

A Review of the Present State of Understanding of Marine Fish Communities

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Abstract

A review of recent literature reveals the problems of perspective on explaining the dynamics of marine fish communities. While tropical reef systems have been examined generally from the small spatial scales such as patch reefs or individual fishes, temperate and boreal systems have generally been observed at very large scales, for example over large tracts of the continental shelf. Neither approach has been totally satisfactory in explaining variations in population and community structures and dynamics. Progress and methods of these two types of studies are discussed.

Introduction

Current fisheries and ecological literature reveal a wide variety of investigations focusing on structuring factors of fish communities. Ecologists are presently debating the importance of relatively deterministic biotic interactions as factors that limit the distribution and abundance of marine organisms in general and fishes in particular. These diverse investigations revolve around the concept of competitive interactions for limiting resources which in turn provide structure to communities. Some studies provide supportive data, while in others, evidence is often circumstantial, contradictory, or lacking. The time seems right to review the history of community studies. The objectives of this paper are to (1) review a historical progression of literature regarding community studies which elucidate our current state of knowledge, and (2) examine the effects of scale and methodological approaches in studies which had opposing conclusions regarding processes affecting community structure and dynamics.

Historical Perspective

Biologists from the late 1800s and early 1900s interpreted data suggesting that some type of underlying principle structured assemblages of organisms (Steere, 1894; Grinnell, 1904). Mathematical models were subsequently developed which demonstrated that for pairs of species utilizing a finite resource, the availability of the resource limited population size (Haldane, 1924; Lotka, 1932) and if competition continued through time, one species population would become extinct. Experiments such as those by Gause *et al.* (1934) provided evidence that the simple model predictions were accurate at least under laboratory conditions. Gause (1934) took the Malthusian population theory and applied it to the next greater level of ecologi-

cal complexity — the community. This neo-Malthusian theory is based on a deterministic density-dependent population model. Gause (1934) and Hardin (1960) also defined the concept of the niche more exactly such that species do not occupy exactly the same niche space but exhibit some displacement along certain resource axes where some species would have a competitive advantage over others.

Basic community theory is based on the assumption that as populations grow, at least one resource is depleted to a point where shortages produce competitive interactions between and within species. That is, competition is a density-dependent phenomenon. With this neo-Malthusian theory in hand, biologists set about collecting data to support it. They were able to collect data on community structure and interpret the structure to be the cause of competitive interactions (Hutchinson, 1959).

Interpretation of the concept of the niche led to another inference, that speciation events were caused by competition between diverging populations and resulted in the species which comprise present communities (Schoener, 1974). The point being that one can sample a community, determine the niches of each of the component species along one or several resource axes, and assume that competition keeps each species in a well-defined niche. The next step is to provide proof of present or ongoing competitive interactions. The question is, are the data on resource partitioning the result of morphological and behavioral limitations imposed by historic speciation events (Connell, 1980)? Biologists are now examining diverse types of communities to determine whether competition is a structuring force or a remnant interaction. Strong *et al.* (1984) presented an extensive review and a discussion on the current problems.

A question of compromise also exists. Do any communities exist at levels where component populations remain at low densities so that competitive interactions do not determine their structure? Such populations may only exhibit competitive mediation occasionally when population numbers increase but interactions would limit potential increases and maintain them at non-competitive levels.

Many recent community studies center on the role of competition as a cause of pattern in resource utilization, distribution, and relative abundance of an animal species. Tests for competition are often indirect (e.g. removal experiments, comparisons of resource utilization of two species where distributions do not overlap), yielding data with patterns consistent with competition theory. Other possible explanations may well exist.

Direct tests are difficult and of undetermined value because they require "reductionist" tactics. This tactic of examining communities also requires the investigator to look at only a few species when communities require a holistic approach. Communities and their resources are not amenable to direct manipulation. Literature commonly requests hypothesis testing of competition with direct field experiments (Connell, 1974, 1975; Weins, 1977; and others).

Finally, with data regarding community structure and change, ecologists look for recurrent, predictable patterns with which to construct community models. Accurate models would be of great use to resource managers and ecologists, there are, however, inherent problems with models. For example, communities with similar taxonomic components may behave similarly, while communities from different geographic regions or with different structuring factors may behave differently. At present, no complete model exists.

