CHAPTER 18

Tropical and Temperate Reef Fishes: Comparison of Community Structures

Alfred W. Ebeling
Department of Biological Sciences and
Marine Science Institute
University of California at Santa Barbara
Santa Barbara, California

Mark A. Hixon
Department of Zoology and
College of Oceanography
Oregon State University
Corvallis, Oregon

I. INTRODUCTION

The structure of a reef fish community—the local distribution, abundance, and functional relations of species—is the product of the regional pool of available species and the processes that influence the establishment and persistence of populations assembled locally from the pool (Sale, 1980a). A large body of literature describes community-level patterns of reef fishes in temperate and tropical habitats, and a more recent spate of papers provides experimental evidence of the processes that may create these patterns. Potentially important processes include competition, predation, recruitment, and abiotic disturbance, which, in some combination, interact in producing the observed structure of a local assemblage. If a reef is "saturated" with fish such that resources are limiting, then competition is a major structuring process, which may be expressed as niche diversification or a competitive lottery, or may be modified by compensatory mortality of superior competitors or shifting of species dominance in a changing environment (Connell, 1978, 1988). If the habitat is unsaturated, then the community may be structured by a host of possible mechanisms, such as the replenishment of individuals from "sources" to "sinks" (Pulliam, 1988), limitation of population sizes by low recruitment (Doherty and Williams, 1988a), or population limitation by physical disturbance or predation (Connell, 1978, 1988).

The rising tide of literature has prompted needed reviews of what is now known of these patterns and processes. Several of these reviews concentrate on the tropical communities associated with coral reefs (e.g., Ehrlich, 1975; Sale, 1980a; Doherty and Williams, 1988a); one treats the temperate communities

in New Zealand (Jones, 1988a). As pointed out by Choat (1982), however, few works compare tropical and temperate reef fish communities, which are derived from noticeably different faunas and environments.

Our aim, therefore, is to compare fish communities of temperate rocky reefs with those of tropical coral reefs, in terms of their environments, structure, and possible regulatory mechanisms, to see if predictable differences occur between latitudes. Do tropical and temperate communities differ fundamentally in structure? Are these communities regulated in basically different ways? Are there enough data of the right kinds to answer these questions? A voyage in the sea of information is worthwhile if for no other reason than to set the course. We limit the scope of our review to systems occurring in analogous habitats. Tropical corals grow in shallow regions about the equator where minimum water temperatures seldom drop below 20°C during the winter; temperate reefs with characteristic forests of large brown algae occur poleward of these isotherms (Fig. 1). Coral reef fishes obviously live among living corals in relatively shallow tropical water. Since temperate reef fishes live on rocky reefs occurring at any depth, we restrict our coverage of temperate communities to those occurring in comparably shallow water where attached macroalgae can grow.

We begin by comparing the environments in which reef fishes assemble as communities. We examine the constraints and potential biases of sampling populations in temperate versus tropical environments as potential sources of systematic error in latitudinal comparisons. We then describe and compare the structure of these communities and evaluate the hypothesized models of regulation of community structure, given the known faunal and environmental differences. We conclude that, despite real differences in the structure of temperate and tropical reef fish communities, there is presently insufficient evidence for a universally appropriate model of community regulation in either system. We close by suggesting directions for future research.

II. Comparison of Environments

A. Habitat Structure

1. Hard Substrata

Temperate rocky reefs and tropical coral reefs are fundamentally different in the composition of their hard substrata. The coral reef is a complex organic matrix with many convolutions that increase spatial heterogeneity, microhabitat variety, and refuges from predation (Fig. 2). The coral itself is a source of food, although relatively few species are so specialized that they depend on
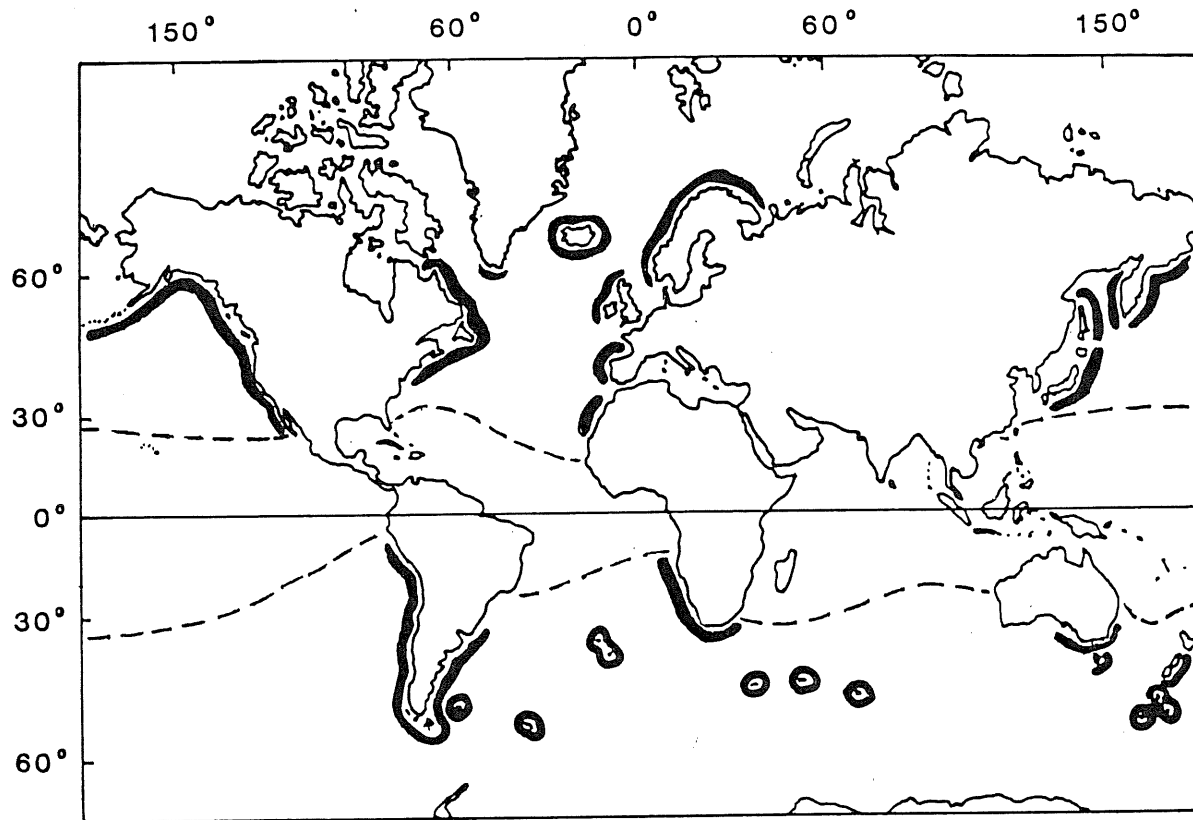
Figure 1 World distribution of kelps (Laminariales) relative to the 20°C isotherm for the coldest month of the year, which marks the boundary between tropical and temperate seas. [Adapted from M. S. Foster and D. R. Schiel (1985, Fig. 2, p. 5). The ecology of giant kelp forests in California: A community profile. U.S. Fish and Wildl. Serv. Biol. Rep. 85(7.2). Redrawn from Womersley (1954), with additional data from Chapman (1970), Briggs (1974), and Michanek (1975).]

the soft parts for their nutrition [some Chaetodontidae (Motta, 1988)]. More important, perhaps, are the interstices formed by coral skeletons that trap plankton and provide shelter for invertebrate food (Abel, 1972). Fish species diversity is often related to coral diversity or topographic complexity (reviewed by Roberts and Ormond, 1987). For example, both the diversity and abundance of Hawaiian reef fishes in Kaneohe Bay, Hawaii, were primarily correlated with coral diversity and bottom relief and only secondarily with such factors as water circulation, light, and substratum hardness (Smith *et al.*, 1973).

Temperate reefs consist of various kinds of rock, often including crevices, holes, and promontories, but lacking the enormous surface complexity of the corals (Fig. 3). Nonetheless, fish abundance and diversity may be linearly related to bottom relief (Ebeling *et al.*, 1980a) or reach an asymptote at intermediate levels of reef height and algal density (Patton *et al.*, 1985). As

Figure 2   View of a fringing coral reef along the coast of Jamaica, showing massive coral
buttresses about 30 m long at 10 m depth and canyons between. [From T. F. Goreau and
N. I. Goreau (1973, Fig. 2, p. 403). Sketch by P. D. Goreau. The ecology of Jamaican
coral reefs. II. geomorphology, zonation, and sedimentary phases. *Bull. Mar. Sci.* **23**, No. 2,
399–464.]

parts of broad coastal headlands, often running virtually uninterrupted along
continental coasts, temperate reefs are usually more continuous than coral
reefs. With the important exceptions of the large barrier reefs associated with
continental margins off Australia (the Great Barrier Reef) and Central
America (the Belize Barrier Reef), coral reefs are relatively patchy along coasts
and are usually associated with small tropical islands. Coral reef habitats may
thereby comprise more patchy environments for fishes, with little or no
migration of smaller individuals from one reef system to another (Barlow,
1981). This patchiness may increase the between-habitat component of fish
diversity (Bradbury and Goeden, 1974; Goldman and Talbot, 1976; Sale,
1980a; Alevizon *et al.*, 1985).

2. Foliage

Besides the hard substrata, the most conspicuous difference between temper-
ate and tropical habitat structures is the extension of macroalgae above tem-
perate reefs (Fig. 4). Forests of large laminarian kelps and fucoid brown algae
are the hallmark of temperate reefs throughout the world (Dayton, 1985;
Schiel and Foster, 1986). In sharp contrast, most algae is cropped back in the
tropics, leaving an unbroken view through clear water above the coral. Vari-
ous vegetation layers or "canopies" in a temperate kelp forest play vital roles in
structuring higher trophic levels (Dayton, 1984; Dayton *et al.*, 1984). The
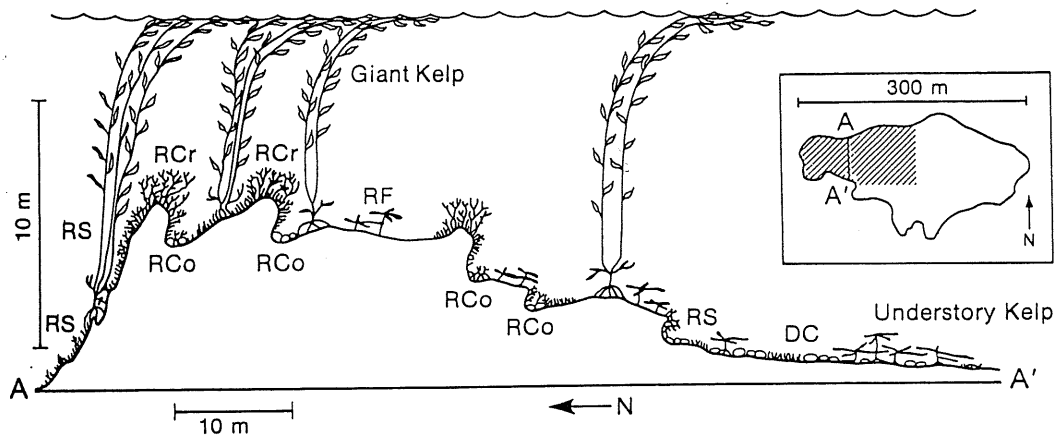
Figure 3 Section of a temperate reef (Naples Reef) off Santa Barbara, southern California, showing microhabitats of deep cobble (DC), depressions or rills with algal turf and kelp plants growing on a cobble base (RCo), the crest of the reef supporting dense bushy stands of red algae and scattered understory kelp plants (RCr), reef flat of relatively level rock base (RF), and reef slope with algal turf, bushy algae, and scattered kelp plants (RS). [From A. W. Ebeling and D. R. Laur (1986, Fig. 1, p. 126). Foraging in Surfperches: Resource partitioning or individualistic responses? *Environ. Biol. Fishes* 16, 126. Reprinted by permission of Kluwer Academic Publishers.]

bottom or crustose layer may play a role in settlement of other organisms (Breitburg, 1984). The second or algal-turf layer, often overgrowing the prostrate crust, is composed of articulated coralline and filamentous or fleshy macroalgae. This canopy provides shelter and food for many small invertebrate grazers and detritivores, which in turn are the principal food of epibenthic fishes (Leum and Choat, 1980; Choat and Kingett, 1982; Laur and Ebeling, 1983; Holbrook and Schmitt, 1984). A third layer of understory kelp may form a dense subsurface canopy in which juvenile fishes shelter (Ebeling and Laur, 1985). In the North Pacific and some regions of the Southern Hemisphere, a fourth layer reaches upward to form a dense surface canopy. Layers of kelp are major contributors to the detritus-based food chain (Gerard, 1976; Mann, 1982; Ebeling *et al.*, 1985; Harrold and Reed, 1985; Duggins, 1988; Duggins *et al.*, 1989). Surface kelp deflects nearshore currents and thereby depresses through-transport of larvae and other plankton (Jackson and Winant, 1983; Bernstein and Jung, 1979; Jackson, 1986). Tropical reefs, on the other hand, have only the first two layers of algae at most and lack the complex filter composed of tall plants (Earle, 1972; Hay, 1981a).

Thus, temperate kelp beds provide a living vertical dimension that coral reefs lack; they extend the space available for substratum-oriented fishes seeking food and shelter among the blades and stipes (Quast, 1968b; Feder *et al.*, 1974; Coyer, 1979; Choat, 1982). Kelp beds generally support a larger biomass of fish than nearby areas without kelp (Quast, 1968c; Estes *et al.*,
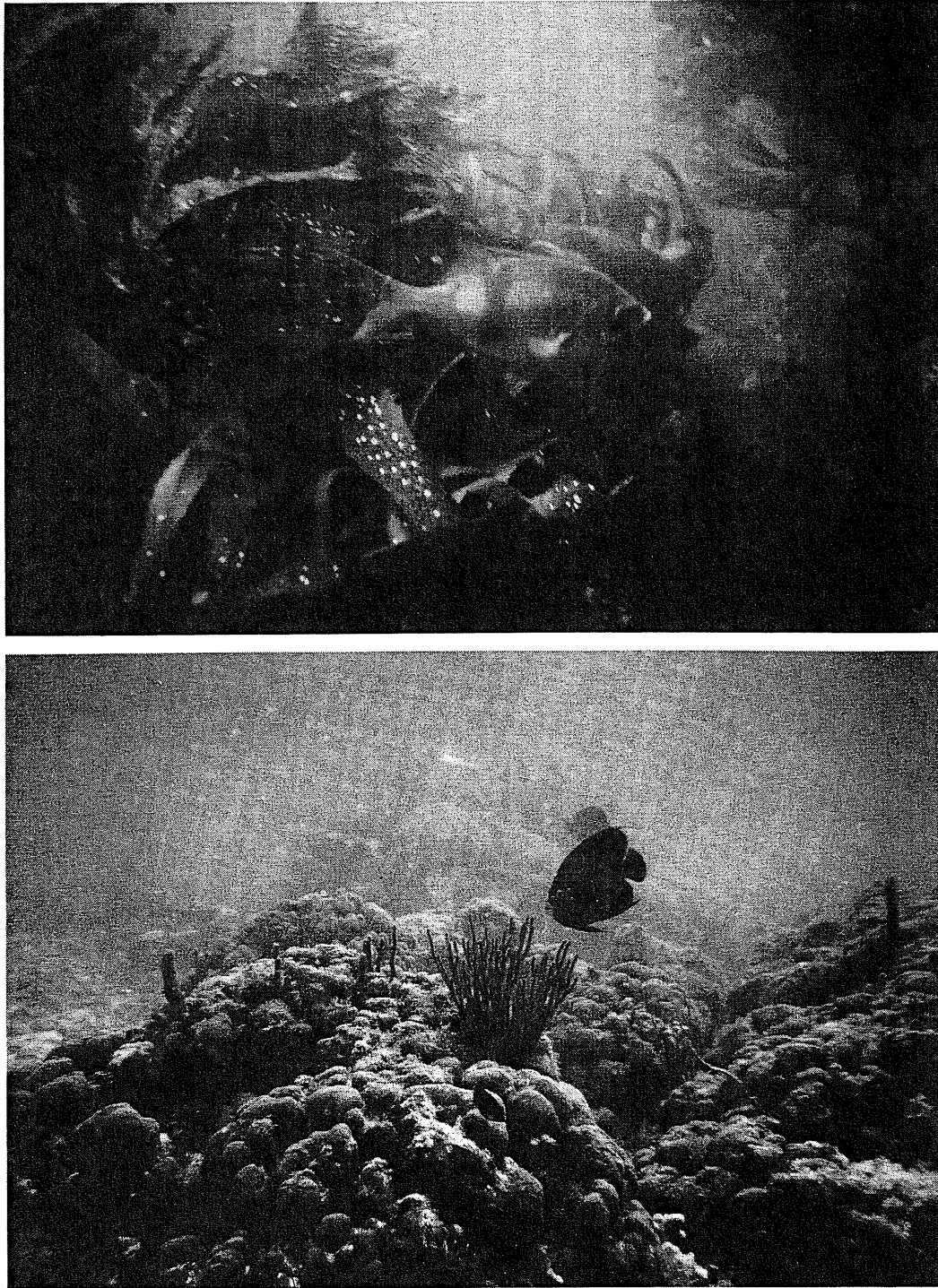
Figure 4 Temperate–tropical contrast of reef structures. The upper photograph is of an area of temperate reef and understory kelp (*Eisenia arborea*), with a pile surfperch (*Damalichthys vacca*) in the foreground, off Santa Cruz Island, California; the lower photograph is of a similar area of coral reef, with a French angelfish (*Pomacanthus paru*) in the foreground, in the Caribbean Sea off Belize. (Photographs courtesy of William S. Alevizon.)

