance of cunner pre-settlement fish in plankton tows conducted at the Isles of Shoals (Levin unpublished data.). This approach is similar to the one used by Connell (1985) and Davis (1988). It suffers from the problem that the number of recruits is constrained by the number of settlers . Consequently, conventional significance tests of the correlation coefficient are not valid (McGuiness & Davis, 1988). However, these data are presented to demonstrate a qualitative change in the recruit-settler relationship over time, and I do not attempt to draw statistical inferences from these data.

I also examined the association between cumulative number of settlers I observed from August 1 through August 17 and the proportion of those settlers still present on the SHUs on August 17, 28 and October 21. The proportion of settlers present on the SHUs was determined by dividing the number of recruits by the cumulative number of settlers. Since fish were considered settlers only if they were still translucent when sighted, this is a conservative measure of settlement which underestimates settlement. Consequently, some proportions were greater than 1. The arcsine transformed data were analyzed using analysis of covariance to examine proportional loss with respect to initial density date, and patch dispersion. An effect of initial density on the proportion of settlers remaining suggests mortality is density dependent (McGuiness & Davis, 1989).

Results

Fine-scale temporal patterns of change and the effect of habitat structure

Each set of 4 SHUs was visually censused on 12 sampling periods, and the change in recruit number between consecutive periods was determined. Fish on both dispersion treatments were easily observed and counted. The change measured is the result of additions due to settlement as well as losses due to post-settlement mortality. Dramatic changes in recruit number were observed on a fine temporal scale; however, there were no consistent differences between clumped and random habitats in the change in recruit number (Fig. 3-1). There was frequently as much as a 10 fold difference in the mean change in recruit number among sampling periods. No pattern in the magnitude of change over the settlement season emerged. Large and small changes appeared interspersed with each other and occurred throughout the settlement season.

The sign of the change (positive or negative) reveals whether larval settlement or post-settlement loss is of greater significance in producing the observed changes. A mean positive change indicates that gains from larval settlement were, on average, relatively greater than post-settlement losses. Likewise, a mean negative change suggests that post-settlement losses were more larger than gains from settlement. Because cunner recruits are site-attached, and migration is rare (Tupper, unpublished data), loss of recruits is assumed to be due to mortality rather than migration. Figure 1 illustrates that the relative importance of settlement versus post-settlement mortality often varies on a daily basis. For example, during the August 6-7 sampling period larval settlement was of greater importance than post-settlement loss on the random treatment, while post-settlement loss was of more importance during the August 7-8 sampling period. The opposite was true for the clumped treatment. Here, post-settlement loss was more important than settlement during the August 6-7 period, while larval settlement dominated the August 7-8 sampling period.

The relationship between change in recruit abundance and initial density

Figure 2 summarizes the results of the 12 regression analyses examining the relationship between the change in initial density and recruit number for all 12 sampling periods. In no instance was the relationship influenced by the dispersion of the SHUs (ANCOVA, $p >> .05$). On 5 of the 12 sampling periods, there was a significant negative relationship between the change in initial density and recruit number (Fig. 3-2). In the other 7 sampling periods no relationship between change in initial density and recruit number could be detected, although in all of these cases the correlation coefficient was negative (Fig. 3-2).

In order to determine if the significant relationships between changes in initial density and recruit number were the result of density dependent processes, I tested the hypothesis that the slopes of the regression lines were more negative than would be expected simply if SHUs with greater densities of fish suffered higher losses. The mean proportional change in recruit number during the settlement season was 0.128. Thus, the line of the change in recruit number regressed against initial density is expected to have a slope of -.872 (Fig. 3-3). The slopes of the observed regression lines were not significantly lower than the expected value for any sampling period (Fig. 3-3), and there is no evidence of density dependence.

The recruit-settler relationship

There was a strong and positive relationship between cumulative settlement and recruitment on August 17 (Fig. 3-4a). One week following Hurricane Bob, the number of recruits was lower than on August 17, but a positive, albeit weaker, relationship between settlement and recruitment still existed (Fig. 3-4b). By October 21, a relationship between settlement and recruitment was no longer evident because few recruits remained on the SHUs (Fig. 3-4c). In fact, by October 21 a total of 10 recruits of the 998 observed setters remained. The loss of 99% of the settlers was presumably due to mortality as a careful search of surrounding habitat also yielded very few recruits. This level of mortality was also observed in natural habitats and is typical for this species in the southern Gulf of Maine (Levin, unpublished data).

There was no relationship between the proportion of settlers that remained on August 17, August 28 and October 21 and the total numbers of settlers I observed throughout the settlement season (Fig. 3-5, Table 3-1). The proportion of fish that survived to the three sampling dates was similar on SHUs of varying densities . Consequently, at this temporal scale, there is no evidence of density dependence.

The dispersion of habitat patches did have an influence on the loss of settlers (Fig. 3-6, Table 3-1). A significantly higher proportion of fish remained on the clumped SHUs than on the randomly dispersed ones. This was particularly evident on August 17 when the average proportion of fish on the clumped treatment was ca. 40% greater than on the random treatment (Fig. 3-6). By October the average proportion of fish remaining was 14 times greater on the clumped treatment than on the random treatment. In fact, 8 of the 10 fish which remained at the end of the experiment were on clumped SHUs.

Discussion

Settlement of post-larval Tautogolabrus adspersus occurs in a brief burst which in 1991 lasted 17 days. During this time I observed 998 individuals settling to 24 m^2 of habitat (ca. 2.5 settlers m^{-2} d^{-1}). The process of recruitment in T. adspersus is very dynamic even at the fine temporal scale examined in this study. The magnitude of changes in recruit number, and the relative importance of settlement versus post-settlement loss both varied daily. Fine scale variability in changes in recruit numbers was density independent and not influenced by the dispersion of the habitat. However, the proportion of settlers remaining at the end of the experiment was influenced by the dispersion of habitat patches. Post-settlement loss was greater in habitats composed of randomly dispersed patches versus aggregated patches. Post-settlement loss was extreme and variable, and the relationship between settlement and recruitment was weak. By the end of the experiment 99% of fish were dead. As a result, there was no realistic chance that variation in settlement could be expressed as recruitment variation.

It is unlikely that the apparent temporal decline in the strength of the correlation between recruitment and settlement was the result of migration from the experimental habitats. The habitats were isolated from each other and from natural habitat by large distances, and these site-attached fish would have to cross large expanses of bare sand in the presence of large schools of pelagic predators. Similar declines in abundances of Tautogolabrus adspersus recruits have been observed in the natural habitat surrounding the experiment as well as in sites throughout the southern Gulf of Maine for the last three years (Levin, unpublished data). For some species, however, emigration from settlement sites may be important to the demography of local populations (Sogard, 1989).

The importance of the recruit-settler relationship for the interpretation of population and community studies

Since all fish populations experience some level of mortality, it is important to know the extent, timing and variability of mortality when inferences about settlement are to be drawn from infrequent recruitment surveys. If the dynamics of Tautogolabrus adspersus populations are typical, then studies that sample frequently may be able to draw inferences about settlement. On the other hand, for species, like T. adspersus, that suffer severe mortality in the first few weeks after settlement (Victor, 1986; Shulman & Ogden, 1987; Sale & Ferrell, 1988; Hixon, 1991), infrequent sampling to examine processes occurring at or around the time of settlement may result in erroneous conclusions (Booth, 1991).

Models of both community and population structure have been developed based on infrequent sampling. Sale and Douglas (1984), for example, proposed a model for the formation of assemblages of coral reef fishes on small patch reefs. From eight censuses conducted during a 33 month period they found that assemblages of fish on patch reefs possessed a structure which was temporally variable and largely independent of the reef structure. They suggested that vagaries in larval supply led to spatial and temporal variation in recruitment, and that assemblages on individual patch reefs were largely a product of this apparently stochastic variation. However, several of the common species found on the patch reefs Sale and Douglas studied suffer high mortality as juveniles while others experience relatively low levels of mortality (Sale & Ferrell, 1988). Consequently, the degree to which the patterns Sale and Douglas (1984) observed actually represented variable settlement may be species specific. Thus, as Sale and Douglas (1984) noted, the composition of assemblages of fish is dependent on both settlement and subsequent loss, but the relative importance of these processes is likely to vary among species with different mortality schedules and cannot be determined from infrequent censuses.

A disintegration over time of the recruit-settler relationship can also influence the interpretation of population studies. Shulman and Ogden (1987) reported levels of mortality for Caribbean grunts similar to the level I observed for Tautogolabrus adspersus. Certainly, after only a short period of time, censuses of recruitment for these species have a great probability of yielding a distorted record of settlement. While extreme mortality may be unusual (cf Hixon 1991), precise data are required to test models of population dynamics. Even moderate levels of mortality, particularly if it is variable, can weaken the recruit-settler relationship thus rendering any conclusions suspect (Warner & Hughes, 1988; Jones 1991; Doherty, 1991).

Implications for models of population dynamics

The principal prediction of the recruitment limitation model is that variation in settlement is expressed as variability in older age classes (Doherty, 1983; Victor, 1983; Doherty & Williams 1988). In order for densities of older fish to be controlled by levels of settlement, the size of the resident population must not affect rates of settlement and the size of the population must be dependent on levels of settlement (Jones, 1991). Previous work (Levin, in press) has demonstrated that the presence of resident conspecifics does not influence levels of settlement in this species. However, because levels of mortality were high, spatial variation in settlement was not expressed as spatial variability in the abundance of older fish. The prediction of the recruitment limitation model is thus not supported for this species at the spatial and temporal scales examined in this study. Since the experiment was conducted for only one year, the significance of interannual variation of settlement on the age structure is unknown. It remains possible that interannual differences in settlement would be reflected as variation in age class strength, and this would be consistent with the tenets of recruitment limitation.

The resource limitation model predicts that shortages of resources should result in density dependent rates of recruitment. No evidence of density dependence was detected in this study. Moreover, the best evidence for density dependence in demersal fishes involves competition for food resources (Thresher, 1983; Jones, 1987; Forrester, 1990). Competition for food appears to affect rates of growth and maturity more than survivorship (Jones, 1987; Forrester 1990). Differential mortality, however, played an obvious and important role in determining the numbers of recruits at the end of the settlement season. Highly mobile predators, particularly pollock Pollachius virens were very common at the study site, and I frequently observed schools of pollock foraging on cunner recruits on SHUs and in natural habitats. It is very likely that much of the post-settlement loss documented in this study was the result of predation. The loss of recruits was much greater on randomly dispersed than clumped SHUs. Despite higher levels of settlement in randomly dispersed habitats (Fig. 3-4 ; Levin, in press), at the end of the experiment 80% of the surviving recruits were on clumped habitats. The increased perimeter of randomly dispersed versus clumped patches may increase the likelihood that mobile predators would detect a habitat patch. Therefore, predator pressure may have been greater on randomly dispersed SHUs. In addition, the increased perimeter of randomly dispersed habitats may decrease the ability of recruits to hide from predators.

The results of this study support neither the recruitment nor resource limitation models, but provide circumstantial evidence for the predation hypothesis. The predation hypothesis predicts that abundances should be negatively related to the intensity of predation. As predation pressure was ostensibly related to the patch structure of the habitat, the results presented here are consistent with this hypothesis. Studies on coral reefs have demonstrated that the architecture of the habitat, particularly hole size and number, are important determinants of predation intensity (Shulman, 1984; Hixon and Beets 1989, 1993). Additionally, on temperate reefs increased biogenic structure is thought to reduce the impacts of predators (Holbrook & Schmitt 1988; Carr, 1991). This study is the first to demonstrate the importance of the spatial arrangement of the habitat on the rate of post-settlement loss. It is important to note, however, that while predators, particularly Pollock, were abundant and I observed Pollock consuming large numbers of cunner recruits, there is no direct evidence that the mortality I observed was predominantly the result of predation.

At present, a cautious interpretation of these results is necessary. The study was only conducted at one site on artificial habitats, and detection of density dependence from a series of consecutive censuses is certainly more equivocal than experimental tests of density dependence. Recruitment (Levin, in press), macrophyte structure (Levin, 1991, in press), and predator abundance (pers. obs.) vary greatly among sites in the Gulf of Maine. Consequently, the relative effects of settlement and post-settlement loss on spatial and temporal variation in abudance may also vary. Nonetheless, this investigation adds to a growing number of studies that have established the necessity of considering post-settlement processes in models of demersal fish populations (Jones, 1987, 1990; Warner and Hughes, 1988; Forrester, 1990; Connell and Jones, 1991; Hixon & Beets 1993; Levin, in press).

Acknowledgements

Many thanks to P.F. Sale, T.P. Good and G.E. Forrester for their extensive comments on various aspects of this work. D. Carlon, G. Forrester, L. G. Harris, M. Hixon, A.C. Mathieson, P. Sale, G. Trussell, and R.R. Warner provided helpful criticism on the manuscript. Thanks also to the Shoals Marine Lab, Capt. Paul Pelletier and the crew of the R/V Jere Chase for their logistical assistance and to D. Lockett, J. Maret, E. Wright and L. Saabe for diving assistance. The support of a NSF Graduate Fellowship, a development grant from New Hampshire/Maine Seagrant, and NSF grant OCE-9102027 to P.F. Sale and P.S. Levin is gratefully acknowledged.

Table 3-1. A two factor analysis of covariance was used to determine if variation in the proportion on settlers remaining on experimental habitats changed with time, between experimental habitats of different patch structure (clumped vs. random), or was influenced by the number of settlers each replicate habitat received. Interaction terms that were not significant (P > 0.1) were removed from the model. Habitat refers to habitat dispersion treatment. * P <.05, *** P < .001.

Source	SS	DF	MS	F
Habitat	.096	1	.096	4.945*
Date	2.027	2	1.013	51.925***
Settlement	.022	1	.022	1.141
Habitat X Settlement	.055	1	.055	2.818
Error	1.288	66	.020	

Figure 3-1. The mean change between censuses in recruit number per set of 4 standard habitat units (SHUs) is plotted for each sampling period. A repeated measures ANOVA revealed that there were significant differences in the average change in recruit density among sampling dates ($F_{11,33} = 5.537$ $P < .001$); however, no difference was detected between clumped versus randomly placed SHUs ($F_{1,3} = 2.597$, $P = .20$). Error bars are ± 1 SE.

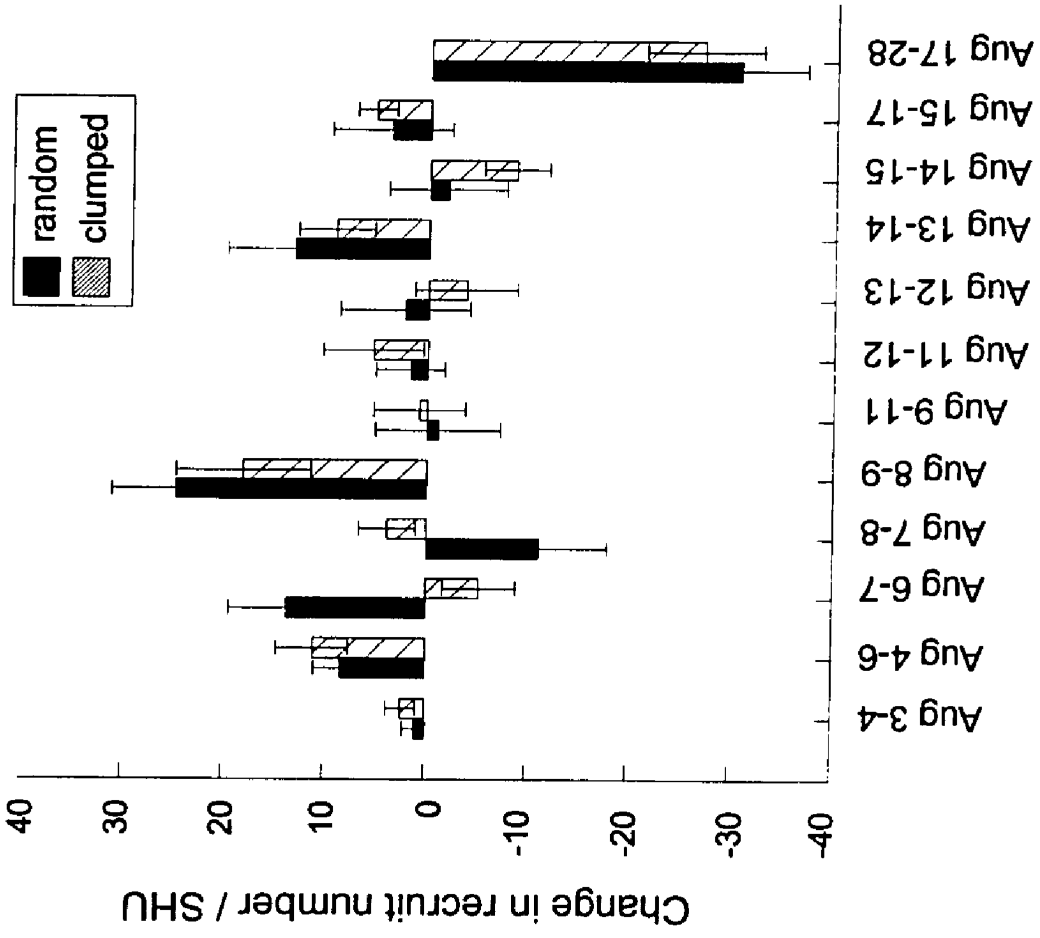

random
clumped
Aug 3-4
Aug 4-6
Aug 6-7
Aug 7-8
Aug 8-9
Aug 9-11
Aug 11-12
Aug 12-13
Aug 13-14
Aug 14-15
Aug 15-17
Aug 17-28
40
30
20
10
0
-10
-20
-30
-40
Change in recruit number / SHU

Figure 3-2. The correlation coefficient between the change in recruit number per group of 4 SHUs and the initial density is plotted for each sampling period. Note that the last sampling period is 11 d while the other 11 sampling periods are 1-2 d. * indicates a significant relationship ($P < .05$) between the change in recruit number and initial density.