The following sections dealing with tropical reef and boreal systems, review selected literature which illucidate our current knowledge of marine fish community systems and discuss problems inherent to various research approaches and our interpretation of data.

Tropical Reef Systems

The study of tropical marine reef fish communities is relatively recent compared to other aquatic and terrestrial systems. Bardach (1959) and Randall (1961, 1963, 1965) pioneered studies of reef fish as ecological groupings and examined the role of habitat and environment on community structure.

At the time these early marine investigations were in progress, terrestrial studies had already hypothesized patterns which would exist in tropical environments. The predicted patterns were that tropical

systems were highly diverse, equilibrial in nature, and competitively organized; the diversity being achieved by narrow partitioning or large overlap of resources by component species (MacArthur, 1965, 1969; Paine, 1966; Pianka, 1966; and others).

Odum and Odum (1955) and Hiatt and Strasburg (1960) described the ecosystem at Eniwetok Atoll in the South Pacific as a stable, equilibrium system with a biotic component which is competitively structured under constant environmental conditions. The same conclusions have been drawn from more recent work (Gladfelter and Gladfelter, 1978; Molles, 1978; Smith, 1978). Investigators then developed hypotheses to explain underlying mechanisms for these apparent patterns. Two examples are stability-time (Sanders, 1969) and predator mediated co-existence (Paine, 1966).

Subsequent studies elucidated aspects of competitive structuring mechanisms through resource limitation and partitioning. Tropical fishes have specialized species-specific space resource requirements, hence space resources are probable limiting factors for fish populations (Ebersole, 1977; Gladfelter and Gladfelter, 1978; Low, 1971; Luckhurst and Luckhurst, 1978; Sale, 1977; Shulman, 1985; Smith and Tyler, 1972; and others). No evidence is presented in the literature which demonstrates food resources to be a direct limiting factor in tropical reef fish populations.

Problems of scale appear in these space resource studies. Sale (1972) showed that the numbers of the pomacentrid (*Dascyllus aruanus*) on isolated coral heads were highly correlated with coral size (indicating space resource limitations). At other larger sites on the reef proper, which had no limitation of coral, no correlation was found.

Smith and Tyler (1975) showed that there was significant seasonal variation in the numbers of fish on a patch reef off Bimini, Bahamas. Sale (1984) argues that this variation indicates that space resources are not limiting throughout the year. This is only one explanation, variation in numbers may also occur as spatial requirements of individuals within species change on a temporal basis, for example, with growth of individuals or through breeding. Under these conditions intense competition for more space or greater defense of the same territory can occur, causing individuals to leave the patch reef for other areas. Short-term changes are also known. For example, Shulman (1985) found temporal scales for aggressive defense of nocturnal shelter sites in the range of hours. In the very short-term, this effects the number of individuals (and probably species) utilizing the shelters. Long-term studies of natural and artificial reefs have yielded similar results (Russell *et al.*, 1974; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980; Williams, 1980). However, without knowing the

behavior of individual components of the system and the reason for emigration, it is not reasonable to assign causal relationships to the observations.

Two theories have consequently developed regarding the structuring of reef fish communities. There is the theory of determinism (order) of fish community structure (Smith, 1977, 1978; Helfman, 1978) based on observations of community composition remaining constant over time. In this theory, fishes have narrow species-specific habitat requirements which reduce competitive interactions resulting in a deterministic community structure. Alternatively, there is a theory with an opposing viewpoint which describes the stochasticity (chaos or lottery) of fish communities on reefs (Sale, 1978; Talbot *et al.*, 1978). Here, the unpredictability of fish community composition is attributed to factors such as predation and death which create ephemeral openings of spatial resources. Colonizers (individuals or species) are recruited by chance processes, although, some priority effects by residents affecting new recruits have been discerned (Shulman *et al.*, 1983). However, unpredictability does not necessarily mean chaos.

Bohnsack (1983) enumerated species turnover rates on artificial and natural coral heads suggesting that understanding turnover, which is central to the MacArthur-Wilson island biogeography model (MacArthur and Wilson, 1967), may reconcile differences between the two theories. He found the rate and length of time of sampling greatly affected perceptions of community changes and suggested that patch reef fish are in "dynamic" equilibrium. The deterministic theory proponents had sampling intervals of one (Smith and Tyler, 1972, 1973) to 13 years (Ogden and Ebersole, 1981), while the stochastic theory proponents sampled at much shorter time scales of monthly to quarterly (Talbot *et al.*, 1978; Sale, 1975, 1978; Sale and Dybdahl, 1975).