1978; Larson and DeMartini, 1984; Ebeling *et al.,* 1980b; Carr, 1989; but see Stephens *et al.,* 1984; Choat and Ayling, 1987). Kelp beds moderate wave action and form productive "edges" where reef residents and pelagic species mingle (Quast, 1968b; Miller and Geibel, 1973; Feder *et al.,* 1974; Ebeling *et al.,* 1980b; Leaman, 1980). The plant surfaces in midwater may provide essential substrata for egg attachment (Limbaugh, 1955; Quast, 1968b) or settlement of fish larvae and pelagic juveniles from out of the plankton (Quast, 1968d; Leaman, 1976; Jones, 1984a,c; Choat and Ayling, 1987; Carr, 1989). On the other hand, coral reef fishes must settle either directly onto the reef or nearby refuges such as seagrass beds (Shulman, 1984, 1985b).

Temperate nursery areas for juvenile fishes are often associated with areas of heavy foliage (Miller and Geibel, 1973; Larson and DeMartini, 1984; Carr, 1989; Holbrook *et al.,* 1989), analogous to peripheral seagrass beds in the tropics (Shulman, 1985b); in both systems, juveniles occur in shallow water, then move into deeper water as they grow older (Sale, 1969; Miller and Geibel, 1973; Jones and Chase, 1975; Choat and Kingett, 1982). Such nursery areas include tidal pools, back reef lagoons, and estuaries, but apparently not tropical mangrove systems to the extent as previously assumed (Quinn and Kojis, 1985). Temperate waters typically provide large offshore mats of drifting kelp and other algae, moving unidirectionally along the surface or bottom and used as rafts by a variety of juvenile fishes (Mitchell and Hunter, 1970; Boehlert, 1977; Jones, 1988a). A diverse assemblage of temperate fishes may shelter in accumulations of detached seaweeds nearshore as well (Lenanton, 1982). The dispersal stages in tropical systems usually drift free in the plankton (Johannes, 1978a; Thresher, 1984) and less frequently associate with detached algae (Robertson and Foster, 1982), unless swept into seaweed sinks such as the Sargasso Sea.

B. Environmental Conditions

1. Seasonality

As the well-traveled diver knows, temperate waters tend to be cold and murky and tropical waters are often warm and clear. This contrast varies seasonally and geographically. In temperate regions, water temperatures experienced by reef fishes may vary annually between 2°C and 20°C along coastal New England (Olla *et al.,* 1974), for example, but only between 10°C and 20°C off southern California (Quast, 1968a; Ebeling and Laur, 1988). Moreover, temperate waters along the western continental coasts are subject to intense upwelling, which may shift temperatures several degrees Celsius within a few hours. For example, the thermally unstable environment off southern California alters fish behavior by inducing fish to seek the bottom and shelter during

exceptionally cold and turbid episodes (Quast, 1968a). Variation in thermal regimes—either seasonal or with depth—may enhance local diversity in transition zones between temperate and subtropical waters by promoting the co-occurrence of cool- and warm-water species (Stephens and Zerba, 1981). In general, temperate continental habitats are characterized by more turbid waters and fewer typical reef fishes than are habitats at offshore islands (Robins, 1971; Gilbert, 1972). Where temperate and tropical faunas overlap in the absence of well-developed coral systems, such as in the Gulf of California, the typical tropical reef species inhabit clear-water areas around precipitous rocky points (Gilligan, 1980).

Temperate fishes show varying degrees of bathymetric movements related to seasonal change in environmental conditions. In shallower water, densities may decrease as fish respond to loss of macroalgae and decreasing food supply during fall and winter (Leaman, 1980; Ebeling and Laur, 1988). Fish may migrate well offshore during the winter in more extreme climates as along New England (Olla et al., 1975). In Puget Sound, where seasonal change is less severe, schooling midwater species such as rockfishes (Sebastes, Scorpaenidae) simply descend a few meters to deeper water, while some benthic species remain in the same shallow (<15 m deep) area of reef and kelp throughout the year (Moulton, 1977). However, in warmer waters off southern California, wherever level bottom separates inshore and offshore reefs, some species migrate inshore to more productive habitats during the winter (Stouder, 1987; Ebeling and Laur, 1988; Ebeling et al., 1990).

Coral reefs grow where the minimum annual surface temperature exceeds about 20–21°C (e.g., Newell, 1971; Goreau and Goreau, 1973) (Fig. 1). Seasonal fluctuations in water temperature are slight compared to in temperate regions. While water clarity is often very high on oceanic reefs, coastal and lagoonal reefs can undergo reduced visibility due to terrestrial runoff, storms, and localized plankton blooms. Although less so than in temperate waters, seasonal change influences tropical systems. Over much of the tropics, two monsoon-related seasons replace the four solar seasons, but are characterized more by changes in patterns of wind, rain, and currents than temperature and day length (Johannes, 1978a). Compared with seasonal enrichment due to large-scale upwelling or overturn of temperate waters, however, open-ocean nutrients in the tropics are consistently low and relatively invariant in all but the eastern parts of the oceans.

In sum, seasonality increases from the tropics through subtropical and warm-temperate climates to cold-temperate zones. The stronger seasonal variation in the higher latitudes elicits greater, albeit predictable, responses in the reef fish assemblages.

2. Disturbance

Superimposed on seasonal events in both tropical and temperate regions are interannual fluctuations in climate. Of major importance on a global basis is the El Niño—Southern Oscillation (ENSO) phenomenon in the eastern Pacific Ocean. It is now thought that couplings between the tropical atmosphere and upper layers of the ocean bring about repeated appearances of warm or cool water in the equatorial eastern and central Pacific at 3- to 5-year intervals (Graham and White, 1988). Episodes may be accompanied by severe storms generated by marked changes in heat transfers between circulating air and water masses. Interannual variability in tropical environments has been ascribed to the quasi-periodic ENSO cycle (Longhurst and Pauly, 1987). During warm-water phases of a cycle, normally cool, upwelled water is displaced in the eastern Pacific. Displacements extending poleward and drastically affecting the temperate oceanographic regimes are called El Niño episodes. The intrusions of warm, nutrient-poor water during an extreme El Niño may cause deterioration of kelp forests and alterations in structure of subtidal reef communities off southern California (reviewed by Tegner and Dayton, 1987). Reduced levels of nitrates and phosphates combined with elevated seawater temperatures tend to disrupt the nitrogen and carbon metabolism of kelp and impair its growth processes (see, e.g., Germann, 1988).

Storms, however, are the major cause of physical disturbance on all shallow reefs. It seems that, at a specific location, storms are seasonally more predictable and frequent in temperate regions, but usually do not match the severity of sporadic tropical hurricanes and typhoons. In higher temperate latitudes, regular cycles of defoliation and regrowth of large algae, with associated shifts in migration and activity patterns of fishes, are correlated with seasonal storm cycles (e.g., Moulton, 1977). However, unusually strong turbulence may cause substantial mortality; for example, large numbers of dead fish from kelp beds were cast ashore with obvious injuries during a major winter storm off central California (Bodkin et al., 1987). In lower temperate latitudes, major disturbances may occur less predictably and cause upheavals of community structure with indefinite recovery periods. In the Southern Hemisphere along coastal Chile, drastic environmental changes wrought by earthquakes, as well as El Niños and sporadic storms, can cause catastrophic mortalities in the intertidal and shallow subtidal reef communities (Castilla, 1988). In the warm-temperate region off southern California, unusually severe storms add a marked unpredictable element to a moderate seasonal regime (Dayton and Tegner, 1984a; Ebeling et al., 1985; Estes and Harrold, 1988). Kelp forest communities were significantly altered by destruction of mature plants by storm surge during periods of unfavorable conditions for growth and altered

patterns of recruitment of both plants and animals associated with a major El Niño episode in 1982–1984 (reviewed by Tegner and Dayton, 1987). Severe storms may trigger processes whereby either existing kelp forests are transformed into urchin-dominated barrens or vice versa, depending on the recent history of the community (Ebeling *et al.*, 1985; Ebeling and Laur, 1988). Thus, storm disturbances may have either deleterious or beneficial effects on kelp forests. The destruction of mature canopies opens space and admits sunlight for rejuvenation of other macroalgal assemblages by means of recolonization and succession (Dayton *et al.*, 1984; Reed and Foster, 1984; Kennelly, 1987a,b, 1989).

Where major storms occur in the tropics, cycles of community perturbation and recovery are very irregular. A host of major physical and biological disturbances, often related to storm activity, tend to perturb coral reef communities unpredictably (Endean, 1976). In the Caribbean region, for example, strong hurricanes may reset the course of ecological succession to alter the long-term patterns of coral distribution and sea urchin grazing (Woodley *et al.*, 1981; Hughes, 1989). Mobile fishes may constitute the least affected group and show most resiliency to perturbation (Springer and McErlean, 1962; Bortone, 1976; Tribble *et al.*, 1982; Walsh, 1983), although the turbulence of major tropical storms can kill fish, and population structure may be temporarily altered (Bortone, 1976; Lassig, 1983; Tribble *et al.*, 1982; Woodley *et al.*, 1981). A severe disturbance during the period of larval settlement may alter the age composition of species populations (Lassig, 1983) or chronically disrupt distributional patterns of sedentary species (Woodley *et al.*, 1981). Sporadic hypothermal events (Bohnsack, 1983a) or episodes of toxic red tides (Smith, 1979) may also be locally catastrophic for subtropical reef fish assemblages.

C. Forage Base

A reef community captures energy in two basic ways: attached plants fix light energy as primary production, and certain animals consume organic matter, including plankton, that is swept over the reef by currents (Odum and Odum, 1955). Some temperate beds of giant kelp (*Macrocystis pyrifera*) have among the highest productivities known for any natural ecosystem (Whittaker, 1970), a capacity equal to or greater than that of coral reefs and seagrass flats (McFarland and Prescott, 1959). This capacity is reflected in the large biomass of fish that temperate reefs support, about equal to or greater than that on tropical reefs (Brock, 1954; Odum and Odum, 1955; Bardach, 1959; Randall, 1963). On coral reefs, concentrations of plankton over coral constitute a major potential source of food (Herman and Beers, 1969; Goreau *et al.*, 1971). Reefs tend to act as highly efficient "filters" or "transducers" in remov-

ing and regenerating particulate organic matter by a combination of processes, including feeding by resident animals, adsorption on mucoid surfaces, trapping in eddies and backwaters, settlement of planktonic larvae, and becoming detritus upon dying (Tranter and George, 1969; Odum and Odum, 1955; Glynn, 1973; Hamner et al., 1988; Hobson, Chapter 4). Recycling of nutrients within a large biomass prevents losses to the ocean and sustains a large benthic productivity (Froelich, 1983; Smith, 1983).

1. Plankton

The density and composition of tropical reef plankton vary with season, water flow over the reef, and time of day (Glynn, 1973). Nocturnal plankton includes not only the smaller daytime forms (copepods, larvaceans), but larger reef-generated forms (polychaetes, larger crustaceans) as well (Hobson, 1968, 1972; Hobson and Chess, 1986). Planktivorous fishes comprise a major means of diverting this wafted energy source into the reef community (Stevenson, 1972; Emery, 1968; Glynn, 1973; Bray, 1981; Hobson, Chapter 4), and as expected of the exploitation of a continuously renewable food supply, planktivory occurs both day and night on both temperate and tropical reefs (Schroeder and Starck, 1964; Ebeling and Bray, 1976; Hobson and Chess, 1976).

Planktivores appear to be efficient at removing plankton swept over reefs in both regions. Glynn (1973) observed that zooplankton volumes were reduced by some 60% in water streaming off a Caribbean coral reef, and Hamner et al. (1988) provided evidence that planktivorous fishes consumed most of the zooplankton passing over a reef on the Great Barrier Reef. Zooplankton was also depleted by resident planktivorous fishes over temperate rocky reefs off California (Bray, 1981) and New Zealand (Kingsford and MacDiarmid, 1988). Such depletion may reduce the supply of invertebrate larvae that would otherwise settle inshore (Gaines and Roughgarden, 1987). On both temperate and tropical reefs, feces generated by diurnal planktivores may be consumed directly by other fishes during the day (Robertson, 1982) or be deposited in reef crevices at night (Bray et al., 1981, 1986), thus facilitating the transfer of allochthonous material and energy to the reef system.

2. Benthos

The most important source of reef-generated production providing food for fishes is the benthic community contained in a matrix of algae, sponges, tunicates, bryozoans, hydroids, and worm tubes covering much of the reef surface. Small animal inhabitants, especially amphipods, constitute the forage base for a host of demersal microcarnivores (Section IV,C). Thus, the well-being of a substantial part of the reef community depends on production associated with this carpet of "turf." On a southern Californian reef, for

example, the distribution of abundant, microcarnivorous surfperches (Embio-tocidae) is closely correlated with the distribution of turf, in both space and time (Ebeling et al., 1985; Stouder, 1987). On coral reefs, the abundance of corallivorous butterflyfishes (Chaetodontidae) is correlated with that of the corals on which they feed (Bell and Galzin, 1984; Bouchon-Navaro and Bouchon, 1989). In the Caribbean, production from surrounding seagrass beds is imported to reefs by daily migrating grunts (Meyer et al., 1983). Foraging over seagrass beds at night, the grunts defecate in their diurnal shelters on reefs, thereby fertilizing nearby corals (Meyer and Schultz, 1985a,b).

Beyond being a source of food, macroinvertebrates may interact directly and indirectly with fishes in ways that affect the benthic forage base. Sea urchins, rather than fishes, appear to be the principal macroherbivores on temperate reefs (e.g., Mann, 1982; but see Horn, 1989). As either small patches or extensive areas, barren grounds (barrens) created by overgrazing due to sea urchins have occasionally displaced kelp forests in temperate waters the world over (Lawrence, 1975; Schiel and Foster, 1986). Zones of barrens and stands of low kelp occur together naturally off New Zealand, where small microcarnivorous fishes forage in the kelp canopy and larger mesocarnivorous fishes eat macroinvertebrates from the barrens (Choat and Ayling, 1987). In the North Pacific, however, barrens often occupy areas where an important predator of urchins, such as the sea otter (Enhydra lutris), has been removed (reviewed by Estes and Harrold, 1988; Estes et al., 1989), although the essential role of this predator in preserving the kelp forest under all circum-stances is still questioned (Foster and Schiel, 1988). Indeed, urchin outbreaks decimate kelp forests in the North Atlantic, where otters have never occurred (e.g., Breen and Mann, 1976). Such outbreaks may be due to unusually strong recruitment cohorts of urchins combined with unusually favorable physical conditions (Hart and Scheibling, 1988). Although herbivorous fishes are thought to be the principal grazers in the tropics (e.g., Bakus, 1969; Hay, 1981a, 1984a), aggregations of urchins may also remove most macroalgae (Hay, 1984b, 1985; Carpenter, 1986; Foster, 1987a; Hughes et al., 1987) or even living corals (Glynn et al., 1979) in local patches or in the absence of their fish predators. In addition, periodic local outbreaks of crown-of-thorns star-fish (Walbran et al., 1989) alter fish community structure by consuming living coral used as food and shelter (Sano et al., 1984a, 1987; Bouchon-Navaro et al., 1985; Williams, 1986a).

On both temperate and tropical reefs, sea urchins may compete directly with fishes for algal food sources. Hay and Taylor (1985) experimentally removed urchins from a reef flat in the Virgin Islands and observed a sub-sequent increase in the abundance of parrotfishes and surgeonfishes. Dam-selfish are able to exclude some urchins from the algal mats within their

defended territories off Jamaica (Williams, 1981), while territories of surfperch can be overrun and decimated by urchins off California (Hixon, 1981).

D. Summary and Conclusions

Temperate reefs lack the enormous structural complexity of coral substrates, but often comprise areas of relatively continuous rock or boulder fields along coastal headlands. Compared to temperate rocky reef fishes, therefore, coral reef fishes often inhabit a more heterogeneous and patchy reef substrate with a greater variety of refuges and microhabitats. On temperate reefs, however, seasonal upwelling of nutrient-rich water supports tall, dense stands of kelp and other macroalgae. Unlike coral reefs, where foliage is mostly restricted to seagrass beds in surrounding sand flats, temperate reefs provide an added dimension of plant canopy for food and refuge, especially for juvenile fishes. Tropical waters are often warm and clear with relatively little seasonal fluctuation in conditions. The greater magnitude of seasonal change experienced by temperate rocky reef fishes is reflected in sharper seasonal peaks in their offshore–onshore migratory behavior. The stronger seasonal variation in the higher latitudes causes progressively greater, but more predictable, responses by resident fishes.