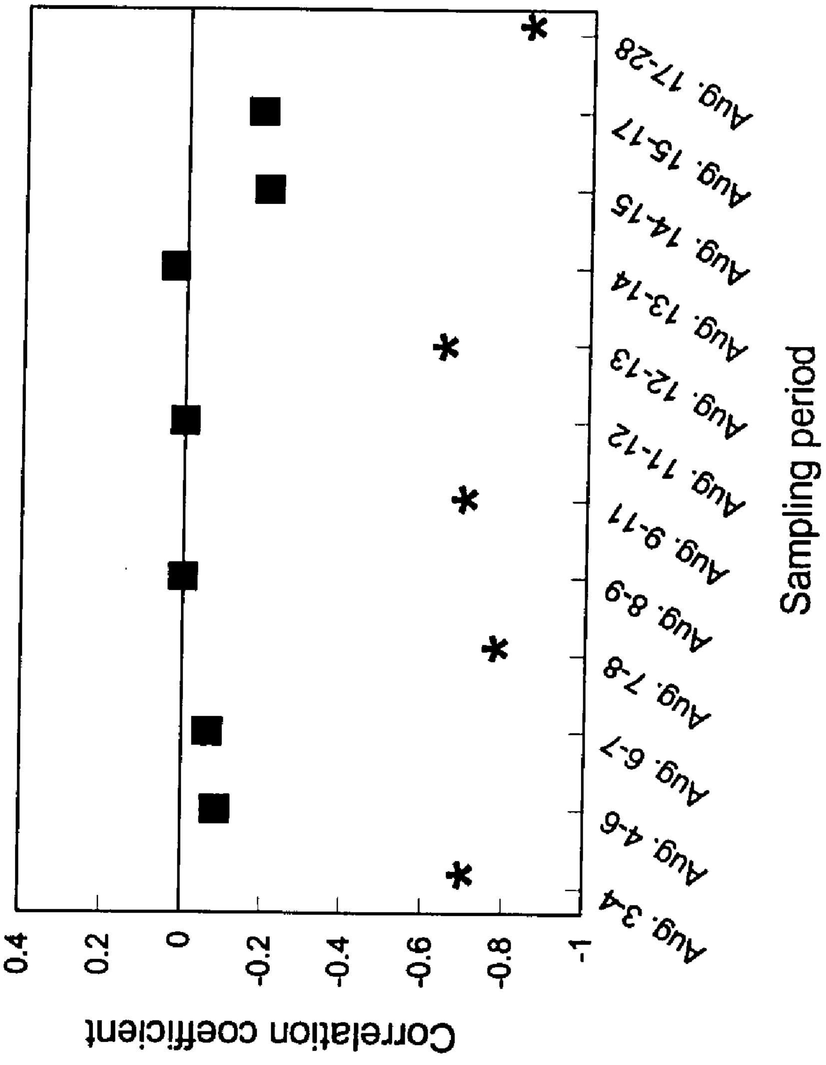

Correlation coefficient
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Sampling period
Aug. 3-4
Aug. 4-6
Aug. 6-7
Aug. 7-8
Aug. 8-9
Aug. 9-11
Aug. 11-12
Aug. 12-13
Aug. 13-14
Aug. 14-15
Aug. 15-17
Aug. 17-28

Figure 3-3. For each sampling period (Fig. 2-2) in which the slope of the regression line was significantly different from zero, the slope of the observed regression line is compared to the line (slope = -.872) expected if the change in recruit number is proportional to the density. For no sampling period tested was the observed slope significantly more negative than expected. (See text for details)

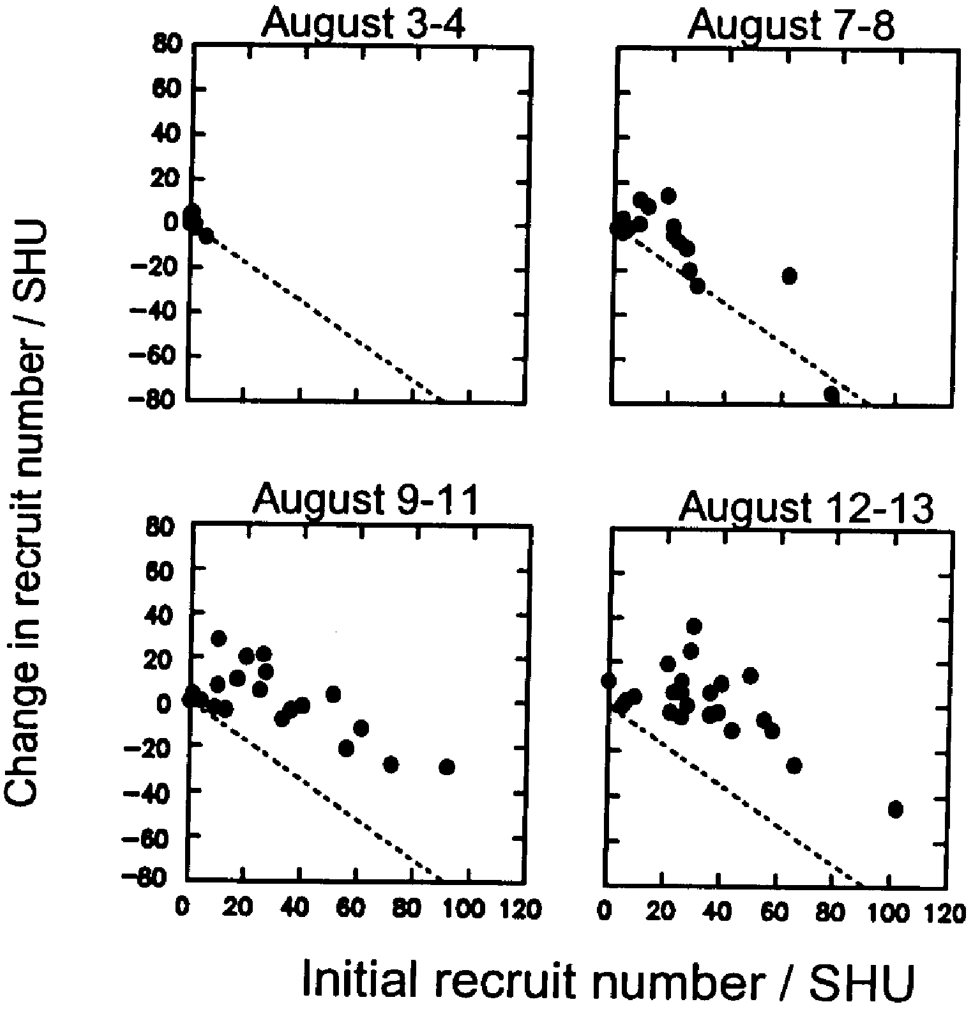

August 3-4
August 7-8
August 9-11
August 12-13
80
60
40
20
0
-20
-40
-60
-80
0
20
40
60
80
100
120
Change in recruit number / SHU
Initial recruit number / SHU

Figure 3-4. Density of recruits on experimental habitats (SHUs) in random and clumped distributions for three sampling dates following the end of the settlement season vs. the total number of settlers observed during the settlement season.

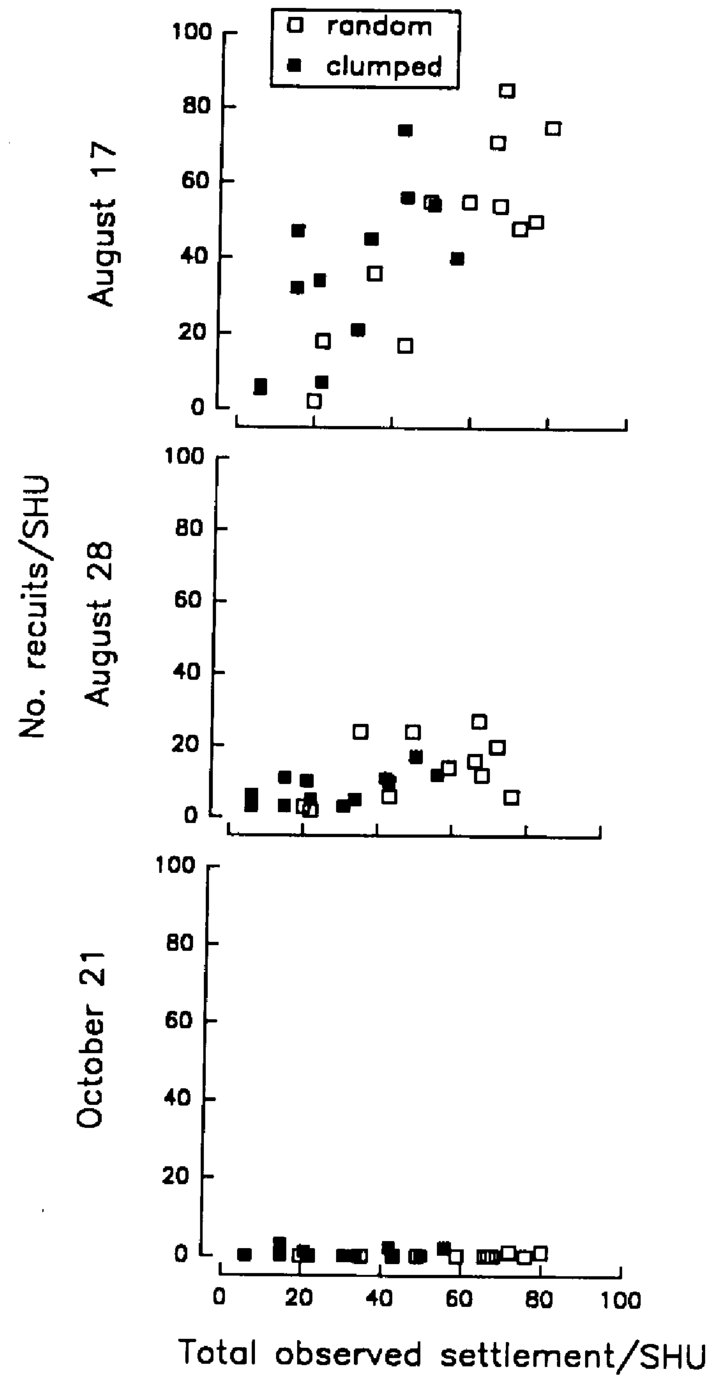

□ random
■ clumped
August 17
August 28
October 21
No. recuits/SHU
Total observed settlement/SHU
0
20
40
60
80
100

Figure 3-5. The proportion of observed settlers still remaining on each of 3 dates is plotted against the total observed settlement on each set of 4 SHUs. Proportions can be greater than 1 since a conservative measure of settlement was used (see methods). The relationship between the proportion of fish remaining and total settlement were not significant (Table 3-1).

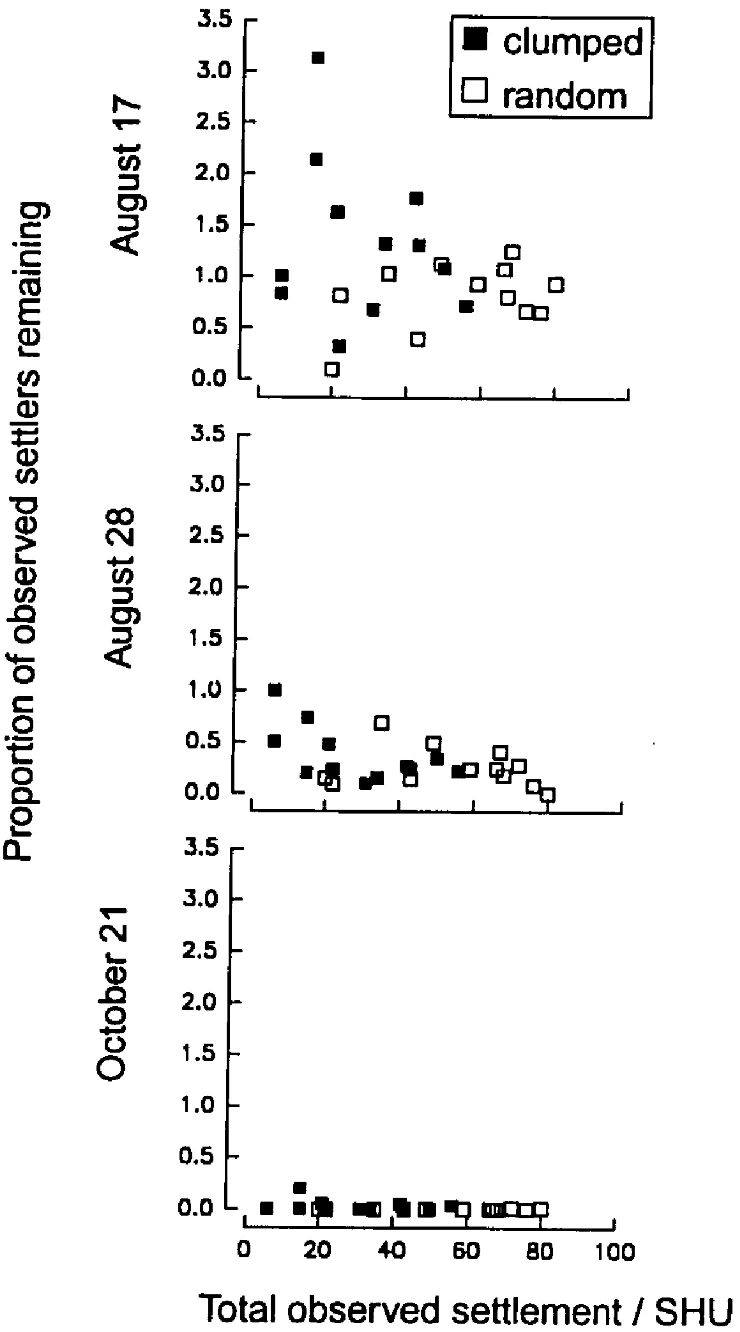
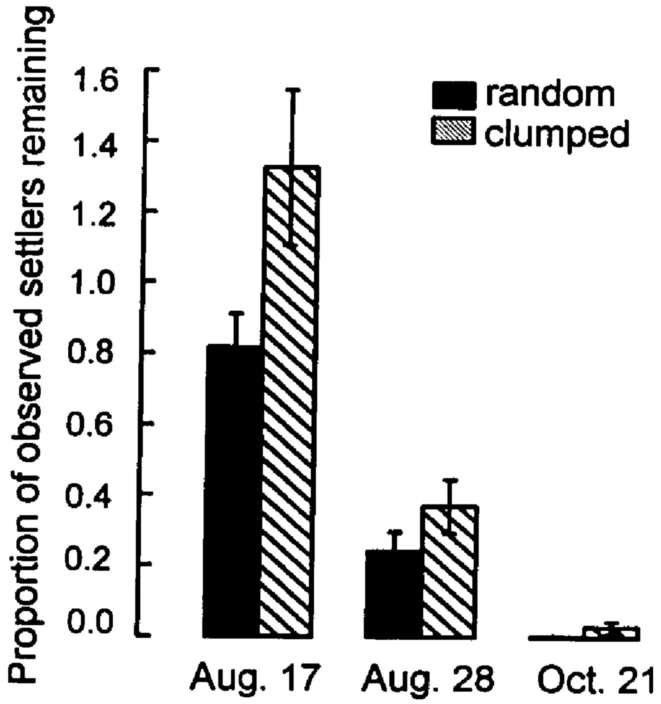

Proportion of observed settlers remaining
August 17
August 28
October 21
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
■ clumped
□ random
0
20
40
60
80
100
Total observed settlement / SHU

Figure 3-6. The mean proportion of settlers remaining on random and clumped SHUs are shown for 3 dates. A significantly higher proportion of fish was lost from the random than the clumped SHUs. There was also a significant decline in the proportion of settlers remaining over time (Table 3-1) Error bars are 1 SE.


Proportion of observed settlers remaining
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
random
clumped
Aug. 17
Aug. 28
Oct. 21

CHAPTER 4

GEOGRAPHIC DIFFERENCES IN THE DEMOGRAPHY OF A TEMPERATE MARINE FISH: INFERENCES ABOUT THE IMPORTANCE OF PRE- AND POST-RECRUITMENT PROCESSES.

Abstract

Three models have been proposed to explain the dynamics of reef fishes. The recruitment limitation model asserts that variability in the supply of larval fish and corresponding variability in the settlement of larvae from the water column to the demersal habitat are the predominant processes influencing spatial and temporal fluctuations in the sizes of fish populations. By contrast, both the resource limitation and predation models suggest that processes occurring after larval settlement can play a major role in determining the sizes of populations. Most tests of these models have been conducted in tropical habitats, on small spatial scales and at single geographic locations. The purpose of this study was to assess the relative importance of pre- and post-settlement processes in a temperate reef fish Tautogolabrus adspersus at multiple spatial scales and in two distinct geographic regions, Newfoundland and the Gulf of Maine.