In large scale contiguous reefs, Williams (1982) and Anderson *et al.* (1981) found significant differences in the composition of fish communities within selected families, at different zones across the Great Barrier Reef of eastern Australia. Differences between major zones across the shelf were much greater than replicates within reefs. In terms of community theory, these differences may be attributed to a compromised view of the stochastic *versus* deterministic theories described by Smith (1978). The fish fauna on any reef is the result of a multi-tiered screening process of the regional fauna. The first screen limits recruits by physico-chemical constraints such as inappropriate microhabitats. The second screen is one of random events. Here recruitment is limited by events such as non-selective predation on recruiting larvae or juveniles, and transport of recruits by currents. The third and final screen is a selective recruitment process,

involving inter- and intra-specific competition for space or food and species-specific symbiotic relationships.

Smith (1978) also suggests that another perspective of this same compromise is "to consider that the local community is made up of a small number of species selected partly randomly and partly deterministically from the regional faunal pool. Only a limited number of species can occur together in a small patch of habitat, but if there are enough patches, a very large fauna can be accommodated. Because of the random effects of the selective process, similar habitat complexes may have quite different faunas that are no less stable". Since successful recruits probably do not often change residence on the reef, these individuals have priority over potential recruits. As fish die or are removed by predation, new recruits will take their place. There is a constant turnover but species number remains relatively constant.

Many theories on methodological comparisons (Bohnsack, 1983), recruitment patterns (Shulman *et al.*, 1983; Doherty, 1987), and discussions of differences in workable theories (Helfman, 1978; Sale, 1978, 1984; Smith 1978), create an information pool which is narrowing in on assembly rules (Diamond, 1975) of coral reef fish communities. It may be, then, that the reef fish community is more than the sum of its parts. That is, larger scale reef tracts have emergent properties not exhibited by small isolated coral heads, and finer scale observations of larger areas would be required to understand limiting factors that are not continuous. Factors such as agnostic interactions influencing recruitment and shelter occupancy (Shulman *et al.*, 1983, Shulman, 1985), territoriality (Ebersole, 1977), variability of larval recruits (Williams, 1980; Doherty, 1983) and small-scale habitat changes (Gladfelter and Gladfelter, 1978) need to be studied over larger scales. Although we have developed the ability to perform hypothesis testing experiments on small reef tracks, or coral heads, we must develop methodologies to perform replicate sampling over large reef tracks and elucidate the scale at which these enumerations are significant.

Temperate and Boreal Systems

While studies of tropical reef fish communities generally take a small-scale *in situ* approach, studies of temperate and boreal fish communities have historically utilized large-scale sampling techniques (e.g. trawl catches) over wide geographic areas (e.g. Overholtz, 1982). The rationale for this dichotomy of scales in approaches is that (1) coral reef fishes generally have limited home ranges and live in a three-dimensional habitat amenable to small-scale census techniques, and (2) temperate/boreal fishes of interest are generally more spatially dispersed, exhibit long distance

migration and live in less spatially complex environments amenable to large-scale census techniques. Factors which cause competitive interactions or allow co-existence, however, still occur at the level of the individual in both systems.

While studies of tropical reef fishes have focused on space resource and interactions limiting access to space, many studies in temperate and boreal waters have focused on food limitation as a structuring factor of communities. Schoener (1971), using optimal foraging models, predicted that food size would decrease asymptotically with decreasing predator size. Several studies demonstrate this prediction (e.g. Hacunda, 1981) while others (Lilly and Fleming, 1981; Sedberry, 1983) indicate that predators in a specific feeding stanza prey on organisms over a set size range through a wide growth phase, or as predator size increases, the size range of prey expands as well while retaining small prey in the diet.