Although El Niño–Southern Oscillation conditions periodically disturb kelp forests, storms are the major source of physical disturbance on both temperate and tropical reefs. At any specific location, storms may be more frequent at higher latitudes, but are usually less severe than the occasional hurricanes and typhoons of tropical regions. In lower latitudes, the worst disturbances cause upheavals of community structure with indefinite recovery periods. Even though assemblages of mobile fishes are less affected by powerful water motion than are the sessile plants and macroinvertebrates, the effects of environmental perturbation may eventually cascade through the entire community.

Allochthonous food energy is imported into both tropical and temperate systems in the form of oceanic plankton consumed by large numbers of planktivorous fishes. Autochthonous energy generated by the rich detrital food chain supports benthic communities associated with algal turf, which harbors the small invertebrate prey of microcarnivorous fishes. Detrital accumulations are much greater on temperate reefs, where, unlike on coral reefs, plant production greatly exceeds consumption. Macroinvertebrates rather than fishes are the principal grazers of benthic algae on temperate reefs. Sea urchins may create "barrens" with an associated decline in fish abundance if, for example, a major storm disturbance removes mature kelp and other detrital food sources for urchins. Urchins may also compete directly with fishes for

access to benthic food sources on both temperate and tropical reefs. Crown-of-thorn starfish can decimate live corals, also affecting fish distributions.

III. ENVIRONMENT-INDUCED SAMPLING CONSTRAINTS AND BIAS

The differences between temperate and tropical reef environments, summarized in the previous section, have ramifications for any attempted comparisons between the fish communities occupying these habitats. The logistic constraints confronting temperate reef fish ecologists are quite different from those facing their counterparts who work in the tropics. Hence, many of the apparent temperate–tropical differences in community structure may be as much or more a function of relative methodological constraints and bias as real differences. With a few notable exceptions, tropical reef systems are remote from the world's major population centers. Yet tropical reefs are eminently more workable because predictably benign conditions allow longer time in the field and greater experimental replication (Sale, 1980a).

A. Seasonal Accessibility and Working Conditions

Access to temperate sites may be severely limited during the winter and spring, when surge, turbidity, and cold curtail the monitoring of experiments and limit observations to periods of fortuitous breaks in the weather. Experimental constructs such as cages are often badly damaged or lost so that long-term data on ecological succession or grazing pressure are usually incomplete and reports must interpret the outcomes of procedural fits and starts (see Breitburg, 1984). Winter fish counts are suspect when made in frigid water of low visibility because the observer is likely disoriented, weak, and nauseous as he or she is tumbled back and forth in a heavy surge. Shallow sites become unworkable, and deeper ones are workable only during reasonably calm periods. This is unquestionably why many temperate sites are sampled mostly during the summer–fall period of maximum calm and water clarity (see Ebeling et al., 1980a,b; Larson and DeMartini, 1984). Conversely, the benign tropics can be sampled in comparable comfort all year, except of course when tropical storms threaten (see Sale, 1980a; Doherty and Williams, 1988a).

Tropical conditions allow more productive time under-water than do temperate conditions. Over many coral reefs, observations can often be made in a shallow, calm, and crystal clear medium. This allows for long, comfortable scuba dives or almost unlimited time simply snorkling at the surface. It provides opportunities for extensive and careful censusing, experiment

tending, or behavioral monitoring by an alert and enthusiastic observer. In contrast to the tropics, the intimidating temperate conditions reduce observational efficiency, accuracy, and precision. It is hard to see fish in a murky milieu. Visibility frequently drops below 3–4 m, the minimum for accurate counts, either by cinetransects or sight transects (Ebeling *et al.*, 1980b; Larson and DeMartini, 1984). And this is not to mention the discouraging prospects for correctly identifying drably colored temperate species in the shade of a kelp canopy, which may eliminate more than 90% of the incident sunlight at midday (Fei and Neushul, 1984).

Divers using the older and thinner neoprene wet suits suffer dyskinesia, distraction, mental disruption, attention loss, and lapse of memory when water temperatures fall below 10°C (Bowen, 1968). This tends to destroy any enthusiasm for the project, let alone a sense of rigorous scientific purpose (A. W. Ebeling, unpublished observations). Observational difficulties when conditions are particularly awful during winter and spring may exaggerate the seasonal effect. In such times and after 20–30 years of watching temperate fishes, an aging ichthyologist tends to "burn (freeze?) out" and become wrongly convinced that temperate systems are hopelessly disturbed and uninviting (A. W. Ebeling, unpublished observations).

B. Sampling Accuracy

The obvious fact that complex substrates contain more nooks and crannies to hide small cryptic species may introduce an unknown amount of bias in temperate–tropical comparisons of reef fish diversity and abundance. Being enormously variegated, convoluted, and ramified, reefs with high coral cover provide a vast potential for concealing fishes of all shapes and sizes (Talbot, 1965). Consequently, attempts have been made to design complete censusing techniques (e.g., Sale and Douglas, 1984). Since many species reveal themselves only at night, a complete census requires around-the-clock observations (Helfman, 1983). Alternatively, combinations of destructive sampling and daytime visual transecting provide total estimates of cryptic and overt coral reef species (Brock, 1954; Bardach, 1959). Yet neither is all revealed on temperate reefs, since they harbor cryptic species in a habitat elaborated by a complex of short and tall algae. Destructive sampling of kelp-bed fishes in California has yielded a host of small cryptic forms, such as clinids, gobies, and clingfishes, that are seldom recorded along standard belt transects (Quast, 1968c). Short of complete censuses, visual belt transects (Brock, 1954) are widely used to estimate fish densities on both temperate and tropical reefs, and much effort has gone into measuring and compensating for the bias of this method (Jones and Chase, 1975; Brock, 1982; Sale and Sharp, 1983; Fowler, 1987; McCormick and Choat, 1987; Lincoln-Smith, 1988).

Because temperate and tropical fish may behave differently, the same sampling techniques may bias samples in different ways. For example, the Rapid Visual Technique (RVT) of Jones and Thompson (1978), which ranks species according to their frequency of encounter, overemphasizes the importance of widespread rare species but underestimates that of patchy but abundant ones (DeMartini and Roberts, 1982). Thus, the technique may bias a tropical census toward evenly distributed species, which are perhaps more consistently visible within the areas censused, but bias a temperate census against abundant species, which tend to move into and out of a target area in large schools. DeMartini and Roberts also point out that human observers tend to consistently underestimate the number of objects in a three-dimensional target such as a dense school of fish. Davis and Anderson (1989) demonstrated this effect dramatically by comparing species abundances estimated by visual transect with "true" abundances determined by marking and resighting fish in systematic censuses of all individuals in a circumscribed area. Visual transect estimates of abundant and aggregated species measured less than half the estimates of "true" abundances. The two estimates of the brightly colored garibaldi (*Hypsypops rubicundus*), which tends to be solitary and spread more evenly, were more in accord.

An additional confounding problem that may render temperate–tropical comparisons difficult stems from the lower regional species richness and larger body sizes of temperate reef fishes (Sections IV,A and B). All else being equal, the same visual sampling method would probably result in fewer errors in species identification and fish abundance estimates in temperate systems.

Because of these biases, tropical–temperate comparisons are suspect even when the same transecting technique was used. For example, Table 1 compares diversity and abundance of tropical western Atlantic (Alevizon and Brooks, 1975) and temperate Californian (Ebeling *et al.*, 1980b) reef fish communities sampled in the exact same way from 2.5-min 8-mm movie strips ("cinetransects"). From this representation, the two assemblages appear similar in local abundance, diversity, and evenness. In total species recorded, the tropical reefs appear to be not much richer than the temperate reefs, although this comparison is probably invalid because of the much smaller number of transects (sample size) filmed from each tropical site. Sample means provide a better basis for comparison: the tropical samples average 67% more species per transect than those from California, even though regional pools of reef fishes contain an estimated 267% more species in the tropical western Atlantic off Venezuela or Florida (Emery, 1978) than off temperate southern California (Quast, 1968b). Although this may represent a real difference between tropical and temperate reef fish communities in their expression of local versus larger-scale patterns of diversity (see Sale, 1980a), the western Atlantic samples may simply be more biased in their underrepresentation of small,

Table 1 Comparison of Cinetransect Samples of Fish Abundance and Diversity between Two Tropical Western Atlantic Coral Reef Sites off Venezuela and Florida[a] and Two Temperate Eastern Pacific Rocky Reef and Kelp Habitats along Coastal California[b]

	Western Atlantic tropical reefs		Eastern Pacific temperate reefs	
	Aves Island, Venezuela	Key Largo, Florida	Santa Barbara, California	Santa Cruz Island, California
Number of transects	32	28	168	185
Mean number of fish	83.3	63.8	64.7	70.6
Total species recorded	44	53	36	34
Rare species (<1.0% of total fish), % of total species	75	64	50	56
Mean number of species	13.0	14.7	8.2	8.4
Mean H' diversity	2.50	2.90	2.42	2.58
Population J' evenness	0.66	0.73	0.74	0.78

[a] Adapted from Alevizon and Brooks (1975).
[b] Adapted from Ebeling et al. (1980b).

cryptic, and nocturnal, or rare and widespread species (see Brock, 1982; DeMartini and Roberts, 1982); the Rapid Visual Technique, wherein such species may be more thoroughly surveyed, yielded substantially higher species numbers in comparable sites off Florida (cf. Jones and Thompson, 1978). Using only the cinetransect samples, therefore, it is difficult to judge whether the tropical western Atlantic assemblage of reef fishes is locally much more diverse than the temperate Californian assemblage, even though the former is derived from a much larger species pool.

More generally, Sale (1980a, Chapter 19) pointed out how different sampling and analytic techniques may influence assessments of degree of similarity among reef fish assemblages in either space or time. We suggest that, in addition, even the identical visual or photographic sampling technique and analysis may tend to distort comparisons of structure between tropical and temperate reef fish communities because of the fundamental differences in their respective habitats.

C. Summary and Conclusions

The marked differences between temperate and tropical environments may contribute to differences in logistic constraints and sampling bias, confounding apparent similarities or differences in their reef fish communities. Counts

of some species may be unrealistically low from many temperate sites where fishes are difficult to observe throughout the year in frequently frigid, turbid, and rough waters overlying bottoms shaded by dense stands of kelp. The usually clearer, warmer, and calmer waters bathing most coral reefs permit longer and more careful censusing and attention to field experimentation. On the other hand, the complex coral substrate (like the macroalgal cover on temperate reefs) may provide more opportunities for cryptic fish species to stay out of sight. All else being equal, moreover, visual species identification and estimates of fish abundances may be less error prone on temperate reefs, which support fewer species and larger fish. Thus, in both systems, a segment of the fish community may remain invisible to nondestructive sampling by transect or quadrat.

Perhaps more attention should be paid to possible behavioral differences between temperate and tropical species of reef fishes. Humans tend to underestimate the number of objects in dense, three-dimensional clusters. If common temperate reef fishes are more likely to move about in dense schools than are their tropical counterparts, for example, the numerical range between abundances of common and rare temperate species observed by nondestructive transect would be artificially small. Yet, the rank or logarithmic transformations of abundance arrays commonly used to obviate this problem tend to mask basic differences in dominance–diversity relations (see e.g., Sale, Chapter 19). Consequently, temperate–tropical comparisons may be suspect even when the same transecting technique was used.

IV. DESCRIPTION OF COMMUNITY STRUCTURE

A. Species Composition and Richness

Regional pools of coral reef fishes are much richer than temperate pools; the number of fish species decreases poleward from the Indo-West Pacific center of tropical diversity (supporting thousands of species), through temperate zones (hundreds of species), to boreal regions (tens of species) (Mead, 1970; Briggs, 1974; Ehrlich, 1975; Springer, 1982). At the low end, boreal rocky reefs of southern New Zealand are dominated by only eight fish species (Kingsford et al., 1989). The latitudinal diversity gradient is correlated with increasing seasonality and frequency of winter storms, and with decreasing solar radiation, geographic area, continuity of productivity, and climatic stability over geologic time in higher latitudes (Emery, 1978). This broad geographic pattern is reflected in regional comparisons. For example, the well-studied tropical western Atlantic and temperate coastal California have regional pools of about 500–600 and 100–200 fish species, respectively

(Emery, 1978; Quast, 1968b). Regional fish diversity also decreases longitudinally on either side of the Indo-West Pacific, with fewer than one-third the species contributing to pools in the Atlantic and eastern Pacific tropics (Briggs, 1974, 1985; Sale, 1980a; Findley and Findley, 1989, for butterfly fishes).

Collectively, tropical reefs have more species per genus (mean = 2.3) and more genera per family (3.0) than temperate reefs (1.5 and 2.1, respectively) (Ross, 1986). Their communities are dominated by perciform and tetraodontiform fishes, which occupy a multitude of niches in their complex habitat. Primarily tropical families, such as the Serranidae, Pomacentridae, Labridae, Gobiidae, and Blenniidae, are among the most diverse for marine fishes (Nelson, 1984). In both the North and South Pacific, temperate reef faunas include warm-temperate or subtropical species derived from the tropics, mostly perciformes, as well as cool- or cold-water species of primarily temperate or boreal origin, such as scorpaeniforms (Mead, 1970). Distinctive tropically derived families occur in temperate regions across the Pacific Ocean. Besides distinct species of pomacentrids, kyphosids, and labrids in both the North and South Pacific, families such as the labridlike Odacidae and Chironemidae (kelpfishes) are typical of the Southern Hemisphere and families such as the Pholidae (eel blennies) and Embiotocidae (surfperches) are abundant in the North Pacific (Mead, 1970).

Relative to temperate reef fish assemblages, this greater diversity of coral reef fishes creates the theoretical potential for more intricate social structures and a greater number of symbiotic relationships (see, e.g., Robertson and Polunin, 1981). However, the role of these interactions in structuring reef fish communities remains unclear (Sale, 1980a), and from what is known of temperate reef fishes, especially of the more recent offshoots from tropical families, many behave much like their tropical counterparts (Sale, 1978a).

The latitudinal increase in richness of reef fish communities between temperate and tropical regions may reflect a decrease in tolerance of environmental variability between temperate and tropical species. Compared to tropical species, temperate species must tolerate much greater ranges of seasonal change and interannual fluctuation in climate. In regions of large seasonal variation, such as the North Atlantic, many temperate fishes pass the winter period of frigid cold, storm turbulence, and loss of cover or food in a state of hiding and torpor (Emery, 1978; Olla et al., 1979). Where seasonal fluctuations are less, such as the eastern North Pacific, adaptations are less extreme. Some species acclimate to seasonal change in the same habitat; others undergo onshore–offshore migrations. Spawning seasons are adjusted, with the more northern species tending to spawn in the winter months and the more southern forms during spring and summer (Tarzwell, 1970; Moulton, 1977; Leaman, 1980). Reanalyzing others' data, Stevens (1989) suggested that

tolerances for broader seasonal conditions account for "Rapoport's rule," which states that a poleward decrease in species richness is accompanied by an increase in species ranges, as among Californian coastal fishes (Horn and Allen, 1978). The greater yearly variation in, for example, temperature at higher latitudes favors the evolution of broader climatic tolerances of the resident species. This "preadapts" them to occupy wider latitudinal ranges as well. Stevens reasoned that if tropical species typically have much narrower environmental tolerances than their temperate counterparts, their equal or greater dispersal abilities would more frequently place them beyond their preferred ranges and into areas where they can compete less successfully. Thus, a steady input of inferior competitors may in itself augment local diversity in the tropics (see Section V,G).

Nonetheless, the richness of some temperate assemblages of reef fishes can be enhanced by the intermingling of species from different faunas historically adapted to different climatic regimes (Quast, 1968b; Choat, 1982; but see Moreno and Jara, 1984). Meridional ranges of warm- and cool-temperate species may fluctuate from year to year with shifting currents and climatic trends (Hubbs, 1974; Stephens and Zerba, 1981; Choat and Ayling, 1987; Ebeling and Laur, 1988; Jones, 1988a). Thus, temperate warm- and cool-water faunas tend to merge in transitional zones of abrupt changes in temperature and other environmental factors, which may vary in magnitude and extent from one year to the next. Warm interannual periods favor species more recently derived from tropical ancestors; cooler periods favor species historically adapted to seasonal fluctuations of temperature and other environmental conditions within a cooler range (Stephens et al., 1970; Patton, 1985). Interannual climatic shifts have occurred, for example, off the western coast of North America over thousands of years, as recorded in long-term temperature records and through strata in aboriginal refuse heaps (Hubbs, 1948, 1960, 1967). In sum, a temperate reef assemblage in the middle latitudes may vary in its relative abundances of cool- versus warm-tolerant species and include summer or winter visitors as well as year-round residents (Moulton, 1977; Olla et al., 1979; Ebeling et al., 1980b; Stephens and Zerba, 1981; Patton, 1985).