We examined a total of 20 sites (100-1000m) nested within 10 locations (10 km) in Newfoundland and the Gulf of Maine. Greater numbers of adult fish were observed in Newfoundland than in the Gulf of Maine; however, higher abundances of both juvenile and newly recruited fish occurred in the Gulf of Maine. In the Gulf of Maine variation in the densities of adults, juveniles and newly recruited fish was most pronounced at the site

scale, but in Newfoundland we detected pronounced variability at both the site and location scales. In both regions there were significant space-time interactions indicating that spatial patterns were not consistent over time. We examined temporal patterns in detail in the Gulf of Maine. For adult and juvenile cunner spatial variation was high so that we were unable to detect significant temporal variation. In contrast, temporal variation in recruitment was extreme. Thus, we detected significant temporal variation but were unable to detect significant levels of spatial variation.

We examined several potential causes of the observed temporal and spatial variability in abundance. Variation in recruitment among sites was not expressed as variability of either juveniles or adults. However, several attributes of the habitat were related to variation in abundance, although the effects differed among ages classes and geographic regions. Variation in abundance of recruits or juveniles was not related to the topographic complexity of the substratum. Likewise for adults in the Gulf of Maine there was no detectable affect of topographic complexity on variation in densities; however, there was a negative relationship between topographic complexity and variability in adult numbers in Newfoundland. Algal height was not associated with variability in the abundances of recruits, juveniles or adults. Algal coverage was also not important in Newfoundland, but in the Gulf of Maine it was an important predictor of variability fish abundance. Adults were negatively associated with kelp cover while juveniles and recruits were associated with branching algae. The supply of larvae competent to settle was also examined. We examined two sites within each of two locations. Although the supply of pre-settlement fish varied in both time and space, it was not concordant with patterns of recruit or older fish abundance. Although there was consistently greater than 2 orders of magnitude difference in densities of pre-settlement fish between the 2 locations, the location that received fewer pre-settlement fish had greater densities of recruits, juvenile and adults. Moreover, abundances of pre-settlement fish varied consistently at the location scale, but this was not reflected in location-scale variability in recruitment.

Our data suggest that pre-settlement processes are not the predominant processes affecting cunner populations in the Gulf of Maine. Rather, we hypothesize that habitat-related differences in predation rates are the most significant process affecting cunner population dynamics in the Gulf of Maine. However, in Newfoundland the evidence gathered thus far supports the hypothesis that episodic recruitment events are responsible for much of the variation we saw there.

Introduction

The processes that limit or generate change in the sizes of populations have been a matter of vigorous debate for decades. The often acrimonious discussions on the relative importance of density dependent and density independent processes are well known. For marine organisms that have a pelagic larval phase, the debate on density dependence versus independence has shifted, and a major challenge facing marine ecologists is distinguishing between the relative importance of processes occurring prior to or after the settlement of larvae in determining the distribution and abundance of adult organisms (Underwood and Denley 1984, Menge and Sutherland 1987, Doherty and Williams 1988, Jones 1991).

Most marine species, including demersal fishes, have complex life cycles in which larvae are pelagic and widely dispersed, while adults are benthic or demersal and relatively site-attached (Sale 1980, Doherty and Williams 1988, Roughgarden et al. 1988). Because of their life history, most marine populations are considered to be open populations in which local production of offspring on a scale of meters to kilometers has little to do with recruitment to that site (Cowen 1985, Warner and Chesson 1985, Roughgarden et al. 1985, Doherty and Williams 1988). It is generally accepted that demersal fish populations consist of local subpopulations connected through larval dispersal (Sale et al. in press). Thus, the arrival of pelagic propagules and subsequent mortality in the demersal population are critical demographic parameters determining the population dynamics of such populations (Roughgarden et al. 1985, Warner and Hughes 1988).

Three general models have been advanced to predict how the distribution and abundance of adult fish will vary in time and space (Doherty 1983, Jones 1987, Hixon 1991). The first of these, the "resource limitation" or "competition" hypothesis is derived from conventional terrestrial ecology and asserts that the size of the adult population is regulated by the availability of resources. According to this model potential settlers are plentiful, and competition for space or food results in density dependent rates of recruitment. The prediction from this model is that larval settlement and/or early post-settlement mortality is inversely related to the densities of conspecifics (Doherty, 1983).

A second model termed "recruitment limitation" asserts that sites are understaturated with new recruits and that upper limits of abundances are set by variability in recruitment (Doherty 1981, 1983, Victor 1983). Additionally, a more restrictive interpretation of this model suggests that populations are not only limited by recruitment, but that recruitment variation causes variation in population abundance. Thus, this model predicts that temporal variation in recruitment is preserved in the age structure of the population, and spatial variation in recruitment is reflected in subsequent patterns of abundance in demersal populations (Doherty 1987, Victor 1986, Mapstone and Fowler 1988).

Most recently a model has emerged that asserts that predation on new recruits and juveniles is the predominant process affecting the dynamics of demersal fish populations (Hixon 1991, Hixon and Beets, 1993). The "predation hypothesis" states that predation pressure on individual fish is intense. Consequently, abundances are kept low enough that competition for non-refuge resources does not frequently occur (Hixon 1991). If predators are abundant and refuges from predators are limiting, this model predicts that there will be competition for refuges (Hixon and Beets 1993). However, when recruitment is low no density dependence should occur. Additionally, when predator abundances are low competition for refuges will not occur.

Although I have presented these three models as mutually exclusive alternatives, recent work has emphasized the need to adopt a more pluralistic approach (Warner and Hughes 1988, Doherty 1991, Hixon 1991, Jones 1991). Single factor explanations are often too simplistic to adequately explain variability in population structure (Strong 1986, Jones 1987, 1990, Forrester 1990, Hixon and Beets 1993). Several workers have suggested that populations may be both resource and recruitment limited in different locations (Jones 1984b, Roughgarden 1986, Nisbet and Bence 1989, Hixon and Beets 1989, 1993). For demersal fishes that are site-attached, the relative importance of recruitment, resource availability and predation pressure may differ in patches that are only separated by a few meters. Additionally, over the geographic range of a species, there is no a priori reason to anticipate that the relative importance of various demographic processes should remain constant. Moreover, fluctuations in recruitment can influence density-dependent post-settlement processes (Jones 1990, Forrester 1990, Hixon and Beets, 1993).

The relative importance of pre- and post-settlement processes on the abundances of adult fishes is likely to be scale-dependent (Smith 1978, Cowen 1985, Doherty 1991, Williams 1991, Fowler et al. 1992). At large spatial scales (10's - 100's km) variation in the delivery of pelagic pre-settlement fish can be affected by oceanographic processes such as variability in current patterns (Cowen 1985). Additionally, mesoscale oceanographic anomalies may produce episodic pulses of recruitment by delivering pelagic propagules to sites that are at the geographical limits of a species range (Dayton and Tegner 1984, Cowen 1985). At small spatial scales (meters) biotic interactions are generally more important than at large scales (Antonovis and Levin 1980, Addicott et al. 1987, Levin 1992). At small scales interactions between settling fish and resident conspecifics can produce variability in recruitment (Sweatman 1985, Booth 1992). Moreover, it is only at small scales where the importance of competition (Jones 1986, 1987, 1990, Forrester 1990) or predation (Hixon and Beets 1993) have been unequivocally documented for fish.

Tests of models that attempt to explain fluctuations in the abundance of demersal fishes have largely been conducted in coral reef habitats, at small spatial scales, and in single geographic locations. Recently, however, some workers have addressed the processes influencing demersal fishes in temperate zones. Unlike coral reefs, a major element of the structure of temperate reefs is macroalgae (Schiel and Foster 1986, Chapman and Johnson 1990). Juvenile temperate reef fish are commonly associated with macroalgae (Wheeler 1980, Jones 1984, Carr 1989, 1991, Holbrook et al . 1990, Levin 1991, in press). The macroalgal structure of temperate reefs is highly variable over a range of spatial and temporal scales, and may be more ephemeral than the structure on coral reefs (Dayton 1985, Schiel and Foster 1986, Witman 1987, Chapman and Johnson 1990, Lambert et al. 1992). The close association of temperate demersal fish with macroalgae may thus have profound consequences on the dynamics of these populations over a range of spatial and temporal scales.

The primary purpose of this study was to assess the relative importance of pre- and post-settlement processes in explaining patterns of adult abundance of a temperate reef fish at multiple scales and in two distinct geographic regions. We accomplished this goal by first describing variability in abundance in space and time of a temperate wrasse (Tautogolabrus adspersus) at numerous sites in the Gulf of Maine, U.S.A. and in

Newfoundland, Canada. We then used a correlative approach to distinguish among models attempting to describe the dynamics of fish populations by testing the following hypotheses.

Hypothesis: *Variation in recruit abundances is reflected as subsequent variation in older age classes*

This hypothesis is a direct statement of the recruitment limitation model (Doherty 1983, Victor 1983). I tested this model by examining the relationship between average levels of recruitment at several sites and subsequent abundances of older fish in future years. Acceptance of this hypothesis is direct support for the recruitment limitation model, while rejection of this hypothesis may be the result of density-dependent post-settlement interactions (e.g. competition for resources) or may arise from differential predation among sites. Thus, it is not possible to distinguish among these alternatives by testing this hypothesis alone.

Warner and co-workers (Warner and Chesson 1985, Warner and Hughes 1988) have directed attention to a potential difficulty in attempting to document effects of recruitment on subsequent population abundance. In long lived organisms much of the interannual variation in recruitment may be masked since the input from settlement is low relative to the size of the adult population (Warner and Hughes 1988). Thus, variability in recruitment will be difficult to detect in the adult population. However, by investigating the relationship between recruitment and subsequent abundance of 1+ year fish, we have circumvented this problem.

Hypothesis: *Abundances of adult fish are related to the structure of the habitat*

Habitat structure can influence the ability of a predator to detect prey (Heck and Thoman 1981, Shulman 1984, Hixon and Beets 1993, Levin in press) as well as the number of refuges available for use by prey (Shulman 1984, Behrents 1987, Hixon and

Beets 1989, 1993). Variation among sites in the structure of the habitat may thus affect the importance of predation. In addition, on temperate reefs fish use macroalgal structure not only for shelter, but also as a foraging substratum (Schmitt and Holbrook 1985, Carr 1991, Levin 1993). Competition for food or shelter sites may thus influence the abundance of recruit, juvenile or adult fish. If the hypothesis that habitat structure affects abundance of fish is rejected then it is evidence that habitat related resources are not significant and thus is evidence for the recruitment limitation model. However, if habitat structure influences abundances of fish then this suggests that either fish choose habitats at settlement or that resource shortages or predation modifies patterns of abundance after settlement. Thus, a positive result from this analysis is ambiguous.

Hypothesis: *Variability in larval supply determines patterns of adult abundance*

Implicit in expositions on recruitment limitation is that variability in larval supply is the ultimate cause of variability in recruitment and subsequent abundance of adults (Doherty 1981, Victor 1984, Sale and Douglas 1984, Jones 1991). If this is true then demersal populations should vary at the same spatial scale as pre-settlement fish (e.g. Victor 1984). Additionally, sites that receive more pre-settlement fish should have higher levels of recruitment and adult densities (Fowler et al. 1992). Rejection of this hypothesis suggests that processes acting after settlement sufficiently modify spatial patterns of larval supply that they can no longer be detected. This is evidence counter to the recruitment limitation model.

STUDY ORGANISM

Cunner, Tautogolabrus adspersus, are prominent members of nearshore communities in the Northwest Atlantic. They occur from depths of greater than 90m (Bigelow and Schroeder 1953) to intertidal zones (Ojeda and Dearborn 1991). Cunner are common from Newfoundland to New Jersey, and are occasionally found as far south as the

Chesapeake Bay (Bigelow and Schroeder 1953). Throughout its range cunner are associated with reefs, sheltered rock substrata or man-made structures (e.g. piers, wrecks, etc.). As young they are often associated with algal cover (Olla et al. 1975, Pottle and Green 1979, Levin 1991, in press). Cunner have relatively small home ranges (Green 1975, Olla et al. 1975, Pottle and Green 1979). Adults limit most of their activity to core areas averaging < 100 m^2 (Pottle and Green 1979, Bradbury 1993). Tagging experiments have shown that juvenile cunner spend their first year within a few square meters (M. Tupper, Dalhousie Univeristy, unpublished data).

Cunner spawn in early and mid summer (Dew 1976, Pottle and Green 1979). Their larval life averages 18-21 days south of Cape Cod (Gleason and Reschiek 1990), but it may be at least 30% longer in the Gulf of Maine (Levin, unpublished data). Cunner spawn during early July in the Gulf of Maine thus settlement occurs in late summer. In Newfoundland spawning occurs in late July and early August (Pottle and Green 1979) followed by settlement 3-4 weeks later. (J. Green pers. obs.).

METHODS

Spatial patterns of abundance

Geographic Scale. Spatial patterns of abundance for adult, juvenile and newly recruited cunner were examined in 1991 and 1992 at 20 sites, ranging in latitude from 43° N to 50° N . Twelve sites were located in Newfoundland, Canada and 8 sites in the central Gulf of Maine, USA, more than 1800 km from Newfoundland. The two regions are considered distinct biogeographic provinces (Vermeij 1978), representing Arctic (Newfoundland) and boreal (Gulf of Maine) zones.

Abundances were estimated by censusing at least 10 haphazardly placed 15m X 1m transects at each site. Because adult and juvenile cunner are less cryptic than recruits, it was necessary to perform separate censuses for these age classes (Lincoln Smith 1989). Thus, at sites with both recruits and adults or juveniles, a total of 20 transects were censused. Data were analyzed with a two-factor ANOVA on log (X+1) transformed data. Geographic region was considered a random factor and year was fixed.

Location and site scales. Locations were defined as places separated by greater than 10 km and sites as places separated by 100 - 1000 m . Two sites were sampled within each of 4 locations in the Gulf of Maine and 6 locations in Newfoundland . Censuses were conducted in 1991 and 1992 as described above. Data were log (X+1) transformed and analyzed with a three-factor ANOVA for each geographic region. Year was considered a fixed factor, while location and site (nested within location) were considered random factors.

Temporal patterns of abundance

Temporal patterns of abundance for adult, juvenile and newly recruited cunner were established by monitoring seven sites in the Gulf of Maine for 3 years . Censuses were conducted as described above for spatial patterns. Data were analyzed with a two-factor ANOVA with both year and site considered random factors.

Causes of variation in abundance

Effects of among-site variation in recruitment on juvenile and/or adult abundance. A positive relationship between recruitment at time t and abundances of juveniles at time t+1 year and adults at time t+2 years is evidence that variability in recruitment contributes to variation in older life stages. To test this we examined the relationship between the mean level of recruitment to 7 sites in 1990 and the average numbers of juveniles in 1991 and adults in 1992. We also examined the relationship between recruitment in 1991 and juvenile abundance in 1992. The 7 sites used in these analyses were the same ones used to describe temporal patterns. Regression analyses were used to determine the proportion of variation in the response variable (juvenile or adult abundance) explained by among-site variation in recruitment. A slope significantly different from zero indicates that recruitment affects the abundance of older stages. However, because cunner are long lived there is an opportunity for the storage effect (sensu Warner and Chesson 1985) to operate, thereby making it difficult to detect effects of recruitment on adult abundance (Warner and Hughes 1988). Negative results from these analyses are thus ambiguous for adults.

Effects of habitat structure on variability of recruits, juveniles and adults. To explore the relationship between habitat structure and the abundance of fish, We first quantified several different attributes of the habitat at sites in Newfoundland and the Gulf of Maine. Because previous work has shown macrophyte cover (Levin 1991, in press) and height (Levin 1991) influence small-scale patterns of distribution in juvenile cunner, these factors were examined in this study. In addition we explored the effect of topographic complexity of the substratum on the abundance of fish.

For algal analyses 4, 7 and 11 sites were examined in the Gulf of Maine during 1990, 1991 and 1992, respectively. Twelve sites were examined in Newfoundland in both 1991 and 1992. Algae were grouped as kelps (Lamanaria sacharina, L. digitata, and Agarum cribrosum) foliose (Ulva lactuca) and branched (mostly Ceramium spp., Polysiphonia spp., Desmarestia spp., Ahnfeltia plicata, Codium fragile). The mean percentage cover at each site was estimated by recording the type of plant at 10 cm intervals along randomly placed 15m transects. A minimum of three transects was sampled at each site. Average cover of each algal type was calculated for each site and a multiple analysis of covariance was used to test for effects of kelp, branched algae and filamentous algae on among-site variation in fish abundance in different years.

Average algal height for each site was determined by measuring the height of plants in at least 30 randomly selected positions. Height was considered to be the distance from the substratum to the apex of a plant in its natural position. An analysis of covariance was used to test the hypothesis that variation among sites in the average abundance of fish in 1991 and 1992 was explained by the mean height of algae.

To determine topographic complexity at each site we adapted a method described by Luckhurst and Luckhurst (1978). A 5 m rope was extended from a randomly selected point and pulled tight. Another line was laid directly under the rope and made to conform as nearly as possible to the contours of the substratum. The ratio of the actual surface distance to the linear distance was used as an index of topographic complexity. Eight replicate measurements were taken at each site. Analysis of covariance was used to test for differences in the relationship between the average abundance of fish and topographic complexity during 1991 and 1992 in the Gulf of Maine and Newfoundland.