Juvenile and adult shelf fishes off the eastern coast of the USA show considerable interspecific overlap in diet, with functionally similar groups of predators feeding on a few principal prey species, although some species-specific selectivity is evident (Tyler, 1972; Ross, 1978; Langton and Bowman, 1980, 1981; Bowman, 1981; Lilly and Fleming, 1981; Sedberry, 1983). Optimal foraging theory predicts that as food becomes scarce, predators will take a wide variety of prey, and the diets of functionally similar predators occupying the same habitat will converge (Pyke *et al.*, 1977). Others (e.g. Tyler, 1972; Jones, 1978) have hypothesized that as food density declines, co-existing predators will specialize on differing prey, hence, decreasing overlap. Considerable food overlap would occur only if prey were abundant. Ross (1977) found that interspecific food overlap in co-occurring searobin species (family Triglidae) was at a minimum during periods of low prey availability, thus supporting the latter hypothesis. Tyler (1972) also found little overlap in principal prey species of a boreal marine fish community off eastern Canada and concluded that specialization of prey resources is a result of a food limited system. Conversely, Sedberry (1983) found overlap lowest in spring when food resources were most abundant.

The results of these studies poses a basic question; is this overlap due to food resource limitation or surplus? Also, there are still the underlying questions; is there competition for food resources among fishes in these temperate/boreal communities, and is this, in part or in total, what structures the community as a whole? Although shelf fishes exhibit interspecific diet overlap, this condition does not necessarily lead to competition unless resources are limiting (Pianka, 1976). Other factors such as small-scale distribution, and interactions between predators and between predators and prey need to be considered.

Factors affecting the prey pool available to individual predators are little understood. Fish feeding on planktonic prey in significant currents have been observed to feed only in an upcurrent direction (Auster, 1985). Depending upon the size of plankton patches and the position of individual predators within the prey field, the possibility of downfield depletion exists.

Consumptive competition (Schoener, 1983) may be common in current dominated environments. Fish use currents in a way which isolates individuals by size class for short periods in order to take advantage of "current sheltered" prey pools (Auster, 1984, 1987). Cyclical changes in tidal current velocity shift the small-scale spatial distribution and change foraging behavior patterns of fish by species and size class. For example, increasing current velocity allowed only increasingly larger classes of cunner (*Tautoglabrus adspersus*) to forage on current exposed surfaces, and restricted the head raised searching posture of winter flounder (*Pseudopleuronectes americanus*) to only those size classes capable of maintaining this position above the substrate. Size class groups within a species are limited in their maneuverability at specific current velocity regimes. Areas exposed to currents limited the foraging behaviors of each species by size class and became ephemeral prey refuges from specific size class fish as current velocity increased. Changes in distribution and behavior continuously shift the potential foraging areas and prey pool for each species size-class group. This phenomenon may provide an isolating mechanism to reduce both inter- and intra-specific competition in a food limited system.

Groups of fishes within communities also switch into prey pools unavailable to other species, when these alternate prey become available. For example, seasonal food overlap values for demersal shelf fishes in the Mid-Atlantic Bight were lowest during spring, when a high abundance of planktonic prey was available near bottom. The normally benthic predators, red hake (*Urophycis chuss*) and Gulf Stream flounder (*Citharichthys arctifrons*) switched to planktonic prey (Sedberry, 1983). On a shorter time scale, Pearcy *et al.* (1984) report that adult ocean salmon, sockeye (*Oncorhynchus nerka*) pink (*O. gorbuscha*), and coho (*O. kisutch*) switch to euphausiids at night, from squid, fish and amphipods during the day. These shifts suggest that salmon are opportunistic and able to exploit food resources when they are encountered. By doing so they reduce pressure on the other common prey pools. This behavior probably has the effect of expanding the prey pool when preferred prey abundance declines. Whether many other species are as opportunistic has yet to be documented.

Movement, migration and habitat

Unlike relatively stable (temporally) tropical coral reef fish communities, temperate and boreal fish com-

munities generally exhibit some large-scale seasonal variability. For example, in the Northwest Atlantic, fish communities show distinct differences in species composition related to seasonal differences in water temperature (Colton, 1972; Colton *et al.*, 1979). It is possible to separate species of a community into year-round residents, winter residents, summer residents, and occasional species (Tyler, 1971). Boreal areas with narrow temperature fluctuations were dominated by year-round residents. However, it is noted that even boreal resident species exhibit inshore-offshore or shallow to deepwater movements on diel and seasonal scales. Areas exhibiting greater annual temperature fluctuations (e.g. south of Cape Cod) on the other hand had more temporary residents, and fewer year-round species.