B. Body Size and Reproduction

There is some evidence that average body size of adult marine teleosts is smaller in the tropics than in cooler temperate regions. Some two-thirds of all small-bodied (<10 cm long) marine teleosts live in the tropics, and the frequency of small-bodied species relative to the total teleostean fauna tends to decrease from about 18% in warm south-temperate waters to about 10% in the tropics, 8% in the warm north-temperate zone, and only 6% in cool

north-temperate waters (Miller, 1979, using data from Lindsey, 1966). Within primarily tropical families such as Pomacentridae (damselfishes) and Labridae (wrasses), the relatively few derived subtropical or warm-temperate species are often larger than their tropical relatives (Choat, 1982). Furthermore, body size may increase with latitude within a single species, as in the hexagrammid *Oxylebius pictus* in the eastern North Pacific (DeMartini and Anderson, 1978).

While the causes of body-size differences are beyond the scope of this review (see Warburton, 1989), the ecological ramifications of this phenomenon may be considerable. Larger, nonterritorial individuals generally move longer distances with greater inclination to go from reef to reef than smaller fish, whether temperate or tropical (Bardach, 1958; Robertson, 1988a). This pattern reflects the fact that larger fish occupy larger home ranges than smaller fish (Sale, 1978a), perhaps due to decreasing food availability with increasing body size (Schoener, 1968). Within-family comparisons between latitudes bolster this conclusion. For example, small tropical damselfishes defend much smaller territories (only about 1 m^2) (Low, 1971; Myrberg and Thresher, 1974; Williams, 1978) than their large temperate counterparts (ca. 10 m^2) (Clarke, 1970; Moran and Sale, 1977; Norman and Jones, 1984).

Along with body size, a latitudinal increase in egg size but decrease in larval dispersal distinguish temperate from tropical demersal spawners (Thresher, 1988, Chapter 15). This difference is less well expressed in pelagic spawning species. Wide dispersal may be less important in temperate species, which need not be distributed among isolated patches of coral (Barlow, 1981) and would not benefit from offshore transport (Parrish *et al.*, 1981). Consequently, perhaps, coastal populations of temperate reef fishes off California seem to show greater genetic differentiation (Davis *et al.*, 1981) than do coral reef species in the western Pacific Ocean (Ehrlich, 1975; Doherty and Williams, 1988a). Temperate faunas also have a higher proportion of viviparous species, including the North Pacific Embiotocidae, whose females bear advanced young occupying the same general habitat type as their parents (Baltz, 1984).

Environmental seasonality (Section II,B) has its greatest effect on the reproductive cycle of reef fishes. Whereas many coral reef fishes spawn all year (Ehrlich, 1975; Johannes, 1978a; Sale, 1980a; McFarland and Ogden, 1985; Doherty and Williams, 1988a), most temperate species spawn during the spring and summer when planktonic productivity providing food for fish larvae is greatest (Lowe-McConnell, 1979; Miller and Geibel, 1973; Stephens and Zerba, 1981; Guillemot *et al.*, 1985; Wyllie Escheverria, 1987; Jones, 1988a). In cool-temperate Puget Sound, for example, spawning of most species peaks during late spring and summer, while only about 25% of the species spawn in fall and winter (Moulton, 1977). Spring and summer herald an influx of first-year juveniles onto temperate reefs (see also Kingett and

Choat, 1981; Stephens *et al.*, 1986; Ebeling and Laur, 1988). Although coral reef fishes have peak spawning periods that coincide with current patterns, productivity pulses, or moon phases and associated tidal cycles (Munro *et al.*, 1973; Johannes, 1978a; Sale, 1980a; Thresher, 1984; Lobel, 1989), they generally show extreme variation in spawning periodicities among species (McFarland and Ogden, 1985). If coral reef species, such as anemonefishes, inhabit subtropical or warm-temperate regions as well, their temperate populations may show more seasonality in their breeding cycles (Moyer, 1980).

C. Foraging Guilds

Temperate and tropical reef fish faunas may differ in trophic structure as well as taxonomic composition (Bakus, 1969; Choat, 1982; Jones, 1988a). Here, we consider five major foraging guilds (*sensu* Root, 1967), as summarized in Table 2. We do not consider several minor guilds, such as detritivores, which are relatively poorly studied.

   Midwater microcarnivores pick small prey off various elevated surfaces. Certain small wrasses and other species often select prey from blades of macroalgae. As opportunistic "cleaner fishes," such species occasionally pick ectoparasites from larger fishes in temperate waters, but may be more specialized as cleaners in the tropics (Limbaugh, 1961; Hobson, 1971; Losey, 1972a; Bray and Ebeling, 1975). Experimental removals of the cleaner wrasse *Labroides dimidiatus* by Youngbluth (1968), Losey (1972a), and Gorlick *et al.* (1987) falsified previous suggestions that cleaning mutualism enhances the local abundance of host species (Limbaugh, 1961).

   Demersal microcarnivores and *mesocarnivores* together constitute the principal carnivore biomass in both temperate and tropical faunas. The microcarnivores select tiny prey from the benthic community with their small mouths, while the mesocarnivores ambush larger motile prey, including small fish, or seek more sedentary macroinvertebrates, such as gastropods and echinoderms. At the family level, the microcarnivores were apparently derived phylogenetically from the more generalized, large-mouthed mesocarnivores (Kotrschal, 1988). Microcarnivores, whose main food is often amphipods in temperate and subtropical systems (Quast, 1968d; Choat and Kingett, 1982; Laur and Ebeling, 1983; Moreno and Jara, 1984; Hallacher and Roberts, 1985; Schmitt and Coyer, 1983; Kotrschal and Thomson, 1986), forage during the day and hide at night; mesocarnivores, such as serranids and scorpaenids, feed during dawn or dusk and at night (Hobson, 1973, 1974; Hobson and Chess, 1976; Ebeling and Bray, 1976; Hobson *et al.*, 1981; Helfman, 1986b). Eastern North Pacific kelp forests also support large numbers of mesocarnivores that may switch among prey types (small fishes, plankton, and substrate-oriented prey) either in midwater among algal fronds or on the bottom

Table 2 Comparison of Foraging-Guild Structure in Temperate Rocky and Tropical Coral Reef Fishes[a, b]

Guild[a]	Temperate reefs	Tropical reefs
Midwater microcarnivores	Small prey picked off large macroalgae and opportunistically off other fish (e.g., wrasses, various juveniles)	Ectoparasites picked off other fish exclusively (mostly wrasses)
Demersal microcarnivores	Most diverse guild in both systems; small invertebrate prey picked off primary and secondary substrates	
	(e.g., surfperches, various juveniles)	(e.g., butterflyfishes, gobies, various juveniles)
Demersal mesocarnivores	No major functional difference between systems; consume macroinvertebrates and small fish	
	(e.g., rockfishes, sculpins, greenlings)	(e.g., scorpionfishes, anglerfishes, hawkfishes)
Macrocarnivores	Mostly transient piscivores (e.g., sharks, electric rays)	Resident and transient piscivores (e.g., sharks, jacks)
Planktivores	Mostly diurnal; consume mostly transient zooplankton (e.g., damselfishes, various juveniles)	Diurnal and nocturnal; nocturnal species consume resident zooplankton (e.g., damselfishes, cardinalfishes)
Herbivores	Low diversity and abundance (e.g., kyphosids)	High diversity and abundance (e.g., damselfishes, parrotfishes, surgeonfishes)

[a] The examples of families in each guild refer to large adult fish, unless indicated otherwise.
[b] From G. S. Helfman (1978). Patterns of community structure in fishes: Summary and overview. *Environ. Biol. Fishes* **3**, 129–148. Reprinted by permission of Kluwer Academic Publishers.

(Love and Ebeling, 1978; Hallacher and Roberts, 1985). The kelp bass (*Paralabrax clathratus*) and various midwater rockfishes (*Sebastes*) make up a substantial proportion of the total mesocarnivore abundance and biomass on some reefs (Love and Ebeling, 1978; Hallacher and Roberts, 1985). There is probably greater predation by mesocarnivores on benthic invertebrates in the tropics (Vermeij, 1978; Choat, 1982). In contrast to temperate reefs, where fishes may have little effect on the overall abundance of benthic invertebrates (e.g., Choat and Kingett, 1982; Laur and Ebeling, 1983; reviewed by Choat, 1982), tropical reefs have prey restricted to small crevices, holes, and other refuges from fish predation (e.g., Menge *et al.,* 1985; Hixon and Brostoff, 1985; reviewed by Hixon, 1986; Choat, Chapter 6).

Macrocarnivores include large piscivorous species, such as sharks and jacks on coral reefs. Hixon (Chapter 17) devotes an entire chapter to this guild and its effects in coral reef fish communities. The evidence suggests that both

piscivory and adaptations among prey fish to minimize the risk of predation are widespread, but that the community-level effects of such predation are largely unknown. On temperate reefs, the dominant piscivores include sharks, electric rays, and larger sea basses (Quast, 1968b; Bray and Hixon, 1978). Pinniped marine mammals join this guild in consuming reef fishes, although the impact of such predation is largely unknown (Section V,C).

Planktivores are either diurnal or nocturnal species that eat plankton imported by ocean currents or generated on the reef itself. Randall (1967) listed 26 families of Caribbean reef fishes containing species that eat zooplankton. Diurnal species that are planktivores as adults include various serranids, pomacentrids, and labrids (Davis and Birdsong, 1973). In addition, almost all the other species consume plankton during early life history stages on both temperate and tropical reefs (Davis and Birdsong, 1973; Hobson, 1982; Singer, 1985). Although numerous planktivorous species inhabit coral reefs, only a few warm-temperate or subtropical species (mostly pomacentrids) are present in higher latitudes (Springer, 1982). Even so, the planktivore biomass is about the same in temperate and tropical habitats (Talbot and Goldman, 1972; Goldman and Talbot, 1976; Russell, 1977; Ebeling *et al.*, 1980b; Hobson, 1982; Kingsford, 1989). On some reefs off California, for example, blacksmith (*Chromis punctipinnis*) (Bray, 1981) and blue rockfish (*Sebastes mystinus*) (Burge and Schultz, 1973; Miller and Geibel, 1973; Hallacher and Roberts, 1985) make up a substantial portion of the total reef fish biomass in southern and central regions, respectively. The relatively few species of obligate and part-time planktivores made up some 67% of the numbers and 50% of the biomass of fishes on a temperate reef off southern California (Ebeling *et al.*, 1980b). Resident nocturnal planktivores are more abundant in coral reef habitats (Helfman, 1986b), although juveniles and adults of some species off southern California enter the reef habitat at night and pick plankton (Hobson and Chess, 1976; Ebeling and Bray, 1976; Hobson *et al.*, 1981).

Herbivores comprise a major foraging guild on coral reefs in terms of both species diversity and biomass (reviewed by Ogden and Lobel, 1978; Horn, 1989). Despite their low standing crop, benthic algae on coral reefs support a diverse guild of herbivorous fishes absent from temperate reefs (see Section IV,C). The high productivity and turnover of closely cropped filamentous algae appear to compensate for low standing crops as a forage base for fishes (Montgomery, 1980). Indeed, the biomass of herbivores rivals that of planktivores in being the largest of any foraging guild (Brock *et al.*, 1979). Many damselfishes, blennies, parrotfishes, surgeonfishes, and rabbitfishes graze algae. Russ (1984a,b) provides a detailed analysis of the distribution and abundance of such fishes over the Great Barrier Reef in Australia, and the activities of these abundant grazers can have major effects on benthic community structure (reviewed by Hixon, 1983, 1986; Choat, Chapter 6).

On the other hand, herbivory is relatively uncommon among temperate reef fishes (Bakus, 1966, 1969; Gaines and Lubchenco, 1982; Choat, 1982; Jones, 1988a). The dearth of herbivorous fishes in cold waters may involve temperature-limited rates of digestion of plant material, which has a lower caloric density and is less easily degradable than animal food, relative to the energetic needs of such large and mobile species (see Mead, 1970; Montgomery and Gerking, 1980; Ralston and Horn, 1986; Horn, 1989). Among cool-temperate fishes off California, for example, the truly herbivorous category seems to be limited to a few, relatively inactive pricklebacks (Stichaeidae), which inhabit algal tufts in the intertidal zone and rarely move from these predictable food sources (Horn *et al.*, 1982; Ralston and Horn, 1986). The large and active plant eaters of temperate waters tend to be more generalized than their tropical counterparts and are more adaptable to a temporally variable and less predictable food supply (Horn, 1989). For example, plant-cropping subtidal species, such as the kyphosids *Girella nigricans* and *Medialuna californiensis*, consume substantial amounts of animal matter along with the algae (Quast, 1968d; Ebeling and Laur, 1988). It is not surprising that the reef fish communities of boreal regions contain no herbivorous species (Briggs, 1974; Moreno and Jara, 1984; Kingsford *et al.*, 1989).

D. Daily Activity Patterns

The structure of reef fish assemblages varies temporally as diurnal, crepuscular, and nocturnal species follow their daily cycles of activity. Hobson (1965, 1968, 1972, 1973, 1974, 1982, Hobson *et al.*, 1981), among others (e.g., Collette and Talbot, 1972), has described the diel changeover: In the evening, the diurnal fishes retire in orderly fashion to refuges in and about the reef, with smaller individuals preceding larger individuals both among and within species; in the morning, the reverse progression ensues. Following a twilight "quiet period" of little activity in the water column, nocturnal species emerge. In general, the diurnal species are more taxonomically derived with specializations of small, protrusible jaws for microcarnivory, or strong jaws and prolonged alimentation for herbivory; nocturnal species are more generalized for mesocarnivory. There are no nocturnal herbivores. Thus temporal partitioning is usually between representatives of different teleostean suborders or even orders. Larger piscivores tend to drive the system in that they are most active in and about the quiet period when the diurnal and nocturnal shifts are most vulnerable (Collette and Talbot, 1972; Hobson *et al.*, 1981; see also Hixon, Chapter 17).

Within this general scheme, the behavior of tropical reef fishes may be more tightly organized or programmed than that of their temperate counterparts (Choat, 1982). For example, Helfman's (1978) review of previous work

indicates that a greater percentage of the tropical reef fish community has a structured cycle of diel activity (Table 3). The twilight changeover between diurnal and nocturnal assemblages may occur more quickly and orderly in the tropics than in temperate regions (see Hobson, 1972, 1973; Ebeling and Bray, 1976; Helfman, 1986b), although this apparent difference may simply reflect the activities of greater numbers of nonsedentary species in the tropical assemblages (Hobson *et al.*, 1981). Coral reef species may have longer and more consistent migratory routes between feeding and sleeping areas (Ogden

Table 3 Temporal Structure in Representative Communities of Temperate and Tropical Reef Fishes, Based on the Species' Feeding and/or General Activity Patterns[a]

Locality	Number of species with a known activity cycle	Percentage with a major period of activity	Percentage diurnal	Percentage nocturnal	Reference
TEMPERATE ROCKY REEFS					
Santa Barbara, California	23	70	57	13	Ebeling and Bray (1976)
Catalina Island, California	10	90	40	50	Hobson and Chess (1976) (planktivores only)
Catalina Island, California	27	93	63	30	Hobson and Chess (1976)
Average =		84.3[b]	53.3	31.0	
TROPICAL ROCKY OR CORAL REEFS					
Southern Gulf of California	53	96[c]	47	38	Hobson (1965, 1968)
Alligator Reef, Florida Keys	159	92[d]	43	44	Starck and Davis (1966)
Lameshur Bay, Virgin Islands	85	88[e]	46	33	Collette and Talbot (1972)
Lameshur Bay, Virgin Islands	61	97	67	30	Smith and Tyler (1972)
Kona, Hawaii	143	97[f]	72	24	Hobson (1972)
Average =		94.0[b]	55.0	33.8	

[a] Adapted and expanded from Helfman (1978, Table 3, p. 133).
[b] Significantly different (t-test of arcsine-transformed values, $P < 0.01$).
[c] Includes nine crepuscular and two nocturnal-crepuscular species.
[d] Includes four crepuscular species.
[e] Includes two crepuscular and four each of diurnal-crepuscular and nocturnal-crepuscular species.
[f] Includes one crepuscular species.