<u>Effects of supply of pre-settlement fish on spatial patterns of abundance</u>. The distribution of pre-settlement fish was examined at the same three spatial scales as demersal fish populations were investigated. A geographic comparison was made between Newfoundland and the Gulf of Maine; a location-scale comparison was made by sampling 2 sites at the Isles of Shoals and 2 sites in Portsmouth Harbor in the Gulf of Maine ; and a site scale was examined by comparing variation among sites within locations.

Pilot studies revealed that pre-settlement cunner are found in surface waters at night. Therefore, we quantified the supply of pre-settlement fish by performing surface ichthyoplankton tows at night with a 1000 μm mesh plankton net fitted with a General Oceanic flow meter. Plankton nets were 1m in diameter. Three replicate 10 minute tows were conducted on 6 occasions during the settlement season. We sampled concurrently in each location in the Gulf of Maine so that spatial trends in abundance were not confounded by temporal patterns. Sampling in Newfoundland was conducted ca. 3-4 weeks later as the settlement season occurs later in Newfoundland than in the Gulf of Maine (J. Green pers. obs.).

Only fish competent to settle were considered in the analysis. To determine the size at which fish were competent to settle, an extensive collection of fish was made at 1 site not used for other analyses in this study. Fish in the water column that were larger than the smallest fish found in the demersal habitat were considered competent to settle. A three-factor ANOVA was used to test for differences in the densities of pre-settlement fish on different dates and among sites and locations. Date was considered a fixed effect, while location and site (nested within location) were both considered random effects.

RESULTS

Spatial patterns of abundance

Geographic Patterns. Distinct differences in the abundance of cunner were found between Newfoundland and the Gulf of Maine. Significantly greater numbers of adults were found in Newfoundland than in the Gulf of Maine and this difference was consistent over time (table 4-1a). The mean density of adults in Newfoundland was 4.17 (.559 SE) fish per transect while in the Gulf of Maine the density averaged 1.316 (.416 SE) fish per transect.

In contrast there were significantly more juveniles in the Gulf of Maine than in Newfoundland (table 4-1b). Like adult abundances, this pattern was consistent between sampling years (table 4-1b). Juvenile density averaged 2.158 (.654 SE) per transect in the Gulf of Maine, while it was .135 (.04 SE) per transect in Newfoundland.

The difference in recruitment between Newfoundland and the Gulf of Maine was striking. In more than 250 censuses during 2 years at 12 sites a total of 3 recruits were observed at only 1 site in Newfoundland. In contrast, recruitment in the Gulf of Maine was high. In 1991 the average density of recruits was 8.316 (1.708 SE), and in 1992 the density of recruits averaged .982 (.242 SE).

Patterns within geographic regions. In the Gulf of Maine variation in adult abundance was most pronounced at the scale of site rather than location (Fig. 4-1, Table 2a). Differences among sites were not consistent between years as evidenced by a significant interaction between site and year (Table table 4-2a). In 1991 Nubble Point had more than 3 times the average density of adults than any other site (Fig. 4-1). However, in 1992 of the sites where adults were present, Nubble Point had the lowest mean density (Fig. 4-1). Despite an absence of adults in 1991, Appledore Island had the highest average density of adults in 1992 with ca. 3 times the density of other sites.

In Newfoundland variation in adult abundance was evident at both the location scale and the site scale (Fig. 4-2, Table 4-2b). During both 1991 and 1992 the Bonne Bay sites had much higher densities than any other site, with densities at Norris Point averaging greater than 25 per transect in 1991 and 17 in 1992. No adults were observed at the east coast location, and other locations generally averaged ca. 3 adults per transect. The magnitude of the difference among locations differed between years producing a significant location - year interaction (Table 4-2b). In particular there was a decline the density of fish in Bonne Bay, but there were generally higher densities at locations in Conception and Trinity Bays (Fig. 4-2).

Patterns of juvenile abundance in the Gulf of Maine were similar to those for adults (Fig. 4-3). Variation in juvenile density was most pronounced at the site scale (Table 4-3a). In 1991, juveniles were most abundant at the Shoals 1, Nubble 2 and Boon 2 sites.

However, in 1992 only Shoals 1 had substantial numbers of juveniles producing a significant site by year interaction in the analysis (Table 4-3a).

Likewise, in Newfoundland the pattern of juvenile abundance was similar to that of adults (Fig. 4-4). Variation was best explained at the location scale (Table 4-3b). In 1991 the highest density of juveniles was at Bonne Bay with an average of ca. 1 individual per transect. However, in 1992 no juveniles were observed.

The pattern of significant site-scale variation in the Gulf of Maine was evident for recruits just as for adults and juveniles (Fig. 4-5, Table 4-4). The Shoals 1 site averaged 37.8 (SE = 7.67) recruits per transect in 1991, and this was more than 4 times the average of any other site. In 1992 recruitment was substantially lower and Nubble 1 had the highest density with an average of 3.6 (SE=.65) fish per transect. Thus a significant interaction between site and year was present for recruits as it was for adults and juveniles.

It was not possible to examine patterns of recruitment in Newfoundland since only 3 recruits were seen in 2 years. However, all of the recruits were observed at Bonne Bay, and this was the location with highest adult and juvenile abundance.

Temporal patterns of abundance. Temporal patterns of abundance were examined for 3 years at 7 sites in the Gulf of Maine. For adult cunner, spatial variation in abundance was more pronounced than interannual variability (Fig. 4-6). The analysis of variance thus identified site as a significant factor but not year (Table 4-5a). However, differences among sites were not consistent over time. In 1990 and 1991 the highest mean density of adults was at Nubble Point, but in 1992 the rank order of abundance changed and Appledore had the greatest density of adults (Fig. 4-6). Because adults were absent from 3 of the sites in each year of the study, we ommitted these sites and re-analyzed the data. The results from this analysis were qualitatively indentical to the original analysis with site indentified as a significant factor, but not year.

A similar pattern was apparent in juvenile cunner (Fig. 4-7). Variation among sites was pronounced so we could not detect a significant difference in abundance among years (Table 4-5b). There were, however, clear shifts in the rank order of abundance among years (Fig. 4-7), producinging a significant interaction between year and site (Table 4-5b).

In contrast to the patterns seen in adults and juveniles, variation in recruitment among years was pronounced while spatial variation was not as extreme (Fig. 4-8). Thus, we could detect significant differences in the density of recruits among years but not sites (Table 4-5c). Recruitment was ca. 15 times lower in 1992 than in either 1990 or 1991. For all 7 sites, 1992 was the year of lowest recruitment (Fig. 4-8). There were clear differences between 1990 and 1991 in the rank order of abundance of recruits. For instance, in 1990 the highest density of recruits occurred at Fort Point with an average of 32.93 (SE = 8.51) fish per transect. Yet in 1991, Fort Point had an average of 4.90 (SE = 1.13) fish per transect, which was significantly lower than 3 other sites (Bonferonni Test, $P < .05$; Fig. 4-8).

Causes of variation between and within geographic regions

Effects of variation of recruitment on variation in juvenile or adult abundances. In order to assess the effects of spatial variation in recruitment on variation in subsequent age classes, we regressed the mean number of recruits in 1990 against the number of juvenile fish in 1991 and the number of adults in 1992. Variation in recruitment among sites in 1990 was not expressed as variability in juvenile density in 1991 (Fig. 4-9). Also, variation in recruitment in 1991 was not reflected as variation of juveniles in 1992. Less than 2% of among-site variation in juvenile density was explained by recruit density in either 1991 or 1992. Likewise, in 1992 among-site variation in adult abundance was not associated with variation in recruitment in 1990 (Fig. 4-10). Additionally, juvenile density in 1991 was not expressed as variation in adult density in 1992.

Effects of habitat structure abundance

Topographic complexity. The topographic complexity of the substratum had no detectable effect on variation in numbers of recruits or of juveniles (r^2=.03, P= .51 for recruits; r^2=.09, p=.13 for juveniles). However, there was a significant effect of topographic complexity on adult density, and the effect differed between the Gulf of Maine and Newfoundland (Fig. 4-11, Table 4-6). In the Gulf of Maine there was a slight trend for increasing adult densities with increasing complexity ($r^2 = 0.19$; $P = 0.1$). In contrast there was a significant negative relationship between adult density and topographic complexity in Newfoundland (Fig. 4-11, Table 6). Indeed, more than 50% of the variation in adult abundance was explained by topographic complexity, and this pattern was consistent over time (Table 4-6).

Algal height. The relationship between algal height and the abundance of recruits, juveniles and adults was investigated in 1991 and 1992. Because most Newfoundland sites were dominated by crustose coralline algae (see below), we investigated the role of algal height only at Gulf of Maine sites. Variation among sites in algal height was not associated with variability in the abundances of recruits, juveniles nor adults (Fig. 4-12). The lack of association between algal height and fish density was consistent between years (Table 4-7).

Algal cover. Variation in coverage of kelp, branched algae and filamentous algae was associated with variation in the density of fish; however the nature of the relationship differed among age classes and geographic region. In Newfoundland there was no effect of algal cover of abundances of any age class, yet in the Gulf of Maine algal cover had a significant effect on among-site variation in abundance (Figs. 4-13, 4-14, 4-15).

Variation in branched algae appeared to have no influence of the density of adults (Fig. 4-13, Table 4-7a). In contrast, adult cunner were abundant in sites with a high coverage of foliose algae (Fig. 4-13, Table 4-7a). In addition there was a significant negative relationship between the abundance of adult cunner and the percent cover of kelp (Fig. 4-13).

The relationship between juvenile cunner and algae was complex. There was a significant positive relationship between cover of branched algae and juvenile density (Fig. 4-14, Table 4-7b), particularly during 1991. The relationship between foliose algae and juvenile density varied among years (Table 4-7b). A negative association was present in 1990, while a positive relationship existed in 1991, and in 1992 no association was apparent (Fig. 4-14). Consequently, no pattern of association between the cover of foliose algae and juvenile abundance was evident over all years (Table 4-7b). Additionally, no relationship between kelp cover and juvenile density was detected (Fig. 4-14, Table 4-7b).

Among-site variation in recruitment was not explained by the cover of foliose algae or kelp (Fig. 4-14, Table 4-7c). This pattern was consistent during the 3 years of the study (Table 4-8c). However, there was a strong relationship between the cover of branched algae and recruitment (Fig. 4-15, Table 4-7c). For example, in 1991, more than 70% of the among-site variation in recruitment could be explained by variability in the coverage of branched algae.

Effects of the supply of pre-settlement fish

Plankton tows were performed in the Gulf of Maine during 1991 and 1992 and during 1991 in Newfoundland. No larvae were captured in Newfoundland nor in the Gulf of Maine in 1992. However, 672 larval and post-larval cunner were captured in 78 tows in the Gulf of Maine during 1991.

In order to estimate at what size cunner were competent to settle, we examined the size frequency distribution of 659 new recruits collected in the middle of the settlement season. Fish ranged in size from 7.0 mm standard length to 24.6 mm with a mean of 12.1 (1.31 SE) (Fig. 4-16). We thus considered fish greater than 7.0 mm to be competent to settle.

Although the supply of pre-settlement cunner competent to settle varied during the settlement season (Fig. 4-17, Table 4-8), no clear temporal pattern emerged. In addition, the abundance of pre-settlement fish varied spatially both at the location and site scales. Significantly greater numbers of fish were captured at the Portsmouth Harbor location than at the Shoals location (Fig. 4-17, Table 4-8). The overall density of fish at Shoals was .02 m^3 (.004 SE) while in Portsmouth the density of pre-settlement fish was .58 m^3 (.14 SE). The interaction between location and date was not significant (Table 4-8), indicating that the pattern of high numbers of pre-settlement fish at the Portsmouth location was consistent throughout the settlement season.

There was also considerable variation between sites within locations (Fig. 4-17, Table 4-8). However, within each location, one site was not consistently higher than the other, producing a significant site-date interaction in the analysis. For example, on August 5, Ft. Point had significantly more fish than Ft. Foster (Fig. 4-17). However, 2 days later on the next sampling date, Ft. Foster had a higher abundance than Ft. Point.

DISCUSSION

Most experimental studies on the demography of reef fishes have necessarily been conducted on small spatial scales (e.g. Doherty 1983, Jones 1984, 1987, Carr, 1989, Forrester 1990, Wellington 1992, Hixon and Beets 1993, Levin1993), and models predicting the dynamics of populations of reef fishes have emerged largely from these small-scale studies (Doherty 1991, Jones 1991). The scale at which investigations are conducted, however, influences the patterns that emerge (Dayton and Tegner 1984, Wiens et al. 1986, Addicott et al. 1987, Menge and Olson 1990, Levin 1992). Moreover, no single mechanism is likely to explain patterns exhibited at different spatial scales (Levin 1992). Thus, the next phase of research on reef fishes must address how well models developed at small-spatial scales explain patterns observed at larger scales.

In this study there were clear differences between geographic regions in densities of recruits, juvenile and adult fish. Although far greater densities of adults were observed in Newfoundland, substantially lower densities of juveniles and virtually no recruits were observed there. The differences we observed between geographic regions were consistent between years. This consistency over time suggests that deterministic processes are functioning at the scale of geographic regions. Similarly the pattern of distribution of fish recruits in different geographic regions along the Great Barrier Reef (Doherty 1987, Fowler et al. 1992) and the southern California (Cowen 1985) appears to persist for several years.

The scale at which we detected variation abundances of fish varied between Newfoundland and the Gulf of Maine. We found significant variability only at the site scale for each age class in the Gulf of Maine, whereas variation was pronounced at both the site and location scales in Newfoundland. In both geographic regions and for each age class, there were significant time X space interactions. The significant interactions indicate that spatial patterns of abundance are not consistent through time. Variability in patterns of abundance of fish are the result of the interactions between the supply of larvae competent to settle, the response of settling larvae to habitat characteristics at a site, and the survivorship of individuals after settlement (Jones 1991). Changes among years in the relative abundances of fish requires that: 1) changes in the habitat of sites or locations make them more or less attractive to settling fish in different years; 2) changes in predator abundance alter the probability of a settling larva surviving to different age classes; or 3) interannual variability in larval supply is reflected as variability in subsequent age classes. The evidence for each of these possibilities is discussed below.

Is variation in the abundance of cunner the result of process occuring prior settlement?

Two lines of evidence suggest that pre-settlement processes are not the predominant processes affecting cunner populations in the Gulf of Maine. Our regression analyses examing the relationship between the density of recruits and older stages showed that less than 2% of the variability in juvenile density was predicted by recruitment. We examined patterns of abundance over time and found significant interannual variation in the densities of recruits; however, we could not detect significant temporal variation in adults or juveniles. Thus, it appears that temporally variable pulses of recruitment are sufficiently modified so that they are no longer apparent in older fish. In order for pre-settlement processes to influence population dynamics, population size should be dependent on levels of recruitment (Doherty 1983, Jones 1991). This was clearly not the case for this species.

Secondly, in the Gulf of Maine variability in the abundance of pre-settlement fish consistently occurred at the location scale, but this was not reflected as location-scale variation in the abundance of recruits, juvenile or adults. Moreover, the average density of pre-settlement fish at the Shoals location was 2 orders of magnitude lower than at the Portsmouth location, yet we did not detect a similar pattern for older fish. In fact, average densities of recruits in 1991 (the year plankton tows were conducted) were actually greater at the Shoals versus Portsmouth.

The situation in Newfoundland is clearly very different from the Gulf of Maine. Despite higher numbers of adults in Newfoundland than in the Gulf of Maine, we observed only 3 recruits in 2 years. In addition, preliminary data on the age structure of cunner populations in Newfoundland indicates that there has not been a substantial pulse of recruitment in 7 years (W. Chiasson, unpublished data). While a cautious interpretation of these data is required, it seems likely that episodic recuitment events are responsible for much of the variation we see in cunner populations in Newfoundland. The location-scale variation we observed in Newfoundland is consistent with the idea that pulses of pre-settlement fish are significant in producing patterns of abundance. We do not yet know how spatially or temporally variable these pulses are nor do we know the extent that these pulses are modified in different locations or sites. Further work monitoring these populations as well as detailed analysis of the age structure of the populations will be essential to demonstrate the significant of pre-settlement process in Newfoundland.

Is variation in abundance the result of post-settlement processes?

Patterns of cunner abundance in the Gulf of Maine were significantly affected by the biogenic structure of the habitat in this study as well as other studies (Levin 1991, 1993). Two alternative explanations of this pattern seem plausible. First, it is possible that fish select specific habitats at settlement. The use of specific microhabitats by reef fishes has been demonstrated both on tropical (Sale et al. 1984, Eckert 1985, Sweatman 1985, Booth 1992, Wellington 1992) and temperate reefs (Carr 1991 Levin 1991, 1993). Moreover, larger scale associations of reef fish with particular habitats are common (Jones 1988, Sale 1991, Ebeling and Hixon 1991).

However, small-scale patterns of abundance created by differential habitat use are not necessarily good predictors of larger scale patterns in cunner. For example, Levin (1991) found that newly settled cunner were associated with microhabitats dominated by filamentous and foliose algae. In a comparison of two sites in the Gulf of Maine separated by ca. 100m, he found that the site with far lower algal coverage had 3 times the density of recruits than the site with higher coverage. However, censuses conducted over the next two years showed that this pattern of recruitment was subsequently reversed such that more juveniles and adults were found in the site with higher algal cover (Levin 1993). Consequently, habitat selection per se did not produce the observed patterns of juvenile and adult abundance. Rather, it appears that differential moratlity in habitats of different patch structure was the mechanism producing abundance patterns of older fish. (Levin 1993). It should be noted, however, that both sites used by Levin in his comparison had relatively high levels of erect macroalgae (> 30%). Certainly, if sites have extremely low levels of plant cover, broad-scale selection of habitats by settling fish should be more important.