Recksiek and McCleave (1973), working in the Sheepscot River-Back River estuary at Wiscasset, Maine, found pelagic fish communities corresponding to Tyler's (1971) community structure groupings. The relatively warm Back River estuary had a summer pelagic component consisting mostly of alewives (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), and Atlantic menhaden (*Brevoortia tyrannus*), while the relatively colder and oceanic Sheepscot River estuary had a summer migrant pelagic component of Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and spiny dogfish (*Squalus acanthias*). Rainbow smelt (*Osmerus mordax*) was the only year-round resident, and Atlantic herring was the only winter resident species. It appears, therefore, that although pelagic and demersal fish assemblages can be divided into similar residency patterns, species composition varies with temperature regime, both within and between latitudes in these temperate and boreal systems.

At even smaller scales, other influences on distribution, such as species-specific substrates, come into play. Using a submersible on a transect over Jeffreys Ledge, Gulf of Maine, revealed partitioning between rock-boulder *versus* cobble-sand substrates of several species (redfish, *Sebastes marinus*; cunner, *Tautoglabrus adspersus*; eel pout, *Macrozoarces americanus*; longhorn sculpin, *Myoxocephalus octodecemspinosus*) demonstrating small-scale discontinuities of species distributions (Auster, unpublished data). The method of assessment was significantly better than usual survey methods (Uzmann *et al.*, 1977) although most of what is known about temperate and boreal fish communities comes from trawl survey data. Problems of gear selectivity and size specific avoidance may give biased samples of species composition and abundance (Byrne *et al.*, 1981). Comparisons of one survey tow to another, in community studies, makes the implicit assumption that the fish are homogeneously distributed over the tow area and all fish are sampled. Also, when comparing tow caught fish within and between

tows for overlap in diet, the implicit assumption is made that the fish all forage within the same prey pool.

Rockfishes (*Sebastes* spp.) of the family Scorpaenidae are an interesting group to examine for the effects of habitat resource partitioning and competition in temperate/boreal environments. The genus contains 100 species reported from the northern Pacific Ocean. As many as 50 species occur in a narrow band between 34°–38° N off central California, USA (Chen 1971, 1975). Many are morphologically similar and co-occur in a variety of habitats, hence the potential for competition and overlap is high (Larson, 1980).

Evidence of direct competition between rockfish congeners has been reported by Larson (1980) and Hallacher and Roberts (1985). They exhibited species-specific spatial zonation in kelp bed habitats, with the exception of several spatial generalists. Food habits reflected the prey pool available in the spatial zones occupied, hence overlap did not signify direct competition for prey resources. Manipulative field experiments by Larson (1980) have demonstrated small-scale range extensions into one congener's habitat when the congener is removed, indicating interspecific competition. The segregation was found to have originated by selective settlement of larvae and maintained by interspecific territoriality.

Segregation to avoid direct competition for food also occurs within habitats by diel partitioning of activity and use of spatial resources (e.g. shelter sites, foraging sites) as in tropical systems. For example, on nearshore rocky reefs off southern New England, USA, there are distinct changes in diurnal and nocturnal fish community structure and activity (Auster, unpublished data). Cunner are typical scan-and-pick feeders during the day but are inactive at night (Olla *et al.*, 1975; Sand, 1982). Other species, such as hake (*Urophycis* spp.) and scup (*Stenotomus chrysops*), move into the area at night for shelter and to forage. Rock gunnel (*Pholis gunnellus*), shanney (*Ulvaria subbifurcata*), and grubby sculpin (*Myoxocephalus anaeus*) also move away from the reef habitat at night to forage on adjacent sand or mud areas.

The community perspective

The foregoing examples of studies at different spatial scales suggest that in trawlable shelf areas where we have a familiarity with the fish community, we are still in the process of identifying factors that may aid in structuring communities. There are groups of fish that have limited home ranges and specific small-scale habitat requirements (like rock reefs). The few studies of these groups in temperate/boreal systems suggest they may behave somewhat like tropical reef systems.

Gascon and Miller (1981) studied the development of fish assemblages on artificial reefs in the nearshore

environment off British Columbia, Canada, using small-scale visual census techniques. Species equilibrium in all cases was reached within 6 months. Assemblages were more stable and predictable than patterns found in several recolonization studies in tropical systems (Russel *et al.*, 1974; Sale and Dybdahl, 1975; Sale, 1977, 1978; Talbot *et al.*, 1978). The authors suggest that the observed stability is a result of a smaller pool of potential colonizers (30 species), as opposed to many more in tropical systems (105 species reported by Talbot *et al.*, 1978). No competitive interactions were reported in this study although winter and summer insular reefs were significantly different. The non-equilibrium (lottery) model of Sale (1977, 1978) may apply in this case although Helfman (1978) suggests that the species pool available for colonization is a major factor controlling similarity between reef systems.