and Buckman, 1973; McFarland *et al.*, 1985; Helfman, 1986b). This trend of decreasing organization in diel activity pattern continues with increasing latitude. For example, the twilight changeover is least structured for kelp-bed fishes in cold-temperate Puget Sound, Washington, where there are no warm-temperate or subtropical species (Moulton, 1977) than off southern California where there are many of both kinds (Ebeling and Bray, 1976) (Fig. 5).
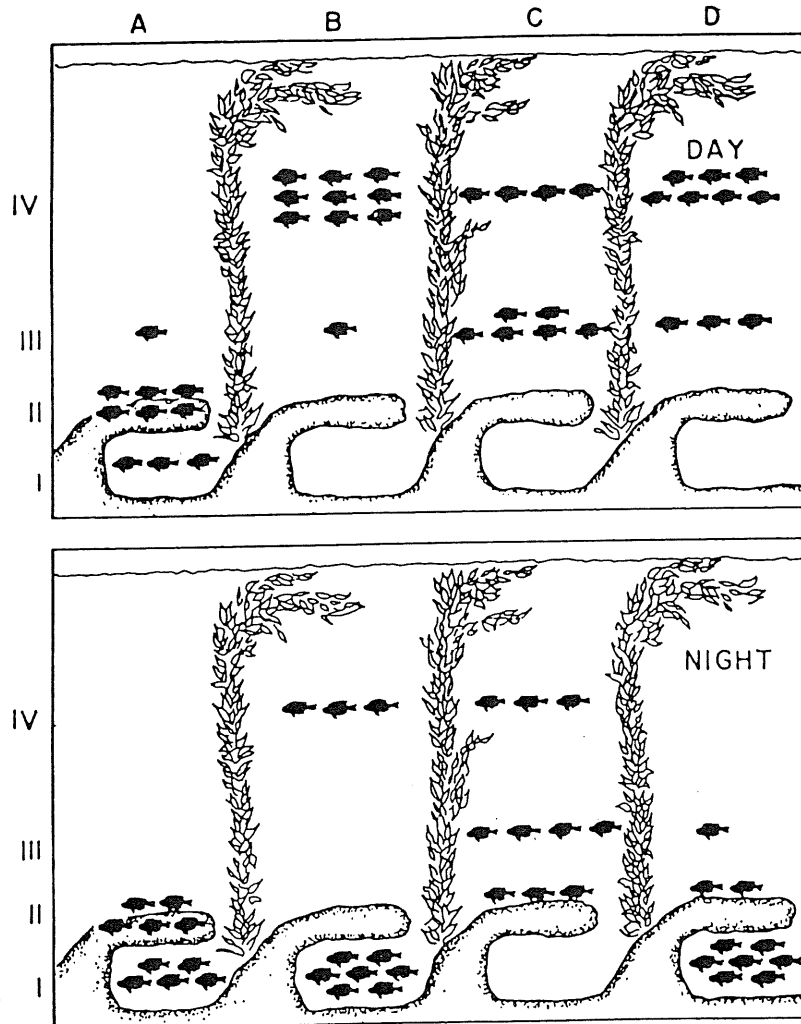
Figure 5   Day and night positions of reef fishes in a kelp forest off Santa Barbara, southern California, comparing (A) seven sedentary bottom species, (B) four mobile mesocarnivores, (C) six mobile demersal microcarnivores, most with primary temperate origins, and (D) five mobile demersal and/or midwater microcarnivores, all with close tropical relatives, observed in shelters (I), exposed on the bottom (II), within 1 m of the bottom (III), or in midwater (IV). Within each guild, one fish represents 10% of observations. [From Ebeling and Bray (1976, Fig. 2, p. 714).]

E. Summary and Conclusions

Tropical regions support more species of reef fishes than temperate areas by at least an order of magnitude. However, there is little evidence that this theoretically greater potential for interactions among coral reef species plays a major role in structuring their communities.

While the coral reef fish fauna is virtually circumglobal, the temperate array of faunas consists of independent elements separated longitudinally by the continental landmasses and latitudinally by the tropics. Along the continental coasts, north–south faunal boundaries fluctuate as warm-temperate and cold-temperate regions overlap in zones of transition. In these zones, species of different faunas mingle to various extents depending on yearly shifts in the oceanographic climate.

Temperate reef fishes tend to attain larger body sizes than their coral reef counterparts. The large numbers of small-bodied teleostean fishes in tropical marine habitats can exploit the diversity of small prey hiding in the myriad nooks and crannies of the coral substrate. Larger-bodied temperate species may tend to be somewhat more vagarious, having larger home ranges and territories. Temperate fish faunas include relatively more viviparous species and may, with some notable exceptions, have less dispersive larval and juvenile stages. Since ranges of temperate species are more one dimensional, there may be less advantage to disperse beyond the immediate coastal zone.

Temperate and tropical communities of reef fishes converge in many trophic characteristics but differ markedly in others. Carnivores are the most abundant and diverse foragers in both communities, but predation on benthic invertebrates may be greater in the tropics. Even though the total abundance and biomass of adult planktivores may be similar in temperate and tropical reef communities, the number of planktivore species is greater in the tropics. Most juveniles are planktivorous in both communities. The main difference in community trophic structure is in herbivory. Although a rich and abundant group of herbivorous species characterizes the coral reef fish communities, relatively few species are strictly herbivorous on cool-temperate rocky reefs. It has been suggested that the dearth of herbivorous reef fishes in cold marine waters may be due in part to restrictions on the rate of digestion, relative to other metabolic processes, at cooler temperatures.

On both temperate and tropical reefs, fishes show pronounced daily cycles in activity. A quiet period at twilight marks the transition between occupation of the water column by specialized species of microcarnivores and herbivores during the day and by generalized species of mesocarnivores at night. Large piscivores are most active in and about the quiet period when the smaller fishes are most vulnerable. This diel behavior pattern appears to be most structured in coral reef fish communities, and progressively less so in warm-temperate

and cold-temperate communities, which are less diverse and contain fewer tropically derived species.

V. REGULATION OF COMMUNITY STRUCTURE

Do temperate and tropical assemblages of reef fishes differ fundamentally in the mechanisms that regulate the patterns of distribution and abundance of their resident species? As members of more diverse assemblages in a presumably stable environment, do coral reef fishes usually coexist by partitioning space, food, and time resources as a result of present or past competitive interactions? As members of assemblages in more seasonally variable habitats, do fishes of temperate reefs co-occur below numbers where competition is important? These questions were often answered in the affirmative before the 1980s (reviewed by Sale, 1980a; Doherty and Williams, 1988a). Within the past decade, however, other models of community regulation have gained favor to the extent that, in a recent review, Doherty and Williams (1988a) averred: "The most important result [of the past decade's experiments] has been the repeated falsification of the hypothesis that populations of coral reef fishes are generally limited by the carrying capacities of reef environments, because this result removes the greatest difference separating studies of reef fishes from those of teleost populations in other neritic environments" (p. 544).

So foretold, we examine the evidence for the hypothesized mechanisms that may regulate the distribution and abundance of temperate and tropical reef fishes (see reviews by Doherty and Williams, 1988a; Mapstone and Fowler, 1988; Sale, Chapter 19). We do not attempt an exhaustive review of the literature. Rather we examine representative studies relevant to each model of community regulation. Thus, the number of studies tabulated in reviewing each model is not necessarily correlated with the validity of that hypothesis. This may be especially true of the circumstantial evidence for "niche diversification" (Section V,A), which was the prevailing research paradigm of the 1960s and into the 1970s (Sale, Chapter 19).

A considerable number of models of community regulation have been proposed. Our list mostly follows that of Connell's (1978) review, but also includes more recent ideas (recent in the sense of being applied to reef fishes), such as "recruitment limitation" (D. M. Williams, 1980; Doherty, 1980, 1982a, 1983a) and "sources and sinks" (Pulliam, 1988). Because there is presently no evidence from reef fish systems (either pro or con) concerning the "circular networks" model from Connell's (1978) review, we do not consider this hypothesis, although the possibility of "predatory networks" (Hixon, Chapter 17, this volume) is intriguing.

A. Competition and Niche Diversification

The "niche diversification hypothesis" maintains that past or present interspecific competition is the predominant process structuring an assemblage. There are basically two versions of this hypothesis. The first states that species have evolved specializations preventing competitive exclusion in an environment where available resources were limited through evolutionary time [the coevolutionary "ghost of competition past" (*sensu* Connell, 1980)]. The second version states that, despite ongoing present-day competition, the environment somehow provides refuges for subordinate competitors or situations where each competitor dominates a particular subhabitat or other subdivision of a limited resource base (reviewed by Colwell and Fuentes, 1975). Thus, in both versions, species are expected to exhibit "resource partitioning," occupying different microhabitats, eating different suites of prey, or being active in different time slots (e.g., Pianka, 1973; Schoener, 1974).

Because the niche diversification hypothesis was the most popular model of community regulation of the 1960s and 1970s, it has received far more attention than any other in studies of reef fish communities. We surveyed the primary literature to test the following predictions from this hypothesis for reef fishes (Table 4). If a community is structured by niche diversification, then: (1) The microhabitat distributions, diets, or perhaps times of activity (covered in Section IV,D) of the component species should show consistently low overlap ("resource partitioning"). Such partitioning should often be expressed as "niche complementarity," where co-occurring species that overlap greatly in one niche dimension (say, diet) separate along another dimension (say, microhabitat). (2) Distributions of potential competitors should be complementary at broader scales; they should displace one another geographically, as conditions favor one species over the other ("geographic complementarity"). Note that such patterns are also consistent with the sources and sinks model (see below). (3) Experimental removal of a species should result in expanded resource use by its competitors ("species complementarity"). (4) Vacated living space should be quickly regained, so patterns of distribution and abundance should be resilient when perturbed ("resiliency"). (5) Succession within newly created sites should culminate in the same equilibrial assemblage ("climax"). (6) The environment should be saturated with fish, to the extent that, for example, all holes and refuges are filled with appropriately sized individuals ("shelter saturation"). (7) An increase in the limiting resource, for example, shelter sites or food, should increase the abundance of fish ("resource limitation").

We present Table 4 as an incomplete and simplified overview of our current predicament regarding each of the preceding predictions. Table 4 does not include studies that focused on possible competition within species

Table 4 Outcomes of Representative Tests of the Predictions from the Niche Diversification Hypothesis of Regulation of Reef Fish Community Structure, Comparing Temperate Assemblages of the Eastern North Pacific with Tropical Assemblages of the Western North Atlantic/Caribbean and Indo-Pacific Regions[a]

Region	Prediction	Group	Prediction supported?	Reference
A. TEMPERATE ROCKY REEFS				
1. Circumstantial Evidence				
Eastern North Pacific	Resource partitioning	All	Yes	Quast (1968b)
		All	Maybe	Hobson and Chess (1976)
		All	Maybe	Yoshiyama (1980, 1981)
		All	Yes	Cross (1982)
		All	Yes	Gascon and Miller (1982)
		All	Yes	Larson and DeMartini (1984)
		All	Yes	Grossman (1986)
		Blennies	Yes	Stephens *et al.* (1970)
		Blennies	Yes	Kotrschal and Thomson (1986)
		Eel blennies	Yes	Barton (1982)
		"Picker-type" fishes	Yes	Bray and Ebeling (1975)
		Rockfishes	Yes	Love and Ebeling (1978)
		Rockfishes	Yes	Larson (1980)
		Rockfishes	Yes	Hallacher and Roberts (1985)
		Sculpins	No	Norton (1989)
		Surfperches	Yes	Alevizon (1975)
		Surfperches	Yes	Ellison *et al.* (1979)
		Surfperches	Yes	Hixon (1980a)
		Surfperches	No	Ebeling and Laur (1986)
		Surperches	Yes	Holbrook and Schmitt (1986)
	Geographic complementarity	Blennies	Yes	Stephens *et al.* (1970)
		Surfperches	Yes	Hixon (1980a)
		Surfperches	Yes	Schmitt and Coyer (1983)
	Resource limitation	All	No	Stephens and Zerba (1981)
		Surfperches	Yes	Schmitt and Holbrook (1986)
		Surfperches	Yes	Stouder (1987)
2. Experimental Evidence				
Eastern North Pacific	Species complementarity	Rockfishes	Yes	Larson (1980)
		Surfperches	Yes	Hixon (1980a)

Table 4 *Continued*

Region	Prediction	Group	Prediction supported?	Reference
		Surperches	Yes	Schmitt and Holbrook (1986)
	Climax	All	Yes	Fager (1971)
		All	Yes	Gascon and Miller (1981)
		All	Yes	Carter *et al.* (1985)
	Resiliency	All	Yes	Thomson and Lehner (1976)
		All	Yes	Grossman (1986)
	Resource limitation	Gobies and midshipmen Surfperches	Yes Yes	Breitburg (1987a) Hixon (1980a)
		Rockfishes	Yes	Larson (1980)
		Wrasse and blenny	Yes	Thompson and Jones (1983)
B. TROPICAL CORAL REEFS				
1. Circumstantial Evidence				
Western Atlantic and Caribbean	Resource partitioning	All	Yes	Smith and Tyler (1973a)
		All	Yes	Parrish and Zimmerman (1977)
		All	Yes	Gladfelter and Gladfelter (1978)
		All	Yes	Luckhurst and Luckhurst (1978a,b)
		All	Maybe	Findley and Findley (1985)
		Angelfishes	Yes	Hourigan *et al.* (1989)
		Butterflyfishes	No	Clarke (1977)
		Butterflyfishes	Yes	Neudecker (1985)
		Damselfishes	Yes	Emery (1973)
		Damselfishes	Yes	Clarke (1977)
		Damselfishes	Yes	Ebersole (1985)
		Groupers	Yes	Roughgarden (1974)
		Squirrelfishes	Yes	Gladfelter and Johnson (1983)
		Surgeonfishes	No	Roughgarden (1974)
	Shelter saturation	All	Yes	Smith and Tyler (1972)
		All	Yes	C. L. Smith (1978)
Indo-Pacific	Resource partitioning	All	Yes	Hiatt and Strasburg (1960)
		All	Yes	Gosline (1965)
		All	Maybe	Talbot and Goldman (1972)

(continued)

Table 4 *Continued*

Region	Prediction	Group	Prediction supported?	Reference
		All	No	Bradbury and Goeden (1974)
		All	Maybe	Goldman and Talbot (1976)
		All	Yes	Harmelin-Vivien (1977)
		All	No	Russell *et al.* (1974)
		Butterflyfishes	Yes[b]	Anderson *et al.* (1981)
		Butterflyfishes	No[b]	Sale and Williams (1982)
		Butterflyfishes	Yes	Harmelin-Vivien and Bouchon-Navaro (1983)
		Butterflyfishes	Yes	Bouchon-Navaro (1986)
		Butterflyfishes	Maybe	Motta (1988)
		Butterflyfishes	Maybe	Findley and Findley (1989)
		Damselfishes	Yes	Fishelson *et al.* (1974)
		Damselfishes	No	Sale (1974)
		Damselfishes	Yes	Robertson and Lassig (1980)
		Damselfishes	No	Tribble and Nishikawa (1982)
		Damselfishes	Maybe	Sale *et al.* (1984a)
		Damselfishes	Yes	Jones (1988b)
		Squirrelfishes	Yes	Vivien and Peyrot-Clausade (1974)
		Surgeonfishes	Maybe	Jones (1968)
		Surgeonfishes	Maybe	Robertson *et al.* (1979)
		Surgeonfishes	Yes	Robertson and Gaines (1986)
		Surgeonfishes and damselfishes	Yes	Robertson and Polunin (1981)
	Resource limitation	Damselfishes	Yes	Thresher (1983a,b, 1985a)
		Planktivores	Yes	Hobson and Chess (1978)
		Planktivores	Yes	Hamner *et al.* (1988)
	Shelter saturation	Damselfishes	No	Sweatman (1983)
2. Experimental Evidence				
Western Atlantic and	Climax	All	Maybe	Bohnsack and Talbot (1980)
Caribbean	Resiliency	Damselfishes	Yes	Williams (1978)

(continued)

Table 4 *Continued*

Region	Prediction	Group	Prediction supported?	Reference
		Damselfishes	Yes	Waldner and Robertson (1980)
	Resource limitation	Herbivores	Yes	Robertson et al. (1976)
		All	Yes	Shulman (1984)
		All	Yes	Hixon and Beets (1989)
Indo-Pacific	Climax	All	Maybe	Nolan (1975)
		All	No	Sale and Dybdahl (1975)
		All	No	Talbot et al. (1978)
		All	No	Sale (1980b)
	Resiliency	All	Yes	Brock et al. (1979)
		All	Yes	Sale (1980b)
		Damselfishes	Yes	Belk (1975)
	Resource limitation	Herbivores	No	Roberts (1987)
		Surgeonfishes	Yes	Robertson and Gaines (1986)
		Damselfishes	No	Jones (1988b)

[a] Predictions of the hypothesis are tested by circumstantial or experimental evidence. Under circumstantial evidence it is indicated whether or not there is support that species within a guild: overlap little in their use of resources ("resource partitioning"), complement one another in geographical distribution ("geographic complementarity"), appear as a group to be limited by resources ("resource limitation"), or appear to saturate available refuges ("shelter saturation"). Under experimental evidence it is indicated whether or not there is support that species within a guild: complement one another when one is removed ("species complementarity"), colonize artificial reefs in similar relative abundances ("climax"), assume original relative abundances after perturbation ("resiliency"), or respond in distribution or abundance to manipulated resources ("resource limitation").
[b] Different interpretations of the same data set.