If the results of previous work on cunner are generalizable, it seems unlikely that habitat selection alone could explain patterns of association of cunner with algal structure. Another plausible explanation for this pattern is that modification of recruitment patterns varies among habitats of different structure. Habitat related differences in the availability of resources (Hixon and Beets 1989) or predation pressure (Shulman 1984, Beherents 1987, Connell and Jones 1991, Hixon and Beets 1993, Levin 1993) may effect the persistence of recruits at a site. Algal structure as been shown to affect the vunerability of young fish to predation within habitats (Carr 1991, Levin 1993); and predator abundance may vary among algal habitats (Carr 1991). In the Gulf of Maine sites mobile predators, particularly Pollock Pollachius virens, were abundant, and we often observed them foraging on cunner recuits. It thus seems probable that differences in algal structure within and among sites affected predator abundance and/or afforded recruits higher quality or more numerous shelter sites.

Our data for recruitment to Newfoundland populations of cunner are sparse, and thus we can draw only limited conclusions about the importance of post-settlement processes in this region. Predation by highly mobile predators on recruits is likely to be less important in Newfoundland than in the Gulf of Maine. Pollock prefer warmer waters (Scott and Scott), and we did not observe them at our Newfoundland study sites. No other highly mobile predators were observed at our Newfoundland sites. Adult mortality, however, may be of greater importance in Newfoundland than in the Gulf of Maine. Cunner enter a state of topor at temperatures below 5° C and overwinter in rock crevices within their home range (Green and Farwell 1971). If the size of overwintering shelters is small, larger adults may not survive the winter (J. Green pers. obs.). Moreover, large numbers of cunner (> 2000) have been killed following winter storms in which fish were dislodged from their shelters by wave action (M. Tupper, pers. comm., J. Green pers. obs). Thus at least at single locations, adult mortality may contribute significantly to fluctuations in the size of local populations.

The generality of population models for reef fishes

Variable replenishment of populations is characterisitic of both temperate (Sissenwine 1984, Cowen 1985, Jones 1988) and tropical (Doherty and Williams 1988, Doherty 1991). The process of settlement is a major event in the recruitment process, and it is not suprising that much attention has focussed on events occurring at or near the time of settlement (e.g. Doherty 1983, Victor 1983, 1986, Shulman 1984, Sale and Douglas 1984, Sweatman 1985, Jones 1987, 1990, Shulman and Ogden 1987, Forrester 1990, Carr 1991, Connell and Jones 1991, Fowler et al. 1992, Wellington 1992, Hixon and Beets 1993, Levin 1993). The paradigm that initially emerged from these studies is that many populations of reef fishes are generally undersaturated as a result of persistently low rates of settlement (Doherty and Williams 1988). Variability and intensity of rates of settlement were thought to be greater than that associated with post-settlement mortality. Consequently, rates of settlement were thought to be the leading determinant of subsequent population size.

This paradigm has been modified in favor of an approach which asks questions concerning the relative contribution of variations in settlement and post-settlement loss (Doherty 1991, Hixon 1991, Jones 1991). Answers to such questions, however, have varied among species (e.g. Victor 1986, Forrester 1990, Connell and Jones 1992, Wellington 1992, Hixon and Beets 1993, Levin 1993), and with the scale of investigation (Fowler et al. 1992). Consequently, we must ask how general models of the population dynamics of reef fishes are? Can the paradigm established largely in tropical systems be extrapolated to temperate or arctic zones? Or are we faced with the impracticable, ineffectual task of creating species or geographically specific models?

It is evident that models that are based solely on rates of settlement are too simple to adequately predict the dynamics of fish populations (Warner and Hughes 1988, Jones 1991). Models that include variable rates of both settlement and post-settlement loss are clearly necessary (Warner and Hughes 1988). However, the recent preoccupation with variability in settlement has lead to a paucity of information about processes occuring after settlement (Jones 1991). Recent mult-factor experiments have directed more attention to proceess occurring after settlement (Jones 1987, 1990, Forrester 1990, Connell and Jones 1991, Wellington 1992, Hixon and Beets 1993). These studies are the first step towards a more comprehensive understanding of population dynamics of fishes and future work that simultaneously examines settlement and post-settlement loss should be encouraged. Thus, generalizations concerning the dynamics of fish populations must await multi-factor descriptive and experimental studies that investigate both pre- and post-settlement processes. Moreover, studies on single species over a range of spatial or temporal scales are rare, and meaningful models of population dynamics should address process occurring at multiple scales (Levin 1992).

ACKNOWLEDGEMENTS

We thank the many people who offered advice on this project especially Peter Sale, T.P. Good, G.E. Forrester, D. Carlon and R.R. Warner. L.G. Harris, A.C. Mathieson, P.F. Sale and R.R. Warner provided many helpful comments the manuscript. Thanks also to the many divers who helped us, especially D. Carlon, T.P. Good, and L. Neveu who braved the frigid waters of Newfoundland just for fun. This research was supported by National Science Foundation Grant OCE-9102027 and National Geographic Society Grant 4625-91 to P.F. Sale and P.S. Levin.

Table 4-1. Analyes of variance on the densities of adult and juvenile cunner in Newfoundland versus the Gulf of Maine (region) in 1991 and 1992. Analyses were performed on log (X + 1) transformed data. *, **, *** indicates significance at the P < .05, .01, and .001 levels respectively.

A. Adults

Source	SS	df	MS	F
year	2.414	1	2.414	1.988
region	30.965	1	30.965	218.06***
year * region	0.142	1	0.142	0.117
error	458.970	378	1.214	

Table 4-1 continuted

B. Juveniles

Source	SS	df	MS	F
year	3.936	1	3.936	3.453
region	7.529	1	7.529	29.524***
year * region	1.140	1	1.140	4.505*
error	95.663	378	.253	

Table 4-2. Analyses of variance examining adult densities in 1991 and 1992 at different locations and sites in the Gulf of Maine and Newfoundland. Data were log transformed prior to analysis. *, **, *** indicates significance at the P < .05, .01, and .001 levels respectively.

A. Gulf of Maine

Source	SS	df	MS	F
year	.372	1	.372	.204
location	6.391	3	2.130	1.776
site{location}	4.794	4	1.199	4.594**
year * location	5.464	3	1.821	1.429
year * site{location}	5.097	4	1.274	4.881**
error	35.505	136	.261	

Table 2 continued

B. Newfoundland

Source	SS	df	MS	F
year	1.196	1	1.196	.257
location	218.331	5	43.666	12.079**
site{location}	21.689	6	3.615	5.562***
year * location	23.235	5	4.647	22.449**
year * site{location}	1.241	6	.207	.318
error	133.948	206	.65	

Table 4-3. Analyses of variance examining juvenile densities in 1991 and 1992 at different locations and sites in the Gulf of Maine and Newfoundland. Data were log transformed prior to analysis. *, **, *** indicates significance at the $P < .05$, .01, and .001 levels respectively.

A. Gulf of Maine

Souce	SS	df	MS	f
year	3.391	1	3.391	6.41
location	9.319	3	3.106	.599
site{location}	20.754	4	5.189	13.912***
year * location	1.587	3	.529	.466
year * site{location}	4.535	4	1.134	3.04*
error	50.775	136	.373	

Table 4-3 continued

<u>B. Newfoundland</u>

Source	SS	df	MS	F
year	.478	1	.478	3.208
locations	.745	5	.149	7.842*
site{location}	.114	6	.019	.032
year * location	.745	5	.149	7.842*
year * site{location}	.114	6	.019	.032
error	6.521	206	.599	

Table 4-4. Analysis of variance examining adult densities in 1991 and 1992 at different locations and sites in the Gulf of Maine. Only 3 recruits were observed in Newfoundland in both years of the study, thus no analysis was performed for this region. Data were log transformed prior to analysis. *, **, *** indicates significance at the P < .05, .01, and .001 levels respectively.

Source	SS	df	MS	F
year	56.439	1	56.439	6.813
location	28.273	3	9.424	.633
site{location}	59.494	4	14.874	26.656***
year * location	24.853	3	8.284	.597
year * site{location}	55.515	4	13.879	24.873***
error	75.941	136	.558	

Table 4-5. Analyses of variance of densities of adult, juvenile and newly recruited cunner in 1990-1993 for 7 sites in the Gulf of Maine. Data were log transformed prior to analysis. *, **, *** indicates significance at the $P < .05$, .01, and .001 levels respectively.

A. Adults

Source	SS	df	MS	F
site	23.605	6	3.934	3.068*
year	.263	2	.132	.103
site * year	15.387	12	1.282	5.477***
error	64.611	276	.234	

Table 4-5 continued

B. Juveniles

Source	SS	df	MS	F
site	56.969	6	9.495	3.543*
year	7.596	2	3.798	1.417
site * year	32.157	12	2.680	6.021***
error	122.844	276	.445	

Table 4-5. continued

C. Recruits

Source	SS	df	MS	F
site	135.765	6	22.628	1.494
year	186.356	2	93.178	6.152*
site * year	181.748	12	15.146	4.238***
error	1475.873	413	3.574	

Table 4-6. A two-factor analysis of covariance of the relationship between adult density and topographic complexity (complexity in the ANOVA table, see text for details) in 1991 and 1992, and in Newfoundland and the Gulf of Maine (region). When interaction terms were non-significant at P > .25 they were pooled with the error mean square (Underwood 1981).

Source	SS	df	MS	F
year	.469	1	.469	.03
region	408.724	1	408.724	25.71***
complexity	291.194	1	291.194	18.317***
region * complexity	388.203	1	388.203	24.419***
error	349.739	22	15.897	

Table 4-7. The results of multple analyses of covariance examining the effects of average percent coverage of branching algae, kelps, and foliose algae on the mean densities of adult, juvenile and newly recruited cunner in 1990-1993. Only sites from the Gulf of Maine were used in this analysis because most Newfoundland sites on very sparse algal coverage. When interaction terms were non-significant at $P > .25$ they were pooled with the error mean square (Underwood 1981). Transect counts of fish were log transformed and percent cover data were arcsine transformed. Data were log transformed prior to analysis. *, **, *** indicates significance at the $P < .05$, .01, and .001 levels respectively.

A. Adults

Source	SS	df	MS	F
year	2.384	2	1.192	3.832*
branched algae	.033	1	.033	.106
kelp	3.089	1	3.089	9.932**
foliose algae	1.684	1	1.684	5.413*
error	4.666	15	.311	

Table 4-7. continued

B. Juveniles

Source	SS	df	MS	F
year	6.225	2	3.112	7.680**
branched algae	2.502	1	2.502	6.172*
kelp	.117	1	.117	.289
foliose algae	.147	1	.147	.362
year * foliose algae	3.552	2	1.776	4.382*
error	5.269	13	.405	

Table 4-7 continued

C. Recruits

Source	SS	df	MS	F
year	3.753	2	1.876	30.270***
branched algae	2.664	1	2.664	42.9777***
kelp	.176	1	.176	2.840
foliose algae	.0002	1	.0002	.004
error	.992	16	.062	

Table 4-8. An analysis of variance of the abundance of pre-settlement cunner on 6 sampling dates in 1991 at 2 sites nested within each of 2 locations. Data were log transformed prior to analysis. *, **, *** indicates significance at the $P < .05$, .01, and .001 levels respectively.

Source	SS	df	MS	F
date	23.203	5	4.641	.0655
location	70.823	1	70.823	20.624*
site{location}	6.869	2	3.434	3.451*
date * location	19.846	5	3.969	.876
date * site{location}	45.316	10	4.532	4.554***
error	47.769	48	.995	

Figure 4-1. The mean number of adult cunner on 15 X 1m strip transects in the Gulf of Maine is plotted for sites (e.g. Boon 1 and Boon 2) nested within locations (e.g. Boon 1 and 2 are a single location) in 1991 and 1992. ANOVA revealed that variation was most pronounced at the scale of site (table 4-2). Error bars are 1 standard error.

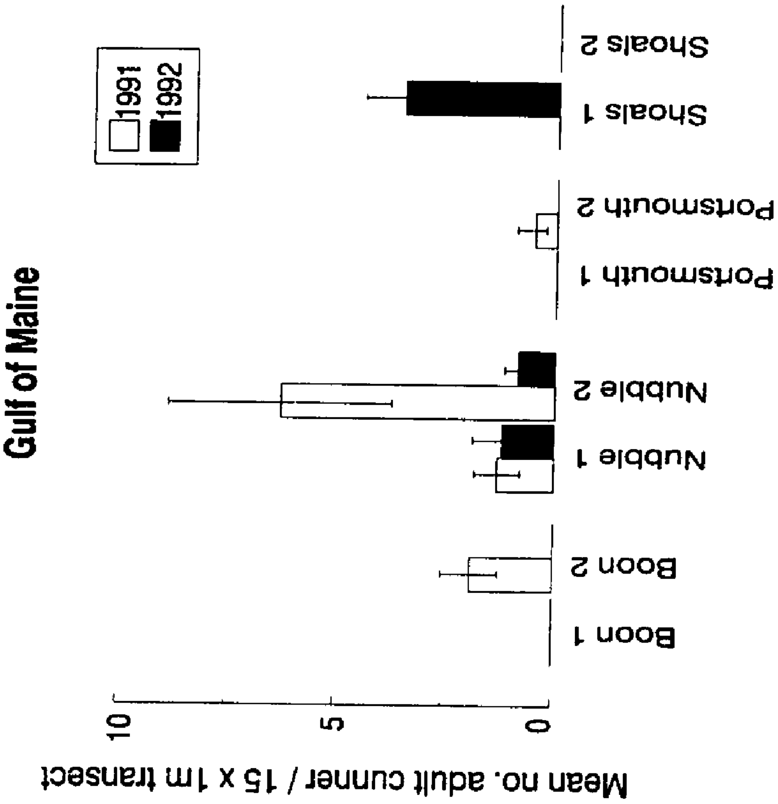

Gulf of Maine
1991
1992
Boon 1
Boon 2
Nubble 1
Nubble 2
Portsmouth 1
Portsmouth 2
Shoals 1
Shoals 2
0
5
10
Mean no. adult cunner / 15 x 1m transect

Figure 4-2. The mean number of adult cunner on 15 X 1m strip transects in Newfoundland is plotted for sites nested within locations in 1991 and 1992. Designation of sites and locations is the same as in figure 4-1. ANOVA revealed that variation was pronounced at both site and location scales (table 4-2). Error bars are 1 standard error.

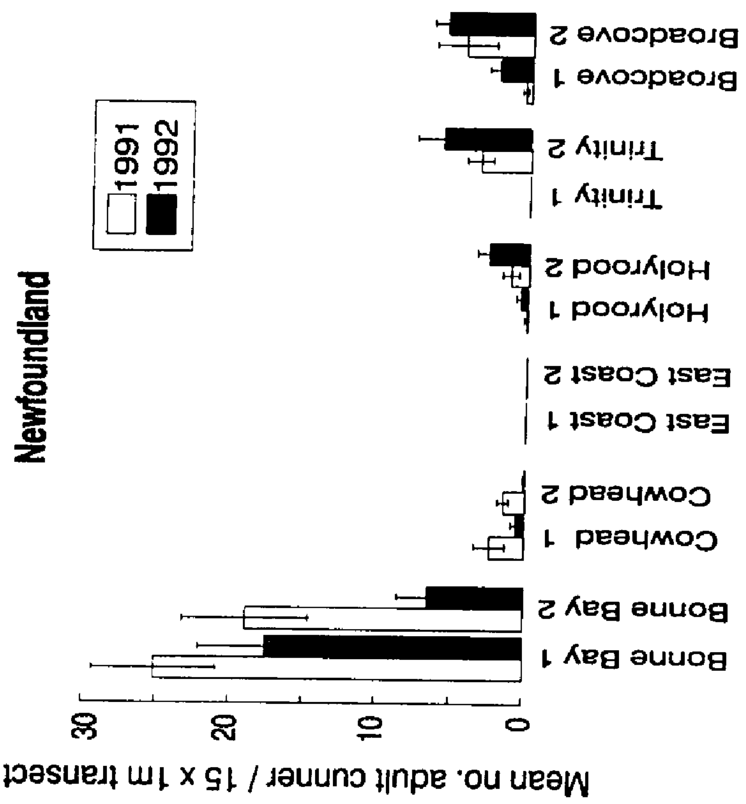

Newfoundland
1991
1992
Mean no. adult cunner / 15 x 1m transect
0
10
20
30
Bonne Bay 1
Bonne Bay 2
Cowhead 1
Cowhead 2
East Coast 1
East Coast 2
Holyrood 1
Holyrood 2
Trinity 1
Trinity 2
Broadcove 1
Broadcove 2

Figure 4-3. The mean number of juvenile cunner on 15 X 1m strip transects in the Gulf of Maine is plotted for sites nested within locations in 1991 and 1992. Designation of sites and locations is the same as in figure 4-1. ANOVA revealed that variation was pronounced at scale of site (table 4-3). Error bars are 1 standard error.