Ebeling *et al.* (1980) also found the same type of pattern in temperate kelp bed fishes off California, USA. This study compared canopy and bottom fish assemblages at an inshore and offshore site, from annual surveys between 1971 and 1974. Variation in species composition was less between years than between habitats or sites. Site- and habitat-specific species composition persisted, although there was significant yearly variation in species abundances. Canopy assemblages, dominated by planktivores (a low number of potential species), were simpler and more variable than bottom assemblages.

These studies suggest that there is some "optimal" or "critical" species pool to draw on for colonizers where community stability would persist. Below some level, communities are less stable and subject to large variations in composition and number. The canopy fish community described by Ebeling *et al.* (1980) drew on the smallest potential species pool and exhibited the greatest variation. However, the kelp canopy is an ephemeral environment subject to variable blade growth, storm breakage, and planktonic prey abundance. This habitat is in itself less stable than their related demersal habitats such as rock-boulder reefs, kelp holdfast and lower blade habitat. The variability of the habitats themselves and their associated "attractiveness" to potential colonizers could contribute to a great deal of the variability of species composition and abundance.

Temperate/boreal assemblages also are stable in structure over the course of years (Ebeling *et al.*, 1980; Overholtz, 1982). In highly perturbed systems (e.g. extensive fishing activity) there have been community responses in which species composition and abundances have shifted to new equilibrium levels. In the Northwest Atlantic, there has been a dramatic increase in sand lance (*Ammodytes* spp.) populations. It has been hypothesized (Sherman *et al.*, 1981) that this is in

response to depletion of herring and mackerel stocks where exploitable fish biomass was reduced approximately 50% from 1968 to 1975 (Clark and Brown, 1977).

Also, in the North Sea it has been hypothesized that high fishing mortality of herring and mackerel stocks during the 1970s was responsible for their replacement by large populations of small, fast-growing, opportunistic plantivorous species such as pollock, sand eel, and eel pout (Andersen and Ursin, 1978). This replacement phenomenon is similar to the results from tropical reef fish studies showing replacement of species on patch reefs, where these niches are refilled by trophically similar species. The resilience of the communities as a system, rapidly moving to new states of equilibrium, demonstrates how complex systems restore components to maximize energy flow.

Studies of other taxa suggest that environmental variability is responsible for the coexistence of species communities (e.g. Dayton, 1971; Caswell, 1978). Similarly, destabilizing environmental parameters by aperiodic high velocity currents, wide temperature fluctuations, fluctuations in salinity, etc. may also be responsible for coexistence of species in fish communities as well (Thorman and Weiderholm, 1983). The coexistence of species in various communities may then be the result of some combination of isolation and instability working in concert to reduce or eliminate competitive interactions.

Conclusions

The preceding review of the fish community literature demonstrates the diverse temporal and spatial approaches used to elucidate the functional aspects of community structure. Problems regarding our understanding of community processes are caused by viewpoints transcending hierarchical divisions (i.e. interpreting small-scale processes through large-scale views and vice versa). Each change in scale in our perspective of a community seems to have its own emergent properties. At the level of individuals, intra- and inter-specific interactions govern recruitment patterns of juvenile fish to open space resources on a reef (Shulman *et al.*, 1983). Temporal changes in sampling alter the view of deterministic *versus* stochastic changes in species composition of fish assemblages on patch reefs (Bohnsack, 1983). Analysis of the gut contents of fish in large-scale trawl collections indicate significant competition for food may occur between species (Langton and Bowman, 1980, 1981), however factors such as differences in time of feeding, areas available for foraging, and opportunistic prey switching (Auster, unpublished observations, 1984, 1985, 1987; Percy *et al.*, 1984) may contribute to reductions in or eliminate competitive interactions at the level of individuals.

Studies of factors governing community dynamics must be conducted at the scale at which the interactions of interest occur. This is often difficult because in many areas of interest (e.g. larval recruitment to juvenile populations), there is a lack of basic understanding of the significant scales regarding the governing interactions.

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