(e.g., Nursall, 1977; Robertson and Sheldon, 1979; Robertson et al., 1981; Sweatman, 1985a; Jones, 1987a,b) because such interactions do not bear directly on niche diversification between species. Our attempt to categorize representative studies as supporting ("yes" in Table 4), partially supporting ("maybe"), or falsifying ("no") each of these predictions emphasizes only temperate systems along the Pacific coast of North America and coral reef systems of the Indo-Pacific and western Atlantic. So limited, this circumstantial and experimental evidence indicates that, contrary to the classic notion that the greater diversity of coral reef fish fauna reflects the narrower and more finely partitioned niches of its species (see, e.g., Mead, 1970; Briggs, 1974), the niche diversification hypothesis may actually apply equally well or even better to temperate reef fish communities. Besides the fact that our review is

not exhaustive, however, we must add the following general caveats: descriptions of patterns of distribution, abundance, and resource use are only suggestive; the lingering results of past competition are not verifiable (Connell, 1980); and the number of positive outcomes in studies of competition is generally high because researchers tend to investigate this process in systems where they suspect that it is likely to occur (Connell, 1983; Schoener, 1983b).

The various kinds of circumstantial evidence for and against the existence of competition and niche diversification suggest that the hypothesis applies equally well to temperate and tropical systems (see "circumstantial evidence" in Table 4). The percentages of outcomes consistent with the hypothesis ("yes" and "maybe" categories) are quite high for "temperate rocky reefs" as well as "tropical coral reefs" (88% of 26 studies and 82% of 44 studies, respectively). The large majority of such evidence pertains to the relatively tenuous prediction of resource partitioning, however. A typical example is of six species of rockfishes (*Sebastes* spp.) co-occurring in kelp forests off central California [Larson (1980) and Hallacher and Roberts (1985) in section A, 1 of Table 4], wherein the species were shown to segregate vertically in the water column as well as by depth along the bottom (Fig. 6). Among all examples relating to resource partitioning in Table 4, percentages of outcomes consistent with the prediction are again very high for the temperate and tropical studies cited (90% of 20, and 82% of 38 studies, respectively). In addition, the partitioning of time as diel patterns of activity occurs in both systems, although the twilight changeover in species occupying the water column appears to be progressively less structured for the simpler reef fish communities at higher latitudes (Section IV,D). Overall, therefore, our results corroborate those of Ross's (1986) more extensive review and analysis of resource partitioning among fishes in general. He also found little difference in patterns between temperate and tropical reef fish assemblages; percentages of temperate and tropical species pairs showing at least one "substantial difference" in use of food, space, or time were 80 and 82%, respectively. Nonetheless, Ross cautioned that such differences may simply reflect chance divergences in the species' evolutionary histories, having nothing to do with competiton (see also Sale, 1979b; Connell, 1980). Peter Sale (personal communication) put the matter more bluntly: "Given that three species of fish on a reef will inevitably differ in some aspect of what they do, how useful is a triumphant documentation of resource partitioning anyway?" (see also Sale, Chapter 19).

The experimental evidence actually suggests that niche diversification may operate more frequently in temperate than in tropical reef fish communities. All 12 experimental outcomes from temperate areas provide evidence for ongoing competition, while only 69% of 16 tropical studies are corroborative (see "experimental evidence" in Table 4). This pattern is not consistent across
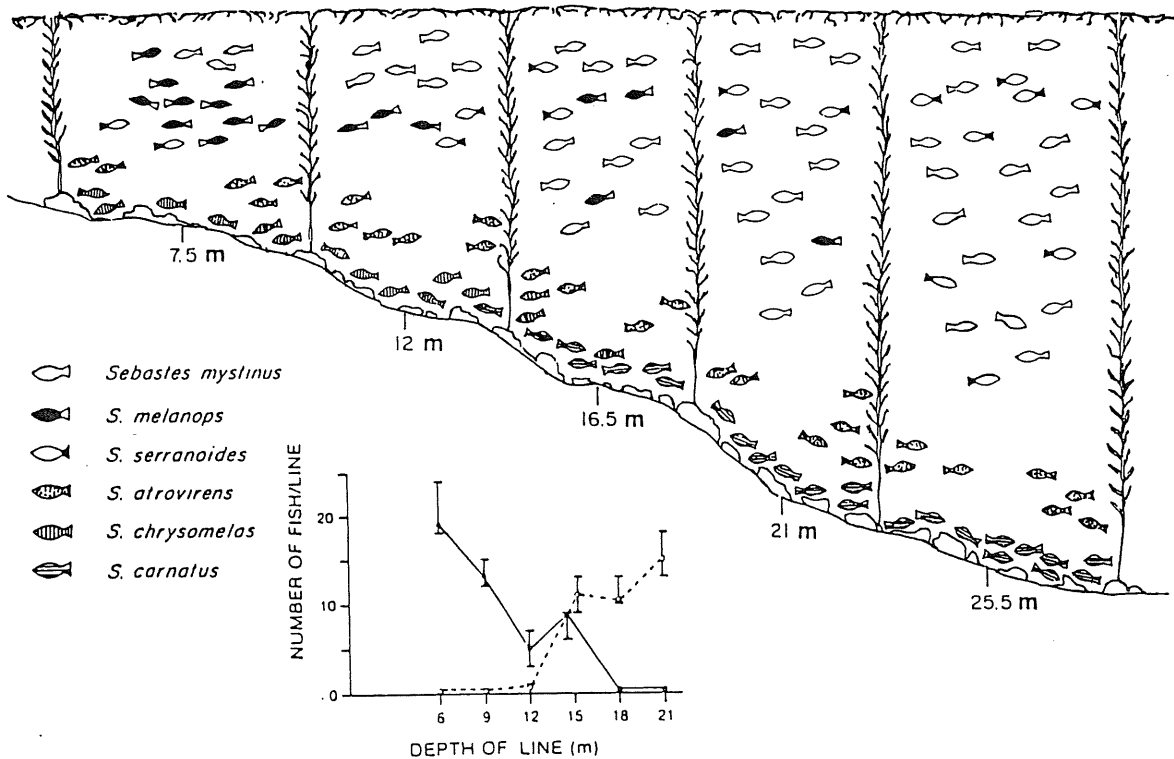
Figure 6 Depth distributions of rockfishes (*Sebastes*) in kelp forests off California. In the picture, species partly segregate by depth in the water column (first four species in the list) or along the bottom (last two species) off central California. [From L. E. Hallacher and D. A. Roberts (1985, Fig. 3, p. 98). Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. *Environ. Biol. Fishes* **12**, 91–110. Reprinted by permission of Kluwer Academic Publishers.] The inset graph shows the bathymetric distribution of the last two species (solid and dotted lines, respectively) off Santa Cruz Island, southern California. [Modified from R. J. Larson (1980, Fig. 2, p. 226). Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. **50**, No. 2, 221–239.]

all predictions of the hypothesis, however. For example, some assemblages of small species show considerable resilience between defaunations whether in temperate rocky intertidal zones or on coral heads in the tropics (Table 4, "resilience"). On the other hand, species assemblages colonizing small experimental reefs stabilized sooner and more predictably in temperate habitats, almost never doing so in tropical studies (Table 4, "climax"). This pattern may simply be a function of the fewer combinations of species available for settlement or to prioritize space in a less diverse fish fauna (see Sale, 1976; Helfman, 1978; Shulman *et al.*, 1983).

Although competition for food among coral reef fishes had often been discounted (Sale, 1980a, 1984), recent experimental and circumstantial evidence indicates otherwise for several tropical and temperate reef fishes (Table

4, "resource limitation"). For planktivorous damselfishes in the western tropical Pacific, data from Thresher (1983b) are suggestive that breeding pairs of *Acanthochromis polyacanthus* spawn earlier in the season and have larger broods of juveniles with greater survival rates on small patch reefs from which potential competitors were removed. G. P. Jones (1986) found that small juveniles of *Pomacentrus amboinensis* show increased growth rates when provided plankton in excess of natural supplies. However, Jones (1988b) could find no evidence of interspecific competition between juveniles of *P. amboinensis* and of another planktivorous damselfish, *Dascyllus aruanus*, manipulated to different densities on patch reefs, even though each species is associated with a different kind of coral and both species grew better on one kind than the other. Others have presented circumstantial evidence that distributions of such planktivores are correlated with plankton abundance (Hobson and Chess, 1978; Thresher, 1983a, 1985a). Using fish-removal experiments, Thompson and Jones (1983) demonstrated that at certain growth stages a wrasse and territorial blenny compete for food in temperate waters off New Zealand, although Roberts (1987) found that a territorial damselfish and blenny apparently did not compete for the benthic algae on tropical coral reefs off Australia. In other studies, foraging and/or shelter sites were shown to be limiting for temperate surfperches and gobies off California (Hixon, 1980a, 1981; Breitburg, 1987a; Behrents, 1987), but not for a tropical wrasse and a territorial damselfish off the Caribbean coast of Panama (Robertson and Sheldon, 1979; Robertson *et al.*, 1981).

Larger scale manipulations of potential competitors between habitat types have been done in temperate communities only. For example, controlled reciprocal removals of each member of closely related pairs of temperate surfperches (Hixon, 1980a; Holbrook and Schmitt, 1986, 1989) and rockfishes (Larson, 1980) off California have demonstrated the existence of present-day interspecific competition (Table 4, "species complementarity"). Predictably, the less aggressive congener of each pair expanded into the more productive habitat of the more aggressive congener when the latter was removed (e.g., Fig. 7). This was corroborated circumstantially for the surfperch studies by "natural experiments" on a geographic scale as well (Table 4, "geographic complementarity"). Wherever the dominant congener is rare or absent, the subordinate congener occupies the habitat range of both (Hixon, 1980a; Schmitt and Coyer, 1983). Comparable population-level experiments and geographical analyses are sorely needed for coral reef fishes.

In conclusion, there is no evidence, except perhaps from temporal partitioning of resources between day and night, that the more diverse communities of fishes inhabiting coral reefs are more competitively organized than the simpler communities of fishes living on temperate reefs. Indeed, the experimental evidence listed in Table 4 indicates that, if anything, temperate reef fishes may

E. lateralis REMOVAL SITE

CONTROL SITE

●——————● *E. jacksoni*
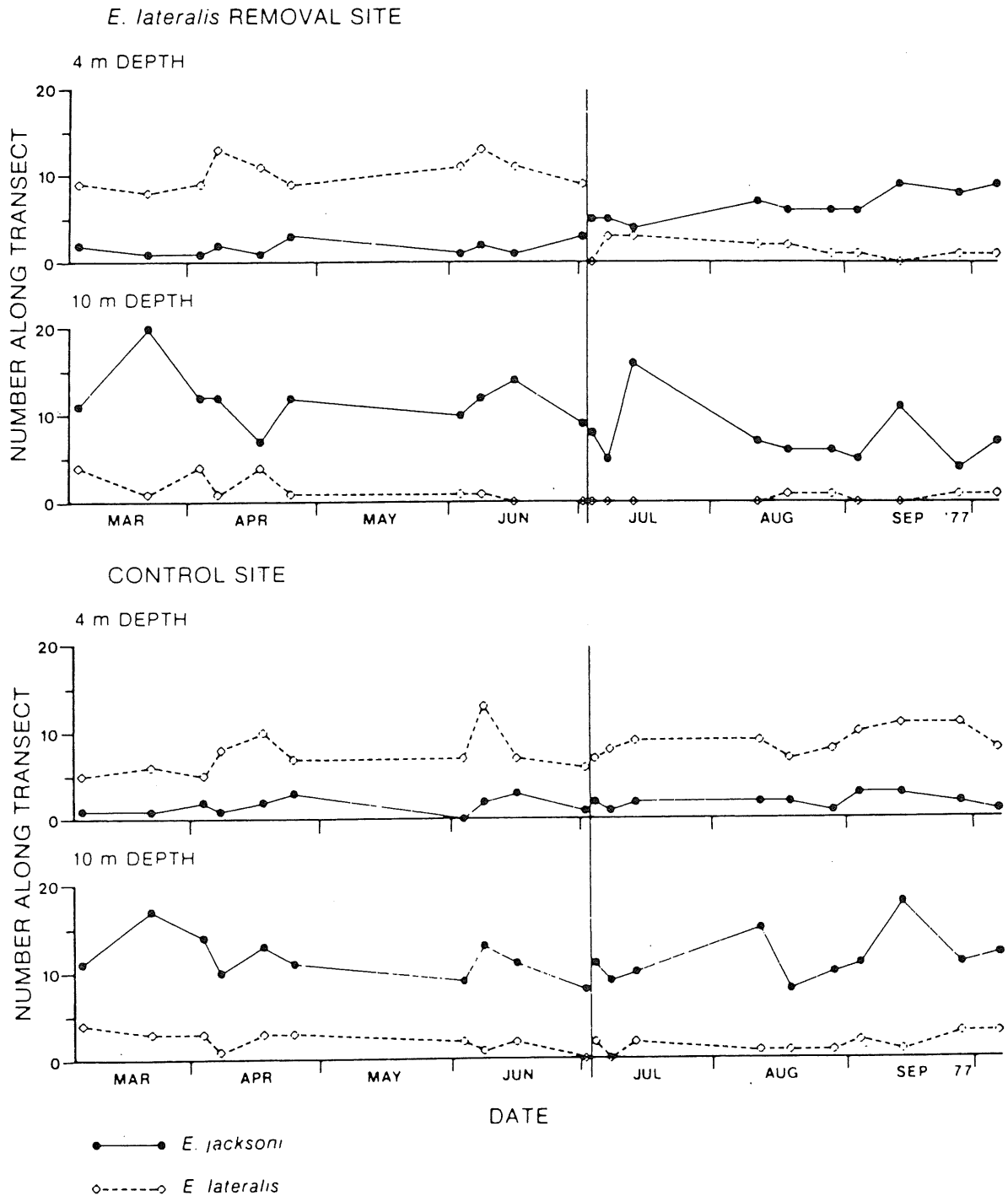
○------○ *E. lateralis*

Figure 7   Counts in time of the black surfperch (*Embiotoca jacksoni*) and striped surfperch (*E. lateralis*) in shallow (4 m depth) and deep (10 m depth) habitats off Santa Cruz Island, southern California. Vertical lines mark the time when the striped surfperch, a specialist on the shallow habitat, was experimentally removed (upper pair of graphs) or left at natural densities (lower pair of graphs) in the presence of its congener. [Modified from M. A. Hixon (1980, Fig. 7, p. 926). Competitive interactions between California reef fishes of the genus *Embiotoca. Ecology* **61**, No. 4, 918–931.]

tend to be more organized by interspecific competition than are their their tropical counterparts. For both systems, the plethora of circumstantial evidence favors an equally large amount of niche diversification by means of resource partitioning due to present or past competitive interactions. Yet, most such evidence is inherently biased. All species must differ to greater or lesser degrees in their autecologies, for the trivial reason that all represent different evolutionary endpoints. It is noteworthy that of the 54 studies in Table 4 that examined only the observed overlap in resource use by different species, 46 (85%) concluded, though often equivocally, that the species partitioned one or more resources. However, four other studies—two each of tropical (Sale and Williams, 1982; Gladfelter and Johnson, 1983) and temperate (Ebeling and Laur, 1986; Norton, 1989) species—tested resource partitioning more objectively. They statistically compared mean observed overlap among species in a guild with a null value assuming species overlapped by amounts that varied randomly (as expected if species' differences in resource use evolved independently). Of these four analyses, only one (Gladfelter and Johnson, 1983) found significant cause to reject the null hypothesis of random overlap.

B. Competitive Lottery

Also referred to as "equal chance" (Connell, 1978) and "multispecies equilibrium" (Doherty, 1983a), the competitive lottery hypothesis of Sale (1974) obviates the requirement of niche diversification to sustain multispecies associations despite ongoing competition among individuals to secure space. Strictly speaking, each species need not have an "equal chance" at recruiting to each site, but only a chance equal to its probability of per capita loss (see Sale, 1977, 1978a, 1979a): "Each species . . . must simply win often enough to avoid going extinct" (P. F. Sale, personal communication). This hypothesis assumes that all species in a guild have similar resource requirements and larval settlement capabilities, and that the availability of settling postlarvae is locally unlimited. Species may differ in competitive ability, however (Sale, 1982a). Furthermore, local larval recruitment is independent of local adult stock, and a strong prior residency effect allows any established recruit to hold space against all comers. Since space is limited, chance vacancies are quickly filled by recruits (analogous to "lottery tickets"), and the unpredictability of the process prevents any one species from excluding another. Thus the species are distributed in a random or patchwork pattern, as vacated spaces are filled with new individuals recruited from the plankton in random order (Sale, 1974). Therefore, although local species populations may vary in size, the species composition and total abundance of fish within the guild should remain fairly constant (in "multispecies equilibrium"). This hypothesis has a quantitative

theoretical basis if any species is able to increase its population size when it is rare and the others are common (Abrams, 1984). This condition is met if the co-occurring species have nonlinear (hump-shaped) stock-recruitment relations (Sale, 1982a), vary in their environmentally affected birth and death rates, and have overlapping generations for "storage" of strong cohorts over unfavorable years (Chesson and Warner, 1981).