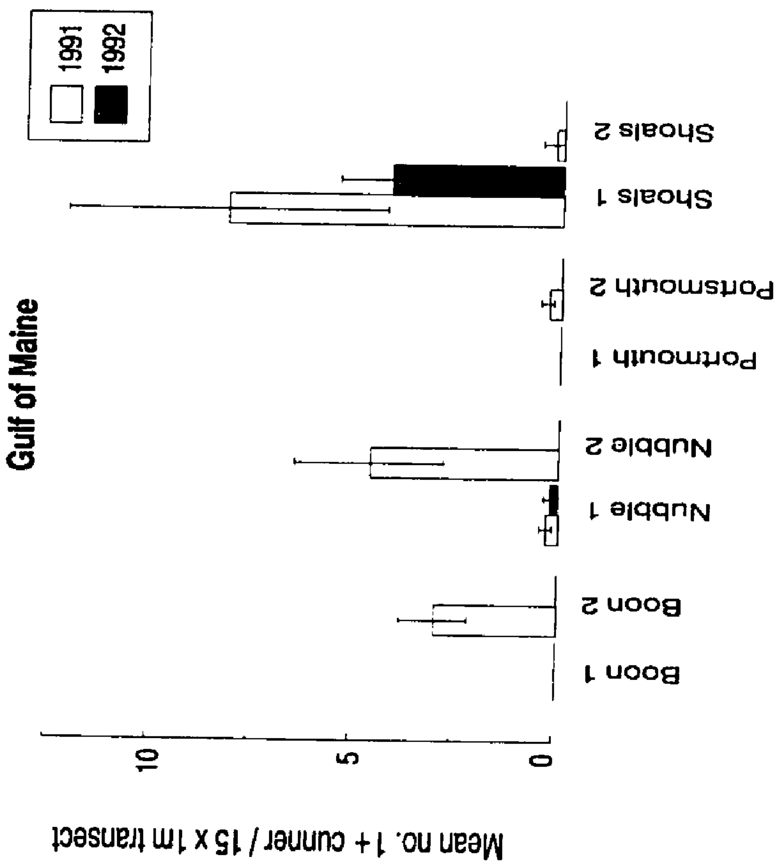

Gulf of Maine
1991
1992
Mean no. 1+ cunner / 15 x 1m transect
0
5
10
Boon 1
Boon 2
Nubble 1
Nubble 2
Portmouth 1
Portsmouth 2
Shoals 1
Shoals 2

Figure 4-4. The mean number of juvenile cunner on 15 X 1m strip transects in Newfoundland is plotted for sites nested within locations in 1991 and 1992. Designation of sites and locations is the same as in figure 4-1. ANOVA revealed that variation was pronounced at both site and location scales (table 4-3). Error bars are 1 standard error.

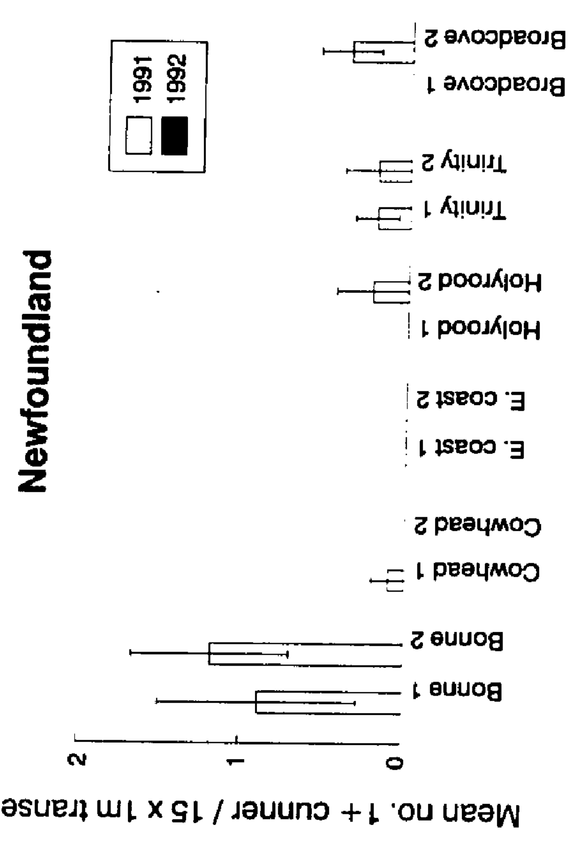

Newfoundland
□ 1991
■ 1992
Mean no. 1+ cunner / 15 x 1m transect
0
1
2
Bonne 1
Bonne 2
Cowhead 1
Cowhead 2
E. coast 1
E. coast 2
Holyrood 1
Holyrood 2
Trinity 1
Trinity 2
Broadcove 1
Broadcove 2

Figure 4-5. The mean number of cunner recruits on 15 X 1m strip transects in the Gulf of Maine is plotted for sites nested within locations in 1991 and 1992. Designation of sites and locations is the same as in figure 4-1. ANOVA revealed that variation was pronounced at scale of site (table 4-4). Error bars are 1 standard error.

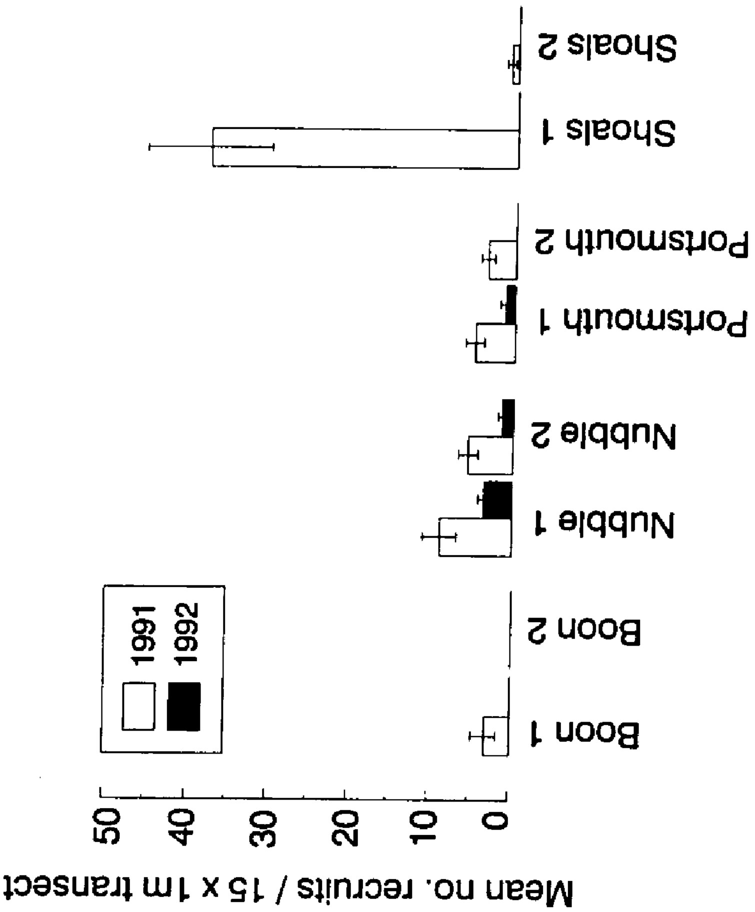

Mean no. recruits / 15 x 1m transect
0
10
20
30
40
50
1991
1992
Boon 1
Boon 2
Nubble 1
Nubble 2
Portsmouth 1
Portsmouth 2
Shoals 1
Shoals 2

Figure 4-6. The mean density of adult cunner is plotted for 3 years at 7 sites in the Gulf of Maine. ANOVA detected significant spatial variability but not significant temporal variation (table 4-5). Error bars are 1 standard error.

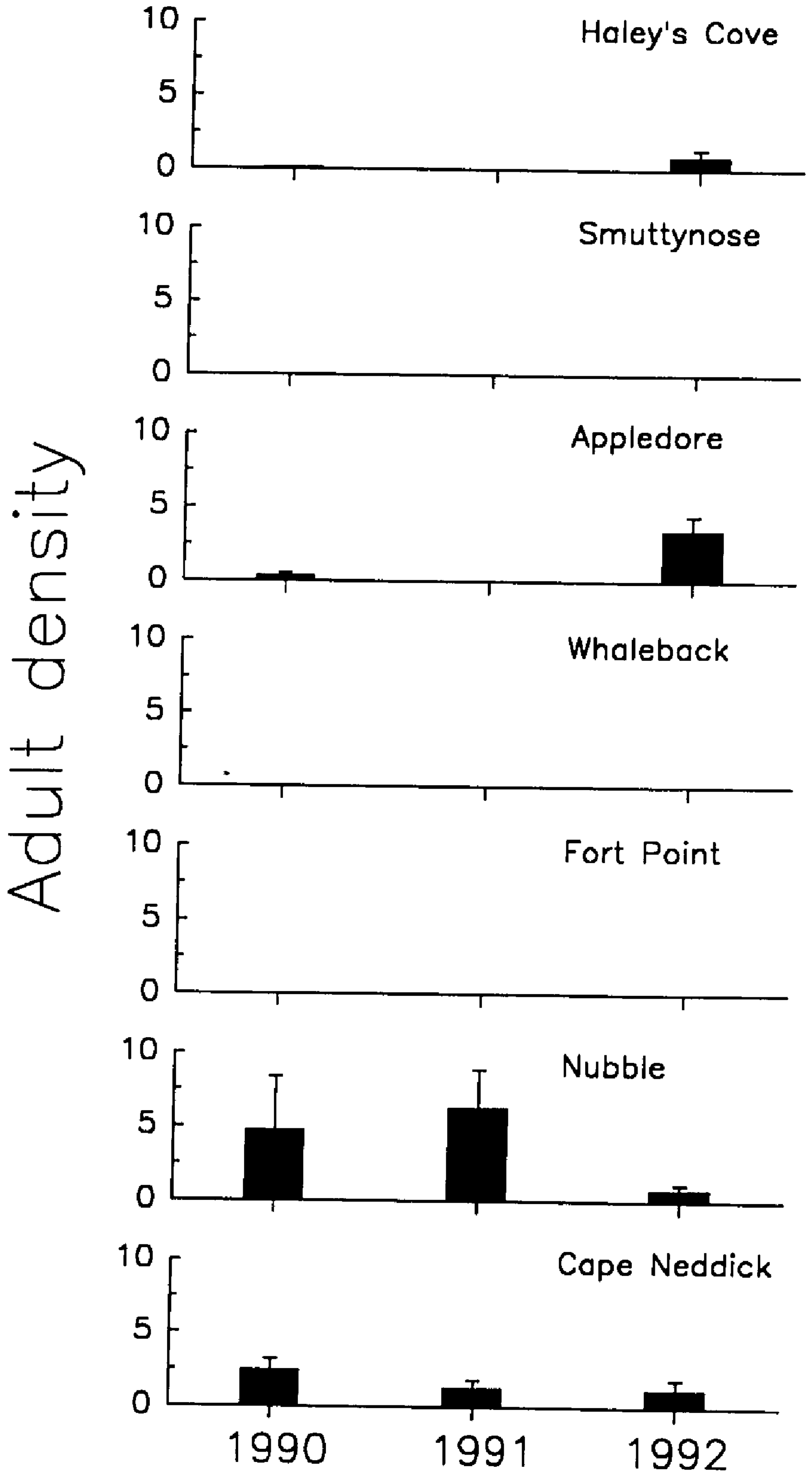

Adult density
10
5
0
Haley's Cove
Smuttynose
Appledore
Whaleback
Fort Point
Nubble
Cape Neddick
1990
1991
1992

Figure 4-7. The mean density of juvenile cunner is plotted for 3 years at 7 sites in the Gulf of Maine. ANOVA detected significant spatial variability but not significant temporal variation (table 4-5). Error bars are 1 standard error.

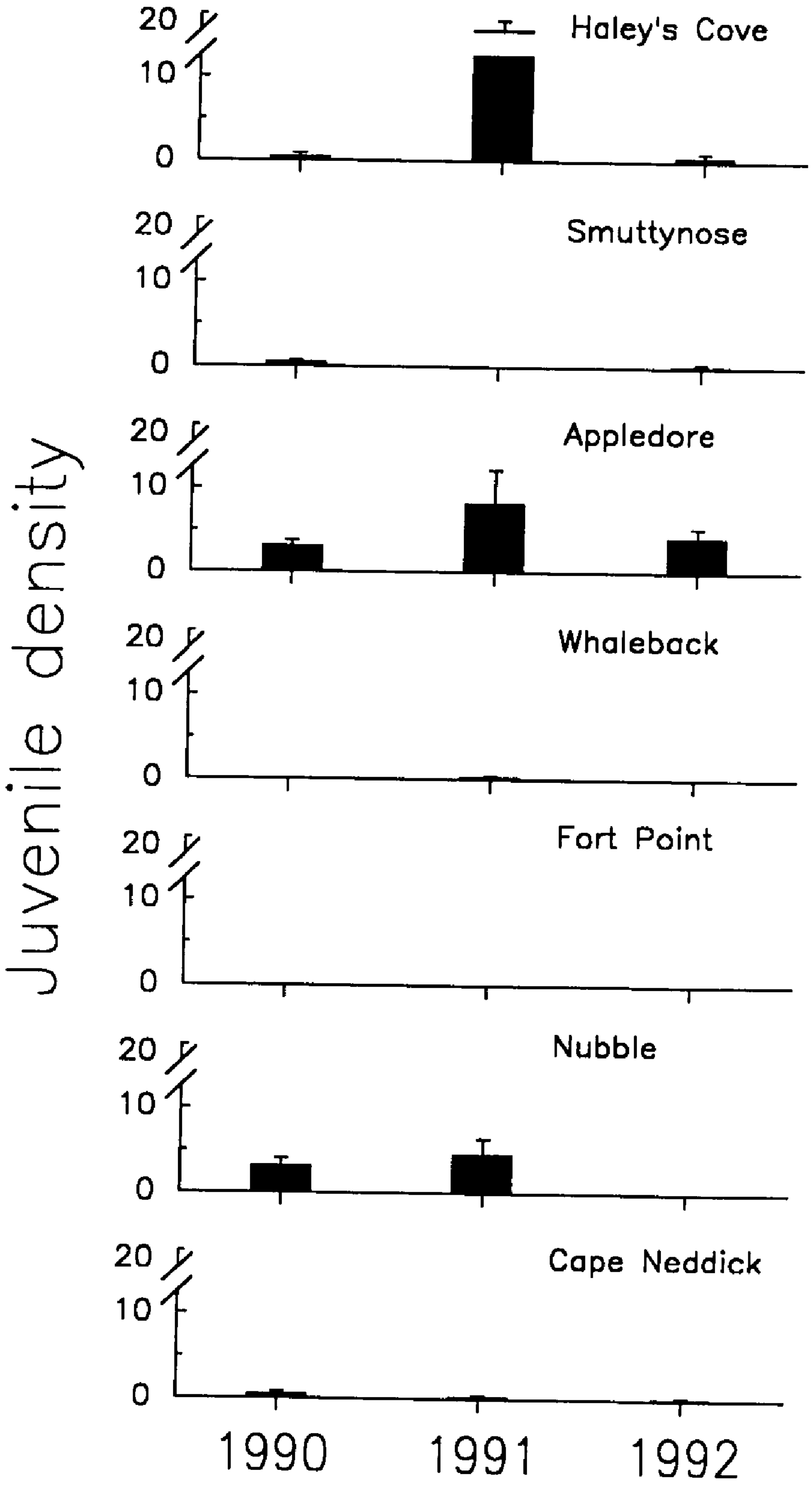

Juvenile density
20
10
0
Haley's Cove
Smuttynose
Appledore
Whaleback
Fort Point
Nubble
Cape Neddick
1990
1991
1992

Figure 4-8. The mean density of newly recruited cunner is plotted for 3 years at 7 sites in the Gulf of Maine. In contrast to the pattern observed for adults (Fig. 4-6) and juveniles (Fig. 4-7). ANOVA indicated that there was significant temporal variation, but we were unable to detect significant spatial variation. Error bars are 1 standard error.