Empirical support for a competitive lottery comes from a guild of territorial herbivorous damselfishes competing for sites on coral rubble patches off Australia (Sale, 1974, 1975, 1977, 1978a; Sale *et al.*, 1980) (Table 5, section B). Total available space remained occupied for more than 3 years, as space vacated by adults was reoccupied by other adults or new recruits apparently at random. Thus three species, *Eupomacentrus apicalis, Pomacentrus wardi,* and *Plectroglyphidodon lachrymatus,* could vary in relative abundance on the same patch while the total number of individuals remained fairly constant (Sale, 1975, 1979a). Observations of their distributions and foraging behaviors indicated that resource needs of these species were nearly equal and their competitive abilities appeared roughly similar, except that the most abundant species, *P. wardi,* tended to compensate for its somewhat inferior competitive ability by securing marginal spaces. Sale (1976) concluded from fish-removal experiments that recruitment of *P. wardi* is in fact limited by the availability of vacant space on which to settle.

Two studies suggest that the damselfish lottery may be a local phenomenon. Robertson and Lassig (1980) provide circumstantial evidence for spatial resource partitioning among the same species near Sale's site. At a different location on the Great Barrier Reef, Doherty (1982b) monitored recruitment and growth of *P. wardi* at different densities among patches. He summarily concluded that because neither recruitment rates nor postrecruitment survival were density dependent, population regulation was nonequilibrial and perhaps determined by the supply of recruits rather than the available space for recruits (Doherty, 1983a; see Section V,H). Therefore, the lottery may not have been operating during Doherty's study.

Our search for temperate examples of competitive lotteries was futile, perhaps because a multispecies equilibrium is difficult to recognize. Most available studies of resource allocation by temperate reef fishes imply that co-occurring species exploit different suites of resources to greater or lesser degrees (see Ross, 1986). In addition, temperate reef fish communities usually lack guilds of several territorial species whose discrete spaces can be monitored for long periods of time. Thus, it may be impossible to demonstrate that a constant number of individuals occupy all available spaces in a pattern that varies in the relative abundances of species through time.

C. Compensatory Mortality and Predation on Common Species

Species with similar requirements can coexist at equilibrium if the most common suffers the greatest mortality due to, for example, differential predation (Connell, 1978). Either the superior competitor is prevented from excluding inferiors by being more vulnerable to predators (or other sources of mortality), or, where competitive asymmetries among prey species are not pronounced, predators switch to the more abundant of alternative prey types in a "type III functional response" (Murdoch and Oaten, 1975). In both cases, the process of competitive exclusion is mitigated. Thus, if predation is the source of mortality, then the prediction of this hypothesis is that the local diversity of reef fishes should increase in the presence of piscivores.

Although predation pressure has often been assumed to be greater in the tropics where antipredator tactics appear to be more highly evolved (Ehrlich, 1975; Johannes, 1978a; Hixon, Chapter 17), there are very few data on how a compensatory response of predator to prey fishes may regulate either tropical or temperate communities (Table 5, Section C). In the only study we know of relating the number of potential prey species to the number of piscivorous fish, Hixon and Beets (1989) found that the local number of prey species declined with increasing piscivore abundance, opposite the prediction of compensatory mortality (Hixon, Chapter 17). However, density-dependent predation of reef fishes has not been investigated; choice experiments offering superior versus inferior competitors as prey have not been performed; and per capita mortality of prey species after altering predator or prey abundances has not been rigorously examined (reviewed by Hixon, Chapter 17).

D. Intermediate Disturbance

This hypothesis views local species diversity as a function of patchy mortality due to disturbance, be it physical (e.g., storms) or biological (e.g., nonselective predation). It states that low-disturbance areas have low diversity because late-successional "climax" species exclude early-successional "fugitive" species, and high-disturbance areas also have low diversity because most species are locally extirpated. However, areas disturbed at intermediate frequency or severity are augmented by both subordinate fugitives and dominant climax species (Connell, 1978). Time between disturbances is an important feature of this model. Succession within an empty habitat patch is seen as proceeding from a low-diversity assemblage of early colonists, to a high-diversity mix of early and late species, to a low-diversity climax assemblage. Each disturbance pushes the successional sequence partway or entirely back to the beginning.

Table 5 Some Key Studies Evaluating the Various Hypotheses on the Regulation of Reef Fish Community Structure[a]

Hypothesis	Species, location, and reference	
	Temperate reefs	Tropical reefs
A. Competition and niche diversification	---------------- see Table 4 ----------------	
B. Competitive lottery	+: none	+: damselfishes Heron Island, Australia (Sale, 1974, 1975)
	−: none	−: damselfishes Heron Island, Australia (Robertson and Lassig, 1980)
C. Compensatory mortality and predation on common species	+: none	+: none
	−: none	−: all species St. Thomas, U.S. Virgin Islands (Hixon, Chapter 17)
D. Intermediate disturbance	+: none	+: none
	−: none	−: none
E. Predation on rare species	+: none	+: all species St. Thomas, U.S. Virgin Islands (Hixon, Chapter 17)
	−: none	−: none
F. Gradual change	+: all species California, U.S.A. (Stephens *et al.,* 1984; Ebeling and Laur, 1988)	+: none
	−: none	−: none
G. Sources and sinks	+: wrasse California, U.S.A. (Cowen, 1985)	+: cardinalfishes Bahamas (Dale, 1978)
	−: none	−: none
H. Recruitment limitation	+: wrasse California, U.S.A. (Cowen, 1985)	+: damselfish One Tree Island, Australia (Doherty, 1983a); wrasse San Blas Islands, Panama (Victor, 1986b)
	−: none	−: grunt St. Croix, U.S. Virgin Islands (Shulman and Ogden, 1987)

[a] Major supportive studies follow a "+" sign; explicitly opposing studies follow a "−" sign; and "none" indicates no available information.

Thus, maximum local diversity occurs where intermediate levels of distur-
bance hold the assemblage occupying each patch at a midsuccessional stage.

Certainly both temperate and tropical reef fishes are displaced or killed by
physical disturbances of various sorts, although the effect on community
structure is difficult to assess (see Section II,B). Indeed, it seems unlikely that
physical damage due to storms and other such events can affect typically
mobile reef fishes severely enough to keep populations chronically low over a
widespread area (Doherty and Williams, 1988a).

Predators probably have constituted a more important source of mortality,
especially in the tropics, as evidenced by the widespread occurrence of spe-
cialized antipredator mechanisms among potential prey and various sources of
correlative evidence (Hixon, Chapter 17). Nonetheless, temperate and boreal
species may more likely fall prey to marine mammals and birds occurring in
large concentrations (Moulton, 1977; Moreno and Jara, 1984) and locally
abundant specialized predators such as electric rays (Bray and Hixon, 1978).
Without proper shelter, juvenile fish become highly vulnerable to predators
on both tropical (Shulman, 1984, 1985a; Hixon and Beets, 1989) and tem-
perate reefs (Ebeling and Laur, 1985; Behrents, 1987). Talbot *et al.* (1978)
attributed the high diversity of fish assemblages on small patch reefs to the
maintenance of species abundances below equilibrium levels by means of
predation, as well as seasonal variation and uncertain recruitment. They con-
cluded that high within-habitat diversity may have been at least partly sus-
tained by the intermediate-disturbance process.

However, none of these observations specifically supports the prediction
that intermediate disturbances promote the diversity of prey fishes. The only
study that we could find to supply pertinent data is that of Hixon and Beets
(see Hixon, Chapter 17) of predatory fishes and their potential prey fish
species inhabiting experimental reefs in the Virgin Islands. In this case,
the relation between predator density and number of prey species was
both inverse and monotonic, not the hump-shaped function predicted by the
intermediate-disturbance hypothesis (Hixon, 1986; Chapter 17). In sum, we
found little convincing evidence, pro or con, that disturbances maintain high
levels of species diversity in either tropical or temperate reef fish communities
(Table 5, section D).

E. Predation on Rare Species

Despite the ideas presented in the previous two sections, increasing levels of
predation are not always predicted to increase local prey diversity. As ex-
plained previously, the intermediate-disturbance model predicts that prey
diversity will decline at very high levels of predation. However, even predation
at low levels can cause an immediate decline in prey diversity if predators

(1) selectively or disproportionately consume the competitively subordinate or otherwise rare species in an assemblage, or (2) consume all prey nonselectively, but rare prey are highly susceptible to predation and are locally extirpated before they can respond favorably to competitive release (Van Valen, 1974; Lubchenco, 1978; Hixon, 1986). These possibilities comprise an alternative hypothesis on the role of predation in regulating community structure. Note that this hypothesis is not mutually exclusive of all others; the initial rarity of a species can be caused by any number of processes, including competition and recruitment limitation (Section V,H). Yet, given that all communities include more rare than common species, predation on rare species can potentially be a major process in determining the diversity of a local assemblage.

The prediction of the predation-on-rare-species hypothesis is that local prey diversity will decline monotonically as the level of predation increases from zero. Here (as in the compensatory-mortality and intermediate-disturbance hypotheses), the level of predation is a measure of the extent to which predators decrease the local population sizes of prey species, and is presumably correlated with predator density.

As summarized previously, a study of fishes occupying artificial reefs in the Virgin Islands provides the only data we could find on the effects of piscivores on the local diversity of reef fishes (Hixon and Beets, 1989) (Table 5, section E). The strong negative relationship between the number of resident piscivores occupying a reef and the maximum number of resident prey species is consistent with the hypothesis of predators extirpating rare species (Hixon, Chapter 17, Fig. 5B). However, the gut contents of the piscivores in this study were not examined, so the precise mechanisms underlying this relationship remain unknown. Moreover, we could find no comparable data from any other tropical or temperate reef system, so this hypothesis remains largely untested.

F. Gradual Change

The gradual change hypothesis states that environmental conditions, which determine the dominance rankings of competitors, eventually change before any one species can exclude others and monopolize resources. The predicted result of this hypothesis is that a gradual change through time in species composition or relative abundances should be correlated with environmental variation (Hutchinson, 1961; Connell, 1978). As a seasonal or longer-term climatic trend alters their environment, species better adapted to the new conditions will increase in abundance but not to the point of excluding others before conditions change once again. Species track the environment but never

come into stable equilibrium because of time lags between resource availability and the realization of the species' exploitative potentials (Boyce, 1979).

This model would seem to be potentially less important in tropical than in temperate regions, which undergo major latitudinal climatic shifts superimposed on more predictable seasonal fluctuations (Section II,B). On temperate reefs, seasonal variation in water temperature may promote a reversal of competitive abilities between species derived from different faunas. The gradual change model may be best expressed in ecotones supporting mixtures of cool- and warm-temperate faunas, where the cool-adapted species perform best during periods of low temperature and the warm-adapted ones are superior during warm episodes. For example, warm water temperatures appear to prevent the competitively dominant, cool-temperate surfperch *Embiotoca lateralis* from locally extirpating the subordinate, warm-temperate *E. jacksoni* at the southern edge of the geographical range of *E. lateralis;* north of this region, *E. lateralis* appears to have completely eliminated its congener from reef habitats (Hixon, 1980a). Although tropical assemblages show some seasonality in environmental conditions, the magnitude of seasonal variation does not approach that of temperate zones (Section II,B). Dominance shifts of tropical species may be less noticeable within the greater diversity of coral reef assemblages (Richards and Lindeman, 1987).

Necessary (but not sufficient) evidence supporting the gradual change hypothesis is variation in the distribution and abundance of reef fishes related to seasonal change and climatic trends. While there is ample evidence of such variation in temperate systems, we found none for assemblages of coral reef fishes. In Puget Sound in the U.S. Pacific Northwest, for example, densities of several species of rocky-reef fishes decrease during the fall and winter as productivity declines and kelp is torn away by strong wave action; a few more generalized carnivores remain abundant throughout the winter when they may eat a greater diversity of benthic prey than the declining specialists (Moulton, 1977). In the subtropical northern Gulf of California, Mexico, marked seasonal change had a greater effect on relative abundances of fish assemblages on small artificial reefs than did rate of colonization or succession (Molles, 1978). More generally, an influx of juveniles during the spring and summer contributes substantially to the predictable seasonal variation in temperate reef assemblages in the Northern Hemisphere (Olla *et al.,* 1975; Miller and Geibel, 1973; Leaman, 1980; Stephens *et al.,* 1986; Ebeling and Laur, 1988) and Southern Hemisphere off New Zealand (Choat and Kingett, 1982; Jones, 1984c). Because many species must adjust to losses of macroalgal cover and food in winter, they migrate to deeper water, become torpid, or seek more productive habitats. The degree of adjustment increases with latitude as seasonal cues and exigencies become more intense (Moulton, 1977). In warm-temperate New Zealand, however, the predictable spatial variation of reef

fishes among habitat types usually exceeds the temporal variation (Kingett and Choat, 1981; Jones, 1988a).

At a given latitude, the composition of temperate reef fish assemblages changes with longer-term shifts in climate, ocean temperature, and current patterns. With episodes of poleward advection and warming, such as El Niño events in the eastern Pacific (Section II,B), recruitment and abundances of subtropical or warm-temperate species increase as those of cool-temperate fishes decrease (Section IV,A). Yet such climatic changes fluctuate with unpredictable frequency, and elements of the one fauna seldom completely displace elements of the other. Off northeastern New Zealand, abundances of subtropical species to the north and more temperate species to the south are correlated with latitudinal gradients in water temperature and current pattern (Choat and Ayling, 1987). At a particular latitude, temporal fluctuations in abundances of subtropical and temperate species reflect shifts in these gradients, and offshore islands support relatively more subtropical elements than the nearby mainland (Choat et al., 1988). Analogous shifts occur off southern California as well. During a warming trend with periodic El Niño episodes of varying strength, abundances of southerly warm-water species increased, those of cool-water species decreased, and those of "central species," perhaps adapted to a more variable regime, remained unchanged (Stephens and Zerba, 1981; Stephens et al., 1984; Patton, 1985; Ebeling and Laur, 1988). A recent shift to a cooler regime seems to have given northern species the advantage once again (A. W. Ebeling, unpublished observations). Since all three categories of species may live in one local area of reef and kelp, they gradually replace one another in numerical dominance.

Despite such evidence for seasonal variation in species composition and relative abundances, there is no evidence that this variation promotes coexistence. Thus, the gradual change hypothesis remains untested for reef fishes (Table 5, section F).

G. Sources and Sinks

Theoretically, inferior competitors can coexist with dominant species in a single locality if there are other areas where the subordinates are at an advantage and can supply surplus recruits to the locality (Abrams, 1984). For reef fishes, Dale (1978) offered an economic analogy called "money in the bank" (local "capital" augmented by foreign "interest"). The hypothesis was recently formalized as allowing coexistence in patches of an environmental mosaic where species vary in their ratios of birth/death rates (Pulliam, 1988). Thus any locality is at one time a "source" for some species populations and a "sink" for surplus individuals produced elsewhere; the local assemblage is as much a

reflection of the conditions in other patches of the mosaic as the local availability of resources. If coexistence depends on this process, local populations should include species recruited from elsewhere along with any locally breeding populations.

Stevens (1989) suggested that this hypothesis is sufficient to account for the maintenance of greater local species richness in the tropics than in temperate areas. Tropical species, which have presumably adapted to more constant environments, may have more narrowly defined and closely approximated source areas where some species have a reproductive or competitive advantage, but have dispersal systems that are as "open" as those of temperate species. Among coral reef fishes, for example, there is some evidence that each species in an assemblage of western Atlantic cardinal fishes (Apogonidae) is most abundant in a different habitat (Dale, 1978). Similarly, a Caribbean damselfish has a refuge from multispecific habitat use by virtue of its broad geographic range (Waldner and Robertson, 1980). In addition, damselfishes recruiting to patches of different quality may form subpopulations varying in reproductive output (Doherty, 1980, 1982a; Wellington and Victor, 1988). Thus, if marginal populations can be maintained at low levels by a continued trickle of immigration, then tropical communities should be relatively sensitive to disturbances that create "habitat islands" with a larger proportion of very rare species (Stevens, 1989). The comparable censuses of temperate and tropical reefs in Table 1 indicate that a substantially larger proportion of tropical species are indeed "rare."

In temperate regions with broad gradients in temperature and other factors, sink populations may be created through expatriation from other sources over a much broader scale. Warm-temperate reefs and kelp beds off New Zealand and California support marginal or nonbreeding populations of species with more northern or southern centers of abundance along with central populations in optimal parts of their ranges (Choat and Ayling, 1987; Jones, 1988a; Patton, 1985; Ebeling and Laur, 1988; Choat et al., 1988). Off southern California, for example, breeding of California sheepshead (Semicossyphus pulcher), a warm-temperate species, is usually more successful to the south (Cowen, 1985), while populations consisting mostly of adults occur commonly on northern reefs, where both successful spawning and recruitment appear to be sporadic (Cowen, 1985; Davis, 1986; Ebeling and Laur, 1988). At the northern sites, marked increases in sheepshead recruitment during 1983 coincided with a major El Niño climatic episode in 1982–1984, when northerly transport of larvae apparently increased (Fig. 8). Expatriate populations of large adults of some southern species inhabit reefs in Monterey Bay, far from their source along southern California (Miller and Geibel, 1973; Hubbs, 1974). On a smaller scale, offshore reefs may be sinks for certain relatively closed populations of viviparous surfperches, whose young are born
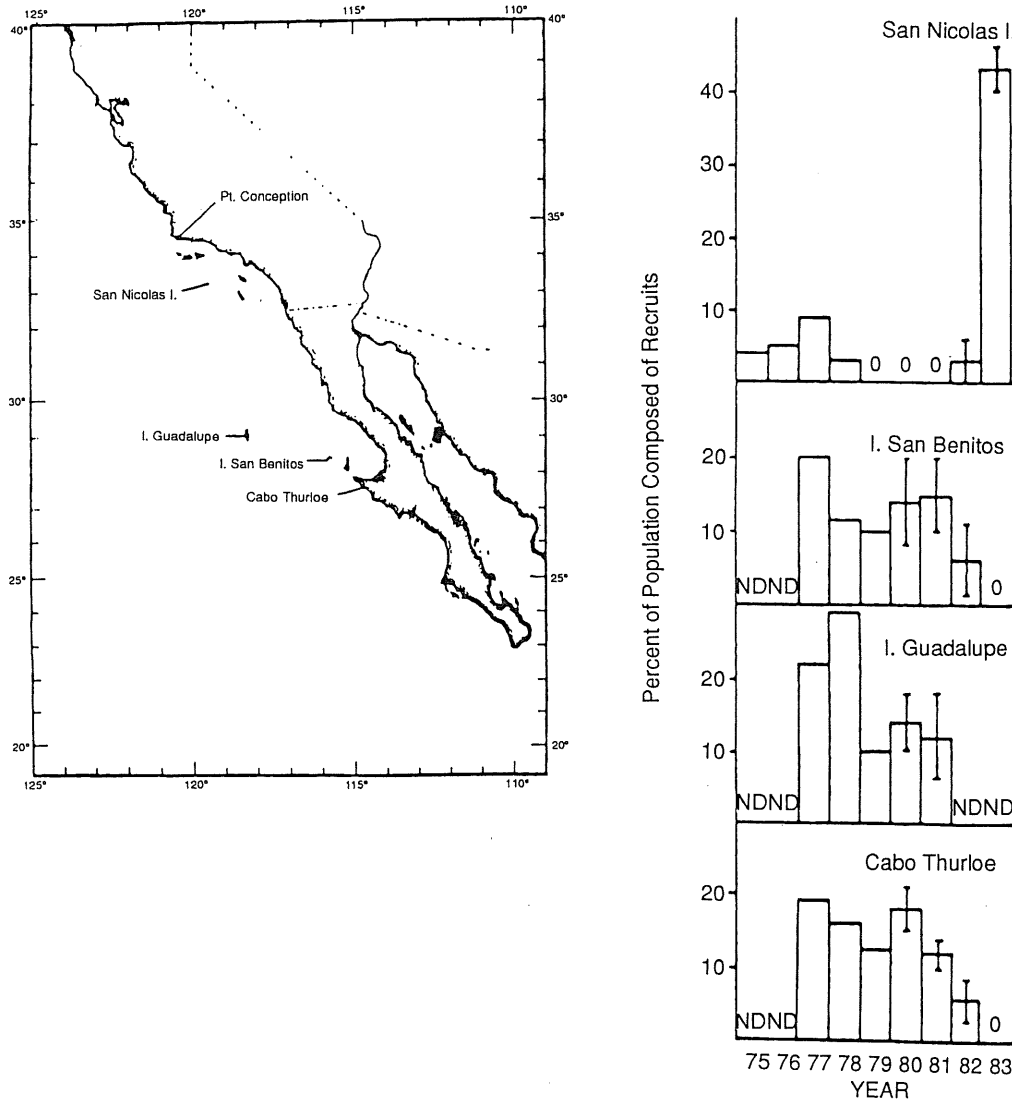
Figure 8 Annual recruitment success of the California sheepshead, *Semicossyphus pulcher*, a warm-temperate fish, at the four longitudinally arrayed study sites off southern California, U.S.A., and Baja California, Mexico, as indicated in the map (inset). Note that relative recruitment increased dramatically at the most northern site (San Nicolas Island) just south of Point Conception during the warm El Niño climatic event of 1982–1984. [Adapted and reassembled from R. K. Cowen (1985, Fig. 1, p. 722, and Fig. 2, p. 725). Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: Causes and implications. *J. Mar. Res.* **43**, 719–742.]

mostly inshore where algal cover is dense (Ebeling and Laur, 1988; Ebeling *et al.*, 1990).

In sum, several lines of evidence from both temperate and tropical reefs are consistent with the sources and sinks model (Table 5, section G). As with the other models, however, rigorous tests have not been forthcoming.

H. Recruitment Limitation

The last model of community regulation that we consider seems to be the most popular at the moment. This hypothesis states that reef fish populations are undersaturated simply because the supply of postlarval recruits is limited (D. McB. Williams, 1980; Doherty, 1980, 1982a, 1983a; reviewed by Doherty and Williams, 1988a). Thus, population sizes virtually never reach levels where competition is important, and local species composition and relative abundances are determined simply by the species and number of postlarvae that happen to settle in a particular location. The idea is seductive. Since most species have planktonic larvae that spend varying periods adrift (Brothers *et al.*, 1983; Brothers and Thresher, 1985; Smith *et al.*, 1987; Victor, 1986a; Wellington and Victor, 1989) in irregular current patterns (Sette, 1960; Lobel and Robinson, 1983; Shapiro *et al.*, 1988), and since targets for settlement are small compared to the expanse of the open ocean (Richards and Lindeman, 1987), the odds that a particular locality is replete with competent larvae may be low. This does not preclude the possibility that some reefs occasionally become overpopulated by occasional dense settlement, perhaps from a particularly rich advected patch (see Doherty, 1983a; Victor, 1986b). One prediction, therefore, is that population density should vary widely among sites and times, without a concordant variation in resources. On reefs with the lowest density of new recruits, competitive interactions among juveniles and adults should be very rare, and changes in resource levels should not alter relative resource use or mortality rates among species. Removal of adults should not affect the recruitment rate, which may be very low; more strictly, residents should not inhibit settlers. [Some settlers may avoid conspecific adults (Talbot *et al.*, 1978; Sweatman, 1985a) or seek such adults (Williams and Sale, 1981; Sweatman, 1985a; Jones, 1987b) on smaller targets like patch reefs (Schroeder, 1987) or on certain substratum types (Sale *et al.*, 1984a).] Population density should be much more sensitive to the number of settlers than to postsettlement mortality. Therefore, adult density should be linearly related to the prior density of juveniles in short-lived species, and the age structure of adults should reflect interannual variation in recruitment in long-lived species (Jones, 1987a; Shulman and Ogden, 1987; Doherty and Williams, 1988a).

There is some debate over how strictly the criteria should be applied to demonstrate "adequately" that a population is recruitment limited (Jones, 1987a). Victor (1983a, 1986b) believes that the demonstration is adequate if the number of first-year adults equals the number of the previous year's recruits, minus a constant density-independent mortality of juveniles. This criterion ignores the role of postsettlement mortality (as opposed to presettlement larval availability) in keeping populations undersaturated. Others

tion densities of surgeonfishes off Caribbean Panama (Robertson, 1988a) and blennies off Barbados (Hunte and Cote, 1989).

The fewer studies of possible recruitment limitation on temperate reefs indicate that this model may not generally apply over the same scales of space and time that the tropical studies have indicated. Although a subtropical wrasse (*Pseudolabrus celidotus*) from northeastern New Zealand varied spatially in recruitment density, this was more likely due to preference for algal habitats than to vagaries of settlement; density-dependent survival of juveniles, perhaps driven by intraspecific competition for food, limited adult densities (Jones, 1984b). In southern California and Mexico, local densities of a congeneric triplet of shallow-living blennies (*Hypsoblennius*), all with long-lived pelagic larvae, are probably determined more by interspecific competition for food and shelter than the supply of settlers (Stephens *et al.*, 1970). Stephens *et al.* (1986) found that recruitment of several species of reef fishes (Gobiidae, Labridae, Scorpaenidae, Serranidae) to a southern Californian breakwater was unrelated to densities of early-stage larvae sampled offshore, although later-stage competent larvae were inadequately sampled and limitation by presettlement mortality was not ruled out. Yet, postsettlement mortality due to predation apparently determined juvenile densities on a small, experimental reef nearby.

In addition, some temperate regions have relatively more live-bearing species without a pelagic dispersal stage. Twenty-six abundant species of viviparous surfperches (Embiotocidae) occur in the North Pacific (Baltz, 1984). Since precocious young are probably born in the same area as their parents, populations are unlikely to be recruitment limited on a local scale, and competition between surfperches has been demonstrated experimentally (Hixon, 1980a; Schmitt and Holbrook, 1986) (Section V,A).

During climatic shifts characteristic of temperate regions, rocky-reef fishes are more likely to show variation in recruitment over larger scales of space and time than their tropical counterparts. Off California, widespread differences in recruitment success may occur between cool- and warm-temperate species as the oceanographic regime changes unpredictably (Radovich, 1961; Hubbs, 1974; Stephens and Zerba, 1981; Stephens *et al.*, 1984, 1986; Ebeling and Laur, 1988). Recruitment of young-of-year blue rockfish (*Sebastes mystinus*), a cool-temperate planktivorous species, and blacksmith (*Chromis punctipinnis*), a warm-temperate planktivorous damselfish, provide examples on a southern Californian reef near Santa Barbara (Fig. 9). Blue rockfish young were abundant during cool years in the 1970s, but virtually disappeared during a warming trend in the 1980s. Densities of young blacksmith, on the other hand, increased dramatically during the climatic shift. Note that such patterns are also consistent with the gradual change model.

The most direct evidence of recruitment limitation on a regional scale is
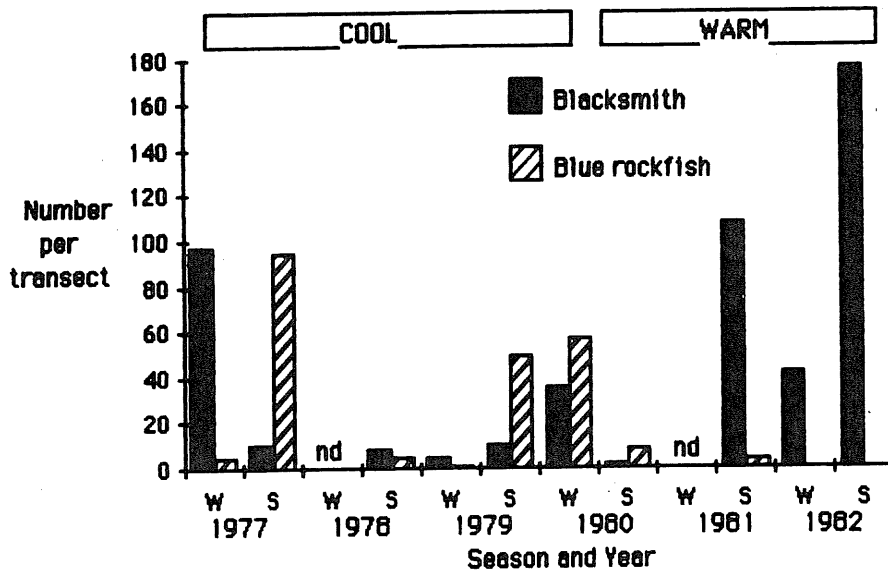
Figure 9   Semiannual densities of young-of-year blacksmith (*Chromis punctipinnis*) and blue rockfish (*Sebastes mystinus*) on Naples Reef near Santa Barbara, southern California, during periods of cool and warm water. Sample size is about 18–27 transects, each with a volume of about 240 × 3 × 3 m (2160 m²) near the base at the ends of the long axis of the reef (see Fig. 3). S, July–December; W, January–June; nd, no data taken. [Transects have been described by Ebeling and Laur (1988).]

from an extensive analysis of unusually large northward recruitment of a warm-temperate wrasse during an intense El Niño episode of northerly transport (Cowen, 1985). Cowen suggested that, in general, recruitment limitation is observed locally whenever the major breeding population is located upcurrent. Thus, widespread recruitment of southern species to the north (and vice versa) is related to major climatic changes associated with reversals in prevailing currents. This causes "expatriation" of adult populations in geographic "sinks" (see Section V,G), where reproductive potential may be "stored" (*sensu* Warner and Chesson, 1985) in long-lived individuals until the next environmental shift (Cowen, 1985). Alternatively, of course, annual variability in recruitment may be due to temperature-related variation of local spawning success (Tarzwell, 1970).

Ultimately, demonstrating presettlement recruitment limitation requires one to show that postsettlement processes, including mortality and competition, do not significantly affect population sizes. Such demonstrations are largely wanting in both tropical and temperate reef fish systems.

I. Conclusions

A careful weighing of the literature on regulation of community structure provides few generalizations. Although there are real differences between temperate and tropical reef fish communities at a descriptive level, there appears to be no universally appropriate model of community regulation for either region. For models where evidence is available from both temperate and tropical systems (competition and niche diversification, sources and sinks, recruitment limitation), a sampling of key studies indicates that each model may apply more or less equally well to both regions. However, for most models (competitive lottery, compensatory mortality, intermediate disturbance, predation on rare species, gradual change), few data are available, the data are only from tropical reefs, and most results are negative. Thus, for the vast majority of reef fish assemblages, there are no data, either pro or con, directly relevant to each model of community regulation (Table 5). All models may operate to greater or lesser extents in temperate or tropical systems, depending on local environmental conditions during the study and during the system's recent history. Any search for "the factor" regulating reef fish community structure is thus doomed to failure and sweeping generalizations should be suspect (Sale, 1979b, Chapter 19; Hixon, Chapter 17; Jones, Chapter 11).

VI. FUTURE RESEARCH

We believe that future research should be directed toward explicitly testing the different models of community regulation for reef fishes in both temperate and tropical regions (see gaps in Table 5). Along with more careful observation over longer periods, multifactorial experiments should be designed to manipulate different populations or resources to find out how processes such as competition and predation may interact to structure fish populations (reviewed by Sih *et al.*, 1985; Hixon, Chapter 17). There should be more effort at discovering when and where recruitment limitation is operative. Determining the relative distributions and abundances through time of postlarvae in the water column versus the substratum would provide valuable data on the mechanisms of recruitment (see McFarland and Ogden, 1985; Eckert, 1985a; Sweatman, 1985b; Kingsford and Choat, 1989; Kobayashi, 1989; Leis, Chapter 8). Testing recruitment limitation, compensatory mortality, intermediate disturbance, and predation on rare species requires measuring the relative mortality rates of different categories of common and rare species (in addition to monitoring recruits). Studies of relative breeding potential may

reveal critical relationships between "source" and "sink" species populations in a particular locality. Little is known about patterns of distribution and abundance of transient species in either temperate or tropical regions. There should be continued effort to map home ranges of fish over their life spans to determine the scales over which processes requiring the interaction of individuals, such as competition and predation, operate.

A critical examination of latitude-associated biases in data gathering is long overdue. Perhaps a more objective comparison of environmental complexity and refuge availability should be made between coral and temperate reefs. More thorough searches for covert individuals would help in interpreting the apparent similarities and differences in species diversity (richness and evenness). More temperate–tropical pairs of studies using the same observational and experimental methods should be employed. Such studies would be particularly valuable if they involved the same personnel (and their associated personal biases) in both regions, such as Menge and Lubchenco's (1981) pioneering temperate–tropical comparison of intertidal systems. Studies comparing sampling methods, such as that by Davis and Anderson (1989), should be made to discover habitat-generated sources of bias, which may differ substantially between temperate and tropical reefs.

Finally, it would do us well to document losses in local diversity due to habitat destruction and overfishing by the human scourge. Natural processes that once structured fish communities may no longer prevail near heavily exploited urbanized areas. Loss of keystone species, such as the earlier depletion of sea otters in the North Pacific, may revolutionize community structure to the extent of indirectly changing the rank order of fish species abundances. Overfishing of predators in the tropics may upset relationships among less exploited prey species. Introduction of exotic species to geographically isolated sites such as Hawaii may destabilize community structure (Randall, 1987). Thus, outcomes of temperate–tropical comparisons should be read in light of the relentless human invasion. A particular example of an important problem for the tropical fish ecologist would be measuring the response of fish assemblages to the destruction of more than 70% of the Philippine coral reefs (McAllister and Rubee, 1986). This environmental disaster was inflicted by sedimentation due to excessive deforestation, and especially by dynamiting and cyanide poisoning of the fauna in response to the lucrative international market for coral habitat and tropical fish aquaria. This might lead one to suggest that the most crucial difference between coral reef and temperate reef fish assemblages is that the smaller and more brightly colored coral reef fishes constitute the more desirable object of such outrages.

ACKNOWLEDGMENTS