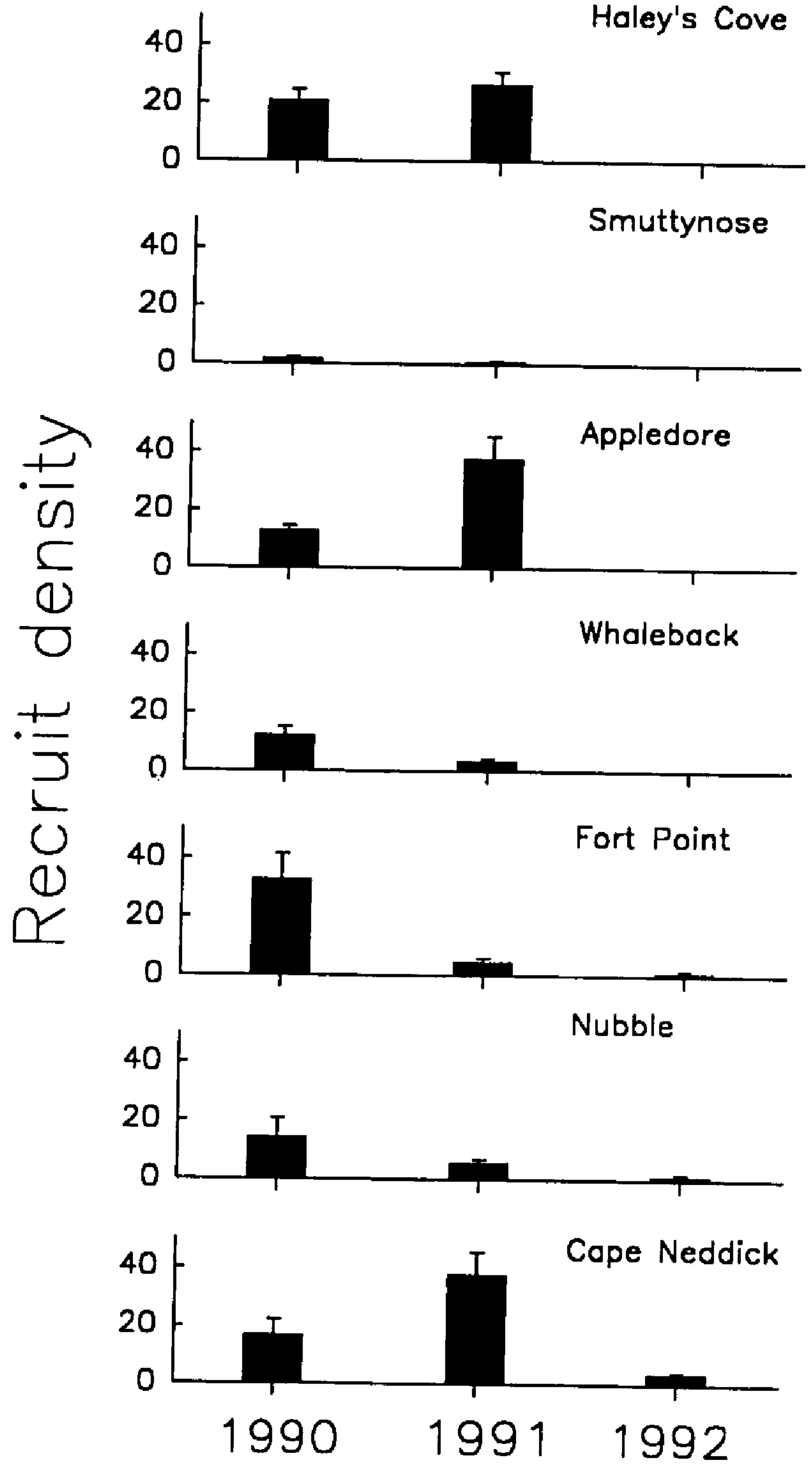

Recruit density
Haley's Cove
Smuttynose
Appledore
Whaleback
Fort Point
Nubble
Cape Neddick
40
20
0
1990
1991
1992

Figure 4-9. The average density of juveniles at each of 7 sites in the Gulf of Maine is plotted against the average recruit density at the same sites. Variation in recruitment was not reflected as subsequent variation in juvenile density.

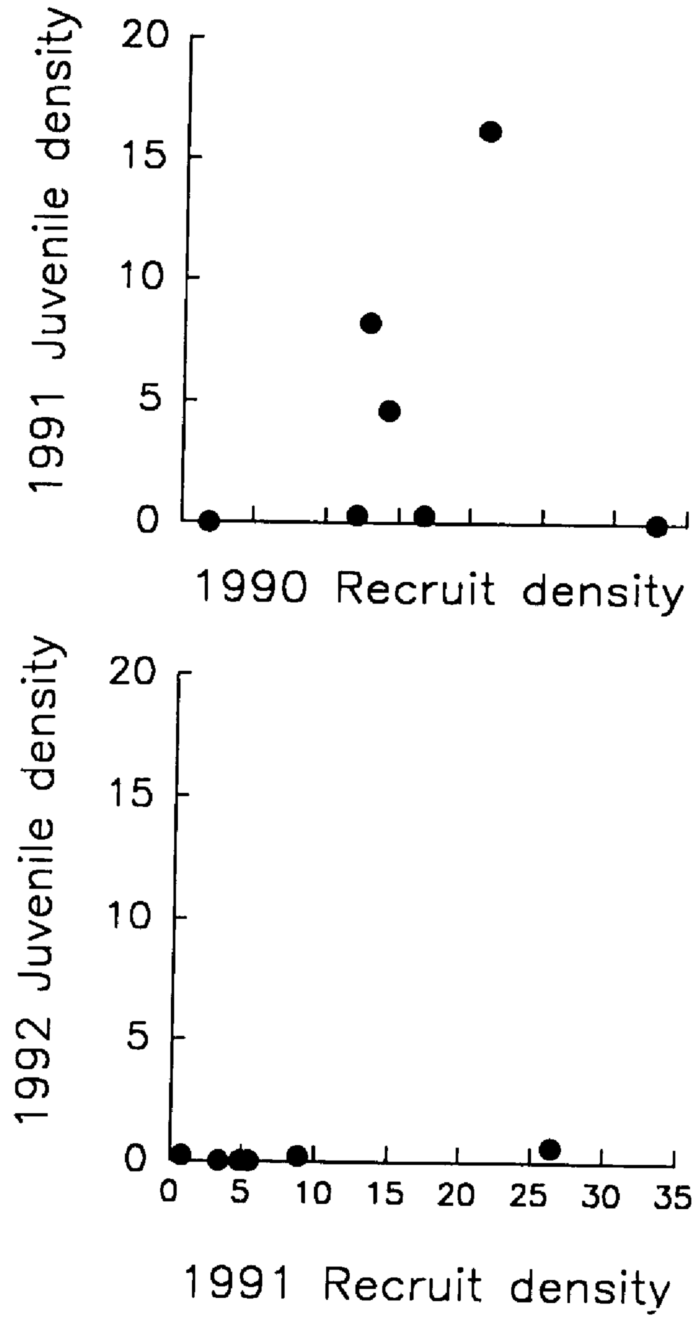
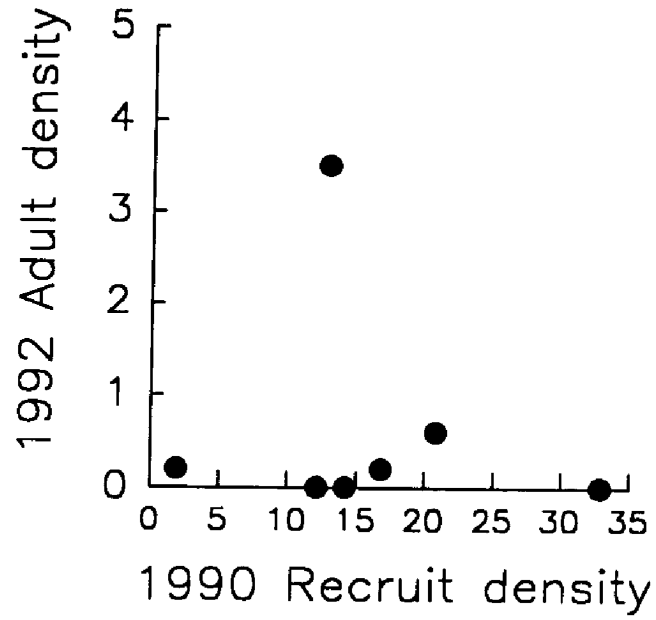

1991 Juvenile density
20
15
10
5
0
1990 Recruit density
1992 Juvenile density
20
15
10
5
0
0
5
10
15
20
25
30
35
1991 Recruit density

Figure 4-10. The average density of adult cunner is plotted against the average density of recruits 2 years earlier and the average density of juveniles in the previous year. Neither variation in recruitment nor juvenile density was reflected as variation in subsequent adult density.


1992 Adult density
5
4
3
2
1
0
0
5
10
15
20
25
30
35
1990 Recruit density

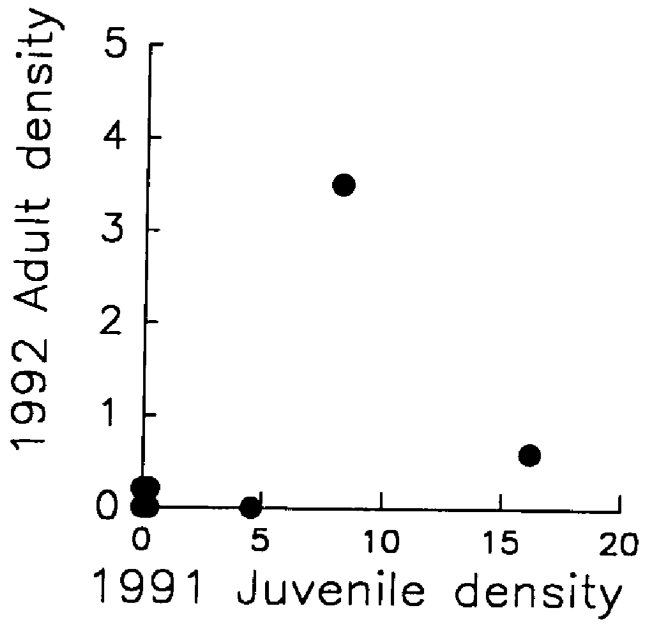

1992 Adult density
5
4
3
2
1
0
0
5
10
15
20
1991 Juvenile density

Figure 4-11. The average density of adult cunner at sites in the Gulf of Maine and Newfoundland is plotted against the mean index of topographic complexity for those same sites. Topographic complexity of the substratum increases with increasing values of the index (see text for details). The relationship between adult density and the topographic complexity of the substratum was not significant in the Gulf of Maine; however, there was a significant negative relationship in Newfoundland.

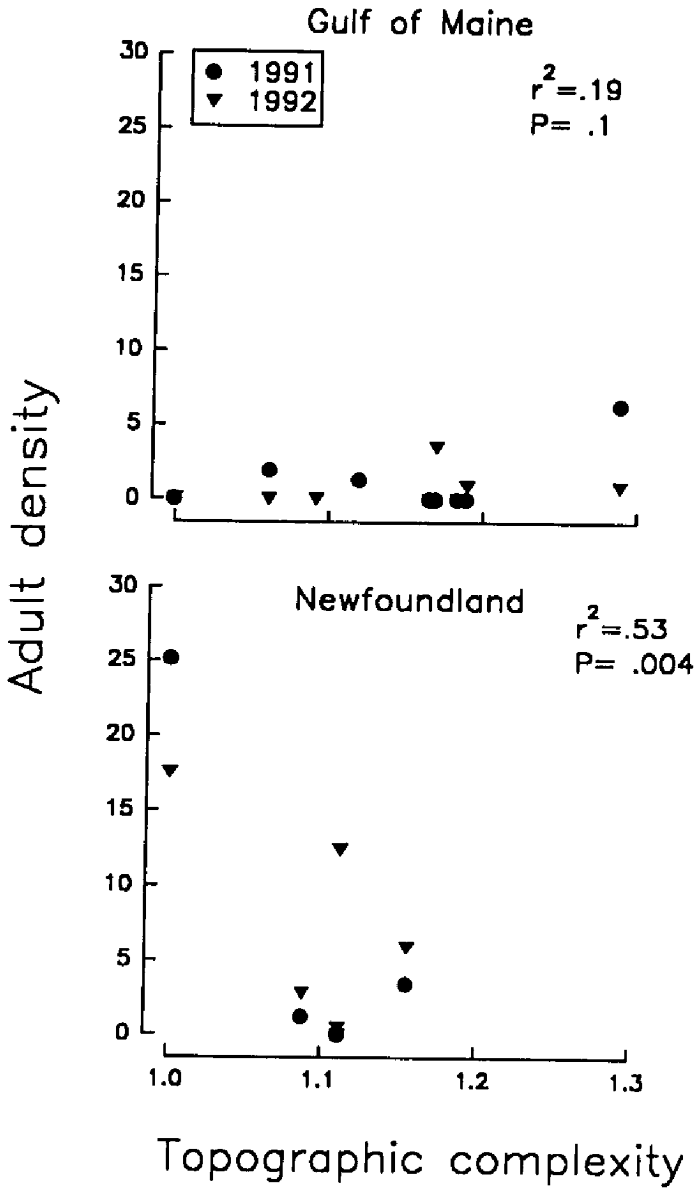

Gulf of Maine
● 1991
▼ 1992
r^2=.19
P= .1
Newfoundland
r^2=.53
P= .004
30
25
20
15
10
5
0
1.0
1.1
1.2
1.3
Adult density
Topographic complexity

Figure 4-12. The mean density of recruits, juveniles and adults at sites in the Gulf of Maine are plotted against the average height of algae at those sites. The relationship was not significant for recruits ($F_{1,11}$=.580), juveniles ($F_{1,9}$=.521) or adults ($F_{1,10}$=.764).

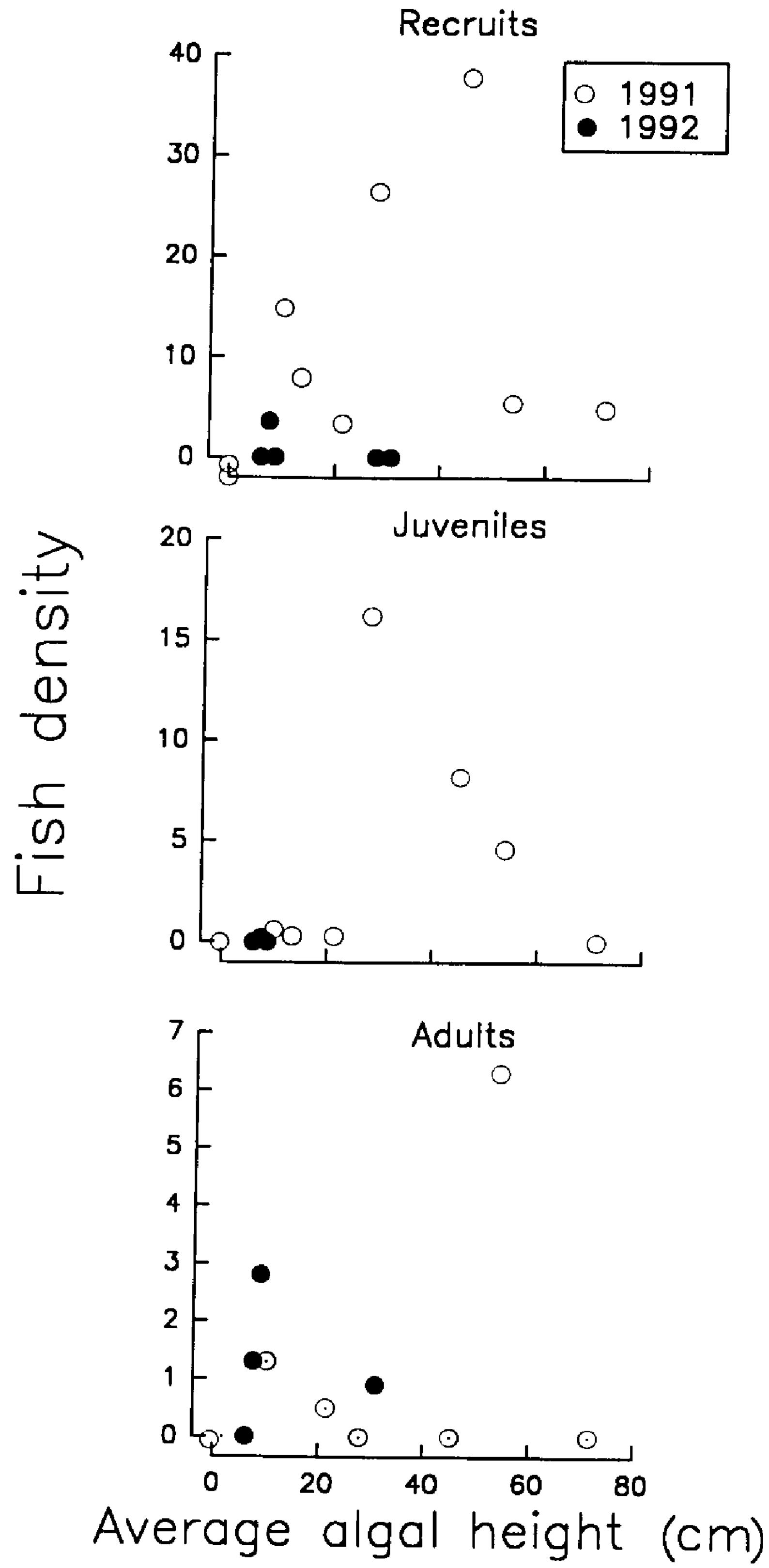

Recruits
40
30
20
10
0
○ 1991
● 1992
Juveniles
20
15
10
5
0
Adults
7
6
5
4
3
2
1
0
0
20
40
60
80
Fish density
Average algal height (cm)

Figure 4-13. Mean adult cunner densities at sites in the Gulf of Maine are plotted against the average percent coverage of branched algae, foliose algae and kelp in 1990-1992. The relationships between adult density and branched and foliose algae were not significant. There was a significant negative relationship between kelp cover and adult density (table 4-7).

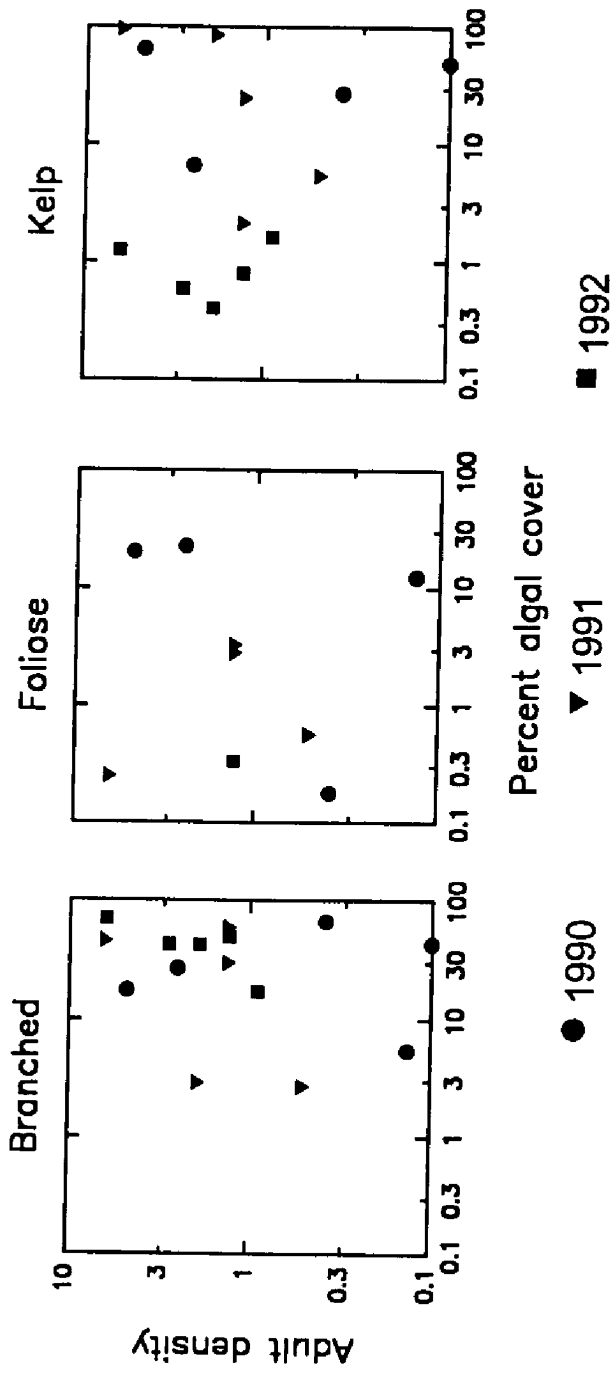

Branched
Foliose
Kelp
Adult density
10
3
1
0.3
0.1
0.1 0.3 1 3 10 30 100
Percent algal cover
● 1990
▼ 1991
■ 1992

Figure 4-14. Mean juvenile cunner densities at sites in the Gulf of Maine are plotted against average percent coverage of branched algae, foliose algae and kelp in 199-1992. The relationships between juvenile density and foliose algae and kelp were not significant. However, there was a significant relationship between juvenile density and the cover of branched algae, particularly in 1991 (table 4-7)

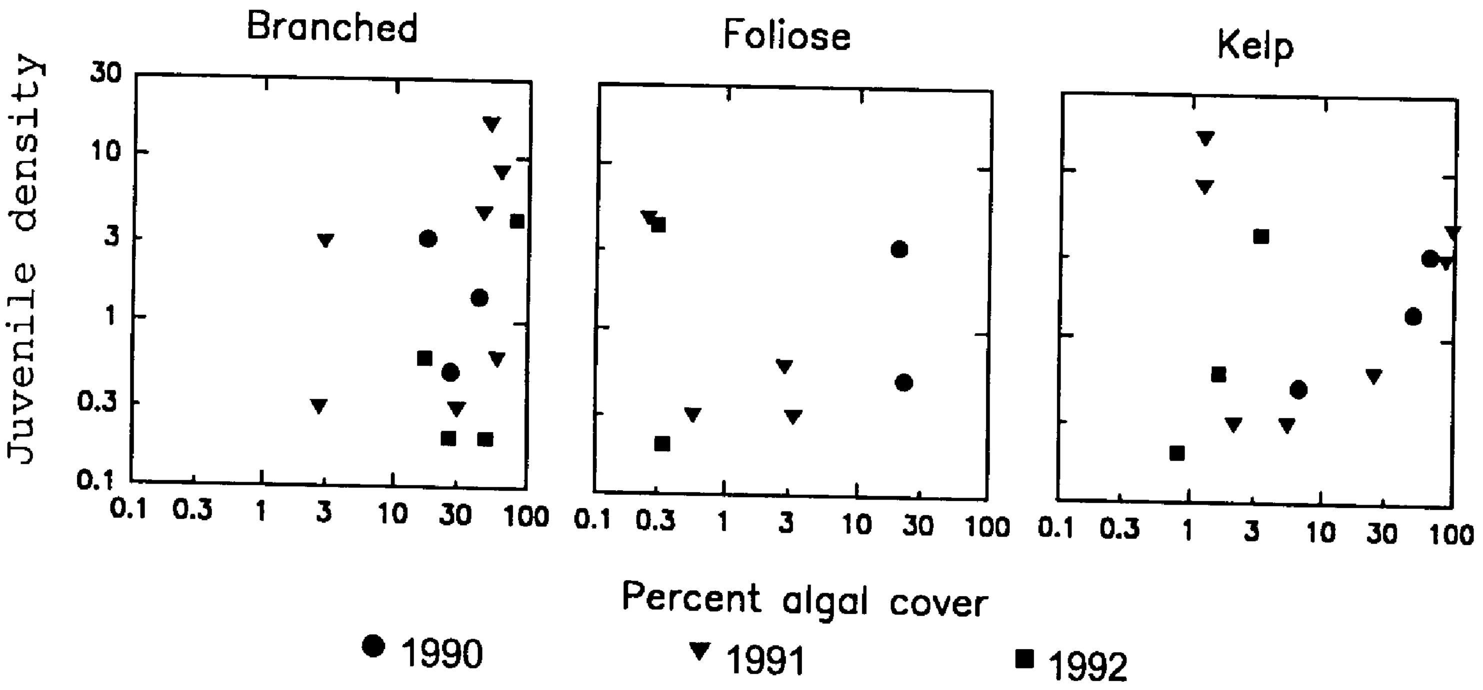

Branched
Foliose
Kelp
Juvenile density
30
10
3
1
0.3
0.1
0.1
0.3
1
3
10
30
100
Percent algal cover
● 1990
▼ 1991
■ 1992

Figure 4-15. Mean densities of newly recruited cunner n the Gulf of Maine are plotted against average percent coverage of branched algae, foliose algae and kelp in 199-1992. The relationships between recruit density and foliose algae and kelp were not significant. However, there was a significant relationship between recruit density and the cover of branched algae (table 4-7).

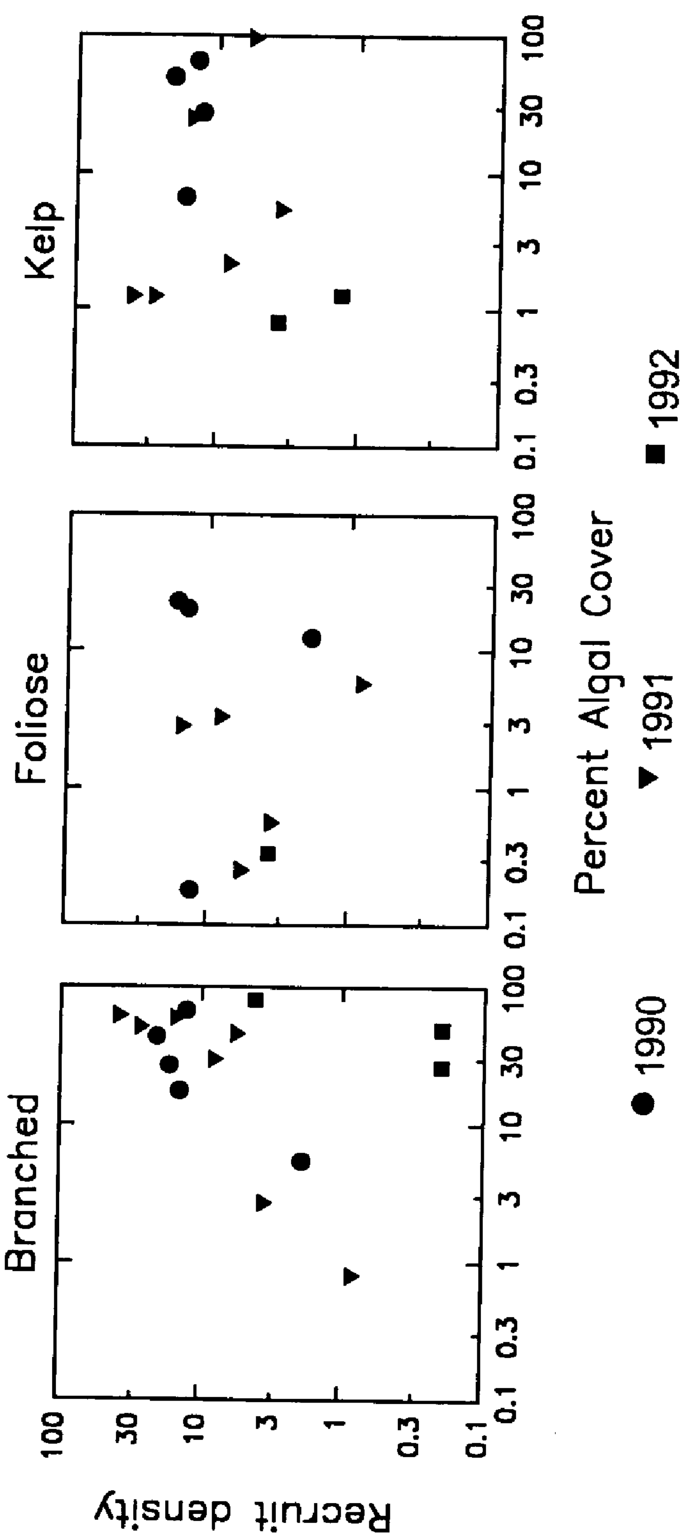

Branched
Foliose
Kelp
Recruit density
100
30
10
3
1
0.3
0.1
Percent Algal Cover
0.1
0.3
1
3
10
30
100
● 1990
▼ 1991
■ 1992

Figure 4-16. A length frequency histogram of newly recruited cunner captured in the demersal habitat in 1989. The mean standard length of cunner from this collection was 12.1 mm (1.31 SE). We used these data to conclude that fish > 7mm in standard length were competent to settle.

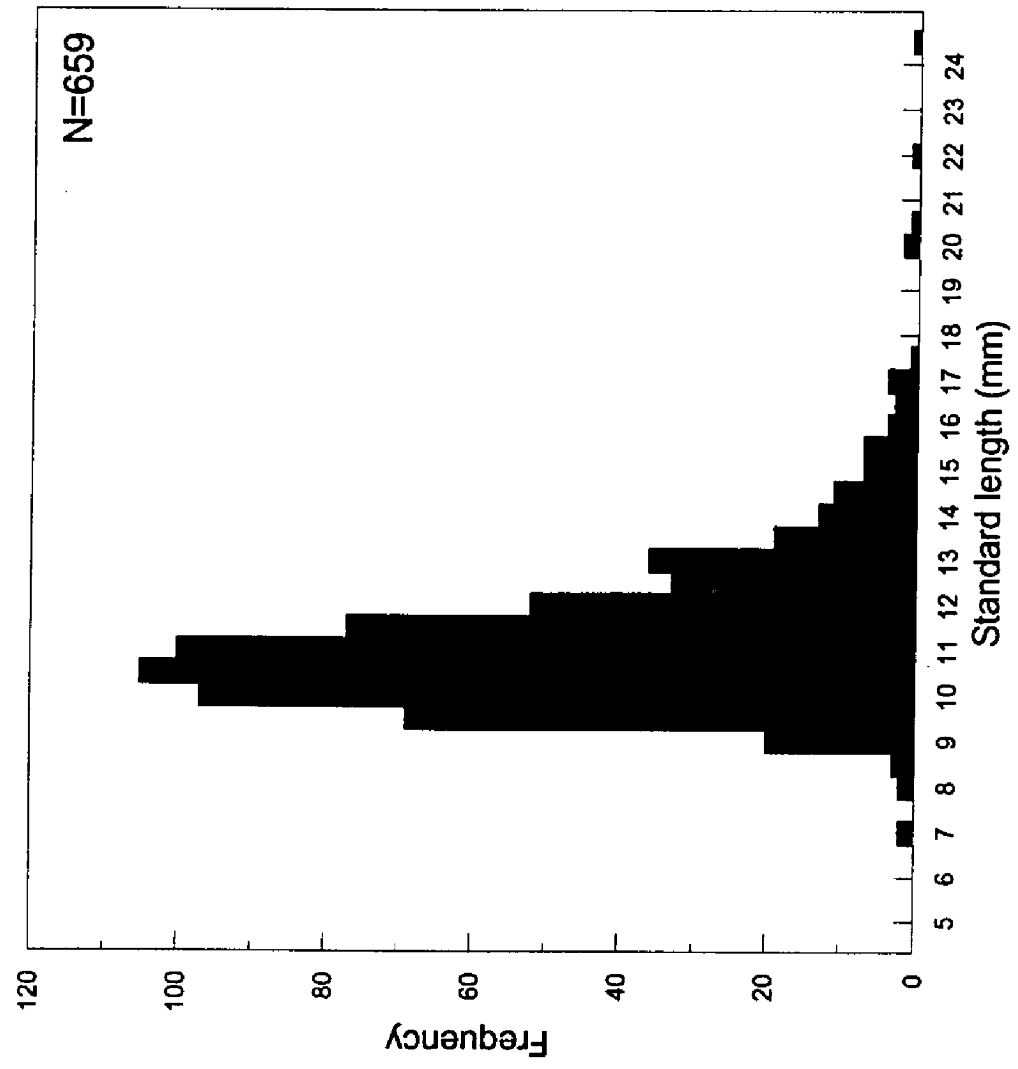
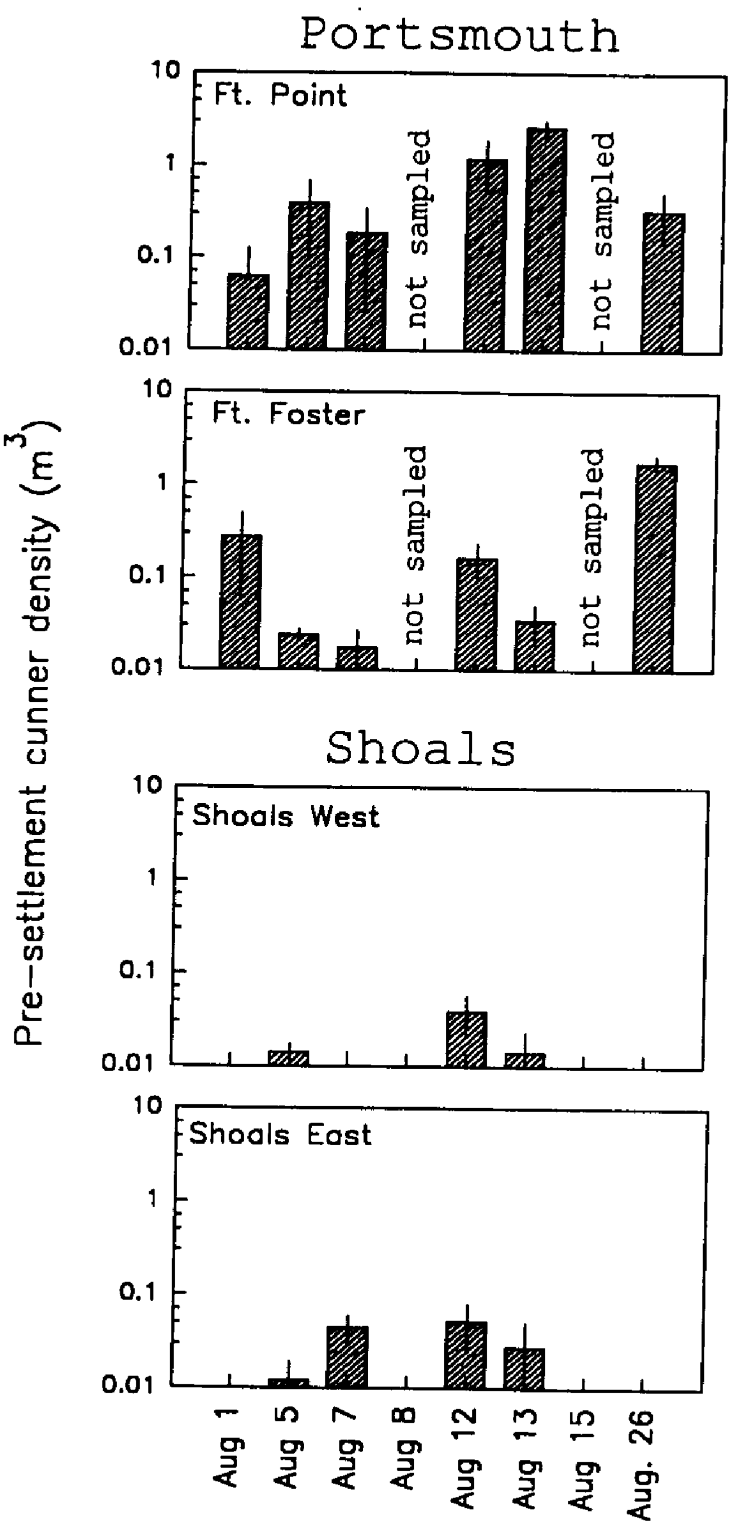

N=659
Frequency
0
20
40
60
80
100
120
Standard length (mm)
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

Figure 4-17. The mean density of pre-settlement cunner collected from replicate (n=3 per date) 10 minute plankton tows is plotted for 2 sites within each of 2 locations for 8 dates in 1991. There were consistently more fish at the Portsmouth location than the Shoals location.


Portsmouth
Ft. Point
Ft. Foster
Shoals
Shoals West
Shoals East
not sampled
Pre-settlement cunner density (m^3)
10
1
0.1
0.01
Aug 1
Aug 5
Aug 7
Aug 8
Aug 12
Aug 13
Aug 15
Aug. 26

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